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STATISTICAL GENETICS
and
PLANT BREEDING

A Symposium and Workshop
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EDITED BY
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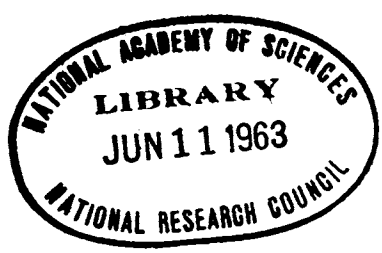
AND
H. F. ROBINSON



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Foreword

THIS symposium on statistical genetics and plant breeding developed from the deliberations of the Committee on Plant Breeding and Genetics, which had been asked by the Agricultural Board of the Division of Biology and Agriculture, National Academy of Sciences—National Research Council, to make an appraisal of the current status of statistical genetic theory and its application to plant breeding. A comprehensive symposium in this broad area of research had not been held for several years. In the meantime many laboratories had been active in both the theoretical and applied aspects of statistical genetics and plant breeding. The committee's decision to conduct such a symposium received encouragement and support from other interested researchers whom it consulted. From the beginning, plans for the symposium were directed toward achievement of two major objectives. First, to provide a general review of statistical genetic theory with special emphasis on recent developments to familiarize the plant breeder with the utility of the approach. Second, a discussion of breeding problems with statisticians should serve the needs of the breeders and should, at the same time, acquaint statisticians of the limitations of methods or inadequacies of theory currently available. The first objective received major emphasis in the symposium and the second in the informal work conference which followed the symposium.

The meetings of the symposium were held March 20–24, 1961 at North Carolina State College, Raleigh, North Carolina. The work conference was held the 27–29 of March. Evening sessions and discussions were held on all but the last day. Approximately 175 persons attended by invitation of the committee. The program consisted of 17 invitational papers, five formal discussions, and a formal résumé. In addition, 25 volunteer contributions were given during the symposium and the workshop. Several of these are included in the proceedings.

The sponsoring committee gratefully acknowledges the financial support received from the United States Atomic Energy Commission, the National Institutes of Health, the National Science Foundation, and the Agricultural Research Service of the United States Department of Agriculture. The encouragement of the Agricultural Board and the Agricultural Research Institute was helpful to the Committee in bringing the Symposium to fruition.

I wish to acknowledge the help of all members of the Committee on Plant Breeding and Genetics. I wish to make especial acknowledgements to H. F. Robinson and G. F. Sprague who were primarily responsible for the development of the final program and work conference and to W. D. Hanson who did the major editing of the proceedings.

I further wish to record my own as well as the committee's appreciation and thanks to all of the formal participants whose papers are presented here; to the discussants B. I. Hayman, Alan Robertson, F. H. W. Morley, C. E. Gates, and G. W. Burton; and, finally, to H. F. Robinson who undertook the major task of organizing and presenting the résumé.

R. P. MURPHY, *Chairman*

COMMITTEE ON PLANT BREEDING AND GENETICS

R. A. Brink
W. M. Myers
F. L. Patterson
H. F. Robinson
W. R. Singleton
G. F. Sprague

R. P. Murphy, *Chairman*

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IN 1955, the Agricultural Board made provisions for a committee on Plant Breeding and Genetics with responsibilities to review this subject and submit proposals for action if the situation warranted. The committee included R. P. Murphy, Chairman, R. A. Brink, F. L. Patterson, H. F. Robinson, W. R. Singleton, and G. F. Sprague with J. L. Lush serving as Advisor. After discussion of what was felt to be the more pressing needs and a consideration of the various ways to meet these needs, the committee proposed the development of two symposia; one dealing with Mutation and Plant Breeding and the second with Statistical Genetics and Plant Breeding. This plan was presented to the Agricultural Board and was approved by the National Academy of Sciences—National Research Council. The Academy Research Council endorsed both the proposal and the budget estimates and authorized the committee to seek the necessary funds. Grants to support the symposia were made by Atomic Energy Commission, Agricultural Research Service, U. S. Department of Agriculture, National Institute of Health, and National Science Foundation. The first of these symposia was held at Cornell University, Ithaca, N. Y., in November 1960 and we are here today at the first meeting of the second symposium which will deal with Statistical Genetics and Plant Breeeding.

The present symposium was organized to meet several interrelated objectives. These were to provide a review of statistical genetic theory and philosophy, to consider developments in certain specific areas of statistical genetics, and to attempt to relate such developments to problems and practices in plant breeding, to stimulate the utilization of the statistical genetic approach in attempts to solve important plant breeding problems, and finally to develop and foster an appreciation of the mutual advantages to be derived from a joint attack upon problems of major importance.

In the sections which follow I propose to present a very brief review of developments in breeding which, I hope, will provide a background for our present situation and the need for further emphasis on statistical genetics. The basic problems, differing only in detail and emphasis, remain much the same regardless of the crop involved. Since my experience has been largely with corn I shall use this crop for my illustration.

Prior to the rediscovery of Mendel's laws plant breeding was primarily an art. The most powerful selection tool devised and utilized by at least some of the workers was the progeny test. Even here some workers believed in the importance of modifications due to environment, or as we would say today, the inheritance of acquired characters. Selection work was done under the most favorable conditions available in the hope that the increased plant vigor, seed size, and quality would be transmitted to the progeny. The ineffectiveness of this procedure was not generally realized until the development of the pure line theory by Johannson.

Following the rediscovery of Mendelism, plant breeders were quick to realize the implications of the rapidly expanding science of genetics to plant improvement. Even when the accumulating information was not directly applicable it served to develop a general understanding and appreciation of the complexities involved. Early in this period a number of papers appeared which indicated that quantitative traits followed the same general pattern of inheritance as qualitative traits as opposed to some type of blending inheritance which had previously been supposed to hold for metric characters.

Progress in plant breeding was equally dependent upon improvements in plot techniques and in experimental statistics. Prior to these developments, there was no real appreciation of the magnitude of environmental variability and techniques for comparing large numbers of selections, or hybrids were inadequate to provide reliable information on mean performance.

Some of the first methods used in corn breeding suffered from either genetic or statistical limitations or both. These limitations minimized realized progress and the conclusion was drawn by some that the limited progress was due to a lack of genetic variability. However, a careful consideration of the data available from either the mass selection or the ear-to-row breeding methods suggests that where there was a lack of significant progress it could readily be accounted for by the inadequacies of genetic control and field plot techniques.

Inbreeding and hybridization was the next breeding method used extensively in corn. Everyone has some familiarity with the results achieved and the accomplishments will not be reviewed in detail. A measure of the success achieved can be appreciated from the knowledge that currently in excess of 95 per cent of the nation's corn acreage is planted to hybrid corn. Total production has increased by at least 25 per cent and this increase has been achieved on 25 per cent fewer acres.

The genetic basis for hybrid corn was laid by the early work of Shull and East who demonstrated the reduction in vigor upon inbreeding and the restoration of vigor upon the crossing. In some cases the vigor of the cross-bred population exceeded that of the parent variety. It was visualized by Shull that such superior hybrids might well be used commercially. The apparent deterrent to this development was the low yield of the parent inbred lines. Although Shull produced and tested double-cross hybrids, he apparently failed to appreciate that this procedure provided a solution to the practical problems imposed

by the lack of vigor of the inbred parents. It remained for D. F. Jones to emphasize the double-cross procedure as a commercially feasible way to utilize hybrid vigor in corn.

When this development was suggested few of the experimental stations had inbreeding programs and the lack of satisfactory lines delayed commercial development for an additional 15 years. Many of the station and commercial programs were started about 1920 and the beginning of sizeable commercial utilization was delayed until the early 1930's. Many important contributions were made in the period from 1920 to 1940. Particularly notable among these were the top cross test for the evaluation of lines and double cross prediction from single cross data by Jenkins. During this period there was a slow and gradual shift from a genic to a population approach in the consideration of breeding problems. Initially, the only parental materials available for inbreeding were the open-pollinated varieties. Following the development of the first commercial hybrids, superior single and double-cross combinations were used as parental material.

Over the next 15 years, extensive public and private programs were concerned largely with the development and evaluation of very large numbers of inbred lines. A succession of improved hybrids was obtained but the successive increments of yield increase were much less than those obtained in the initial improvement. Again we hear the viewpoint that genetic variability for yield has been exhausted and that further improvements will involve only such ancillary attributes as disease and insect resistance. If such a belief were justified, it would require a complete re-evaluation of corn breeding programs involving both procedures and the relative priorities of the various objectives. Before any such drastic reorganization is initiated, it may be desirable to speculate as to whether the reduced rate of progress requires the assumption of limited genetic variability or indicates merely an inadequate knowledge of genetic variability and the procedures required for efficient control and manipulation.

We may list the factors which limit progress under the following general headings:

1. Large number of genes involved.
2. Type of gene action.
3. Genotype-environment interaction.

Since some aspects of these topics will be considered in detail by other speakers, we shall be concerned here only with broad generalities.

Information on number of genes conditioning such quantitative traits as yield, resistance to lodging, and disease resistance, to name only a few, is completely lacking. Experience would suggest, however, that the number is large. One can calculate that in a population heterozygous at 10 loci a sample requiring approximately 90 acres would need to be grown to provide an even chance for the occurrence of the homozygote possessing the desired allele at each locus. If 20 or 30 loci were heterozygous, the land areas required to provide an even chance of obtaining the desired homozygote would be in excess of

90,000,000 acres or the land mass of the earth, respectively. Some workers have argued that with the large total number of lines which have been isolated, lines approaching the yield level of open-pollinated varieties should have been obtained. Yield trials of inbred lines have not been extensive, so critical data on this point are lacking. Observation would suggest, however, that lines approaching the yield level of open-pollinated varieties have been obtained at various times. None of these has proved valuable in hybrid combinations but this limitation has been for reasons other than the yielding ability of the line.

The possibility of a large number of genes poses problems additional to the probability relationships just mentioned. One of the most important of these is linkage. In the original sampling of open-pollinated varieties it may be assumed that such varieties were in approximate linkage equilibrium. This equilibrium would not exist in the back-cross or second cycle populations which largely replaced the direct varietal sampling. Lines contributing to superior F_1 yields would be expected to possess strong genetic dissimilarities and the consequent departures from linkage equilibrium would impose an important barrier to progress through selection. Improvements would come largely from substitution of whole chromosomes or large chromosome segments rather than from gene substitutions made possible by recombinations. The limited progress which has been made by the various forms of cyclic selection involving the direct isolation of lines from F_2 or backcross progenies is not surprising, but possibly it should have been expected.

If the number of genes conditioning important attributes is large, this will also have a bearing on the effectiveness of the selection practiced. Expected changes in gene frequency become less, with a given intensity of selection, as the number of loci involved increases. The selection pressures actually applied may be much less than generally assumed. It is common to measure progress in terms of yield improvement, the implicit assumption being that the entire selection pressure has been applied to yield performance at the hybrid level. This may have been largely true with the first commercial hybrids developed, since the major requirement at that period was performance superior to open-pollinated varieties. As work continued, however, additional criteria of performance were added. Hybrid combinations were required to possess resistance to root lodging, stalk breaking, ear dropping, leaf blight, and a number of other diseases and insect pests and also to possess an acceptable seed parent. With the addition of each new criterion of evaluation the selection pressure applied for yielding ability would be expected to decrease unless there was a corresponding increase in the number of items evaluated. If selection is practiced simultaneously for n attributes, the selection pressure for each is $\frac{1}{\sqrt{n}}$ of that which could have been applied had only a single attribute been involved. On the basis of information available it is not possible to assign a specific value to n since all variables do not receive equal consideration in each yield trial evaluation. It seems probable,

however, that selection pressure for yield is less than commonly assumed and within any single program it may actually have been steadily decreasing during the past 20 years.

Information on types of gene action has been derived from a number of procedures. It should be obvious that adequate information is needed on this point for the development of breeding systems having maximum efficiency. The procedures used in providing estimates differ in their underlying assumptions, and the studies have also differed in the parental material used. The analysis of diallel crosses and certain types of bi-parental progenies has been used to supply information on the relative magnitude of additive and non-additive genetic variance.

Information is needed at two different levels: for random mating populations at linkage equilibrium and for groups of hybrids involving selected inbred lines. Relatively little information is available from random mating populations. The limited data which are available suggest the importance of partial and complete dominance and the relative unimportance of overdominance and epistasis. Useful as such information may be as a basis for decisions between alternative breeding schemes, the estimates represent the average condition for the population. They provide no satisfactory guide as to the maximum deviation from this average condition that may be expected in a particular inbred line isolated from some random mating population. It would be conceivable that the gene action characterizing some specific single cross combination might represent a marked deviation from the average estimates from the parental varieties. This problem remains to be investigated.

Studies involving selected lines are probably most useful in providing an explanation for the actual observed differences. However, they provide a somewhat hazardous basis for extrapolation to a hypothetical random mating population or to other seemingly comparable hybrid populations. The results obtained from a group of other than random lines are subject to an unknown bias, this bias arising from the past selection history and the effect of such selection on the degree of departure from the average situation characteristic of the parental population.

Studies involving single crosses between highly selected inbred lines have indicated the importance of non-additive gene action. It seems unlikely that any sizeable fraction of the non-additive variances is associated with true overdominance. This leaves epistasis as the most likely causal factor. Attempts to estimate the importance of epistasis in contrasts involving single cross and three-way cross means indicate an average contribution of epistasis to the mean yield level of approximately 10 per cent, and in individual contrasts this contribution may exceed 30 per cent. If these estimates are substantiated by more extensive data, it may well suggest a re-assessment of the importance of epistasis and a re-evaluation of the whole problem of choice of testers.

Considerable evidence has accumulated suggesting the importance of genotype-environment interactions. The most extensive and possibly the most

reliable data have been accumulated from replicated field plantings involving a series of diverse populations, each of uniform genotype. Data from heterogeneous populations provide information which is not amenable to precise interpretations. With heterogeneous material a uniform replication of genotypes within a plot is not feasible. Thus, any differential response of genotypes comprising a given plot, or series of plots, tends to be averaged out, yielding a minimum estimate if plot totals or means are used. If an attempt is made to estimate the within plot variance, the problem becomes one of separating genetic and environmental variation. This is commonly attempted by using one or more uniform genotypes, inbred lines or hybrids, to estimate the environmental variance.

An estimate of genetic variance is then obtained by subtraction. This procedure assumes that all genotypes exhibit similar reactions to varying environment. If such an assumption were completely valid, there would be no genotype-environmental interaction to measure. The assumption of uniform response to environment appears to be particularly hazardous in normally cross-pollinating organisms where large differences in vigor and somewhat lesser differences in maturity may be involved at the inbred and hybrid level. Thus, each of the presumably uniform populations may actually be sampling different environmental sequences. It should come as no surprise, therefore, when uniform inbred or F_1 populations provide widely differing estimates of environmental variance. This estimating procedure possibly may have somewhat more validity in the normally self-pollinating species where parents and F_1 are more nearly alike in vigor and yielding ability. One is plagued, however, by the rather disturbing feeling that each genotype may have its own characteristic environmental response. Whether this is true, it appears that the problem of genotype-environment interaction has received much less attention than its importance may justify.

The present situation in corn breeding represents something of a paradox. In certain areas practice has progressed beyond the development of adequate theory. This undoubtedly has been an important contributing factor to the reduced rate of progress experienced in recent years. However, reduced progress has led neither to a wide-spread, critical re-evaluation of the several possible limiting factors, nor has it stimulated a general realization of the need for further extension and evaluation of theory. The general absence of such a critical evaluation is perhaps not too surprising since plant breeding has evolved at least as much through empirical trial and error procedures as through a close dependence upon confirmed genetic theory.

A word of caution may be in order. Statistical genetic studies have been pursued somewhat more extensively in corn than with many other economic crops. There has been a tendency to assume that information and procedures arising from corn studies can be transferred bodily to other crop species. It should be remembered that any estimates obtained from corn populations have been influenced by population structure and size, gene frequency, past selection history, linkage equilibrium, and various other circumstances. Attempts to trans-

fer corn techniques and population estimates to other species without a critical evaluation of possible differences in population structure or ultimate use may serve to delay progress and regiment procedures to an unwarranted extent. This could lead to unjustified conclusions as to the inadequacies of the statistical genetic approach. Basic principles have a wide range of applicability but the utilization of such principles must be guided by the population and use characteristics of the specific crop.

This brief résumé purposely has been kept very general since the several topics mentioned are to receive detailed consideration during the course of this symposium.

In conclusion I should like to reemphasize the following points:

1. Progress in plant breeding during any particular period has been dependent on the genetic information of that period and the extent to which such information has been utilized.

2. At the present time statistical genetic theory is not completely adequate to provide answers to all of the important breeding problems. Of more importance, however, is the fact that a very considerable body of theory is available which is not being used adequately by plant breeders.

3. The failure of a more extensive use of available theory may be due to several causes.

This symposium was designed to minimize any limitations arising from either a lack of familiarity with statistical genetic theory and philosophy or from a lack of appreciation of the utility of statistical genetic methodology in the solution of breeding problems. It is not generally known, but the reciprocal recurrent selection technique was developed as a result of problems posed at a plant breeding conference held in Raleigh, N.C. in 1948. It is to be hoped that these meetings will provide stimulation for new advances in theory and its subsequent practical utilization.

PART I–SYMPOSIUM

Biological and Statistical Concepts of Genetic Theory

R. P. MURPHY, *Chairman*

Modes of Reproduction and Their Genetic Consequences[1]

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LIVING organisms must reproduce to perpetuate themselves. There are, however, a variety of reproductive techniques and which one a species chooses determines to a large extent the variety of genotypes found within it. Both the variety of genotypes and that of phenotypes found in a population is a function of its breeding structure and of the complexity of the environments with which it must cope. Our talk is to deal in a general way with the interrelations of breeding structure and genetic variation. We impose one restriction on our discussion. The only type of gene to be discussed is that which affects fitness. It is only with such genes that we can make statements as to their expected frequencies in populations.

SEX AND PLOIDY

Sex confers an enormous evolutionary advantage upon organisms. "Sex," for our purpose, includes all mechanisms which permit the recombination of genes of diverse origins. The advantage derived from sex is the rapidity with which new gene combinations can be formed and subjected to natural selection.

Let us assume that the frequencies of genes a and b in a population of asexual, haploid organisms are the same (p) but that no ab individuals exist. What is the frequency with which ab individuals will be found in the following generation? In the absence of gene recombination the frequency of this class of individuals will depend upon mutation rate. Assuming that A mutates to a and B to b at approximately the same rate (u) the frequency of ab individuals in the next generation will be roughly $2up$.

In a sexually reproducing population, on the other hand, given equal frequencies of a and b (p), the frequency of ab individuals in the next generation will be p^2. As long as p is greater than $2u$, p^2 is greater than $2up$. Even in haploid organisms a mutant gene must be semilethal or worse if its frequency at equilibrium is to be less than twice its rate of mutation.

Sex permits a relatively high proportion of novel genotypes to be formed in every generation, that is, a frequency of novel genotypes which is related to

[1]Contribution No. 422, Dept. of Plant Breeding, Cornell University.

gene frequencies rather than to mutation rates. These conclusions are not original. They have been discussed earlier by Muller (14) and Haldane (7), among others.

Wherein lies the advantage of diploidy? The generally accepted version of the advantage of somatic diploidy (ascribable to Svedelius, 20; according to Stebbins, 17, p. 173) is based on the fact that deleterious genes can be sheltered in heterozygous condition. Therefore, new and possibly advantageous combinations of these genes can be formed, even though some of the intermediate gene combinations might be selectively disadvantageous. Suppose, the argument goes, both AB and ab represent adaptive gene combinations for a haploid organism whose normal constitution is AB; the organism may never form ab if the combinations Ab and aB are disadvantageous. In contrast, $aabb$ diploid organisms can arise since they will occur as offspring of $AaBb \times AaBb$ matings.

If haploid organisms may utilize sexual reproduction, the argument given above for the advantage of the diploid state is not valid. The frequency of the genes a and b in a haploid population (assuming that mutation rates (u) and selective disadvantages (s) of the two genes are the same) will be u/s. The frequency of ab individuals will be $(u/s)^2$. In a diploid population the frequency of aa or bb individuals will be u/s each (making the same assumptions about equality of mutation rates and selective disadvantages) and, therefore, the frequency of $aabb$ individuals will also be $(u/s)^2$. Obviously for a completely recessive gene, haploid and diploid organisms produce the same proportions of novel genotypes.

If the dominance of the "normal" genes is not complete, diploids offer a less favorable field for testing novel gene combinations than do haploids. The reason for this is readily apparent: Any gene which is unfavorable in heterozygous individuals will have a lower frequency in a population than if it were unfavorable in homozygotes alone. Thus, the frequency of $aabb$ individuals, the only genotype supposed to represent a new, selectively advantageous gene combination, will be lower if dominance of the normal genes (A and B) is incomplete than if it is complete. Thus, it seems as if diploidy offers no advantage over haploidy by virtue of the "sheltering" of deleterious genes in heterozygous condition if the new homozygotes ($aabb$) are the sole possessors of the novel, advantageous phenotype.

In seeking an alternative advantage for diploidy, the suppression of the mutational load appears as one obvious explanation. The fitness of a haploid population at equilibrium is decreased $u/s \times s$ or u for each locus. Considering all loci, the fitness of a haploid population at equilibrium is lowered as a result of mutation to an extent equal to total mutation itself. If, within such a population, haploid genomes could be associated at random, the average fitness of the resulting diploid combinations would be lowered by only $(u/s)^2 \times s$ or u^2/s. This "load" is only u/s as large as before. We can conclude, therefore, that if mutational load plays an important part in natural selection, the utilization of diploidy could reduce this load to a small fraction of its original value.

The possibility described above, if true, represents a "makeshift" solution to a perplexing situation confronting a population. Once mutation re-establishes equilibrium frequencies in the new diploid population, the genetic load becomes twice its original size. At best, assuming complete dominance of all normal genes, the new mutational load will be precisely what it was in the original haploid population. If dominance is incomplete, tetraploids, octoploids, and other higher ploids will eventually bear genetic loads 4, 8, or more times greater than do haploid organisms. This would seem to suggest that the majority of higher plants and animals have fallen into a enormous evolutionary trap.

There may exist, however, another possible advantage of diploidy. Diploidy, because of the presence of two alleles at each locus, may open evolutionary vistas not available to haploid organisms. There are at least two ways in which this may happen. First, the gradation of phenotypic expressions of genes may be much finer when these effects result from two genes acting in concert than when they are produced by single alleles. This requires nothing more than the usual dominant-recessive relationships with intermediate heterozygotes. To be sure, there may exist an allele, A_1, which when homozygous will duplicate the action of a given heterozygote, A_mA_n. However, the mere existence of this allele results in the formation of additional heterozygotes, equal in number to that of already existing alleles, any one of which may be advantageous in its own right under the proper conditions. The gradation of phenotypic expression can never be as fine for single genes as for their diploid (including heterozygous) combinations.

The second way in which the diploid state may confer an advantage lies in the phenomenon of over-dominance or heterosis. Two alleles may produce phenotypic effects which cannot be duplicated by the single alleles of haploids (or of homozygotes). According to this view, diploidy offers entirely new opportunities to an organism, not merely a refinement or possibilities already inherent in the haploid state.

LIMITATIONS OF HETEROSIS

For the moment, we will assume that heterosis does indeed exist. By "heterosis" we mean that the interaction of a pair of alleles, a' and a'', produces a higher fitness than does homozygosis for either allele alone, $a'a'$ or $a''a''$. It is not necessary to assume that every combination of two alleles at a given locus exhibits heterotic properties; it is necessary to assume only that highly fit individuals carry two different alleles.

What limits the extent to which a population may utilize heterotic systems, or more specifically, these systems at different loci? Account must be taken of the loss of zygotes during development. If none are lost, there is no heterosis nor, indeed, is there any selection at all. It is impossible to have heterosis by virtue of non-defective alleles (East, 5) where fitness is the trait under consideration. If zygotes are being lost during development because of selection, then the factor which limits the use of heterosis as an important genetic feature of a population is the average number of zygotes a pair of parents in the population

can produce. In a biparental species, each female must leave on the average two surviving offspring if the population is not to become extinct. In a two-allele system where gene A has a frequency p while a has a frequency q, and where the fitnesses of AA and aa individuals are $1-s$ and $1-t$, respectively, loss of zygotes ascribable to heterosis equals $sp^2 + tq^2$. More generally, if the adaptive values of all homozygotes are equal $(1-s)$, the zygotic wastage ascribable to a single locus becomes s/n where n equals the number of alleles participating in heterotic combinations. For N independent loci, the proportion of surviving individuals equals $\left(1 - \frac{n}{s}\right)^N$. In Table 1 are listed the number of fertilized eggs each female

TABLE 1.—THE APPROXIMATE NUMBER OF ZYGOTES (FERTILIZED EGGS) A FEMALE OF A BIPARENTAL SPECIES MUST PRODUCE ON THE AVERAGE IN ORDER TO MAINTAIN HETEROTIC SYSTEMS INVOLVING A GIVEN NUMBER OF INDEPENDENT GENE LOCI AND GENES WITH SPECIFIED DELETERIOUS EFFECTS WHEN HOMOZYGOUS. UPPER FIGURES GIVE THE REQUIREMENTS IF THERE EXIST ONLY 2 ALLELES PER LOCUS; THE LOWER, IF 20 ALLELES PER LOCUS INTERACT HETEROTICALLY.

Disadvantage of Homozygotes	Number of loci			
	1	10	100	1000
1	4	2000	$> 10^{30}$	$> 10^{300}$
	3	3	340	$> 10^{22}$
.5	3	36	$> 10^{12}$	$> 10^{124}$
	3	3	25	$> 10^{10}$
.1	3	3	340	$> 10^{22}$
	3	3	4	300
.01	3	3	4	300
	3	3	3	4
.001	3	3	3	4
	3	3	3	3

of a biparental species must produce on the average in her lifetime if populations of that species are to tolerate heterotic systems (a) involving various numbers of loci ($N = 1$ to $N = 1000$), (b) in which homozygotes suffer various disadvantages ($s = 1$ to $s = .001$), and (c) in which the number of alleles involved at each locus (n) is either 2 or 20. For most plant species, the number of zygotes produced per female would be roughly one half (to the next higher whole number) than that shown in the table. In making these calculations we have allowed for no zygote wastage except that needed for the heterotic system itself.

The main conclusion which follows from calculations such as those in the table is as follows: If the optimal fitness is a property of a genotype heterozygous for genes at many gene loci, the number of offspring produced per

female must be very high (a) if many gene loci are involved and (b) if the selective differentials are large ($s = .10$ or more). This situation is especially pronounced if only two alleles exist at each locus. If, instead of 2, there are 20 alleles which give heterotic combinations at each locus, the fertility requirements for the species are alleviated somewhat. Nevertheless, in a system involving 20 alleles per locus at each of 1,000 independent loci where homozygotes possess 50 per cent fitnesses of the heterozygotes, the demands are much too high for most land animals to meet. It is doubtful that any organism could meet these demands, since we have allowed for no wastage of zygotes except that required for the heterotic systems themselves.

Before leaving this topic we may consider whether a species can circumvent the need for colossal fertilities in order to utilize heterosis. There are two obvious possibilities each of which acts to eliminate the independence of loci assumed in our calculations.

The first way in which this situation is improved is a mechanical one, namely linkage. If, within a population, there exist two heterotic systems, the highest average fitness (or, the least loss of zygotes) is achieved if the components of the two systems are linked. Thus, if there are two heterotic systems, A and A' and B and B', in each of which the homozygotes are at a selective disadvantage s, the average fitness of the population is raised from $(1 - s + s^2/_4)$ to $(1 - s + s^2/_2)$ by absolute linkage. This fact may be involved in the observation by Professor Carl Epling (personal communication) that one rare gene arrangement (TL) in populations of *Drosophila pseudoobscura* inhabiting southern California has an exceptionally high frequency of lethals and, besides, a high frequency of allelism. It may also be involved with the fact that chromosomes of most species are numbered neither in the thousands nor, generally, in the hundreds.

Linkage is not the only method by which the independence of heterotic systems is reduced. Physiological interactions, specifically those which follow the law of diminishing returns, may make the heterosis exhibited by genes at one locus dependent upon the number of loci for which an individual is heterozygous. For example, heterotic combinations of alleles may exist at any one of a thousand loci. However, if genes at any 10 of these 1,000 are in fact heterozygous, heterozygotes and homozygotes at the remaining 990 loci may be virtually equal in fitness. A system of this sort has been proposed by Tantawy and Reeve (21) who claim that the fixation of genes at one locus as the result of inbreeding makes it increasingly difficult to fix genes at the remaining loci. Some of our own work, to be discussed in the next section, has led us to a similar conclusion.

HOW COMMON IS HETEROSIS

Calculations in the preceding section show that a pronounced heterosis at a large number of independent loci is unlikely since most living things simply do not produce enough eggs to support the demands of differential survival inherent in such a system. Nevertheless, we can devise experiments to determine

how common the phenomenon of heterosis is. The answer given by our own experiments, at least, is "very common".

This is not the place to discuss experimental techniques in detail as these can be found in an earlier publication (Wallace, 27). We will simply point out that in some species of Drosophila it is possible to manipulate wildtype chromosomes at will by utilizing files carrying specially-constructed, genetically-marked "laboratory" chromosomes. Utilizing these techniques one can make individuals homozygous for a given wildtype chromosome, heterozygous for two different chromosomes obtained from the same population, or heterozygous for two chromosomes obtained from widely separated localities. With each of these different types of flies one can obtain a precisely corresponding type except that one of the two chromosomes is derived from a parent exposed to radiation. Thus, mutations induced by radiation can be studied in heterozygous condition in a background which is either homozygous, heterozygous to the extent characteristic of natural populations, or heterozygous to an extent obtainable in inter-population hybrids.

The rationale of this type of experiment is the following: If heterosis is a rare phenomenon, most gene loci in wildtype chromosomes of large populations will be occupied by normal genes. Radiation-induced mutations will be deleterious in this case. Most deleterious mutations are supposed to be expressed to some extent in heterozygous individuals. Consequently, flies carrying an irradiated chromosome should have impaired viability.

Results of experiments testing the validity of the above argument have already been published (Wallace, 26, 27). The new mutations in these studies seemed to increase the average viability of individuals otherwise homozygous for an entire chromosome. This effect can scarcely be explained if heterosis does not exist or exists only at a limited number of loci. On the contrary, heterosis must be an exceedingly common phenomenon to give this result. Some doubt about the validity of conclusions based on these experiments arose because new mutations apparently improved the viability of flies already heterozygous for two dissimilar chromosomes.

In Table 2 are listed the results of some new experiments. The conclusions are tentative even yet because the number of cultures is small. No statistical tests of significance for these new data are available. Nevertheless, it is interesting to note that the data for homozygous cultures bear out the earlier results, the apparent improvement of homozygotes accompanies an exposure as high as 2,250 *r*. The intra-population heterozygotes, as expected, seem to react differently to new mutations than do homozygotes; there is no evidence that the viability of these heterozygotes is improved by radiation and 2,250 *r* seems to be somewhat deleterious in its effect. The results for inter-population heterozygotes are disappointingly erratic. There is no indication that the newly induced mutations are either beneficial or deleterious for these flies nor for the curly-lobe flies which are, in a sense, a special type of inter-population heterozygote.

TABLE 2. THE AVERAGE VIABILITY OF FLIES (*Drosophila melanogaster*) HOMOZYGOUS OR HETEROZYGOUS FOR WILDTYPE CHROMOSOMES AND HETEROZYGOUS AS WELL AS FOR GENE MUTATIONS INDUCED BY FOUR LEVELS OF RADIATION: 0 *r* (CONTROL), 250 *r*, 750 *r*, AND 2,250 *r*. (STANDARD VIABILITY (= 1.000) IS THAT EXHIBITED BY CyL/Pm FLIES, A MUTANT APPEARING IN EACH CULTURE).*

Genetic Structure	Level of radiation			
	0 *r*	250 *r*	750 *r*	2,250 *r*
Wildtype; homozygous for entire 2nd chromosome:	1.139	1.149	1.155	1.182
Wildtype; heterozygous for two 2nd chromosomes of same locality:	1.297	1.307	1.293	1.284
Wildtype; heterozygous for two 2nd chromosomes of widely separated geographical origins:	1.401	1.431	1.397	1.414
Curly Lobe; heterozygous for wildtype chromosome and "laboratory" chromosome genetically marked with genes "Curly" and "Lobe":	1.093	1.098	1.104	1.096

*As mentioned in the text, these data have not been subjected to statistical analysis.

COADAPTATION AND INTROGRESSION

In determining the fitness of individuals, genes do not act independently of one another. Genes at one locus interact with those at others, so that in speaking of the adaptive value or fitness $(1 - s)$ of a given gene, we are really speaking of an average value; the variance in fitness exhibited by one gene in a variety of genetic backgrounds may be tremendous. To the extent that genes carried in the gene pool of a population are selected so that individuals will on the average carry well-adapted genotypes, we say that the components of the gene pool of the population are coadapted. Coadaptation of this sort can be demonstrated experimentally by a breakdown in average viability following inter-population hybridization. Positive results for *Drosophila* have been obtained by Brncic, (1); Vetukhiv, (22, 23, 24); Wallace, (25); Wallace and Vetukhiv, (29); and King, (9, 10). Furthermore, utilizing a different experimental approach, Dobzhansky and Pavlovsky (4) were able to show that hybrid populations containing the same two gene arrangements from each of two localities tend to lose one of these arrangements. Recombination destroys the genetic basis upon which the retention of two gene arrangements in a population is based. In addition to these experiments, however, there are a number of attempts to demonstrate coadaptation which have failed: Robinson *et al.* (corn), (15); Merrill (Drosophila), (12).

Coadaptation may, in theory, arise irrespective of the breeding structure of the population. The heterosis exhibited by a pair of alleles at one locus may depend upon alleles at another locus just as well as the beneficial effect of homozygosity for a given allele at one locus may depend upon genes occupying other loci. Crow (2) has argued, however, that coadaptation which involves epistatic interactions between genes at different loci should be more important

in a clonal organism than in an outcrossing species. In a comparative study of the development of resistance to chloramphenicol in *E. coli* and DDT resistance in *D. melanogaster,* Crow found that inter-strain bacterial crosses resulted in an appreciable loss of resistance to chloramphenicol while no comparable loss of DDT resistance was observed in inter-strain Drosophila crosses. It is interesting to apply Crow's arguments to introgression in plants.

A variety of facts dealing with hybridization, polyploidy, and introgression presented by Grant (6) have been summarized in Table 3. The point which

TABLE 3. THE INTERRELATIONS OF SELF OR CROSS FERTILIZATION; ANNUAL, BIENNIAL, OR PERENNIAL HABIT; AND POLYPLOIDY, INTROGRESSION, AND APOMIXIS IN PLANTS. (A CONDENSATION BASED ON GRANT, 6).

Growth habit	Selfing	Crossing
Annual	Polyploids-common Very little introgression	Introgression
Biennial	(no examples)	Polyploids rare or absent Introgression
Perennial	(no examples)	Polyploidy* Introgression Apomixis-all common

*Polyploidy more common among crossing perennials than among selfing annuals.

seemingly supports Crow's arguments is the prevalence of introgression in all cross-fertilizing groups and the lack of it in self-fertilizing annuals. Polyploidy bears upon this situation only to the extent that in being a common phenomenon in selfing annuals it shows that an opportunity for introgression to occur actually exists in that group. The annual selfers, however, do not avail themselves of this opportunity. Utilizing Crow's arguments, one can speculate that the high level of coadaptation, of the interdependence of genes at one locus on the presence of particular genes at other loci, in the self-fertilized species causes introgression in these groups to lead to a breakdown in fitness too great to be tolerated.

The occurrence of introgression in outcrossing species does not indicate that coadaptation does not exist in these forms. (Indeed, where Crow failed to detect coadaptation in Drosophila, King found excellent evidence for its existence.) The demonstration of coadaptation in Drosophila has been based, in most experiments done so far, on the average viability of all progeny offspring. The experiments have not been designed to test the range of viabilities of the individual members of hybrid progenies. In a given cross one can generally say that the average viability of the resulting progeny is lower than that of F_1 hybrids of the parental flies, but one cannot say that every individual offspring of the given cross has impaired viability. In a study of experimental populations containing two interfertile Drosophila species, *D. mojavensis* and *D. arizonensis,*

Mettler (13) found that most of these hybrid populations retained blocks of genes from both species. Obviously, certain "exotic" gene combinations conferred high fitness on their carriers in these studies.

Cross-fertilizing plants which show considerable introgression may rely upon only a small fraction of their total seeds for population replacement. Certain interspecific or intervarietal gene combinations may make up a considerable proportion of this small fraction. The tolerance of introgression as a feature of normal reproduction, if the intercrossing of different strains leads to many inviable gene combinations, must be subject to the same limitations as that of heterosis discussed earlier. Enough seeds must be produced per individual to allow for the elimination of ill-adapted genotypes.

SELF- AND CROSS-FERTILIZATION

The study of the genetic consequences of inbreeding and outbreeding began with Mendel and has continued, on increasingly higher levels of complexity, to the present time. It seems reasonable to restrict our present comments to consequences of importance to natural rather than artificial populations.

It seems to be well established that self-fertilizing plants have arisen from cross fertilizing ancestors (Darwin, 3; Stebbins, 19). It is well known from many experiments that a regime of self-pollination imposed upon a normally outcrossing species leads to "inbreeding" depression. Kimura (8) has calculated that the presence of one lethal-equivalent per gamete on the average is an effective barrier to the adoption of selfing by an outcrossing species. Since most cross-fertilizing species of animals studied have proved to carry more than this number of lethal-equivalents, the adoption of self-fertilization by a plant species probably represents the breaking of a real biological barrier.

Under what circumstances can there be an advantage in a mode of reproduction which is generally disadvantageous? This advantage occurs probably in situations where cross-fertilization itself is a disadvantageous trait. This may occur because the vagaries of chance which accompany cross-fertilization in an annual species. Accidental failure of fertilization in any one season would be a real calamity for such a population. We may add here the situation which exists wherever terrain suitable for habitation occurs only as isolated patches; cross-fertilization between such isolated patches may well be impossible so that self-fertilization becomes a necessity. Still a third possibility has been suggested by Stebbins (17, p. 177): Self-pollination permits rapid exploitation of environments which are uniform within a growing season but which are subject to drastic changes from year to year. The uniformity of self-fertilizing plants insures that a few survivors of one season can re-populate the entire area when conditions are suitable once again.

To the above I would add still another, perhaps somewhat paradoxical, situation. Cross-fertilization, despite the fact that it permits the retention of many mutant genes in population, is essentially a conservative method of reproduction for a population confronted by many environmental situations through-

out its distribution range. The conservative aspect of crossing arises from the fact that no individual is free of the selective influences operating on all other individuals (Mayr, 11). This statement, in fact, is merely the converse of the argument we used in explaining the advantage of sex. Sex, the recombination of genes of diverse sources, offers the most efficient technique for constructing new gene combinations; mutations occurring anywhere in a sexually reproducing population have an opportunity to form novel gene combinations with those arising elsewhere in the population. In asexual populations, on the contrary, mutations must arise in tandem sequence in order to form various combinations. However, new gene combinations cannot be formed by recombination without useful combinations being destroyed. Thus, when a population of cross-fertilizing plants has occupied an area encompassing a variety of environments, the same process which underlies the advantage of sex leads to the disruption of adaptive genotypes and limits the further exploitation of additional environments.

In discussing this contention, I will lean heavily upon a personal communication from Professor Harlan Lewis which deals primarily with those groups (*Clarkia* and *Amsinkia*) with which he is familiar. In this communication Lewis states that "when closely related taxa differ in breeding habit, one group being outcrossed and the other self-pollinated, the selfers very often (but by no means inevitably) have the greatest geographical area of distribution, occur in the greatest numbers, and occupy the most diverse habitats." This statement is followed by the qualification that of the examples which come to mind the wide ranging selfers are polyploid. In contrast, self-pollinating diploids tend to have more restricted areas of distribution than their outcrossing relatives. Furthermore, the selfing polyploids which range widely relative to their outcrossing diploid progenitors are polyploids from near relatives; selfing polyploids from distantly related species have relatively restricted areas of distributions.

The case of the self-pollinating diploids may be considered first. Knowing that inbreeding is generally a derived condition and that the adoption of inbreeding as a means of reproduction leads to a decline in fitness, I would claim that in the case of these diploids selfing was adopted as a "last resort." Perhaps restriction in numbers of individuals had already preceded self-pollination so that the species were relatively homogeneous at the time the selfing habit was adopted.

Of greater interest is the wide ranging distribution and flourishing numbers of selfing polyploids carrying genomes from close relatives. Since these polyploids start from hybrids, they cannot initially have been genetically homogeneous. Next, polyploidy lessens the rate at which homozygosity sets in following self-fertilization. Third, as Lewis has pointed out to me, inter-genomic recombination must supplement mutation as a source of new variability for an extended period of time. The net result of these factors is the origin of a widespread complex variable from location to location, each local population of which is adapted to its own micro-habitat. Each local population exists with

no restrictions imposed by alien gene combinations arising under different selective forces in other environments.

Finally, to conclude this line of argument, we must consider the selfing polyploids whose genomes come from distantly related species. These polyploids have relatively restricted geographical distributions. Such polyploids, following the initiation of self-fertilization, approach complete homozygosity at the same rate as do diploids. Furthermore, inter-genomic recombination cannot occur. In this case (and in the preceding one as well) I would ascribe the initial advantage of selfing to the avoidance of crossing with diploid progenitors (crossing which if it occurred, would lead to sterile triploids). However, in the present case selfing is associated with many more disadvantages than in the case of polyploids from close relatives, an association which is reflected subsequently in the relative success of the two types of selfing polyploids.

If recombination of gene combinations selected initially under diverse environmental conditions results in the destruction of their usefulness, one might predict that the dispersal of pollen or seeds of cross fertilizing species would be subject to control by natural selection, that there might exist an optimal dispersal range for locally adapted gene combinations.

It is difficult to see just what observations are necessary to test the validity of the above prediction. One argument might run as follows: Granted that both selfers and crossers produce more seed than are essential for maintaining population size, selfers suffer very little from possessing mechanisms for wide seed dispersal while crossers (because of the breakdown in fitness accompanying inter-population recombination) would suffer relatively more. Data given by Stebbins (17, Table 3) seemingly support this argument: 85 per cent of the self-fertilizing species of Gramineae studied have efficient means for seed dispersal while only 35 per cent of the cross-fertilizing species studied of the same family were similarly equipped. However, in his personal communication H. Lewis states specifically that no comparable distinction exists in seed dispersal mechanisms of the groups with which he is familiar. My own experiences are totally inadequate for evaluating the variables (total seed production and environmental variation between seasons, to name two) which must be involved in this problem.

ASEXUAL REPRODUCTION

My comments on asexual reproduction will be exceedingly brief; they will touch only on the more-or-less formal relationship between this type of reproduction and genetic variability. Biological problems, that is, problems concerning the origin of, genetic basis for, or the establishment of apomixis in a particular species,—will not be considered here (see, however, Stebbins, 17, Chapter X).

In an earlier section dealing with heterosis, we raised the question as to the ability of a species to support a number of heterotic systems at different gene loci. The problem of affording a given genetic system recurred in our discussion of coadaptation and introgression. In each case the genetic system

under consideration was one which produced disadvantageous as well as highly fit ("normal") individuals; to assure numbers of the latter sufficient for perpetuating the population, reproducing individuals need produce many more zygotes than will eventually survive. We suggested, in fact, that the lack of introgression reported by Grant among selfing plants reflected a breakdown of coadapted gene combinations too great for these plants to tolerate. Our account of marginal conditions for a cross-fertilizing species is part of the same argument: The margin exists where the cost of recombination becomes too high.

Species hybridization and subsequent interspecific gene recombination impose the greatest possible strain on coadapted gene system; the harmonious gene combinations of each species can be destroyed by gene recombination following hybridization. At times, however, this recombination is tolerated; introgression is the name given to the extensive utilization by one species of genes obtained from another. In many interspecific crosses, however, the products of recombination are so poor on the average that the populations involved cannot tolerate the concomitant wastage of gametes. Various isolating mechanisms arise as a consequence of and as a means for preventing this wastage.

Granted that the variation in fitness is sufficiently great, however, there is a technique—asexual reproduction—by which a population can successfully utilize the recombination genotypes (including aneuploids) of interspecific hybridization with little or no regard for the mean fitness of these recombinants. As Haldane (7, p. 177) pointed out, intense selection selects the more variable population rather than the population with the higher mean. Asexual reproduction allows selection to operate the maximum intensity; a single desirable genotype can be perpetuated asexually in enormous numbers. This fact has been appreciated by plant breeders; for example, Rollins, Catcheside, and Gerstel (16) recommend initiating artificial selection in guayule by making the initial variability as great as possible. When one considers the frequent association of hybridization, polyploidy, and aneuploidy with apomixis, it appears obvious that nature anticipated this recommendation.

EVOLUTIONARY GENETICS AND PLANT BREEDING

It is customary, I believe, for evolutionary geneticists to summarize general accounts such as this one by citing the implications their work has for artificial breeding programs. This is fair enough. However, excellent articles of this sort already exist (for instance, Stebbins, 19, as well as Stebbins, 17, pp 290ff, 369ff, and 417ff). Of the topics discussed by us, heterosis, coadaptation, and asexual reproduction warrant further amplification in this concluding section.

Perhaps the most unexpected data discussed here was that of the effect of newly induced mutations in heterozygous condition on viability in Drosophila. Under certain circumstances these mutations seem to increase viability. These data appear to offer strong evidence in favor of "single-gene" heterosis. We should consider once more the rationale of the experiment which yielded these

data. Flies were made homozygous for a chromosome (about two fifths of the entire genome) carrying a sample of genes occurring in a large population. The observed improvement in average viability accompanying heterozygosis for newly induced mutations implies that the genes of the original population were not "normal" when homozygous. Carrying the argument an additional step, the results imply that these genes in the original population occurred primarily in heterozygous condition. It must be made clear that these results do not suggest that every inbred strain nor hybrids between inbred strains will be improved by the induction of new mutation. Inbred strains do not contain random samples of genes which exist in the initial material from which these strains are drawn. Inbred strains carry gene combinations which when homozygous produce viable and fertile individuals. Considering the replicate cultures used in perpetuating inbred material and the frequency with which these replicates fail to produce anything, one can see that surviving inbred material is most likely to be highly selected material.

Coadaptation, our second topic, has certain theoretical implications for the practical breeder but, in this case, the breeder is in a position to inform the evolutionist rather than the reverse. In transferring certain traits from one strain of plants to another by backcrossing, how often does the trait vanish? How often does it appear in distorted frequencies relative to those expected on the basis of intra-strain crosses? How does the efficiency of the backcross method vary from species to species? These questions arise in the mind of the evolutionary geneticist because the backcross technique is one which closely resembles introgression. It is a technique which should destroy coadapted gene combinations if these are responsible for the traits in question.

The implications of my brief remarks on asexual reproduction are fairly obvious. In working with apomicts or with vegetatively reproducing material, it is as important (if not more so) to know the range of variation which will come from a certain sexual cross as it is to know where the mean lies. In this case the breeder is looking for a single individual. The individual plant which represents the extreme upper tail of a highly variable distribution may greatly exceed any individual member of a more uniform distribution regardless of the relative positions of means.

Finally, in conclusion, I would like to pose for myself the following question: If any phenomenon—inbreeding, outcrossing, hybridization, polyploidy, apomixis, or the like—has been found to be an important evolutionary phenomenon, does it necessarily follow that it will be a useful device as well in a plant breeding program? I am inclined to answer "No."

First, the requirements of man and of nature are really quite different. The individual members of a natural population are confronted with the two problems, surviving and reproducing. Meeting both of these problems successfully requires the harmonious interaction of a multitude of genes whose pleiotropic effects touch on all facets of life. The more extensive the array of interactions, the less likely it is that any one allele will be optimal for each and every

demand placed upon it. Thus, heteroallelism within large, cross-fertilizing populations may be considerable. The wasteful aspect of such diversity is unimportant as long as sufficient numbers of normal individuals remain each generation after the culling of aberrant genotypes.

In contrast to the above situation, man's ingenuity has removed many problems of survival from his cultivated material. In many instances, the breeder has but a single goal (for example, maximum yield) which his material must meet. Although probably still great in actual numbers, the pleiotropic interactions between genes in cultivated material, especially in relation to the breeders primary goal, must be few in comparison with those in natural populations. Consequently, it is reasonable to expect that, in cultivated material, there exist at more gene loci, single alleles capable of functioning properly in homozygous condition.

Under a regime of mechanization, man demands uniformity of his agricultural products. To achieve uniformity, many breeding programs utilize two or more distinct populations such as the breeding stocks themselves and a commercially valuable hybrid population. This is a maintenance scheme which is virtually impossible in nature. More and more, plant and animal breeders are utilizing breeding stocks which give successful hybrids as measured by immediate demands. And, thus, the resemblance between artificial and natural populations becomes less and less.

Still another reason for answering "No" to the question posed above lies in the reasons *why* given phenomena have proven useful in nature. In many cases I suspect these reasons encompass a breakdown of a pre-existing system rather than (or, as much as) positive contributions of the new system. For example, under conditions which exist at and just beyond the extreme margin of a species' distribution range, the normal genotypes found in nearby populations must be lethal. In the case of cross-fertilizing species gene recombination may be largely responsible for the failure of marginal populations to achieve lasting adaptation to local conditions (Wallace, 29). Many of the reproductive techniques which we have considered may attain importance by solving the really pressing problem of marginal populations, the inadequacy of the normal genotype. Generally speaking, comparable situations of inadequacy do not exist in most breeding programs. Either man himself assumes many of the responsibilities of survival or, if one type of material is totally inadequate under given circumstances, man finds himself a more suitable substitute.

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DISCUSSION

H. E. SCHAFFER: Have any of the X-rayed chromosomes from the "homozygous" flies been extracted and put in homozygous state to check if the changed alleles (which have increased viability) are deleterious?

BRUCE WALLACE: In our experiments on the second chromosome of *D. melanogaster* we have not tested the irradiated chromosomes in homozygous condition. We know from past experience that radiation-induced mutations are overwhelmingly deleterious when homozygous; for a given exposure to X-rays one recovers a certain proportion of lethal mutations and an even greater proportion of mutations with smaller effects on viability. A prohibitive amount of work would be required to test each irradiated chromosome on a scale which would accurately characterize its effect on viability when homozygous and then to re-test it on an even larger scale to reveal its effect in heterozygous condition.

By using the X-chromosome it has been possible to determine the average effect of irradiated chromosomes in males (where they are present in hemizygous condition) and in females (where they are present with an unirradiated homologue). Here we find that the irradiated chromosomes lower the viability of males but so far we have no good evidence that they either increase or decrease the viability of females.

H. L. CARNAHAN: There must be different measures of viability in Drosophila. Did you use more than one measure of viability in your irradiation experiment relating to overdominance? If so, was there agreement in results obtained for different attributes of fitness?

BRUCE WALLACE: Our measure of viability is based on the relative numbers of adult flies of different genotypes which hatch in our cultures by the 17th day after mating. One genotype (CyL/Pm) is constant in all cultures and is taken as the standard for all genotypes. Our measure, then, includes egg hatching, larval, pupal, and (to some extent) adult viability, as well as speed of development. Past work has shown that there is a correlation between different measures of fitness; that this correlation cannot be perfect, however, is illustrated by sterile flies which otherwise are apparently normal.

R. E. COMSTOCK: You have stated that as fixation of genes proceeds, the ones remaining become progressively harder to fix. What is the best evidence you know of on this?

BRUCE WALLACE: The evidence supporting the claim that it becomes increasingly difficult to fix genes as more and more genes are actually fixed comes primarily from the Edinburgh group: Robertson and Reeve (1955. Z.I.A.V. **86**: 439–458), Tantawy and Reeve (1956. Z.I.A.V.**87**: 648–667), Tantawy (1957. Genetics **42**: 121–136). Illustrations of the diminishing

returns of increasing amounts of heterozygosity can be found in Robertson and Reeve (1952. Nature **170**: 296–298) and Robertson (1954. Caryologia, Suppl. Vol.: 1237–1238). [Subsequent to the Raleigh meetings a paper touching on this problem has been published by Reeve (1961. Evolution **15**: 145–152).]

R. E. COMSTOCK: In your irradiation work relating to heterosis, you noted significant response in homozygotes but not in heterozygotes. Was the difference in response found statistically significant?

BRUCE WALLACE: The new data on the viability effects of mutations in heterozygous condition have not been analyzed statistically; this has been emphasized in the text but can stand repetition here. These recent experiments involve six chromosomes of diverse origins; the amount of data available for each chromosome in each of tested combinations (homozygous, intra-population heterozygous, and inter-population heterozygous) and with each level of radiation is simply too small to make an analysis useful at this point.

H. F. ROBINSON: How do you (if you do) distinguish between overdominance and epistasis? Give definition of overdominance and synonymous meaning of overdominance and heterosis.

BRUCE WALLACE: In general I do not make a hard and fast distinction between overdominance and epistasis. I feel that the properties exhibited by alleles at any one locus are determined by genes at other loci; hence, overdominance may be exhibited by a pair of alleles in one genetic background but not necessarily in another.

[During this same period of discussion both H. F. Robinson and Alan Robertson made a distinction between "heterosis" (the observed phenomenon, equals "hybrid vigor") and "overdominance" (one possible genetic explanation for heterosis); the comments of Sewall Wright which follow were directed toward this portion of the discussion. At the time I was willing to accept this restriction of the use of "heterosis" and later began changing the terminology in the manuscript—a fact to which the Editor can ruefully attest. However, the result was so cumbersome that I soon reverted to my usual philosophy (that if a term is clearly defined in a paper it can be used according to that definition) and to my original terminology. To the dismay of some, then, the "heterotic" alleles of my paper are the "overdominant" alleles of other workers.

I wonder whether this flexibility of terminology isn't worth keeping at the present time when we know so little about the "basic" causes of hybrid vigor, "basic" in the sense that a molecular biologist would use the term? By insisting that "overdominance" is one cause of "heterosis", aren't we obscuring the interactions between loci which determine the degree of dominance (including overdominance) of genes at any one locus? Further-

more, are not we in danger of accepting the term as an explanation much as the physician who tells a patient with a rapid pulse that he is suffering from tachycardia?]

H. F. ROBINSON: Defining "heterosis" and "overdominance" as synonymous in meaning seems, to me, to add confusion to the literature and is actually the wrong usage from several standpoints. "Overdominance" or "superdominance" as defined and used by East and Hull was restricted to the superiority of the heterozygote at the individual locus level. Intra-allelic gene interaction is clearly intended here in contrast to inter-allelic gene interaction or epistasis. Whether or not we have any clear understanding of the basic causes of hybrid vigor or heterosis does not bear on the issue of the use of the term "overdominance" as used by Dr. Wallace. The fact that "heterosis" is a phenomena concerned with phenotypic expression from the total genotype and "overdominance" concerns the genotypic effects at a single locus is a distinction that cannot be disregarded.

SEWALL WRIGHT: I agree with Alan Robertson and Robinson and may add that George Shull, who coined the term heterosis, stated very emphatically at the Symposium on "Heterosis" at Ames, Iowa a few years ago that overdominance was not a synonym. It had been intended merely as a descriptive term for hybrid vigor, irrespective of mechanism. Its use as a descriptive term does not imply acceptance of the idea that Shull himself, as well as East, had of a physiological stimulus from mere difference between alleles at any locus. It also by no means necessarily implies overdominance.

F. H. W. MORLEY: Selfing is probably seldom complete, most species which are selfers having a low frequency of cross fertilization. This is probably of great evolutionary significance as well as being important in adjustment to short term environmental variations. Natural populations of selfers frequently display great variability (Discussion in C.S.H. Symposium 24) and for high degree of selfing may be by no means an evolutionary dead-end. The change from crossing to selfing might be facilitated by a gradual unloading of the load of deleterious mutants. The equilibrium frequency of lethals is reduced to little more than the mutation rate by even moderate levels of selfing (Wright, 1931). There are several obvious short-term advantages for selfing, and the disadvantages may be relatively minor in populations which have a history of some selfing, unless overdominance is common or extreme in few loci.

The Role of System of Mating in the Determination of Means, Variances, and Covariances in Genetic Populations[1]

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INTRODUCTION

FISHER (4) obtained the variance of individuals and some of the simpler covariances of relatives in random mating populations under a simplifying assumption of epistasis arising only between pairs of loci, which he termed "dual epistasis." Cockerham (1, 2) gave a formula for covariances of relatives in a random mating population for the case where there are 2 alleles at each locus with an arbitrary number of loci. Kempthorne (6, 7) gave a more general solution for this case in that the number of alleles at each locus could be an integer. Kempthorne (8) gave a partial solution to the theoretical covariances of relatives in a random mating autotetraploid population, and he gave a fairly general form for the covariances of relatives under selfing (10). Kempthorne (9) examined the covariances of relatives under a regular full-sib inbreeding system, and Horner (5) did the same thing for a parent-offspring inbreeding system. The effects of linkage are essentially untreated, with the exception of some equilibrium theory in which gene effects are assumed to be small (Fisher, 4; and Cockerham, 3). Linkage has been examined by Mather (12) for some special cases related to populations arising from two inbred lines. A general treatment of linkage is long overdue, but in the work to be reported here linkage is assumed to be absent.

The present paper was prompted by the idea that there should be a unified way by which problems of the type reviewed above can be solved in a reasonably routine way. An approach will be described which leads to the solution for all the cases so far worked out, and to formulae for an autotetraploid population under selfing. It appears to be of very general applicability as long as mating is based solely on consanguinity. The full details by which each case is worked out will not be given except for the case of an autotetraploid population. The detailed development for this case will illustrate the general process, as well as give results of interest in themselves.

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ASSUMPTIONS

In the following development it will be assumed that the mating is entirely on the basis of pedigree and that segregation follows regular Mendelian rules with the absence of linkage, differential variabilities, and selection of any sort. It will also be assumed that the populations are infinite. In other words, the genetic possibilities as regards offspring of a particular mating are exactly realized. Sex-linked effects and maternal effects will not be considered, though the inclusion of these cases present no new problems.

The basic idea is that the situations of relevance arise in the development of populations by means of certain definite inflexible genetic operations, as for instance,

(a) mate each individual to a random member of the population,
(b) mate each individual with a full-sib,
(c) mate each individual to itself.

Each such operation will be denoted by a symbol, as for instance, R for random mating, F for full-sibbing, and S for selfing.

It will be shown that consideration of the genetic properties of the particular operation leads to a model for the genotypic value of the starting individual(s), for the genotypic value of individuals arising by repeating the operation an arbitrary, n, times, and hence to variances and covariances of relatives.

RANDOM MATING WITH DIPLOIDS

Consider a population in which only one locus is segregating and denote the alleles at this locus by $A_1, A_2, \ldots, A_m$ with frequencies $p_1, p_2, \ldots, p_m$. Consider an individual X with genes a, b at this locus. Then the offspring of X from random mating have the genotypic array,

$$\begin{pmatrix} 1 & 1 \\ -a + -b \\ 2 & 2 \end{pmatrix} (\Sigma p_s A_s).$$

We write,

$$R(ab) = \begin{pmatrix} 1 & 1 \\ -a + -b \\ 2 & 2 \end{pmatrix} (\Sigma p_s A_s). \tag{1.1}$$

It is easy to see that

$$R^2(X) = R(R(X)) = \begin{bmatrix} 1 & 1 & 1 \\ -a + -b + -\Sigma p_s A_s \\ 4 & 4 & 2 \end{bmatrix} \begin{bmatrix} \Sigma p_s A_s \end{bmatrix}.$$

Consider now the operation R on the whole population:

$$R\{(\Sigma p_s A_s)^2\} = (\Sigma p_s A_s)^2, \tag{1.2}$$

which is merely the Hardy-Weinberg law in an unusual form.

Also, we have

$$R\,[a\,\Sigma p_s\,A_s] = \left[\frac{1}{2}-a+\frac{1}{2}\Sigma p_s\,A_s\right]\left[\Sigma p_s\,A_s\right];$$

so,
$$R\,[(a-\Sigma p_s\,A_s)(\Sigma p_s\,A_s)] = \frac{1}{2}(a-\Sigma p_s\,A_s)(\Sigma p_s\,A_s). \tag{1.3}$$

Finally,

$$\begin{aligned} R[(a-\Sigma p_s\,A_s)(b-\Sigma p_s\,A_s)] &= R(ab) - R(a\Sigma p_s\,A_s) - R(b\Sigma p_s\,A_s) + R((\Sigma p_s\,A_s)^2) \\ &= \left(\frac{1}{2}-a+\frac{1}{2}-b\right)(\Sigma p_s\,A_s) - \left(\frac{1}{2}-a+\frac{1}{2}\Sigma p_s\,A_s\right)(\Sigma p_s\,A_s) \\ &\qquad - \left(\frac{1}{2}-b+\frac{1}{2}\Sigma p_s\,A_s\right)(\Sigma p_s\,A_s) + (\Sigma p_s\,A_s)^2, \end{aligned}$$

so

$$R[(a-\Sigma p_s\,A_s)(b-\Sigma p_s\,A_s)] = 0 \tag{1.4}$$

Now the relationships (1.1), (1.2), (1.3), (1.4) can be interpreted in two ways, both of which are correct for the use we shall make of them.

Firstly, there is no ambiguity about relationship (1.2). Everyone understands the Hardy-Weinberg law, that if every member of a population is exposed to random mating, the population reproduces itself. Similarly the relationship (1.3) means that if we consider two populations, one of them with genotypic structure $(a\,\Sigma p_s\,A_s)$, the other with genotypic structure $(\Sigma p_s\,A_s)^2$, and mate each to the whole population at random, we shall get two populations, and when the second resulting population is subtracted from the first the remainder is $\frac{1}{2}-a\,(\Sigma p_s\,A_s)$ occurring positively and $\frac{1}{2}(\Sigma p_s\,A_s)^2$ occurring negatively. In the case of (1.4) consider four populations:

(1) ab
(2) $a\Sigma p_s\,A_s$
(3) $b\Sigma p_s\,A_s$
(4) $(\Sigma p_s\,A_s)^2$

Mate each to the whole population, calling the resultant populations 1′, 2′, 3′, 4′, and then form the population

$$1' - 2' - 3' + 4',$$

and it will be found to contain all possible genotypes with zero frequency. Algebraically, one can look upon an expression like $(a-\Sigma p_s\,A_s)(\Sigma p_s\,A_s)$ as a generalized population in which some genotypes have positive frequencies, and some have negative frequencies. Genotypes with positive frequency beget genotypes of positive

frequency while genotypes of negative frequency beget genotypes of negative frequency, all absolute values of frequencies of offspring being what Mendelian rules indicate.

Secondly, we can replace genotypic symbols by genotypic values. We then assert that the mean genotypic value of offspring of $X = ab$, is equal to

$$\left(\begin{matrix}1\\-a\\2\end{matrix} + \begin{matrix}1\\-b\\2\end{matrix}\right)(\Sigma p_s A_s),$$

in which the expression is to be expanded and genotypic values inserted in place of genotypic symbols.

Consider the identity

$$(ab) = (\Sigma p_s A_s)^2 + (a - \Sigma p_s A_s)(\Sigma p_s A_s) + (\Sigma p_s A_s)(b - \Sigma p_s A_s) + (a - \Sigma p_s A_s)(b - \Sigma p_s A_s).$$

Interpreting the symbols as genotypic values, we have

$$(ab) = \mu + \alpha_a + \alpha_b + \delta_{ab},$$

where

$$\begin{aligned}\mu &= (\Sigma p_s A_s)^2,\\ \alpha_a &= (a - \Sigma p_s A_s)(\Sigma p_s A_s),\\ \alpha_b &= (\Sigma p_s A_s)(b - \Sigma p_s A_s), \text{ and}\\ \delta_{ab} &= (a - \Sigma p_s A_s)(b - \Sigma p_s A_s)\end{aligned}$$

(the last term is often denoted by d_{ab}, "d" denoting dominance), and where

$$\begin{aligned}R(\mu) &= \mu,\\ R(\alpha_a) &= \frac{1}{2}\alpha_a,\\ R(\alpha_b) &= \frac{1}{2}\alpha_b, \text{ and}\\ R(\delta_{ab}) &= 0.\end{aligned}$$

Thus, we have partitioned the genotypic value of the individual (ab) into four parts, each of which is affected in a very simple way, namely, by multiplication, by the operation R. It is clear that

$$R^2(\mu) = \mu,\ R^2(\alpha_a) = \frac{1}{4}\alpha_a,\ R^2(\alpha_b) = \frac{1}{4}\alpha_b,\ R^2(\delta_{ab}) = 0,$$

and in general

$$R^n(\mu) = \mu,\ R^n(\alpha_a) = \left(\frac{1}{2}\right)^n \alpha_a,\ R^n(\alpha_b) = \left(\frac{1}{2}\right)^n \alpha_b,\ R^n(\delta_{ab}) = 0.$$

It follows from this that if we have a subpopulation, say π_0, which we mate to the whole population at random getting π_1, we then mate π_1 to the whole population

and get π_2, and so on, and if we denote the means of these populations by μ_0, μ_1, μ_2, . . . respectively, then

$$\mu_0 = \mu + A + D,$$

$$\mu_1 = \mu + \frac{1}{2}A, \text{ and}$$

$$\mu_2 = \mu + \frac{1}{4}A,$$

and so on.

It also follows that the covariance of an individual (ab) and its *k-th* degree offspring under random mating in every generation is equal to

$$\text{Cov}\left[\mu + a_a + a_b + \delta_{ab},\ \mu + \frac{1}{2^k}(a_a + a_b)\right]$$

$$= \text{Cov}\left[(a_a + a_b + \delta_{ab}),\ \frac{1}{2^k}(a_a + a_b)\right]$$

$$= \frac{1}{2^k}\text{V}(a_a + a_b) + \frac{1}{2^k}\text{Cov}(\delta_{ab},\ a_a + a_b).$$

If X is a random member of the population $(\Sigma p_s A_s)^2$, then
Prob [a is A_j] = p_j and
Prob [b is A_k] = p_k independently of a,

so that a_a and a_b are uncorrelated and have the same variance say, $\frac{1}{2}\sigma^2_A$.

Also,

$$\text{E}(a_a) = \text{E}(a_b) = \text{E}(\delta_{ab}) = 0$$

and $\text{E}(a_a\,\delta_{ab}) = \text{E}(a_b\,\delta_{ab}) = 0.$

If we denote $\text{E}(\delta^2_{ab})$ by σ^2_D,

then $$\text{V}(X) = \sigma^2_A + \sigma^2_D$$

and $$\text{Cov}\,[X,R^k(X)] = \frac{1}{2^k}\delta^2_A.$$

In considering covariances of relatives in general, if two individuals X and Y are denoted by (ab) and (cd) respectively, then

$$\text{Cov}(X,Y) = \text{Cov}(a_a + a_b + \delta_{ab},\ a_c + a_d + \delta_{cd}).$$

This covariance consists of nine terms:

$\text{Cov}(a_a,a_c)$, $\text{Cov}(a_a,a_d)$, $\text{Cov}(a_b,a_c)$, $\text{Cov}(a_b,a_d)$, $\text{Cov}(a_a,\delta_{cd})$, $\text{Cov}(a_b,\delta_{cd})$, $\text{Cov}(a_c,\delta_{ab})$, $\text{Cov}(a_d,\delta_{ab})$, and $\text{Cov}(\delta_{ab},\delta_{cd})$.

If now X and Y are random members of the population subject only to a particular relationship, and with a zero coefficient of inbreeding, these terms are easily worked out, and we get

$$\mathrm{Cov}(ab, cd) = 2r_{XY}\,\sigma^2_A + \mu_{XY}\,\sigma^2_D$$

where $r_{XY} = \frac{1}{4}\{P(a=c) + P(a=d) + P(b=c) + P(b=d)\}$

and $u_{XY} = P(a = c, b = d) + P(a = d, b = c)$.

The extension to multiple loci is clear in terms of genotypic arrays. If (ab) denote alleles at the A locus, $(a'b')$ denote alleles at the B locus, at which the alleles are $B_1, \ldots B_m$, with frequencies

$p'_1, p'_2, \ldots, p'_m$, then

$$R[(ab)(a'b')] =$$
$$[(\Sigma p_s A_s)^2 + (a - \Sigma p_s A_s)(\Sigma p_s A_s) + (\Sigma p_s A_s)(b - \Sigma p_s A_s) + (a - \Sigma p_s A_s)(b - \Sigma p_s A_s)]$$
$$[(\Sigma p'_{s\cdot} B_{s\cdot})^2 + (a' - \Sigma p'_{s\cdot} B_{s\cdot})(\Sigma p'_{s\cdot} B_{s\cdot})$$
$$+ (\Sigma p'_{s\cdot} B_{s\cdot})(b' - \Sigma p'_{s\cdot} B_{s\cdot}) + (a' - \Sigma p'_{s\cdot} B_{s\cdot})(b' - \Sigma p'_{s\cdot} B_{s\cdot})]$$

because of our assumption of independent segregation. This expression can be expanded and similar operations performed. It follows, for example, that

$$\begin{aligned} X = \mu &+ \alpha_a + \alpha_b + \delta_{ab} + \alpha'_{a\cdot} + \alpha'_{b\cdot} + \delta'_{a\cdot b\cdot} \\ &+ (\alpha_a\,\alpha'_{a\cdot}) + (\alpha_a\,\alpha'_{b\cdot}) + (\alpha_a\,\delta'_{a\cdot b\cdot}) \\ &+ (\alpha_b\,\alpha'_{a\cdot}) + (\alpha_b\,\alpha'_{b\cdot}) + (\alpha_b\,\delta'_{a\cdot b'}) \\ &+ (\delta_{ab}\,\alpha'_{a\cdot}) + (\delta_{ab}\,\alpha'_{b\cdot}) + (\delta_{ab}\,\delta'_{a\cdot b\cdot}) \end{aligned}$$

where, for example,

$$\alpha_a = (a - \Sigma p_s\,A_s)(\Sigma p_s\,A_s)(\Sigma p'_{s\cdot}\,B_s')^2$$

and

$$(\alpha_b\,\delta'_{a\cdot b\cdot}) = (b - \Sigma p_s\,A_s)(\Sigma p_s\,A_s)(a' - \Sigma p'_{s\cdot}\,B_{s\cdot})(b' - \Sigma p'_{s\cdot}\,B_{s\cdot}).$$

From the properties of the operation R it is clear that

$$\begin{aligned} R(X) = \mu &+ \tfrac{1}{2}\alpha_a + \tfrac{1}{2}\alpha_b + \tfrac{1}{2}\alpha'_{a\cdot} + \tfrac{1}{2}\alpha'_{b\cdot} + \tfrac{1}{4}(\alpha_a\,\alpha'_{a\cdot}) + \tfrac{1}{4}(\alpha_a\,\alpha'_{b\cdot}) \\ &+ \tfrac{1}{4}(\alpha_b\,\alpha'_{a\cdot}) + \tfrac{1}{4}(\alpha_b\,\alpha'_{b\cdot}). \end{aligned}$$

So, if the genotypic value of X is

$$X = \mu + A + D + (AA) + (AD) + (DD)$$

then

$$R^k(X) = \mu + \frac{1}{2^k}A + \left(\frac{1}{4}\right)^k (AA).$$

Similarly, if we consider the populations π_0, π_1, π_2, etc. mentioned earlier, exactly the same functional relationship represents the successive means μ_0, μ_1, μ_2, and so on. These formulae hold for any number of loci, though with more loci there will be additional terms. The details of working out the general formula for the general case are given by Kempthorne [10 or 11].

RANDOM MATING OF AUTOTETRAPLOIDS

We shall consider the case when there is no double reduction. The results when taking double reduction into account present nothing new.

We double an arbitrary individual by $(a\ b\ c\ d)$. We suppose individuals are mated to the population $(\Sigma p_s A_s)^4$ at random, so the population always contributes the gametic array $(\Sigma p_s A_s)^2$.

Then,

$$R(a\ b\ c\ d) = \frac{1}{6}(ab + ac + ad + bc + bd + cd)(\Sigma p_s A_s)^2.$$

It can be seen fairly easily that

$$R[(\Sigma p_s A_s)^4] = (\Sigma p_s A_s)^4,$$

$$R[a(\Sigma p_s A_s)^3] = \frac{1}{2}a(\Sigma p_s A_s)^3 + \frac{1}{2}(\Sigma p_s A_s)^4,$$

$$R[ab(\Sigma p_s A_s)^2] = \frac{1}{6}ab(\Sigma p_s A_s)^2 + \frac{1}{3}a(\Sigma p_s A_s)^3 + \frac{1}{3}b(\Sigma p_s A_s)^3 + \frac{1}{6}(\Sigma p_s A_s)^4,$$

$$R[abc(\Sigma p_s A_s)] = \frac{1}{6}ab(\Sigma p_s A_s)^2 + \frac{1}{6}ac(\Sigma p_s A_s)^2 + \frac{1}{6}bc(\Sigma p_s A_s)^2 + \frac{1}{6}a(\Sigma p_s A_s)^3 + \frac{1}{6}b(\Sigma p_s A_s)^3 + \frac{1}{6}c(\Sigma p_s A_s)^3,$$

and

$$R(a\ b\ c\ d) = \frac{1}{6}ab(\Sigma p_s A_s)^2 + \frac{1}{6}ac(\Sigma p_s A_s)^2 + \frac{1}{6}ad(\Sigma p_s A_s)^2 + \frac{1}{6}bc(\Sigma p_s A_s)^2 + \frac{1}{6}bd(\Sigma p_s A_s)^2 + \frac{1}{6}cd(\Sigma p_s A_s)^2.$$

The following complete set of relations therefore hold:

$$R[(\Sigma p_s A_s)^4] = (\Sigma p_s A_s)^4, \tag{2.1}$$

$$R\,[(a - \Sigma p_s A_s)(\Sigma p_s A_s)^3] = \frac{1}{2}(a - \Sigma p_s A_s)(\Sigma p_s A_s)^3, \tag{2.2}$$

$$R\,[(a - \Sigma p_s A_s)(b - \Sigma p_s A_s)(\Sigma p_s A_s)^2] = \frac{1}{6}(a - \Sigma p_s A_s)(b - \Sigma p_s A_s)(\Sigma p_s A_s)^2, \tag{2.3}$$

$$R[(a - \Sigma p_s A_s)(b - \Sigma p_s A_s)(c - \Sigma p_s A_s)(\Sigma p_s A_s)] = 0, \text{ and} \tag{2.4}$$

$$R[(a - \Sigma p_s A_s)(b - \Sigma p_s A_s)(c - \Sigma p_s A_s)(d - \Sigma p_s A_s) = 0. \tag{2.5}$$

If now for brevity we write

$$\nu = \Sigma p_s A_s,$$

then

$$abcd = (\nu + a - \nu)(\nu + b - \nu)(\nu + c - \nu)(\nu + d - \nu)$$

and expand, we have the model given by Kempthorne (6 p. 168).

If the genotypic value of an individual or group of individuals π_0 is denoted by μ_0 and successive backcrosses to the population by π_i with means μ_i, then

$$\mu_0 = \mu + A + D + T + F, \tag{2.6}$$

$$\mu_1 = \mu + \frac{1}{2}A + \frac{1}{6}D,$$

$$\mu_2 = \mu + \left(\frac{1}{2}\right)^2 A + \left(\frac{1}{6}\right)^2 D,$$

$$\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots, \text{ and}$$

$$\mu_k = \mu + \left(\frac{1}{2}\right)^k A + \left(\frac{1}{6}\right)^k D.$$

The relationship (2.6) expresses the genotypic value of an individual (or average genotypic value of a group) in terms of population mean, additive effect, dominance effect, trigenic effect, and quadrigenic effect.

The consequences as regards covariances of relatives are easily worked out, the single locus case being given by Kempthorne (6 p. 171). Extension to multiple loci is clear.

SELFING OF DIPLOIDS

I have written about this topic before (10, 11) and the only purpose of doing so here is to show that the approach then used is that advocated here for the general solution of a large class of problems[2].

[2]In passing it is perhaps not inappropriate for me to express my surprise that the statistical methodology in these references has not been considered seriously as far as I know by even one biologist.

The basic idea is that of a selfing operator S where

$$S(ab) = \frac{1}{4}aa + \frac{1}{2}ab + \frac{1}{4}bb,$$

so $S(aa) = aa$, $S(bb) = bb$, and

$$S\left(ab - \frac{1}{2}aa - \frac{1}{2}bb\right) = \frac{1}{4}aa + \frac{1}{2}ab + \frac{1}{4}bb - \frac{1}{2}aa - \frac{1}{2}bb$$

$$= \frac{1}{2}ab - \frac{1}{4}aa - \frac{1}{4}bb$$

$$= \frac{1}{2}\left(ab - \frac{1}{2}aa - \frac{1}{2}bb\right).$$

Hence,

$$S^2\left(ab - \frac{1}{2}aa - \frac{1}{2}bb\right) = \frac{1}{2^2}\left(ab - \frac{1}{2}aa - \frac{1}{2}bb\right)$$

and

$$S^k\left(ab - \frac{1}{2}aa - \frac{1}{2}bb\right) = \frac{1}{2^k}\left(ab - \frac{1}{2}aa - \frac{1}{2}bb\right).$$

Finally,

$$S^k(ab) = S^k\left\{\left(\frac{1}{2}aa + \frac{1}{2}bb\right) + \left(ab - \frac{1}{2}aa - \frac{1}{2}bb\right)\right\}$$

$$= S^k\left(\frac{1}{2}aa + \frac{1}{2}bb\right) + S^k\left(ab - \frac{1}{2}aa - \frac{1}{2}bb\right)$$

$$= \left(\frac{1}{2}aa + \frac{1}{2}bb\right) + \frac{1}{2^k}\left(ab - \frac{1}{2}aa - \frac{1}{2}bb\right).$$

If we then wish to consider what happens in quantitative inheritance under selfing, we write

$$ab = \left(\frac{1}{2}aa + \frac{1}{2}bb\right) + \left(ab - \frac{1}{2}aa - \frac{1}{2}bb\right)$$

$$= G_2 + (G_{11} - G_2).$$

Then, G_2 is multiplied by unity and $(G_{11} - G_2)$ by $\frac{1}{2}$ for each generation of selfing.

So, if one has any initial group of material with mean μ_0, the mean in successive generations is

$$\mu_k = \mu_0 + \left(\frac{1}{2}\right)^k X_1.$$

If there is two-locus epistasis, this result is obviously generalized to

$$\mu_k = \mu_0 + \frac{1}{2^k} X_1 + \frac{1}{2^{2k}} X_2.$$

Many general formulae can be developed and some are given in the papers already cited.

SELFING OF AUTOTETRAPLOIDS

I shall consider the case of regular autotetraploid inheritance with no double reduction.

The elementary segregation fact about the present situation is that the genotype $a_i\, a_j\, a_k\, a_l$ gives a gametic output

$$\frac{1}{6}(a_i\, a_j + a_i\, a_k + a_i\, a_l + a_j\, a_k + a_j\, a_l + a_k\, a_l),$$

so that

$$S(a_i\, a_j\, a_k\, a_l) = \left(\frac{1}{6}(a_i\, a_j + a_i\, a_k + a_i\, a_l + a_j\, a_k + a_j\, a_l + a_k\, a_l)\right)^2.$$

Now define the following formal quantities:

$$G_4 = \frac{1}{4}(a_i a_i a_i a_i + a_j a_j a_j a_j + a_k a_k a_k a_k + a_l a_l a_l a_l),$$

$$G_{31} = \frac{1}{12}(a_i a_i a_i a_j + a_i a_i a_i a_k + a_i a_i a_i a_l + \ldots + a_l a_l a_l a_i + a_l a_l a_l a_j + a_l a_l a_l a_k),$$

$$G_{22} = \frac{1}{6}(a_i a_i a_j a_j + a_i a_i a_k a_k + \ldots + a_k a_k a_l a_l),$$

$$G_{211} = \frac{1}{12}(a_i a_i a_j a_k + a_i a_i a_j a_l + a_i a_i a_k a_l + \ldots + a_l a_l a_i a_j + a_l a_l a_i a_k + a_l a_l a_j a_k), \text{ and}$$

$$G_{1111} = a_i a_j a_k a_l.$$

These may be regarded as all the possible symmetric groups of genotypes which are derivable from G_{1111} by selfing.

Now consider some initial group of N individuals (N can be unity) which we might denote by

$$(a^1{}_i a^1{}_j a^1{}_k a^1{}_l),\ (a^2{}_i a^2{}_j a^2{}_k a^2{}_l), \ldots,\ (a^N{}_i a^N{}_j a^N{}_k a^N{}_l).$$

Let G(1111) denote the average genotypic value of this group. Let G(211) be the average of the G_{211} quantities for each such individual, G(22), G(31), and G(4) the corresponding quantities. Then, denoting by S the selfing of a group, we have

$$S[G(4)] = G(4),$$

$$k[G(31)] = \frac{1}{4}G(4) + \frac{1}{2}G(31) + \frac{1}{4}G(22),$$

$$S[G(22)] = \frac{1}{18}G(4) + \frac{1}{2}G(22) + \frac{4}{9}G(31),$$

$$S[G(211)] = \frac{1}{36}G(4) + \frac{8}{36}G(31) + \frac{9}{36}G(22) + \frac{1}{2}G(211), \text{ and}$$

$$S[G(1111)] = \frac{1}{6}G(22) + \frac{4}{6}G(211) + \frac{1}{6}G(1111).$$

Expressing these equations in matrix form we have

$$S\begin{bmatrix} G(1111) \\ G(211) \\ G(22) \\ G(31) \\ G(4) \end{bmatrix} = \begin{bmatrix} \frac{1}{6} & \frac{2}{3} & \frac{1}{6} & 0 & 0 \\ 0 & \frac{1}{2} & \frac{1}{4} & \frac{2}{9} & \frac{1}{36} \\ 0 & 0 & \frac{1}{2} & \frac{4}{9} & \frac{1}{18} \\ 0 & 0 & \frac{1}{4} & \frac{1}{2} & \frac{1}{4} \\ 0 & 0 & 0 & 0 & 1 \end{bmatrix} \begin{bmatrix} G(1111) \\ G(211) \\ G(22) \\ G(31) \\ G(4) \end{bmatrix}.$$

We now proceed to find linear functions of the G's that are changed by a simple multiple during selfing.

First we want a function which contains G(1111) and others, then one that contains G(211) and *succeeding* ones, and so on. On first going through the manipulations it appears that there are many solutions. Actually there is only one:

$$G(1111) - 2\,G(211) + \frac{1}{4}G(22) + G(31) - \frac{1}{4}G(4) \text{ is decreased to } \frac{1}{6} \text{ of its}$$

value by each generation,

$$G(211) - \frac{1}{2}G(22) - G(31) + \frac{1}{2}G(4) \text{ is decreased to } \frac{1}{2} \text{ of its value,}$$

$$G(22) + \frac{4}{3}G(31) - \frac{7}{3}G(4) \text{ is decreased to } \frac{5}{6} \text{ of its value,}$$

and G(4) is unaffected.

Also,

$$G(1111) = \left\{G(1111) - 2G(211) + \frac{1}{4}G(22) + G(31) - \frac{1}{4}G(4)\right\}$$
$$+ \{2G(211) - G(22) - 2G(31) + G(4)\}$$
$$+ \left\{G(31) + \frac{3}{4}G(22) - \frac{7}{4}G(4)\right\}$$
$$+ G(4).$$

If we call the successive terms on the right hand side X, Y, Z, and T, then

$$G(1111) = X + Y + Z + T,$$

$$S[G(1111)] = \frac{1}{6}X + \frac{1}{2}Y + \frac{5}{6}Z + T,$$

$$S^2[G(1111)] = \left(\frac{1}{6}\right)^2 X + \left(\frac{1}{2}\right)^2 Y + \left(\frac{5}{6}\right)^2 Z + T,$$

and, in general,

$$S^k[G(1111)] = \left(\frac{1}{6}\right)^k X + \left(\frac{1}{2}\right)^k Y + \left(\frac{5}{6}\right)^k Z + T. \qquad (*)$$

This relationship is true for any individual or group of individuals.

Suppose we take an individual or group, obtain a measurement of their average phenotype, self successively each time getting the average phenotype of the progeny, we then shall have numbers μ_0, μ_1, μ_2, etc. to which we can fit the relationships (*).

We shall then be able to estimate T, X, Y, and Z.

Also, we can get the variance of *k-th* degree offspring, by selfing the covariance of an original set and its *k-th* degree offspring and, so on.

All these variances and covariances will involve

$$V(X), V(Y), V(Z), V(T)$$

$$\text{Cov } (X,Y), \text{Cov } (X,Z), \text{Cov } (Y,Z), \text{Cov } (X,T), \text{Cov } (Y,T), \text{Cov } (Z,T)$$

and these will be *parameters* in the expressions for variances and covariances. Just what form these will take will depend on the initial population. I regret that factors have not enabled me to explore these matters to their logical conclusion. I do hope, however, that I have said enough to indicate that the line of development leads to the formulation of parameters which describe both the first-order and second-order statistics that can arise in a wide class of situations in the study of quantitative inheritance.

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DISCUSSION

W. D. HANSON: In true autotetraploids, chromosome transmission may not be regular. Would not the abnormal chromosome transmission and corresponding abnormal phenotypes make the estimation of genetic parameters in tetraploid data difficult to interpret?

D. L. HARRIS: Yes. As in nearly all theoretical developments of statistical genetics as well as other statistical problems, it was necessary here to limit the problem to a set of situations which would be manageable. For this reason, Professor Kempthorne has "assumed" regular chromosome transmission. Thus, the results presented are rigorously applicable only to situations involving regular chromosome behaviour. The extension of this theory to include irregular chromosome behaviour or, at least, the assessment of the influence of irregular behaviour seems quite difficult but, of course, would be highly desirable for the interpretation of tetraploid data where the basic assumptions used here are not valid. What has been presented here is a "first step" toward development of tetraploid theory.

Concepts and Definitions in Relation to Selection Schemes

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THE theory of plant breeding is based on Mendelian inheritance of genes whose frequencies are viewed as determined by mutation, selection, migration, and chance. Genes themselves are treated as delineated entities existing at a few thousand loci and located in chromosomes, but modern conceptions of the gene do not mesh perfectly with this simple model. Rapid recent advances, based largely on experiments with microorganisms (see for example Benzer, 1), demand at least a cursory review of the postulates of ordinary population genetics theory. According to the newer concepts, essential constituents of the genetic material are pairs of nucleotides arranged linearly in helical structures. The traditional gene of classical genetics must, on this concept, embrace thousands of nucleotide pairs, 25,000 or 50,000 being recent estimates in the case of Drosophila (Rudkin and Schultz, 25). Yet, in phage and bacteria, it appears that each nucleotide pair may constitute a potential mutation site. These sites fall into a hierarchy of functional groups, not always unambiguously defined, one important criterion being complementation behavior. Recombination is found to occur within such groups as well as between them. The unit defined by crossing over or mutation in experiments with microorganisms is almost incomparably smaller than the traditional gene. Even those groups defined, where possible, by noncomplementation of mutated nucleotides, seem much smaller than the entities long accepted as genes in higher plants and animals.

Experiments in higher organisms, particularly those of Taylor (29), offer general support to the basic Watson-Crick model of double helices of paired nucleotides. A good many experimental data, however, conflict with the hypothesis that a series of genes on a chromosome of such organisms is essentially a continuous sequence of an immense number of nucleotide pairs subject to individual mutation and to recombinations at roughly similar frequencies between adjacent pairs (Green, 11, 12; Lewis, 18). Nevertheless, there is ample evidence that crossing over can separate into smaller units entities earlier considered to be single genes. Such separations do not seem to continue indefinitely down to the nucleotide level, and one may judge that the smallest units so far separated by crossing over in Drosophila and in maize must themselves contain hundreds if not thousands of nucleotide pairs. In Drosophila a group of pseudoallelic loci,

because of non-complementarity, may perhaps, for the purposes of population genetics, be considered the approximate functional equivalent of a single locus of the traditional type with many alleles. An individual heterozygous for two different pseudoalleles in the trans-position is phenotypically altered, just as though heterozygous for two recessives of the same system of alleles. An exception to this equivalence is the rare production of double mutants and reversions by crossing over, which for the purpose of breeding predictions is not very different from an assumption of reverse mutation. The situation at the *A* and the *R* loci in maize (Emmerling, 9; Laughnan, 17), involving complicated and even bewildering evidence of unequal crossing over, may be less easily accommodated into the simple model, but these phenomena may or may not be common ones at other loci or in other organisms.

Gene partitioning, of course, does not constitute the only challenge to the simple basic model. The activator mutator systems first discovered by McClintock (19, 20), the paramutations of Brink and associates (2), and the growing evidence of meiotic drive and other segregation abnormalities (Cameron and Moav, 3; Dunn *et al.* 7, 8; Sandler *et al.* 24), are cases in point. These variant phenomena, generally ignored by population geneticists, may be of negligible importance to breeders, but this comfortable supposition still remains to be established. In the meantime, while every unusual situation that may be encountered does not necessarily have to be forced into the common mold, it is perhaps profitable in many cases to proceed under the slightly uneasy assumption that the conventional model is an adequate one. That is, a gene can be defined as a unit of crossing over and mutation, or as an equivalent group of non-complementary pseudoalleles; that mutation rates are not often subject to sudden and violent changes; and, that meiosis is usually regular.

SOME GENERAL CONSEQUENCES OF THE BREEDING STRUCTURE OF POPULATIONS

You have already heard a stimulating analysis of the possible effects of breeding structure on population genetics. Let us restrict our consideration for the moment to some of the simpler consequences ensuing from a long history of cross breeding or inbreeding, with especial reference to population size and breeding goals. The proportion of completely recessive deleterious genes due to mutation pressure that are homozygous and come to expression under conditions of theoretical equilibrium is the same in crossbred as in inbred populations. However, the ratio of the numbers of such genes that are heterozygous in the two classes of population is very different. The proportion of such genes that are heterozygous to those that are homozygous in self-fertilized populations, is $2s$, whereas this ratio in random mated populations is almost $\sqrt{s/u}$, where s is the selective disadvantage and u the mutation rate. Thus, there are more heterozygous recessives in the crossbred population by a ratio of approximately $1/(2\sqrt{us})$, which has a minimum value of 500 if u is as low as 10^{-6}. Assuming for illustrative purposes that $u = 10^{-6}$ at 5,000 loci and that $s = .01$, individuals

in the inbred population would contain on the average 1 mutant gene while those in the random bred population should contain on the average about 100 of them, mostly unexpressed. The parametric assumptions are, of course, fictitious but moderate ones in that mutations with such minor effects could well occur more frequently.

Let us suppose now that the large random bred population were reduced in size, and specifically that 50 hermaphroditic individuals are crossed *inter se,* a similar number being used as parents in succeeding generations. It is easily calculated that among the 5,000 loci, the original randomly selected group of 50 plants would contain at least one deleterious recessive gene at about 3,160 loci, and that the mutant would be present once at about 1,840 of these loci, twice at 920 loci, three times at 307 loci, and so on. Some of these genes, although selected against, would be fixed by chance. Using a formula of Kimura (16) as expanded by Robertson (21), it turns out that eventually about 17 of the mutant genes would become fixed and homozygous in all 50 individuals.

This result can be viewed in different contexts. It indicates that crossbred varieties of plants which in their early history, may have been restricted in population size for a number of generations, could easily be homozygous throughout for a number of deleterious recessives. Robinson *et al.* (22) suggested this as a possibility to account for the large boost observed in yield of varietal crosses in maize. It also illustrates the difficulty of producing, from a highly crossbred variety, an inbred having favorable economic qualities. Even by inbreeding at the very slow rate of about one per cent per generation, as in the above example, there is no assurance of weeding out a sufficient number of the harmful recessives. Also the production of a very large number of inbred lines and selection among them does not constitute a solution of the evident difficulties. The population number in such lines would have to be small for economic reasons. If self-fertilization were used, almost 50 deleterious genes would be fixed on the average based on the hypothesized parameters. In this event only about 1 such line in over 300 billion could be expected to have as few as 5 fixed deleterious genes on the assumption of independent assortment, even neglecting the hindrance of linkage.

It is true that some naturally crossbred varieties are also subject to considerable natural inbreeding, in which event the accumulation of deleterious recessives may have been held in check. In such cases, the production of inbred varieties may not be difficult, as in some of the cucurbits (Whitaker and Bohn, 30). It appears, however, that in a species like maize it would be a gargantuan task to shift the population in a way that would permit economically desirable properties in the homozygous state. Other methods than those discussed would probably be necessary. This is apart from whatever influences might be attributable to overdominance.

At this point it may be worth considering briefly the situation that would exist in populations if mutations occurred with approximately equal frequency at each nucleotide or small group of nucleotides, as is possibly the case, and

where any 2 mutations separated by as few as 50 or so nucleotides are usually complementary in heterozygotes, a situation that is less likely. In this case, the number of effective loci would be greater than usually hypothesized and mutation rate per locus lower. Allowing 100 nucleotide pairs to the presently envisaged effective locus, the equivalent assumptions to those above would be a mutation rate of 10^{-8} and 500,000 loci. The average number of slightly deleterious mutants per individual, mostly heterozygous, in very large randomly mated populations would then be 1,000 instead of 100. In this case it would be essentially impossible to produce offspring by self-fertilization, or perhaps even by brother sister matings, and highly inbred lines of normally crossbred organisms would not be produced by ordinary methods. If the total map length of all chromosomes were 1,000 crossover units, there would be an average of one deleterious mutant in each crossover unit of each chromosome or its homolog. The effects of linkage would be exaggerated, and in cases of slight or moderate linkage disequilibrium the system would behave as though multiple alleles with overdominant effects on fitness were to exist at many loci. The extreme situation just postulated, as regards higher plants, is belied by data, but a partial approach to this condition is not excluded.

STABILITY OF SMALL POPULATIONS

Just as a small population derived from a large randomly mated one will gradually result in the fixation of hitherto only rarely expressed deleterious recessives, so also will a small population accumulate and fix new mutations that may occur. While this is well known in theory, the rather considerable population sizes necessary to prevent accumulations of deleterious genes seems not generally appreciated. The probability of a neutral mutation being fixed eventually in a population of effective size N is $1/2N$; a large population would then, when equilibrium rates were established, fix unselected mutations at the same rate as a small one, because decreasing chances of fixation are exactly balanced by the increasing number of loci that can mutate. If the mutant gene is unfavorable it will, of course, be selected against, but selection will be relatively ineffective unless the population size is at least equal to the reciprocal of the selection intensity. Thus, in a population of size 50, an additively acting selective disadvantage of 1 per cent permits the elimination of 41 per cent of the genes that otherwise would have been fixed; if size is increased to 100, selection becomes 78 per cent effective, and if increased to 200, the figure is about 92 per cent. If a homozygous recessive gene creates the same disadvantage as a homozygous additive one, selection will be roughly two-thirds as effective in preventing fixation, providing s is not too large, based on Robertson's expansion of Kimura's formula (21). There is no absolute limit at which populations will not in theory occasionally absorb a deleterious mutant. That even very large populations persist more or less indefinitely despite presumed occasional fixations of undesirable genes must be due to the occasional occurrence of favorable mutations offsetting the rare fixation of unfavorable ones.

EFFECTS OF POPULATION SIZE ON SELECTION

Clearly, a large population is superior to a small one in any selection scheme except, possibly, a backcross program aimed at transferring an individual gene to a single pure line. Aside from and superimposed upon, changes in allelic frequencies attributable to selection pressures are random fluctuations, indifferent in direction. The variances of these fluctuations, other things being equal, are inversely proportional to population number. While the genes are dancing around by chance, they may also be systematically nudged in one direction by selection. This nudging will be unimportant in comparison with the random undirected movement if the gene effect or the population number is small. Where such conditions exist, large proportions of favorable alleles can be lost by chance, and inferior ones fixed. Such losses of desirable genetic material can obviously seriously limit the ultimate gains achievable by selective breeding.

Robertson (21) has analyzed this problem of ultimate gains, and the time necessary for their realization. His discussion is directed toward animal breeding, in which individuals are selected as parents either on the basis of their own phenotypes or on data from relatives, such as their family means. His treatment considers the cases of additive and recessive genes. It is true that in much of plant breeding for measurable characters such as yield, non-additive effects must be of great importance. This is certainly the case for selection among inbred lines, for which situation Robertson's analysis has only a special indirect application to be considered briefly later. In the selection of crossbred varieties his analysis is basically applicable to plants as well as animals. It also should apply, with slight modifications, to the important cases of recurrent selection for combining ability with an inbred line or variety and, to a degree, with reciprocal recurrent selection for combining ability. Alleles in a selected parent having even overdominant relations with alleles of a recurrent parental strain or variety, or involved in epistatic relations leading to combining ability, will act additively in terms of cross performance (Comstock *et al.* 5). As selection proceeds, especially in reciprocal recurrent selection, and as gene frequencies shift, the degree, and even in some cases direction, of apparent additivity may change. To this extent the theory is imperfect; however, it appears to offer at least a sound basis for approximation and a reference for the study of exceptions.

Robertson shows from his own analysis, and also from that of Kimura, that the eventual fixation of a selected gene present initially in some proportion q is a function only of q and the product of N, the effective population size, and s, the selective advantage. The maximum advance possible may be expressed as $s(1-q)$ if s is constant. The proportion of this maximum advance eventually achieved is shown to be over 93 per cent if $Nsq>2$, and over 70 per cent if $Nsq>1$.

N in this expression may be replaced by Tv, where T is the total population number and v is the proportion selected. Also, as originally shown by Haldane, in the case of breeding to increase a measurable character or index by truncation selection, the reproductive advantage s conferred by an allele can

be expressed in terms of the gene effect a, the variance of the character σ^2, and the average improvement of the character or index among the selected parents. The approximate equivalent of s, where a is small compared to σ and the distribution normal, is $\bar{\imath}a/\sigma$, where $\bar{\imath}$ is the improvement of the character in standard units. Also, assuming normality, $\bar{\imath}$ may be replaced by z/v where z is the ordinate of a unit normal distribution at the point of truncation. Making these substitutions the expression Nsq becomes $Tzqa/\sigma$. To insure that the value of this expression is adequately high for genes of importance, preferably over two, the breeder can control the first two terms by varying total population number and proportions of measured or tested individuals used as parents.

If maximum ultimate gain were the only criterion for a given value of T, the ordinate z should be a maximum, and hence half the population is used as parents. Robertson has, however, investigated the relationship between ultimate gain and point of truncation and shows that a very considerable increase in selection intensity can often be obtained at a trivial cost in ultimate selection limits. The ultimate gain is shown to be from $2N$ to $4N$ times the gain in the initial generation of selection for additive genes and may be many times this figure in the case of very rare favorable recessive genes. The number of generations theoretically necessary to achieve half the total gain varies from about N to $2N$, or if one quarter of the population is selected from $T/4$ to $T/2$. Both the selection limits in terms of first generation gain and number of generations required may be much lower if Nsq is large.

As Robertson points out, there are many difficulties in the practical utilization of these relationships in actual programs. Gene number and frequency are often inestimable where gene effects are small. In theory, one gains some information from the shape of the curve of advance over many generations; in practice cessation of gains may occur due to causes other than exhaustion of genetic variance. Nevertheless, some criteria may have practical utility. Robertson points out that if Nsq is unity or lower, but not too low, crossing replicate lines after several generations of selection, should provide a boost in rate of gain. After one or more such crosses, the ultimate achievable advance, if carried on with the population number of the replicates combined, will generally be the same as though selection had been carried on in a single line with the larger number from the start. Crosses of replicates then can furnish a clue as to the adequacy of population number and a possible remedy if it is too small. If no increase in rate of advance is obtained, T may be adequately large. If an increased rate does occur, T may be so small as to seriously limit selection. If the boost in rate is large, new replicates from the original population may be worth starting for later crossing. Further general conclusions are as follows: restriction of population size in early generations may greatly reduce ultimate gains, but as selection progresses, rare alleles tend to become lost or increased in frequency and population size can be safely reduced. Smaller populations should also be adequate where the foundation population is the result of crosses between, say, two or four highly inbred lines, so that q cannot be much less than one quarter.

The work discussed clearly illustrates the proposition that not all gains from selective breeding have equivalent values. If achieved by very intense selection, the population may be depleted of the ingredients necessary for further advance. Very strong selective pressures may have other deleterious effects not considered in the model, such as in the prevention of new combinations of linked genes, and loss of fitness due to correlated response. Lowered selection intensities are of value, however, only if achieved by increasing T, the total population size, and not through decreasing N, the number of selected parents.

EPISTATIC VARIANCE

An implicit assumption in some of the foregoing discussion is that non-allelic interactions, or epistatic variance, could safely be ignored. This assumption is not always without justification. In a crossbred population, selection in general can be expected to act chiefly on additive variance. Temporary gains which have to be maintained by repeated selection may result from non-random combinations of genes (Griffing, 13), especially when linkage is involved. In addition, the presence of epistatic interactions can lead to shifts in the additive values of particular alleles, or in theory even to reversals in sign, as the genetic background alters in the course of selection. Selection between inbred lines, and especially between pure lines, takes full account of favorable epistatic combinations, although in rapid inbreeding with $Nsq = s/2$ for the case of selfing, selection is relatively ineffective within lines being selfed. A parallel to epistatic interactions of genes is the interaction between complete genotypes, in the sense of Sakai (23), and here the difficulties of utilizing individual interactions by selections among pure lines are somewhat analogous to the problems of utilizing epistatic gene interactions by selection within a variety.

Selection based on performance in crosses also takes account and makes use of favorable gene combinations, although a semantic difficulty arises; epistasis in the sense analyzed by Cockerham (4), Kempthorne (15), and others is definable only in terms of specified populations. In the broader meaning, all selection acts on gene combinations, and an allele selected for in one population may be selected against in another. Thus, selection works toward an "integrated gene pool" (Dobzhansky, 6).

The theoretical and no doubt the practical difficulties of increasing the frequency of, or establishing desirable epistatic combinations in a segregating population are very great. Gains based on additive variance, as pointed out by Wright, are not apt to lead the population toward the most favorable epistatic peak (31). Even where selection is applied to a large number of inbred lines or clonally reproduced genotypes that have been produced in large numbers by selfing hybrids, the best gene combinations may occur very rarely and therefore be lost before the total number of combinations is reduced sufficiently to permit effective testing. Favorable and unfavorable epistatic combinations have, of course, a chemical or physical basis, and should these be known, the possibility exists of selecting for the necessary components. Efficient utilization of the

breeding potential represented by epistatic variance may thus require a detailed knowledge of developmental genetics, largely unavailable at the present time.

CORRELATED RESPONSE

As is well known, correlated variation of two characters may be due to similar actions on both characters by genes or chromosomes on the one hand or by environmental influences on the other. The two components may be separated statistically by a comparison of the covariance between related individuals, one set of covariances being based on different characters in the relatives and the other on the same characters in the relatives. If genetic correlation is high, it is sometimes useful to increase character A by selecting for B. Favorable circumstances are high heritability and ease of selection for B, and high genetic correlation between it and A. One example is the selection of awns in wheat, with the aim of increasing yield (Suneson *et al.* 28). An example not related to a single gene is the sometimes successful use of bulk selection in grains, such as those of Suneson in barley (27). Here, fitness under cultivation is the automatically selected character B, whereas the sought for character A is yield. Since correlation in this case must be far from perfect, exhaustion of the possibilities of indirect selection does not necessarily preclude subsequent direct selection of A.

An important case of correlated response is that between fitness and a selected character or index. Fitness in a population with reasonably stable environment is apt to approach a peak after long continued natural selection. Many components of fitness as pointed out by Wright (31) may have averages near their optima, and variance of fitness, due to genetic fluctuations of such characters, is largely epistatic. Selection of such a component, either directly or by correlated response, is necessarily away from its optimum and can be expected to reduce fitness. The genetic fluctuations which before were epistatic with respect to fitness now become additive. The effect of any genetic correlation induced between fitness components and a selected character or index is therefore highly likely to reduce fitness. Fitness is usually reduced by long continued selection, although this is not invariably the case. In some examples, relaxation of selection has led to spontaneous recovery of fitness with only moderate reduction in the selected character or index. According to Robertson's theory of selection limits (21), continued moderate selection with a given total population size T should lead to greater ultimate gains than strong selection followed by relaxation. His theory, however, does not encompass epistasis and does not predict the effects of relaxation on fitness. Intuitively continuous moderate selection would seem superior, but more experimental data are needed.

Correlations between selection of multiple objectives or between component characters related to economic objects are important in index construction. The problem of efficient selection indices was first studied by Smith (26), using a discriminant function and later by Hazel (14) using Wright's path coefficients. In general, the optimum weight assigned to an index component is

larger as: (a) its direct economic value is high, (b) its heritability is high, (c) its genetic correlation with other economically important components of low heritability is high, and (d) its environmental correlation with other economically important components is low or negative.

CONCLUSION

An attempt has been made to consider some of the basic concepts of population genetics as related to plant breeding. In brief, it is concluded that recent studies of the nature of genetic material may lead to some modifications of the basic Mendelian models implicitly assumed by most population geneticists, but the extent and importance of the necessary changes remain to be determined. Breeding structure leads to important differences between populations, placing strong limitations on practicable goals. Size limitations on breeding populations and extreme selection pressures may severely limit the probable limits of selection, particularly in varietal selections and in recurrent selections for combining ability. Computation of the optimum sizes of breeding populations depends on information not readily available, although crosses of replicate lines may provide some pertinent information. Relation of epistatic variance and correlated variables to selection theory was discussed very briefly.

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DISCUSSION

H. L. CARNAHAN: In several Drosophila selection experiments, the gain in the first few generations has been great and then leveled off suggesting exhaustion of genetic variability. Then suddenly a second major advance is made. How do you account for this in terms of selection intensity?

E. R. DEMPSTER: I think the explanation usually proposed for a sudden resumption of gains is that a crossover has occurred between plus and minus genes. However, leveling off after only a few generations, if actually due to loss of genetic variance, suggests that effective population size may have been quite low. With a small population and/or a few genes with large effects, sampling variation could lead to considerable irregularities.

TIMOTHY PROUT: In the expression giving the ultimate selection limit, "Z" is a maximum when 50 per cent of the population is saved. Is the expression still valid when "Z" diminishes due to the saving of more than 50 per cent of the population?

E. R. DEMPSTER: Yes, if the assumptions are valid.

Discussion: Models in Quantitative Genetics

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DR. SPRAGUE has said that this is a symposium on statistical genetics and plant breeding but nearly every letter I have received from the organizers has emphasised that this is *not* a symposium on statistical genetics. Nevertheless, I *am* going to talk about statistical genetics and about its place in this symposium.

Dr. Sprague has outlined the objectives of this symposium to you, and I would like firstly to talk around his outline, perhaps summarizing a little and perhaps extending a little. What are we here for? We are here to establish close contact between statistical geneticists and plant breeders. Here plant breeders can tell statistical geneticists about their problems and discover if statistical genetics can help them. Statistical geneticists in their turn can tell plant breeders about their theories and discover whether they are of any practical use. You will notice that my last two statements carry the implication that statistical geneticists and plant breeders work independently of each other to some extent. I think that this is inevitable in a science such as genetics that is only beginning to develop its mathematical theory and neither group of workers should decry all the independent efforts of the other group. Let plant breeders try new experiments without a full mathematical investigation (we have no full theory), and let statistical geneticists wander off in theories that seem impractical at present. Two conditions are that neither group ignore the established work of the other group and that both groups work to extend the area of their cooperation. This is why we are here.

Dr. Sprague has already made these comments in other words, but I would like to specify and detail the four areas of genetics we are here to discuss, from the point of view of a statistical geneticist. The four areas of discussion are:

(a) Plant breeding genetics for which an adequate statistical theory exists.
(b) Plant breeding practices based on biological theory.
(c) Statistical genetical theory not yet applied to plant breeding.
(d) Other areas of genetics.

We wish to enlarge the first area at the expense of the others.

What is the present common area of statistical genetics and plant breeding? I will ignore major qualitative genes which are not the center of interest here.

We can describe how additive and dominance gene action affect most

genetical experiments, and various controlled experiments provide estimates of average measures of these two kinds of gene action. Comstock and Robinson and Mather have described such experiments. Epistasis is also fully described, as Dr. Kempthorne has shown, and some measures of epistasis have been obtained. This is probably the furthest direction in which useful advance in statistical genetics has been made, and it is probably the most important because knowledge of the modes of gene action is basic to any other theoretical advance. It would be easier to develop a selection theory for heterosis if we knew what caused heterosis.

Dr. Kempthorne's method of evaluating the genetic expectations of various statistics is valid for a wide range of breeding systems. This means that one mathematical technique replaces the collection of techniques developed separately in the past for each breeding system. In other words, the theory of breeding systems has been advanced by his paper. During my recent visits in this country, I noticed that several workers were comparing breeding systems. This was usually in the context of a selection experiment, and Dr. Kempthorne is not concerned with selection here, but I think that his paper means that soon we may be able to extend the quantitative theory of selection in randomly mating systems to other mating systems.

Another direction in which progress has been made is in the study of additive variation in populations. Wright and many others have given us a good understanding of random mating, inbreeding, heritability, selection, and drift in such populations. Here, theory and practice are working well together.

The second area is where plant breeders are working without any exact statistical theory and depend more on their genetical knowledge. I think that Dr. Sprague was being kind to statistical geneticists when he said that genetical theory is not completely adequate to provide answers to all important breeding problems. During this symposium plant breeders will doubtless indicate many points where they think theory to be inadequate. I can mention a few gaps in theory.

There are no general usable theories of selection, polyploids, mutation, or genotype-environment interaction. Remember, that I am excepting the theory of one or two major genes. Many of the attempts to construct these theories have assumed equal values for the parameters of each gene. This is only a small start to general theories because the interesting genetic systems do *not* contain genes with the same dominance or the same selective advantage.

Selection theory has been confined until recently to additive and dominance variation. Unlike Kempthorne's theory of gene action it is also restricted to genes of small effect unless dominance is absent. In view of Powers' discovery that some continuous characters are controlled by a few major genes, a more exact theory is needed for when dominance occurs.

The failure of selection advances to match theoretical predictions has forced plant breeders to adjust the above theory on the basis of their knowledge of genetical disturbances such as epistasis and natural selection to explain, at

least qualitatively, some of their difficult results. Griffing's (1) recent investigation of selection in the presence of epistasis between pairs of genes has brought the theory nearer to practice and has quantified and corrected some of the breeders' explanations. In particular, he has shown how epistasis may cause the response to selection to taper off and also cause a regression when selection is relaxed. However, a general theory of selection and epistasis is still needed. Kimura's (3) general theory is not easy to apply in practice.

Mutation does not appear at first sight a difficult concept to parametize—one or two parameters would be needed for each gene. However, if we remember that mutation may be under genetic control, the parameters may become as complex as for gene action.

Theoretical work on gene number is also lacking. Powers and others have developed the partitioning method of genetic analysis which supplies the number of genes when the quantitative character is controlled mainly by a very few genes. Mather's estimates of gene number are based on quantitative theory, but their statistical sampling errors are very high. Except when Powers' methods are applicable, much more theoretical work is needed. Since a group of tightly linked genes behaves much as a single gene, we can probably measure only the number of these groups, or effective factors in Mather's terminology. Theoretical advance in the estimation of number of effective factors depends on advance in the theory of linkage in quantitative inheritance.

The third area contains theories in statistical genetics which have not found application in plant breeding. The more extensive ramifications of Dr. Kempthorne's theory of gene action are an obvious example. I think it is a good thing to have this theory developed and waiting for use. It can supply models for experiments, and it should also suggest new experiments to measure gene action.

Linkage work was at a very low ebb until recently. On the theoretical side we could only discuss models involving linkage between pairs of genes. This limited us to means in epistatic models and variances in non-epistatic models. On the practical side I know of no experiments which can measure linkage or average linkage in a multifactorial genetic system. The best that can be done is to test for its presence. Geiringer did construct a general specification of linkage, but this contained redundant parameters and, either for this or other reasons, found little application. Recently Jones (2) devised a new linkage specification. This contains no redundant parameters and is eminently suitable for tying into the present theory of quantitative inheritance. This seems to be a real break-through on the theoretical front. I have been able to apply it to any number of genes and manipulate it in a general mathematical way. Since this specification applies to qualitative as well as to quantitative genetics, we can make some estimates of the higher order parameters from experiments with major genes. It seems that Kempthorne's restriction to no linkage in his model of gene action and Griffing's restriction to two genes in his selection model can now be relaxed.

Kimura (3) has proposed a set of fitness parameters with additive components, dominance components, and epistatic components of fitness paralleling Kempthorne's action parameters. Now, Dr. Wallace has pointed out that we cannot ascribe a single measure of fitness to one gene—each combination of genes has its own fitness and interaction between the fitnesses of genes may maintain complex polymorphisms in balance. This type of discussion would gain in precision by recasting in terms of Kimura's fitness parameters.

The fourth area of discussion includes all those parts of genetics which might be incorporated in either statistical genetics, or plant breeding, or both, sometime in the future. Detailing this area is really crystal-gazing, and once again I will leave the practical side to more competent people. On the theoretical side I would like to mention two possible predictions.

The first is an attempt to answer Dr. Sprague's question, "How can we predict the maximum deviation from the average of an inbred line isolated from a randomly mating population?" A follow-up question might be, "How can we predict the maximum heterosis in crosses between inbred lines developed from a randomly mating population?" Now, I am not going to give you an answer to these questions, but I am going to suggest a new way of looking at the quantitative genetics of populations that might lead to an answer.

We usually look at a population of individuals in terms of the distribution in the population of the alleles at each locus. All the theory of additive action that I mentioned earlier is based on such a single gene theory which is adjusted to quantitative theory by summation over all loci concerned in the inheritance of the character under investigation. Measures of variation are concerned with differences from individual to individual to each locus.

Suppose we turn our thinking around and look at the loci in one individual. Instead of comparing individuals let us compare loci. The genes under investigation each have properties measured by parameters such as we have been discussing. Some parameters such as additive and dominance measures, frequency in the population, degree of inbreeding, and mutation rate may be specific to individual genes. Others such as epistatic action and fitness may concern several genes simultaneously. With a large number of genes we can construct a distribution for each parameter and then describe this distribution by two or three statistics. For instance, if the distribution over the loci of additive action is normal, it would be described by a mean and a variance. Similarly, we can describe the distribution of gene frequencies in a population. We can even go a step further and describe the joint distribution of gene frequency and additive action if these two parameters are correlated. From such joint distributions it should be possible to predict the chance of achieving an inbred line or a hybrid combination deviating from the population mean by a given amount. If it is possible to estimate the distributions of these parameters from suitable experiments, we can answer Dr. Sprague's question.

My other prediction has more confidence. In my work in statistical genetics I am continually surprised by the mathematical complexity of genetically

simple problems. Selection seems to be the most difficult phenomenon to handle. A recent development is to by-pass these theoretical difficulties by simulating genetical experiments on an electronic computer. Setting the parameters of the model up in a computer, repeating the experimental procedure many times, and averaging the results achieves the same end as a purely mathematical investigation. The main difficulty is that no general relation between the parameters of the model and the experimental result is obtained. However, the speed and capacity of a computer are such that a range of models containing several numbers of genes, various linkages, measures of gene action, etc., can be run through and so achieve an approximation to a mathematical formula. This method is not as good as a complete theoretical solution, but it is very much better than no solution.

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DISCUSSION

A. ROBERTSON: I was very interested that Dr. Hayman introduced the notion of the distribution of gene effects and gene frequencies, but I disagree with some of his suggestions as to what we might find. In particular, I would suggest that we are very likely to find a distribution of gene effects of a J-shaped kind. That is to say, there will be very few genes having really marked effect on the character that we are concerned with, and that as we move to genes with smaller and smaller effects we will find larger and larger numbers of genes contributing. In fact, I would almost take it as an axiom in this business that, as organisms are complicated, every gene affects every character. With regard to gene frequencies the problem is a little more difficult. I think we have some evidence from our bristle selection experiments in Drosophila, that the genes that we eventually fix in both high and low directions were themselves at low frequencies in the initial population. If we, therefore, draw a diagram of the frequency of positively-acting alleles in the initial population, we might find again a curve with maxima at the two extremes. The evidence on which this is based is that of the persisting variation in

a wide cross, in which, as one might expect, the variance in the F_2 generation is extremely high, but after even 20 generations of recombination the variation still remains at a level of four or five times that in the base population. Now, in the wide cross, the genes concerned must be at frequencies of about 50 per cent, which would suggest that in the initial population they are at extreme frequencies. We hope to get some further evidence on this matter from our analysis of the effect of restriction of population size on final response to selection.

Estimation and Interpretation of Genetic Parameters

D. S. Robson, *Chairman*

Estimation of Genetic Variances[1]

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INTRODUCTION

GENETIC variances are estimated in the following manner. Relatives are developed by some system of matings, the mating design, and they are grown in a set of environmental conditions, the environmental design. A quadratic analysis of the observations leads to estimates of components of variance and covariance of the design which are interpreted genetically and environmentally. While this description is complete if one considers asexual propagation to be a system of mating, the ramifications are many. Not just any mating design or any environmental design lends itself readily to interpretation. The purpose of this paper is to review some of the commonly used and simpler designs and to discuss generally the estimation of genetic variances.

Although obvious, it is sometimes overlooked that estimates are of variances in a population from which the experimental material is a sample. This is the reference population, both of genotypes and of environments, and it is in terms of its variances that the various procedures and designs are interpreted. Only under a few circumstances can variances be translated from one population to another. The reference population of genotypes may be from a cross of two homozygous lines or from the genetic mixture of many homozygous lines. It may be a variety or a racial mixture of varieties. Further, within these categories, there is a reference population for each generation of inbreeding. We shall, for the most part, limit our considerations to diploid reference populations ranging from non-inbred to homozygous for reasons that will become obvious.

It is natural that the mating designs most often employed are those which can be readily analyzed by standard statistical procedures and interpreted into components of variance of the design. To interpret genetically the components of variance of the design it is easiest to first translate them into covariances of relatives. This is purely a statistical device with general application in expressing the expected or average values of quadratic forms such as sums of squares and products or mean squares and products. It is the covariances of

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relatives which are often readily interpretable into components of genetic variance. As we shall see, it is also the covariances of relatives which serve as a yardstick in relating various mating designs as to the information available.

MATING DESIGNS WITH UNRELATED MATES

By following the simple rule that all mates are unrelated by pedigree, many mating designs are available which can be readily analyzed by standard statistical procedures.

The progenies are initially non-inbred since the mates or parents are unrelated, and thus the reference population is the non-inbred generation. If the progenies are further inbred by some regular system of inbreeding then the reference population is the inbred population corresponding to the inbreeding of the progenies. These reference populations for the progenies are independent of the reference population of the mates or parents as far as inbreeding of the parents is concerned; that is, the parents may be inbred but the initial progenies will not be as long as mates are unrelated.

Two factor mating designs

The two parents of bi-parental progenies operate much as factors in the design of experiments. They are the sources of variation among progenies from which inferences can be made about genetic variances. However, inferences about genetic variances and the comparison of various designs is accomplished most easily by using covariances of relatives.

Diallel matings—design (AA)—To exemplify the various relationships among relatives from a group of unrelated parents, consider progenies from diallel or all possible matings among a group of parents including reciprocal matings but not selfs. Let X_{ij} represent an individual from mating parent i used maternally with parent j used paternally. Two different individuals, X_{ij} and $X_{i'j'}$, may be related as shown in Table 1.

TABLE 1.—RELATIONSHIPS AMONG RELATIVES, X_{ij} AND $X_{i'j'}$, IN A DIALLEL WITH RECIPROCALS BUT NO SELFS.

Conditions	Description	Designation of covariance
$i = i', j = j'$	Full sibs	C_f
$i = j', j = i'$	Reciprocal full sibs	C_{rf}
$i = i', j \neq j'$	Maternal half sibs	C_{ms}
$i \neq i', j = j'$	Paternal half sibs	C_{ps}
$\begin{bmatrix} i = j', j \neq i' \\ i \neq j', j = i' \end{bmatrix}$	Reciprocal half sibs	C_{rs}

Estimation of the covariances will be illustrated by the following analysis of variance. Let Y_{ijk} be the plot mean of the progeny X_{ij} in replication k ($i, j = 1, 2 \ldots p$, $k = 1, 2 \ldots k$). The pertinent sums of squares, analysis of variance

and expectations of mean squares appear in Table 2. The replacement of a subscript by a dot indicates summation over that subscript. Two analyses, designated as primary and alternate, are given. In the primary analysis the maternal and reciprocal sums of squares are the same as those of Yates (41) and the general and specific sums of squares are the same as found in several places (Griffing, 15; Kempthorne, 26; and Matzinger, 31). In the alternate analysis the maternal and reciprocal sums of squares of the primary analysis have been pooled as is often done. This is an orthogonal partitioning of the sums of squares in each analysis. The components of variance in each analysis are defined in terms of the expectations of the mean squares and are translated into the covariances of Table 1. The new features here are the expectations of the mean squares for the primary analysis and the translation of the components of vari-

TABLE 2.—SUMS OF SQUARES, ANALYSES OF VARIANCE, AND EXPECTATIONS OF MEAN SQUARES FOR A DIALLEL EXPERIMENT WITH RECIPROCALS BUT NO SELFS.

$\sum_{i,j} Y^2_{ij}./k = s_1$, $Y^2.../kp(p-1) = s_5$, $\sum_{i} (Y_{i..} - Y_{.i.})^2/2k(p-1) = s_2$

$\sum_{i<j} (Y_{ij.} + Y_{ji.})^2/2k = s_3$, $\sum_{i} (Y_{i..} + Y_{.i.})^2/2k(p-1) = s_4$

Source	df	Sums of squares	Expectations of mean squares
		Primary Analysis	
Replications	(k-1)		
General	(p-1)	$S_4 = \frac{(p-1)}{(p-2)}(s_4 - 2s_5)$	$\sigma^2 + k\sigma^2_r + 2k\sigma^2_s + k(p-2)\sigma^2_m + 2k(p-2)\sigma^2_g$
Specific	p(p-3)/2	$S_3 = s_3 - S_4 - s_5$	$\sigma^2 + k\sigma^2_r + 2k\sigma^2_s$
Maternal	(p-1)	$S_2 = \left(\frac{p-1}{p}\right)s_2$	$\sigma^2 + k\sigma^2_r + kp\sigma^2_m$
Reciprocal	(p-1)(p-2)/2	$S_1 = s_1 - s_3 - S_4$	$\sigma^2 + k\sigma^2_r$
Error	(k-1)(p^2-p-1)	S_0 = usual manner	σ^2

σ^2 = error variance, $\sigma^2_r = C_f - C_{rf} - (C_{ps} + C_{ms} - 2C_{rs})$

$\sigma^2_m = (C_{ps} + C_{ms})/2 - C_{rs}$, $\sigma^2_s = C_{rf} - 2C_{rs}$, $\sigma^2_g = C_{rs}$

		Alternate Analysis	
Replications	k-1		
General	p-1	S_4	$\sigma^2 + 2k\sigma^2_{s'} + 2k(p-2)\sigma^2_{g'}$
Specific	p(p-3)/2	S_3	$\sigma^2 + 2k\sigma^2_{s'}$
Reciprocal	p(p-1)/2	$S_2 + S_1$	$\sigma^2 + k\sigma^2_{r'}$
Error	(k-1)(p^2-p-1)	S_0	σ^2

$\sigma^2_{r'} = \sigma^2_r + 2\sigma^2_m = C_f - C_{rf}$, $\sigma^2_{s'} = (\sigma^2_r + 2\sigma^2_s)/2 = (C_f - C_{ps} - C_{ms} + C_{rf} - 2C_{rs})/2$

$\sigma^2_{g'} = \sigma^2_g + \sigma^2_m/2 = (C_{ps} + C_{ms} + 2C_{rs})/4$

ance into covariances of relatives involving reciprocals. The covariances of relatives serve to compare different definitions of the design components of variance. Other definitions of the design components of variance could be put forward but the ones of the primary analysis appear to be the most informative.

Factorial matings—design (AB)—This is the mating design II of Comstock and Robinson (7, 8) where each of a group of parents used maternally are mated to each of another group of parents used paternally. The expectations of the mean squares for a replicated experiment in a single environment are given in Table 3. Details of the analysis and interpretation of this design are given by Cockerham (4).

TABLE 3.—EXPECTATIONS OF MEAN SQUARES FOR DESIGN (AB).

Source	df	Expectations of mean squares
Replications	k−1	
Paternal parents	(p−1)	$\sigma^2+k\sigma^2_{MP}+km\sigma^2_P$
Maternal parents	(m−1)	$\sigma^2+k\sigma^2_{MP}+kp\sigma^2_M$
M x P	(p−1)(m−1)	$\sigma^2+k\sigma^2_{MP}$
Error	(k−1)(mp−1)	σ^2

$\sigma^2_{MP} = C_f-C_{ps}-C_{ms}$, $\sigma^2_M = C_{ms}$, $\sigma^2_P = C_{ps}$

Three covariances and three components of variance are estimable. The relationships between the components of variance of this design and of the diallel, if all of the parents of both designs are equally inbred, are

$$\sigma^2_{MP} = \sigma^2_r+\sigma^2_s, \qquad (\sigma^2_M+\sigma^2_P)/2 = \sigma^2_m+\sigma^2_g.$$

Nested matings—design (A/B)—This is the mating design I of Comstock and Robinson (7, 8) where each member of a group of parents used paternally (maternally) is mated to a different group of parents used maternally (paternally). In Table 4 the expectations are given for two experiments. In one experiment

TABLE 4.—EXPECTATIONS OF MEAN SQUARES FOR DESIGN (A/B) OR (B/A).

Source	df	Expectations of mean squares
Replications	k−1	
Paternal	p−1	$\sigma^2+k\sigma^2_{M/P}+km\sigma^2_P$
Maternal within Paternal	p(m−1)	$\sigma^2+k\sigma^2_{M/P}$
	or	
Maternal	m−1	$\sigma^2+k\sigma^2_{P/M}+kp\sigma^2_M$
Paternal within Maternal	m(p−1)	$\sigma^2+k\sigma^2_{P/M}$
Error	(k−1)(m−p−1)	σ^2

$\sigma^2_P = C_{ps}$, $\sigma^2_M = C_{ms}$, $\sigma^2_{M/P} = C_f-C_{ps}$, $\sigma^2_{P/M} = C_f-C_{ms}$

the maternal parents are nested within the paternal parents and in the other experiment the paternal parents are nested within the maternal parents. Further details are found in (Cockerham, 4).

Reciprocal effects—To avoid undue complexities, reciprocal effects will be dispensed with before proceeding to other designs. Reciprocals could have been included in designs (A/B) and (AB) just as they were in the diallel. In such case the same estimates are available in the analysis of variance as in the diallel. The analysis of variance is easily accomplished. The sums of squares are partitioned in the same way as they are without reciprocals but are partitioned once on the sum of the reciprocals and once on the difference between reciprocals with some care exercised on the sign of the reciprocal difference and with an extra factor of two in the divisor.

It is not within the scope of this paper to review and develop procedures which will account for all types of reciprocal effects. The subject has received considerable development, reviewed by Dickerson (9), in terms of maternal effects in animals. However, the direct, as opposed to transmitted, effects of the maternal parent found in animals is probably of little importance in plants. Fortunately, also, for many species of plants, reciprocal effects have been found to be insignificant.

If one is concerned about reciprocal effects, then one of the three previous designs with reciprocals and with all of the parents equally inbred can be used to estimate and test for these effects. Tests of significance are available (see the primary analysis of Table 2,) for the hypothesis that $\sigma^2_r = 0$ and that $\sigma^2_m = 0$. If σ^2_r is not zero, it indicates an interaction of reciprocal effects. If σ^2_r is zero, σ^2_m is most likely due to maternal effects in addition to paternal ones. If reciprocal effects are entirely maternal and additive to the paternal effects, then

$$C_{ms} > C_{ps} = C_{rs}, \qquad C_f - C_{rf} = C_{ms} - C_{ps}, \qquad \sigma^2_r = 0,$$

$$\sigma^2_m = \frac{1}{2}(C_{ms} - C_{ps}), \qquad \sigma^2_s = C_{rf} - 2C_{ps} = C_f - C_{ms} - C_{sp}, \text{ and } \sigma^2_g = C_{ps}.$$

In this case, design (AB) without reciprocals contains the same information as the diallel with reciprocals.

$$\sigma^2_P = \sigma^2_g, \qquad \sigma^2_M = 2\sigma^2_m + \sigma^2_g, \text{ and } \sigma^2_{PM} = \sigma^2_s.$$

In the case of no reciprocal effects of any kind,

$$C_{rf} = C_f, \qquad C_{ps} = C_{ms} = C_{rs} = C_s, \qquad \sigma^2_P = \sigma^2_M = \sigma^2_g = C_s, \text{ and}$$

$$\sigma^2_{PM} = \sigma^2_s = \sigma^2_{M/P} - \sigma^2_P = \sigma^2_{P/M} - \sigma^2_M = C_{fs} - 2C_s,$$

and each of the three experiments without reciprocals contain the same information.

Since reciprocal full sibs and reciprocal half sibs have only genic contributions common, it is these covariances, C_{rf} and C_{rs}, which are given genetic interpretations. In the absence of reciprocal effects they have the same interpretations as C_f and C_s, which is the terminology to be used in subsequent designs

in which reciprocal effects will receive no consideration. For designs (A/B) and (AB), when reciprocal effects are assumed absent, the A and B designations may be used to distinguish different inbreeding coefficients in the two groups of parents, where the inbreeding coefficients of all the parents in group A is F_A and of all the parents in group B is F_B. There is, of course, only one group of parents in design (AA). To avoid confusion, new designations, Table 5, are given to the covariances and components of variance when reciprocal effects are assumed absent.

TABLE 5.—DESIGNATION OF COMPONENTS OF VARIANCE AND COVARIANCES OF RELATIVES FOR DESIGNS (AA), (AB) AND (A/B) WHEN RECIPROCAL EFFECTS ARE ASSUMED ABSENT.

Relationship of relatives	Symbol for covariance
Full sibs, both A and B parents common	C_{fAB}
Full sibs, both A parents common	C_{fAA}
Half sibs, parent A common	C_{sA}
Half sibs, parent B common	C_{sB}

Components of variance for designs (AA), (AB) and (A/B)

$\sigma^2_A = C_{sA}$, $\sigma^2_B = C_{sB}$, $\sigma^2_{AB} = C_{fAB} - C_{sA} - C_{sB}$,

$\sigma^2_{A/B} = C_{fAB} - C_{sB}$, $\sigma^2_g = \sigma^2_A = C_{sA}$, $\sigma^2_e = \sigma^2_{AA} = C_{fAA} - 2C_{sA}$

Chain block matings—incomplete design (AA)—This design is a variant of the diallel where each parent has the same number of progenies but all possible matings among the parents are not made. Two variations of this design for eight parents appear in Table 6 where matings are made only where an x

TABLE 6.—INCOMPLETE DESIGN (AA)—ONE VARIATION ABOVE THE DIAGONAL AND ANOTHER BELOW THE DIAGONAL.

Parent	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8
A_1		x						x
A_2	x		x					
A_3		x		x				
A_4	x		x		x			
A_5		x		x		x		
A_6	x		x		x		x	
A_7		x		x		x		x
A_8	x		x		x		x	

occurs. Many variations are available depending on the number of parents. The variations, their analyses and comparisons for reliability of estimates are considered in detail by Kempthorne and Curnow (29). In each variation, estimates are available of C_f and C_s.

It may be helpful to note the relationship between design (AA) and designs (A/B) and (AB) in Table 7. From this viewpoint designs (AB) and (A/B) represent certain patterns or samples from an overall diallel.

TABLE 7.—DESIGNS (AB) AND (A/B) VIEWED AS SEGMENTS OF DESIGN (AA); DESIGN (A/B) ABOVE DIAGONAL, DESIGN (AB) BELOW.

Parent	A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8
A_1				x				
A_2				x				
A_3				x				
A_4								
A_5	x	x	x	x				x
A_6	x	x	x	x				x
A_7	x	x	x	x				x
A_8	x	x	x	x				

Incomplete design (AB)—All possible matings need not be made in design (AB). An example is given in Table 8, ignoring the small blocks, for two groups of eight parents where each parent has three progenies with a connected mating pattern much the same as the chain block for the diallel. Analysis of this design will provide estimates of C_f and C_s as do the others. It may be noted that design (B/A) is obtained by considering only the matings in the small blocks in Table 8 which are unconnected sets of matings, or in other words, the B parents are completely confounded within the A parents.

Suffice it to say that as long as there are full sib, one or two types of half sib, and unrelated progenies in an experiment, estimates can be obtained of C_f and one or two C_s's or alternatively of two or three components of variance. The difficulties are those usually encountered in the analyses of non-orthogonal data.

Three factor mating designs

By exercising control of at least one of the grandparents as well as of the parents in making up matings a third factor is introduced which allows

TABLE 8.—INCOMPLETE DESIGN (AB).

Parent		Parent A_1	A_2	A_3	A_4	A_5	A_6	A_7	A_8
	B_1	x						x	x
	B_2	x	x						x
	B_3	x	x	x					
	B_4		x	x	x				
	B_5			x	x	x			
	B_6				x	x	x		
	B_7					x	x	x	
	B_8						x	x	x

the estimation of additional genetic variances or covariances among relatives. These designs require two generations to produce the seed for the progenies in contrast to the two factor designs which require only one generation or nursery season.

Factorial matings—design (A(BC)—For this design, let an additional group of individuals which are to be used in the matings be designated as C. First, mate each C_l ($l = 1, 2, \ldots m$) individual to each B_j ($j = 1, 2, \ldots n$) individual. Next, mate each A_i ($i = 1,2, \ldots p$) individual to a single offspring of each mating (B_jC_l). This gives altogether *pnm* progenies, one for each mating ($A_i(B_jC_l)$). The order in which the matings are made is from right to left in the designation (A(BC). The types of relatives in this mating pattern and their designations are put in Table 9. The expectations of mean squares for a replicated experiment are given in Table 10. The analysis of variance is the usual one for a three factor factorial and the expectations of the mean squares are the usual ones for an all random model of effects. Altogether, seven components of variance and covariances of relatives are estimable when the inbreeding

TABLE 9.—DESCRIPTION OF COVARIANCES OF RELATIVES FOR DESIGN (A(BC).

Relationship of relatives	Designation of covariance
Full sib, parent from mating CB and parent A both common	$C_{fA(BC}$
Three quarter sibs, both parent A and grandparent B common	C_{sAcB}
Half sibs, parent A common	C_{sA}
Half sibs, parent from mating BC common	C_{sBC}
Cousins, grandparent B common	C_{cB}

TABLE 10.—EXPECTATIONS OF MEAN SQUARES FOR DESIGN (A(BC).

Source	df	Expectations of mean squares
Replications	k−1	
A parents	p−1	$\sigma^2+k\sigma^2_{ABC}+kn\sigma^2_{AC}+km\sigma^2_{AB}+knm\sigma^2_A$
B grandparents	n−1	$\sigma^2+k\sigma^2_{ABC}+kp\sigma^2_{BC}+km\sigma^2_{AB}+kmp\sigma^2_B$
C grandparents	m−1	$\sigma^2+k\sigma^2_{ABC}+kp\sigma^2_{BC}+kn\sigma^2_{AC}+knp\sigma^2_C$
A x B	(p−1)(n−1)	$\sigma^2+k\sigma^2_{ABC}+km\sigma^2_{AB}$
A x C	(p−1)(m−1)	$\sigma^2+k\sigma^2_{ABC}+kn\sigma^2_{AC}$
B x C	(n−1)(m−1)	$\sigma^2+k\sigma^2_{ABC}+kp\sigma^2_{BC}$
A x B x C	(p−1)(n−1)(m−1)	$\sigma^2+k\sigma^2_{ABC}$
Error	(k−1)(pnm−1)	σ^2

$\sigma^2_A = C_{sA}$, $\sigma^2_B = C_{cB}$, $\sigma^2_C = C_{cC}$, $\sigma^2_{AB} = C_{sAcB}-C_{sA}-C_{cB}$
$\sigma^2_{AC} = C_{sAcC}-C_{sA}-C_{cC}$, $\sigma^2_{BC} = C_{sBC}-C_{cB}-C_{cC}$
$\sigma^2_{ABC} = C_{fA(CB}-C_{sAcC}-C_{sAcB}-C_{sBC}+C_{sA}+C_{cB}+C_{cC}$

coefficients are different in the three groups of parents. If parents B and parents C are equally inbred, then

$$\sigma^2_B = \sigma^2_C, \quad \sigma^2_{AC} = \sigma^2_{AB}, \quad C_{cB} = C_{cC}, \text{ and } C_{sAcB} = C_{sAcC}.$$

If, in addition, the same number of parents is used in groups B and C, i.e., $n = m$, the mean squares for B and C may be pooled together, and the mean squares A × B and B × C may be pooled together, since, in each case, the two have the same expectations. This gives five components of variance or covariances of relatives that are estimable.

When none of the parents are inbred there are only four distinct covariances of relatives because $C_{sA} = C_{sBC}$ since C_{sBC} is the covariance between half sibs from a non-inbred parent, BC.

Nested matings—designs (A/B/C) and (A/B/C)′—These represent an extension of the nested two factor matings. For design (A/B/C) each C_l individual is mated to a different subset of the B_{jl} individuals. An offspring of each mating $B_{jl}C_l$ is mated to a different subset of the A_{ijl} individuals. The *ijl*th progeny is from the mating $(A_{ijl}(B_{jl}C_l)$. It may be noted that the order of matings was from right to left in the designation (A/B/C) of the design. There is of course the reverse mating order which is to be designated as (A/B/C)′. In this design a different subset of A_{ijl} individuals is mated to each B_{jl} individual, and the offspring of a different subset of B_{jl} individuals are mated to each C_l individual. The *ijl*th progeny is from the mating $(C_l(B_{jl}A_{ijl})$. In each design there are m individuals in group C, nm in group B and nmp in group A, giving a total of nmp progenies.

The analysis of variance is the same for the two mating designs, but the components of variance of the two designs have different interpretations. These are given in Table 11.

Mixed matings—designs (A(B/C) and (A/(BC)—A mixture of nested and factorial matings is used in the designs. For design (A(B/C) each individual

TABLE 11.—EXPECTATIONS OF MEAN SQUARES FOR DESIGNS (A/B/C) AND (A/B/C)'.

Source	df	Expectations of mean squares
Replications	k−1	
C	m−1	$\sigma^2+k\sigma^2_{A/B}+kp\sigma^2_{B/C}+kmp\sigma^2_C$
B within C	m(n−1)	$\sigma^2+k\sigma^2_{A/B}+kp\sigma^2_{B/C}$
A within B	mn(p−1)	$\sigma^2+k\sigma^2_{A/B}$
Error	(k−1)(mnp−1)	σ^2

For design (A/B/C) the components are:
$\sigma^2_C = C_{cC}$, $\sigma^2_{B/C} = C_{sBC}-C_{cC}$, $\sigma^2_{A/B} = C_{fA(CB}-C_{sBC}$
For design (A/B/C)' the components are:
$\sigma^2_C = C_{sC}$, $\sigma^2_{B/C} = C_{sCcB}-C_{sC}$, $\sigma^2_{A/B} = C_{fC(BA}-C_{sCcB}$

in the C group is mated to a different subset of B individuals. A single individual from each $B_{jl}C_l$ mating is mated to each individual in the A group, giving again nmp progenies, the *ijl*th one being from the mating $(A_i(B_{jl}C_l)$. The analysis of variance for this design in Table 12 is the usual one for a mixed factorial and nested design. Altogether, five components of variance or covariances of relatives are estimable.

TABLE 12.—EXPECTATIONS OF MEAN SQUARES—DESIGN (A(B/C).

Source	df	Expectations of mean squares
Replications	k−1	
A parent	p−1	$\sigma^2+k\sigma^2_{AB/C}+km\sigma^2_{AC}+kmn\sigma^2_A$
C grandparent	m−1	$\sigma^2+k\sigma^2_{AB/C}+kp\sigma^2_{B/C}+kpn\sigma^2_C$
A x C	(p−1)(m−1)	$\sigma^2+k\sigma^2_{AB/C}+kn\sigma^2_{AC}$
B within C	m(n−1)	$\sigma^2+k\sigma^2_{AB/C}+kp\sigma^2_{B/C}$
A x B/C	m(n−1)(p−1)	$\sigma^2+k\sigma^2_{AB/C}$
Error	(k−1)(pnm−1)	σ^2

$\sigma^2_A = C_{sA}$, $\sigma^2_C = C_{cC}$, $\sigma^2_{AC} = C_{sAcC}-C_{sA}-C_{cC}$
$\sigma^2_{B/C} = C_{sBC}-C_{cC}$, $\sigma^2_{AB/C} = C_{fA(BC}-C_{sBC}-C_{sAcC}+C_{cC}$

The design (A/(BC) has the A parents nested within the factorial matings BC. This design will have a slightly different analysis and of course a very different interpretation from design (A(B/C). It is definitely inferior to the other designs.

Triallel or three-way matings—design (A(AA)—This is the extension of the diallel to all possible three-way crosses from a single group of individuals. If the individuals are inbred lines, then it is all possible three-way hybrids. With p individuals or lines, the combinations of three are $p\ (p-1)\ (p-2)/6$. For each combination A_i, A_j, A_l there are three ways or orders in which the progenies can be produced,

$$(A_i(A_jA_l), \quad (A_j\ (A_iA_l), \text{ and } (A_l(A_iA_j),$$

giving altogether $p(p-1)(p-2)/2$ progenies.

Nine covariances of relatives may be distinguished from this design and seven components of variance can be estimated from an orthogonal partitioning of the sums of squares. Their estimation and details of the analysis of variance are given by Rawlings and Cockerham (32).

Mixed matings—designs (A(BB) and (A(AB)—It is always to be understood that when the same group of parents are used in combinations of matings such as (AA), (A(AA), or (A(AB) that no matings are ever to be made which involve the same individual more than once in the pedigree of any progeny. This is necessary to meet the requirement that mates are unrelated.

These designs, (A(BB) and (A(AB), are in a sense mixtures of the triallel and factorial. Design (A(BB) involves mating each of a group of A individuals to an offspring of each of the diallel matings (BB). Design (A(AB) involves mating an offspring of each mating A_iB_j to all A_l except $l = i$. The analyses of these designs will not be given. For design (A(BB) five covariances of relatives can be estimated if the two groups of parents differ in inbreeding; otherwise, four covariances are estimable. Seven covariances of relatives can be estimated in design (A(AB) with $F_A \neq F_B$, otherwise only four.

Incomplete three factor mating designs—Just as in incomplete designs (AA) and incomplete designs (AB), incomplete matings can be used in the three factor mating designs. The analogy between confounding in the design of experiments and that of using partial mating patterns should be apparent by now. It is of course desirable that the connected mating patterns be balanced in such a way that the estimates are not too difficult to obtain. This is true for the most extreme cases of confounding the three factors, which are designs (A/B/C) and (A/B/C)′.

Four factor mating designs

By exercising control over grandparents on both sides of the pedigree or of one or more great grandparents a fourth factor is introduced which leads to more types of relatives and to more covariances of relatives or components of variance. The number of different variations in the four factor designs is appalling even without considering the primed ones or order of matings and the incomplete designs. Most of these variations are collected in Table 13 along with the two factor and three factor designs.

The designations in Table 13 of the four factor designs are an extension of, and should be clear from, the designations of the two and three factor designs. Matings are made in order from right to left. Enclosure by parenthesis [(] on the left indicates factorial or all possible matings with the group of individuals to the immediate left of the enclosure. A slash mark [/] indicates matings nested within or divided among the individuals to the immediate right of the slash mark. Double division by parentheses [)(] means matings factorially between both sides such as in (AB)(CD).

Some general comments will be made about only a few of the designs. The completely nested design (A/B/C/D) has the usual hierarchal or nested

TABLE 13.—SUMMARY OF TWO, THREE AND FOUR FACTOR DESIGNS.

Number of factors	Designs			Number of covariances of relatives
	Column 1	Column 2	Column 3	
Two:	(AA)	(A/B)	(AB)	2 to 3
Three:	(A(AA) (A(AB) (A(BB)	(A/B/C) (A/B/C) (A/(BC)	(A(BC) (A(B/C)	3 to 7
Four:	(A(A(AA) (A(A(BA) (A(B(AA) (B(A(AA) (B(B(AA) (B(A(BA) (C(B(AA) (C(A(BA) (A(C(BA)	(A(A(BC) (A(B(CD) (A/B/(CD) (A/B(CD) (A(A(B/C) (A(B(C/D) (A(B/C/D) (A/B/C/D)	(AA)(AA) (AA)(AB) (AA)(BB) (AB)(AA) (AA)(BC) (AB)(AC) (AB)(CD) (AA)(B/C) (AB)(C/D) (A/B)(C/D)	4 to 15

analysis of variance. It, of course, has an inverted mating order (A/B/C/D)'. Four components of variance and four covariances of relatives are available in each design. This represents the minimum number of covariances for a four factor design.

The factorial design (A(B(CD) has the usual four factor factorial analysis of variance. Fifteen components of variance are estimable in terms of 15 distinct covariances of relatives providing the 4 groups, A, B, C, and D, have different inbreeding coefficients. The same is true, and of course the same analysis of variance is made, for design (AB)(CD) except that there are 14 instead of 15 distinct, $C_{sAB} = C_{sCD}$, covariances of relatives. When each of the four groups are equally inbred, only five distinct covariances of relatives are available in design (AB)(CD). The 15 covariances of relatives represents the maximum number that are estimable from the 4 factor designs.

Design (AA)(AA) represents all possible double crosses of a group of parental individuals. If inbred lines are used in making the matings, it represents all possible double cross hybrids. There are eight covariances of relatives, but only seven components of variance are estimable from an orthogonal partitioning of the sums of squares. The analysis of variance, expectations of mean squares, covariances of relatives and components of genetic variance are given in (Rawlings and Cockerham, 33).

Extremes of the covariances of relatives for four factor designs will be helpful in the comparison of designs. The least related relatives in all of the designs in columns 1 and 2 of Table 13 are those with a single great grandparent common which will be denoted as $C_{c'A}$. The most related relatives of these designs are full sibs, for example from the mating $(A_i(B_j(C_kD_l)$ to be

denoted as $C_{fA(B(CD}$. All other covariances of relatives in these designs (columns I and 2) are intermediate between these two, and many of them are the same as encountered in the two and three factor designs.

For the designs in column 3 of Table 13 the most distant relatives are those with a grandparent common, which were encountered in the three factor designs, and the covariance was designated as C_{cA}. The most closely related relatives are full sibs or members of the same progeny and to be denoted as $C_{fAB)(CD}$. The covariances for the other types of relatives are intermediate between these two.

It takes three generations of matings to produce the progenies for the designs in columns 1 and 2 in Table 13 because some great grandparental control is exercised in each of the designs. In contrast, two generations are required for the designs in column 3 for which complete control or accounting of all four grandparents of each progeny is exercised.

One factor mating designs

These designs, Table 14, should be included for completeness. Only one component of variance for progenies or covariances of relatives can be estimated. If unrelated full sib progenies are used in a replicated experiment, then the

TABLE 14.—ONE FACTOR MATING DESIGNS.

Source	df	Expectations of mean squares
Replications	k−1	
Progenies	p−1	$\sigma^2+k\sigma^2_p$
Error	(k−1)(p−1)	σ^2

component of variance, σ^2_p, due to progenies is equivalent to the covariance of full sibs, C_{fAB}. Many other progenies may be used. For unrelated progenies of the types (A(BC) or (A(B(CD) or (AB)(CD), the component of variance due to progenies is equivalent to $C_{fA(BC}$, $C_{fA(B(CD}$, or $C_{fAB)(CD}$, respectively.

If the progenies are clonal propagations of individual plants, σ^2_p represents the total genetic variance, providing of course that the mechanics of clonal propagation does not affect the component of variance due to clones.

Co-designs

The inclusion of one or more common groups of ancestors for the matings in two or more designs allows an analysis of covariance between related progenies of the different designs. There is then available an analysis of variance of each design and an analysis of covariance of each pair of designs. This device can be used to obtain extra information on the covariances of relatives and keep the mating designs simple. Except for a few special cases it is doubtful that these co-designs offer any additional advantages over the regular designs.

One co-design which should receive more attention in plant breeding

is the covariance, C_{po}, of parent and offspring, and possibly even, the covariance, C_{gpo}, between grandparent and grand offspring. For annuals, the parents and grandparents must be measured in different years from offspring and grand-offspring, but as we shall see, this is a good feature.

Flexibility in making the matings

For some species individual plants can be used only one or two times as females, which makes it impossible to make the matings for the factorial designs with individual plants. However, the same result is accomplished by using the selfed progeny of the individual. A random gamete from the selfed progeny should be the same as a random gamete from the parent except for linkages. The recombination from selfing reduces the effects of linkages on the covariances of relatives, however.

By using selfed progenies many more designs can be accomplished for some species than could be otherwise. Even species which are naturally self fertilized and which are difficult to cross fertilize can be adapted with some effort to the cross mating designs.

Ideally, only a single gamete should be used from each member of a selfed progeny. The argument was developed in (Cockerham, 5), however, that as many as six members of a selfed progeny contributing equally in bulk to all crosses should be sufficient. More than six would of course be more desirable.

In the more complicated three and four factor designs, for matings of the type $(A_i(B_jC_l)$, a single individual was indicated to represent B_jC_l in matings with all A's. This is still true but the selfed progeny of a single individual from B_jC_l instead may be used in cross matings with all the A's. Thus, a selfed progeny may be used to represent each of the B's and each of the C's in the factorial matings of the B's with the C's, but a single individual or its selfed progeny of each B_jC_l combination must be used for all matings with the A's. There is, of course, another alternative. If each B_j and C_l are represented by selfed progenies in producing the B_jC_l matings, then each B_jC_l could be represented by the bulk crosses of the two selfed progenies, rather than a single individual or its selfed progeny, in the matings with the A's. This procedure will change the interpretation of some of the covariances of relatives to be given for the mating rules outlined. The reader is referred to (Cockerham, 5) for interpretations of the covariances of relatives when bulk matings are followed.

GENETIC CONTENT OF COVARIANCES OF NON-INBRED RELATIVES

The analyses of variance of the various mating designs in the previous section were characterized and related in terms of covariances of relatives. The only assumption employed was that the ancestors in a group, A, B, C, or D, were unrelated random members of that group. Note, it is the mating design that produces the relatives, and covariances of these relatives may be estimated

regardless of the ploidy of the species or other qualifying assumptions. Many of the designs have common types of relatives and thus furnish estimates of the same covariances. Further note, when reciprocal effects have been ruled out or accounted for and proper precaution has been taken to insure no environmental correlations among relatives, that the covariances of relatives are genetic in origin. For some purposes this level of interpretation may be sufficient. Generally, however, one desires an interpretation at the level of the genes. To do this much more exacting specifications and assumptions are required.

Interpretation at the level of the genes depends, of course, on the ploidy of the species. Most of our knowledge in this connection is for diploids. Kempthorne (28) gives the translation of covariances of some autotetraploid relatives from non-inbred parents into components of genetic variance for a single locus and indicates the extension to multiple interacting loci. The results are more complicated than for diploids, but the same procedure to be illustrated for diploids is followed, as it is for any other ploidy. The mating designs lead to the covariances of relatives. These are translated into genetic variances appropriate for the population.

A general formulation, in terms of genetic variances, of the covariances of relatives in the previous section may be employed provided that the following assumptions are met:

(a) regular diploid and solely mendelian inheritance.
(b) no environmental correlations among relatives.
(c) no linkages.
(d) the relatives are not inbred.
(e) the relatives can be considered to be random members of some non-inbred population.

Other assumptions are: no position effects and no competitional effects not wholly accounted for by the error component of variance. It is very difficult to delimit all possibilities.

Diploid inheritance in assumption (a) also includes amphidiploids. Reciprocal effects were considered previously and will be assumed to be absent or to have been accounted for. Environmental correlations are avoided by randomization. The method of constituting the progenies in the various designs insures assumption (d). Assumption (e) is necessary as a base population of reference. It is particularly important when inbred parents or lines are used to constitute the progenies. To maintain the same reference population for all progenies, it must be assumed that the only difference between inbred generations of parents is that due to the theoretical consequence of inbreeding. When the parents are homozygous, for example, they are assumed to be a random sample of doubled gametes from the non-inbred reference population. The assumption (c) of no linkages, implying also linkage equilibrium, is the most troublesome. While some comments on the effects of linkages will be made later,

this assumption is necessary for the following relatively simple formulation of the covariances of relatives:

$$C = \alpha\sigma^2_a + \delta\sigma^2_d + \alpha^2\sigma^2_{aa} + \alpha\delta\sigma^2_{ad} + \delta^2\sigma^2_{dd} + \alpha^3\sigma^2_{aaa} + \ \ldots$$

The covariance is C and σ^2_a, σ^2_d, σ^2_{aa} and so on are the components of genetic variance, additive, dominance, additive by additive, and so on for the non-inbred reference population. More details and information on their formulation are given in (Cockerham, 2; Kempthorne, 27). The coefficients, involving α and δ, of the genetic components of variance depend on the relationships of the relatives. The coefficients are given in Table 15 for the relatives of the mating designs in the previous section.

TABLE 15.—COEFFICIENTS OF THE ADDITIVE AND DOMINANCE COMPONENTS OF VARIANCE IN THE COVARIANCES OF NON-INBRED RELATIVES.

Covariance	In designs*	Coefficient		Maximum		Minimum	
		α	δ	α	δ	α	δ
$C_c{}'_A$	4	$(1+F_A)/64$	0	1/32	0	1/64	0
C_{cA}	3, 4, 4′	$(1+F_A)/16$	0	1/8	0	1/16	0
C_{sA}	2, 3, 4	$(1+F_A)/4$	0	1/2	0	1/4	0
C_{sBC}	3, 4, 4′	1/4	0	1/4	0	1/4	0
C_{sAcB}	3, 4	$(5+4F_A+F_B)/16$	$(1+F_A)(1+F_B)/16$	5/8	1/4	5/16	1/16
$C_{fAB)(CD}$	4′	1/2	1/4	1/2	1/4	1/2	1/4
$C_{fA(B(CD}$	4	$(2+F_A)/4$	$(1+F_A)/4$	3/4	1/2	1/2	1/4
$C_{fA(BC}$	3	$(2+F_A)/4$	$(1+F_A)/4$	3/4	1/2	1/2	1/4
C_{fAB}	2	$(2+F_A+F_B)/4$	$(1+F_A)(1+F_B)/4$	1	1	1/2	1/4
C_{fAA}	2	$(1+F_A)/2$	$(1+F_A)^2/4$	1	1	1/2	1/4
C_{po}		1/2	0	1/2	0	1/2	0
C_{gpo}		1/4	0	1/4	0	1/4	0

*The covariances appear in the designated 2, 3, 4 and 4′ factor designs, where 4 indicates the four factor designs in columns 1 and 2 of table 13 and 4′ those in column 3.

Two covariances for half sibs and five for full sibs are given in Table 15. In each category they are the same if none of the parents are inbred. It may be noted that for C_{sBC} the half sibs have a parent from the mating B_jC_l common. The parent is not inbred since B_j and C_l are not related. By the same argument for $C_{fAB)(CD}$, the two common parents of the full sibs are not inbred.

There remains some explanation of the error component of variance, σ^2, of the designs. The following explanation is completely dependent on the absence of effects of competition, and should be utilized, if ever, with extreme caution. The error component consists of a plot component of error variance, σ^2_e, and the variance, σ^2_w, among individuals within plots,

$$\sigma^2 = \frac{\sigma^2_w}{w} + \sigma^2_e,$$

where w is the number of individuals in each plot. The variance within plots

consists of plant to plant environmental variance, $\sigma^2_e{}'$, and the genetic variance, σ^2_{wG}, among members of the same progeny,

$$\sigma^2_w = \sigma^2_e{}' + \sigma^2_{wG}.$$

The genetic variance among members, full sibs, of the same progeny is the remaining part of the total genetic variance, σ^2_{TG}, not accounted for by the other components of variance of the design,

$$\sigma^2_{wG} = \sigma^2_{TG} - C_f,$$

where C_f is the full sib covariance appropriate for the design. In summary,

$$\sigma^2 = \frac{(\sigma^2_{TG} - C_f) + \sigma^2_e{}'}{w} + \sigma^2_e.$$

Inbred parents

The main reason for the inclusion of inbred parents in the mating designs is that they are an excellent aid in the estimation of genetic variances (Cockerham, 4). Without them, the maximum coefficient in the covariances of non-inbred relatives, Table 15, is ½ for additive and ¼ for dominance. With them, these coefficients can be increased to one, and also to one for the coefficients of all components of genetic variance, which permits the estimation of the total genetic variance, an obviously desirable feature. With the same number of progenies, the use of homozygous parents as compared to non-inbred parents will reduce the variances of some estimates of genetic variances by a factor of four or more. To estimate specific components or types of genetic variances, variation is needed in the coefficients from one covariance of relatives to another. By varying inbreeding of the parents in the designs or between designs used simultaneously, considerable variation in the coefficients or "handles of estimation" are obtained.

All of these advantages of utilizing different degrees of inbreeding are for naught, however, if the assumptions cited previously about the inbred parents are not met. The situation is probably not so bad when all parents are from the same generation of inbreeding even if there are some changes in gene frequencies with the generation of inbreeding. This means that the reference population for the progenies changes some with the generation of inbreeding of the parents, but the biases that can occur in estimating functions of genetic variances will be small compared to those that can occur when different degrees of inbreeding in the parents are employed.

The elimination of unfavorable recessive genes is a well known consequence of inbreeding. Whether there are enough of these and at high enough frequencies to account for a significant amount of variation is a matter of speculation and probably varies much among species. Certainly, one should be concerned about the use of different generations of inbreeding in species for which the normal mode of reproduction is by cross fertilization. Unfortunately, it is for these species that the mating designs of the previous sections are most adaptable. Changes in gene frequencies with inbreeding in normally self fertilizing species are probably not of any particular consequence.

COMMENTS ON GENE EFFECTS AND VARIANCES AND THE COVARIANCES OF DIPLOID RELATIVES

There is a minimal two fold purpose in the definition of genetic components of variance. One is that they are reflective of gene action and the other is that they are estimable. Another feature, considered almost essential by some, is that the effects and variances be phrased in terms of quantities that are invariant with inbreeding, or that are invariant with the distribution of genotypes as long as gene frequencies remain the same. This feature cannot be attained with any generality in the genetic model. It does not take much reflection, however, to realize that the intuitive appeal of this feature may be misleading. The additive effect of a gene loses some of its meaning when there is interaction of alleles, dominance. Its effect then depends somewhat on its companion. If there is little interaction, slight dominance, the significance of the average effect is little marred. If there is a large interaction, overdominance, the average effect has little meaning and one must refer to specific combinations of alleles. With several alleles dominance may not have simple connotations. Similarly, additive and/or dominance effects of alleles at a locus begin to lose their simplicity and meaning when non-alleles interact, epistasis. With more interactions less significance can be placed in additive and dominance average values or effects. These facts are unavoidable and should be reflected in their definitions and of course in their variances. The effects and variances should also be reflective of the situation in the population of reference. It is meaningless to talk about the dominance variance in a population of homozygous genotypes. Gene effects and variances change with the population of reference. Sometimes they can be translated from one population to another, sometimes they cannot. If they cannot be translated, this is as it should be, and they must be estimated for the desired reference population.

Genetic effects, and their variances, are used in the sense defined by Fisher (11) and Wright (40) for additive, dominance and epistasis, except the epistatic effects and variances are further partitioned into component parts (Cockerham, 2; Kempthorne, 27). These definitions are reflective of gene action. If there is no epistasis, then there is no epistatic variance, regardless of the reference population. If, in addition, there is no dominance, then there is no dominance variance. It is true that with considerable dominance and/or epistatic variance one cannot make reference to the exact genetic situation. This was the point being stressed earlier. With interactions, simplicity in interpretation is lost. The exact situation is uncovered only by identifying and measuring each combination or genotype. With this type of information one would resort entirely to mean comparisons or to gene effects, and never to the less sensitive measures such as genetic variances. For quantitative characters, however, whether it be viewed as fortunate or unfortunate, it appears that genetic variances are the most sensitive general measures of gene action that are estimable.

There is no difficulty (Cockerham, 2) in defining these effects and variances in an arbitrarily inbred linkage equilibrium diploid population. There is difficulty, however, in relating them from one generation to another. As an illustration, consider the genetic components of variance for a single locus with two alleles in Table 16. Even in this simple situation variances cannot be translated from one generation of inbreeding to another unless gene frequency is one half or there is no dominance, $\Delta = 0$. In either case, the additive variance is $(1+F)\,\sigma^2_a$. The dominance variance is zero if there is no dominance, and varies with $(1-F^2)\sigma^2_d$ if gene frequencies are one half.

TABLE 16.—VARIANCES FOR A SINGLE LOCUS WITH TWO ALLELES.

Genotype	AA	Aa	aa
Frequency	$p^2 + F_{pq}$	$2pq(1-F)$	$q^2 + F_{pq}$
Genotypic value	Y_2	Y_1	Y_0

Let $\Theta = (Y_1-Y_0)/2$, $\quad \Delta = (2Y_1-Y_2-Y_0)/4$

$$\text{Additive variance} = 2pq(1+F)\left[\Theta+\left(\frac{1-F}{1+F}\right)(q-p)2\Delta\right]^2$$

$$\text{Dominance variance} = \frac{16pq(p+Fq)(q+Fp)(1-F)}{(1+F)}\Delta^2$$

Gene frequencies of one half

With epistasis or non-allelic gene interaction the situation is more complex. When all gene frequencies are one half, however, many simplifications occur and the effects and variances may be defined as in Table 17. The additive effect θ_i and the dominance effect Δ_i for the ith locus are the same as defined in Table 16. The additive by additive effect, θ_{2ij}, for the ith and jth loci is the following comparison of mean genotypic values,

$$\theta_{2ij} = (A_iA_iA_jA_j - A_iA_ia_ja_j - a_ia_iA_jA_j + a_ia_ia_ja_j)/4.$$

One more comparison, additive at the ith locus by dominance at the jth locus, $\overline{\theta_i\Delta_j}$, will suffice to illustrate the definitions of the effects. $\overline{\theta_i\Delta_j} = [(A_iA_iA_jA_j - 2A_iA_iA_ja_j + A_iA_ia_ja_j) - (a_ia_iA_jA_j - 2a_ia_iA_ja_j + a_ia_ia_ja_j)]/8$. The effects are defined for the non-inbred population in Table 1, $F = 0$, and corresponding effects, denoted by the additional subscript F, for inbred generations are expressed as a function of those when $F = 0$. In each case the effect in the inbred generation is equal to the one when $F = 0$ plus additional ones times some power of F. The additional ones always involve a higher order of dominance interaction with other loci. The summation is over all such interactions or loci.

The various types of genetic variances are given in the lower portion of Table 17 in terms of the effects. The summation is over all loci or the appropriate

combinations of loci, and the subscripts identifying these loci have been dropped.

The effects vary with the degree of inbreeding unless there are no epistatic effects with dominance in their nomenclature. In this case the total genetic variance is comprised of only additive, dominance, and all additive types of epistatic variances. These variances can now be translated from one generation of inbreeding to another.

TABLE 17.—GENETIC EFFECTS AND VARIANCES FOR GENE FREQUENCIES OF ONE-HALF AND ARBITRARY INBREEDING.

Type	F = 0	F = F
	Effects	
a	Θ_i	$\Theta_{iF} = \Theta_i + F\Sigma\overline{\Theta_i\Delta_j} + F^2\Sigma\overline{\Theta_i\Delta_{2jk}} + \ldots$
d	Δ_i	$\Delta_{iF} = \Delta_i + F\Sigma\Delta_{2ij} + F^2\Sigma\Delta_{3ijk} + \ldots$
aa	Θ_{2ij}	$\Theta_{2ijF} = \Theta_{2ij} + F\Sigma\overline{\Theta_{2ij}\Delta_k} + F^2\Sigma\overline{\Theta_{2ij}\Delta_{2kl}} + \ldots$
ad	$\overline{\Theta_i\Delta_j}$	$\overline{\Theta_i\Delta_{jF}} = \overline{\Theta_i\Delta_j} + F\Sigma\overline{\Theta_i\Delta_{2jk}} + F^2\Sigma\overline{\Theta_i\Delta_{3jkl}} + \ldots$
dd	Δ_{2ij}	$\Delta_{2ijF} = \Delta_{2ij} + F\Sigma\Delta_{3ijk} + F^2\Sigma\Delta_{4ijkl} + \ldots$
aaa	Θ_{3ijk}	$\Theta_{3ijkF} = \Theta_{3ijk} + F\Sigma\overline{\Theta_{3ijk}\Delta_l} + F^2\Sigma\overline{\Theta_{3ijk}\Delta_{2lm}} + \ldots$
aad	$\overline{\Theta_{2ij}\Delta_k}$	$\overline{\Theta_{2ij}\Delta_{kF}} = \overline{\Theta_{2ij}\Delta_k} + F\Sigma\overline{\Theta_{2ij}\Delta_{2kl}} + F^2\Sigma\overline{\Theta_{2ij}\Delta_{3klm}} + \ldots$
.	.	.
.	.	.
.	.	.
	Variances	
a	$\frac{1}{2}\Sigma - \Theta^2$	$(1+F)\frac{1}{2}\Sigma\Theta^2_F$
d	$\Sigma\Delta^2$	$(1+F)(1-F)\Sigma\Delta^2_F$
aa	$\frac{1}{4}\Sigma - \Theta^2_2$	$(1+F)^2\frac{1}{4}\Sigma\Theta^2_{2F}$
ad	$\frac{1}{2}\Sigma - \overline{\Theta\Delta}^2$	$(1+F)^2(1-F)\frac{1}{2}\Sigma\overline{\Theta\Delta}^2_F$
dd	$\Sigma\Delta^2_2$	$(1+F)^2(1-F)^2\Sigma\Delta^2_{2F}$
aaa	$\Sigma\Theta^2_3$	$(1+F)^3\frac{1}{8}\Sigma\Theta^2_{3F}$
aad	$\Sigma\overline{\Theta_2\Delta}^2$	$(1+F^2(1-F)\frac{1}{4}\Sigma\overline{\Theta_2\Delta}^2_F$
.	.	.
.	.	.
.	.	.

Restriction of genetic model

A genetic model with no additive by dominance or all dominance types of epistasis is fairly restrictive. Before examining this, first consider the genetic model with only additive and all additive types of epistatic effects. With two alleles, two loci, for example, the following relationship among genotypic values must hold,

$$AaBb = (AABb+aaBb)/2 = (AaBB+Aabb)/2 = (AABB+AAbb+aaBB+aabb)/4.$$

That is, the single heterozygotes are always intermediate between corresponding homozygotes and the double heterozygote is intermediate between single heterozygotes. In other words, all genotypic values are determined by the genotypic values of the complete homozygotes. Now this statement is not confined to two alleles and two loci but is true for any number of alleles and loci—all genotypic values involving heterozygotes are completely specified by those of the complete homozygotes. For many genetic models one or more components of genetic variance may go to zero depending on gene frequencies and distribution of genotypes in the population. However, the previous definition of the additive and additively epistatic genetic model is the only one for which the dominance and dominance types of epistatic variance are universally zero, gene frequencies of one half or otherwise, and is the one implicitly assumed when only additive and additive types of epistasis are assumed. It may be noted that this is the correct model for homozygous populations since they contain no heterozygotes.

With the addition of dominance to additive and all additive types of epistasis in the genetic model, all genotypic values are completely specified by those of the complete homozygotes plus a single heterozygote, homozygous elsewhere, for each pair of different alleles (there may be several pairs of different alleles at each locus). For two loci, two alleles each, the model is completely specified by the four complete homozygotes and any two single heterozygotes, and for two loci, three alleles each, by the nine homozygotes and by six different single heterozygotes.

With all types of gene effects in the model except all dominance types of epistasis, the genotypic values of the double, triple, and so on, heterozygotes are specified by those of the other genotypes.

These simple descriptions are often helpful in visualizing the limitations placed on the genetic model by making assumptions in the additive-dominance terminology.

The complications that arise when gene frequencies are not one half are further illustrated by considering the additive effects when there are no epistatic interactions involving more than two loci,

$$\Theta_{iF} = \Theta_i+(q_i-p_i)\left(\frac{1-F}{1+F}\right)2\Delta_i+F\Sigma p_jq_j4\overline{\Theta_i\Delta_j}+(q_i-p_i)\left(\frac{1-F}{1+F}\right)F\Sigma p_jq_j\Delta_{2ij},$$

and the additive variance is

$$(1+F)\Sigma 2p_iq_i\theta^2_{iF}.$$

Even dominance by dominance effects of the non-inbred generation enter into the additive effects of the inbred generation now.

The most general genetic model for which genetic components of variance can be translated from one generation of inbreeding to another without specifying gene frequencies or number of alleles is the additive and all additive type of epistatic model. The variances are then

$$(1+F)\sigma^2_a, \qquad (1+F)^2\sigma^2_{aa}, \qquad (1+F)^3\sigma^2_{aaa}, \quad \ldots$$

Covariances of relatives

When relatives are not inbred and subject to the assumptions of the previous section, the covariances can be expressed as linear functions of components of genetic variance without specifying anything about gene frequencies, including the number of alleles, or the genetic model. This, unfortunately, is not the case when the relatives are inbred, and particularly so, when they are in different generations of inbreeding. While covariances of relatives can always be expressed as functions of components of genetic variance plus covariances of different types of genetic effects, the situation is complicated enough without having to reckon with covariances of different types of genetic effects.

To be outlined now are the conditions necessary for expressing the covariances of inbred relatives as linear functions of components of genetic variance. The minimal assumptions to begin with are the first three of the previous section

(a) regular diploid and solely mendelian inheritance
(b) no environmental correlations among relatives
(c) no linkages

plus a relaxation of assumption

(d) the progenies or relatives may be considered to be random members of some generation of self fertilization.

Actually, the ensuing comments are accurate for other regular systems of inbreeding but self fertilization is the one of importance in plants, and the only one of importance in the estimation of genetic variances. Further assumptions or restrictions depend on the type of relatives. Two types are distinguished, those in the same generation of inbreeding and those in different generations of inbreeding. A further distinction of those in the same generation of inbreeding according to the inbreeding coefficient are made in Table 18. In this table the further minimal assumptions about gene frequencies and the genetic model necessary for the covariances of relatives to be expressed as a linear function of components of genetic variance are listed.

The first situation in Table 18 for relatives in the same generation of inbreeding and not inbred, $F = 0$, is the previously considered case of non-inbred relatives. If the relatives are partially inbred, then $O < F < 1$. Although they are in the same generation of inbreeding, the covariances cannot be expressed as a linear function of genetic variances without assuming something about either gene frequencies or the genetic model (Cockerham, 2). The trouble is, if gene

TABLE 18.—SITUATIONS FOR WHICH THE COVARIANCES OF RELATIVES CAN BE EXPRESSED AS A LINEAR FUNCTION OF COMPONENTS OF GENETIC VARIANCE.

Relatives	Inbreeding Coefficient	Gene Frequencies	Genetic Model
In the same generation of inbreeding	$F = 0$	Unspecified	Unlimited
	$0 < F < 1$	Unspecified	Additive and all additive types of epistasis
	$F = 1$	Unspecified	Unlimited but includes only additive and all additive types of epistasis
	$0 \leq F \leq 1$	One-half	Unlimited
In different generations of inbreeding		Unspecified	Additive and all additive types of epistasis
		One-half	Additive, dominance, and all additive types of epistasis

frequencies are not one half, different types of genetic effects of the relatives are correlated unless the genetic effects are entirely additive and/or all additive types of epistatic effects. With this genetic model and any number of alleles the covariances of relatives can be expressed as a linear function of components of genetic variance, which will, of course, consist only of σ^2_a, σ^2_{aa}, σ^2_{aaa}, and so on.

When the relatives or progenies are inbred to homozygosity, $F = 1$, their covariances can always be expressed as linear functions of components of genetic variance without specifying anything about gene frequencies or the genetic model. The genetic model includes only additive and all additive types of epistatic effects, however, since there are no heterozygotes.

When gene frequencies can be assumed to be one half, meaning also only two alleles at every locus, as is the case in populations stemming from two homozygous parents or lines, the genetic model need not be limited. The covariances of relatives in the same generation of inbreeding are expressible as linear functions of all types of components of genetic variance. This situation is analogous to the one for non-inbred progenies as far as the use of covariances of relatives is concerned. Just as many different types of relatives and all inbred to a certain generation can be obtained, although probably not as easily as can be for the non-inbred progenies, and the same estimation techniques can be used. This point is stressed here because it is believed to have been generally overlooked.

For the covariances of relatives in different generations of inbreeding to be expressible as a linear function of components of genetic variance, it is necessary that the components of genetic variance can be translated from one generation of inbreeding to another. This is not required for relatives in the same generation of inbreeding where the components of genetic variance are

defined for each generation of inbreeding. The genetic model is limited to additive and all additive types of epistasis when gene frequencies are not assumed to be one half. Even if gene frequencies are assumed to be one half, only single factor dominance effects of genes can be further incorporated into the genetic model and have the covariances of the relatives expressible as linear functions of genetic variances.

COVARIANCES OF INBRED DIPLOID RELATIVES FROM THE MATING DESIGNS OF UNRELATED MATES

For the cross mating designs of unrelated mates the initially non-inbred progenies are now inbred for one or more generations by bulk selfing. The selfed progenies are the ones grown in the experiment. For each design the same analysis of variance, components of variance for the design, and covariances of relatives are appropriate except the covariances are now of the inbred relatives of the selfed progenies. We wish to express the covariances of these relatives in the previous form

$$C = \alpha\sigma^2_a + \delta\sigma^2_d + \alpha^2\sigma^2_{aa} + \alpha\delta\sigma^2_{ad} + \delta^2\sigma^2_{dd} + \cdots$$

This can be done subject to the conditions outlined in Table 18.

When gene frequencies can be assumed to be one half, meaning generally that the parental plants of the mating design are from populatings stemming from two homozygous lines, no restrictions need be placed on the genetic model. The additive coefficient, α, takes the same value for the inbred relatives as it does in Table 15 for non-inbred relatives. The appropriate dominance coefficient, δ, is the one in Table 15 multiplied by $(1-F_g)^2$ where F_g is the inbreeding coefficient of the progenies or of the relatives. The variances are now defined strictly in terms of gene effects for the inbred generation, however. The identifications of the following can be made from Table 17,

$$\sigma^2_a = \frac{1}{2}\Sigma\Theta^2_F, \qquad \sigma^2_d = \Sigma\Delta^2_F, \qquad \sigma^2_{aa} = \frac{1}{4}\Sigma\Theta^2_{iF}, \qquad \sigma^2_{ad} = \frac{1}{2}\Sigma\Theta\Delta^2_F, \text{ and so on.}$$

With these definitions, components of genetic variance can be estimated for any inbred generation in the same way as they were for the non-inbred generation.

If no assumptions are made about gene frequencies and number of alleles, then the model must be reduced to that of additive and all additive types of epistatic effects. The coefficients for α are those in Table 15 and δ is of course zero, or not needed. If the progenies were selfed for many generations, F_g assumed to be one, then this would be the complete genetic model regardless of gene frequencies. The number of generations of selfing does not really have to be many before the additive and all additive type of epistatic model is probably a close and reasonable fit. The coefficient for the dominance variance in the covariance of inbred relatives in the same generation contains $(1-F_g)^2$. This is 1/64 for three generations of selfing and 1/256 for four generations of selfing. The coefficients for epistatic variances involving dominance contain

$(1-F_g)^2$ or higher powers of $(1-F_g)^2$. The coefficient (Cockerham, 2) for the correlated portion of additive with dominance in the covariance of inbred relatives also contains $(1-F_g)^2$. It was these correlated portions in the covariances of relatives which caused us to make some assumptions concerning either the model or gene frequencies in order to maintain a manageable formulation. However, to total up the above considerations, it would seem generally to be a safe working rule to forget dominance or dominance types of epistasis in the covariances of relatives when the progenies have been selfed for as many as four generations, $F_g = 15/16$. This conclusion does not apply to relatives of self fertilization in general but to those developed by bulk selfing of non-inbred progenies.

NESTED DESIGNS OF SELF FERTILIZATION

These are the designs often employed for the normally self pollinating species since they are a natural consequence of this method of reproduction. The starting point for these designs as a base of reference will be the non-inbred or S_0 generation. These may be F_2 plants of a cross of two homozygous lines or they may be plants from crosses of unrelated parents from, for example, a variety. In any case, the base non-inbred generation for counting purposes is zero. The S_0 plants are selfed. These progenies may be selfed in bulk on to any generation or pedigrees may be maintained of the S_1 parent plants so that their progenies can be traced to each S_1 and S_0 plant. Pedigrees may be maintained for as many generations of selfing as desired and the progenies may be further selfed in bulk for any number of generations. It is not necessary to start out with S_0 plants. One may start with any generation of plants, S_1, S_2, S_3, and so on, but they should never be related meaning that they should all trace to different S_0 plants.

Analysis of variance and covariance

The analysis of an experiment will be illustrated for progenies in the *gth* generation from parents in the t, t', and t'' generations with $t'' > t' > t$. Ordinarily t' will equal $t + 1$ and t'' will equal $t' + 1$, that is, successive generations, but this is not mandatory. If t' is more than one generation away from t, then each plant in t' should trace through different parents to a plant in t, otherwise t is incorrectly labeled. These may appear to be petty details but they are necessary for accuracy of the results.

The expectations of mean squares for the analysis of variance appear in Table 19. The analysis of variance is the same as that for design (A/B/C) in Table 11 and the pattern of the coefficients and variance components in the expectations of mean squares is the same. The components of variance are translated into covariances of relatives at the bottom of Table 19. The generation of the progenies or relatives is introduced into the notation of the covariance because it makes a difference in their covariances. The designation of the covariances is fairly common (Cockerham, 2; Horner, 24), where C_{tgg} is the

TABLE 19.—EXPECTATIONS OF MEAN SQUARES OF DESIGN ($S_{t''}/S_{t'}/S_t$).

Source	df	Expectations of Mean Squares
Replications	k−1	
Between S_t	n_t-1	$\sigma^2+k\sigma^2_{t''/t'}+kn_{t''}\sigma^2_{t'/t}+kn_{t''}n_{t'}\sigma^2_t$
$S_{t'}$ within S_t	$n_t(n_{t'}-1)$	$\sigma^2+k\sigma^2_{t''/t'}+kn_{t''}\sigma^2_{t'/t}$
$S_{t''}$ within $S_{t'}$	$n_tn_{t'}(n_{t''}-1)$	$\sigma^2+k\sigma^2_{t''/t'}$
Error	$(k-1)(n_tn_{t'}n_{t''}-1)$	σ^2

$\sigma^2_t = C_{tgg}$, $\sigma^2_{t'/t} = C_{t'gg}-C_{tgg}$, $\sigma^2_{t''/t'} = C_{t''gg}-C_{t'gg}$

covariance of progeny means or of relatives in the g th generation whose last common parent in the selfing chain was in the t th generation. The same definition of course holds for $C_{t'gg}$ and $C_{t''gg}$ except the last common parent is in the t' and t'' generations, respectively. Relatives in different generations are accommodated by priming one of the g's, e.g., C_{tgg}'.

The extension of the design to include more generations of control or pedigreed parents is straight forward and should be apparent, as should shortening of the design, using only t parents or t and t' parents. Often, only one generation of control parents, for example S_0, is used, but several generations of progenies. Considering the same parental controls, S_t, S_t' and S_t'', as before, the expectations of mean products for the analysis of covariance of two sets of progenies in different generations of inbreeding are shown in Table 20. The

TABLE 20.—EXPECTATIONS OF MEAN PRODUCTS OF PROGENIES IN DIFFERENT GENERATIONS FOR DESIGN ($S_{t''}/S_{t'}/S_t$).

Source	df	Expectations of Mean Squares
	In the same replications	
Replications	k−1	
Between S_t	n_t-1	$\bar{\sigma}+k\bar{\sigma}_{t''/t'}+kn_{t''}\bar{\sigma}_{t'/t}+kn_{t''}n_{t'}\bar{\sigma}_t$
$S_{t'}$ within S_t	$n_t(n_{t'}-1)$	$\bar{\sigma}+k\bar{\sigma}_{t''/t'}+kn_{t''}\bar{\sigma}_{t'/t}$
$S_{t''}$ within $S_{t'}$	$n_tn_{t'}(n_{t''}-1)$	$\bar{\sigma}+k\bar{\sigma}_{t''/t'}$
Error	$(k-1)(n_tn_{t'}n_{t''}-1)$	$\bar{\sigma}$
	In different experiments	
Between S_t	n_t-1	$\bar{\sigma}_{t''/t'}+n_{t''}\bar{\sigma}_{t'/t}+n_{t''}n_{t'}\bar{\sigma}_t$
$S_{t'}$ within S_t	$n_t(n_{t'}-1)$	$\bar{\sigma}_{t''/t'}+n_{t''}\bar{\sigma}_{t'/t}$
$S_{t''}$ within $S_{t'}$	$n_tn_{t'}(n_{t''}-1)$	$\bar{\sigma}_{t''/t'}$

$\bar{\sigma}_t = C_{tgg'}$, $\bar{\sigma}_{t'/t} = C_{t'gg'}-C_{tgg'}$, $\bar{\sigma}_{t''/t'} = C_{t''gg'}-C_{t'gg'}$

analysis of covariance is accomplished exactly as the analysis of variance except corresponding products are used instead of squares. The analysis of covariance is given for two situations. For the uppermost analysis in Table 20 the two sets of progenies are randomized in the same replications. For the lower analysis the two sets of progenies are grown in different experiments and the analysis is of

progeny means over replications. The error component of covariance, $\overline{\sigma}$, in Table 20 is often zero, in which case, the lower analysis is satisfactory when the two sets of progenies are in the same experiment. With more than two sets of progenies in different generations of inbreeding, there is an analysis of covariance of each pair of sets, and, of course, an analysis of variance of each set.

Genetic interpretation of the covariances of relatives

As previously, the covariances of relatives are to be expressed in the form

$$C = \alpha\sigma^2_a + \delta\sigma^2_d + \alpha^2\sigma^2_{aa} + \alpha\delta\sigma^2_{ad} + \delta^2\sigma^2_{dd} + \ldots$$

Gene frequencies of one half—For C_{tgg}, that is for relatives in the same generation, g, and which trace to the last common parent in generation t, the additive coefficient is simply,

$$\alpha = (1+F_t).$$

It depends only on the inbreeding of the parent in generation t and is not affected by the generation of the progenies or relatives. The dominance coefficient is

$$\delta = \frac{(1+F_t)}{(1-F_t)}\ (1-F_g)^2,$$

which is affected by both the generation of the parent and of the offspring. Expressing the coefficients, α and δ, as functions of the inbreeding coefficients may be more informative than the usual manner in which they have been expressed (Cockerham, 2; Horner, *et al.* 24) by substituting $(2^{g-1}-1)/2^g$ for F_g, and $(2^{t-1}-1)/2^t$ for F_t.

The genetic components of variance are now defined for the generation of the offspring, and are identified from Table 17 as

$$\sigma^2_a = \frac{1}{2}\Sigma\Theta^2_g, \qquad \sigma^2_d = \Sigma\Delta^2_g, \qquad \sigma^2_{aa} = \frac{1}{4}\Sigma\Theta^2_{2g}, \qquad \sigma^2_{ad} = \frac{1}{2}\Sigma\Theta\Delta^2_g, \quad \ldots,$$

where F has been replaced by g in denoting the effects in the inbred generation g. Remember, these effects vary with the generation of inbreeding unless the genetic model consists of only additive and additive types of epistatic effects, in which case, these variances are for the non-inbred generation.

For $C_{tgg'}$, that is, for relatives in different generations, g and g', the coefficients are

$$\alpha = (1+F_t) \text{ and } \delta = \frac{(1+F_t)}{(1-F_t)}(1-F_g)(1-F_{g'}),$$

which of course also includes the situation when the relatives are in the same generation. When they are in different generations, however, the genetic variances are not really variances but are sums of products of genetic effects,

$$\sigma^2_a = \frac{1}{2}\Sigma\Theta_g\Theta_{g'}, \qquad \sigma^2_d = \Sigma\Delta_g\Delta_{g'}, \qquad \sigma^2_{aa} = \frac{1}{4}\Sigma\Theta_{2g}\Theta_{2g'}, \quad \ldots,$$

if there are any additive by dominance and all dominance types of epistatic effects. If not, the genetic variances,

$$\sigma^2_a = \frac{1}{2}\Sigma\theta^2, \quad \sigma^2_d = \Sigma\Delta^2, \quad \sigma^2_{aa} = \frac{1}{4}\Sigma\theta^2_2, \quad \sigma^2_{aaa} = \frac{1}{8}\Sigma\theta^2_3, \quad \ldots,$$

are for the non-inbred generation since the effects do not change with the generation of inbreeding.

Gene frequencies general—The only genetic model that can be accommodated satisfactorily here is the additive and additively epistatic one. Only one coefficient is needed for $C_{tgg'}$,

$$\alpha = (1+F_t),$$

and the additive variance and additive types of epistatic variances are defined for the non-inbred generations.

The inbreeding needed in the progeny for the additive and all additive type of epistatic model to be a reasonable approximation depends also on the generation of the last common parent because the dominance coefficient contains

$$\frac{1+F_t}{1-F_t}(1-F_g)^2.$$

It was observed earlier that as many as four generations of self fertilization should be sufficient to insure that errors would be negligent in assuming gene effects to be additive and additively epistatic. However, the progenies were non-inbred initially and then selfed by bulk so that F_t for the part $(1+F_t)/(1-F_t)$ corresponding to the last common parent was zero, i.e., $F_t = 0$. This same argument for accuracy of the model holds then for C_{044}, or when the last common parent is not inbred.

When inbred parents are to be used in the estimation of the covariances of relatives, the progenies should be in more than the fourth generation of inbreeding in order to ignore dominance and dominance types of epistasis. Consider the following approximate δ's for various covariances of relatives:

Covariance	δ
C_{144}	$3/256 \doteq 1/85$
C_{155}	$3/1024 \doteq 1/340$
C_{244}	$7/256 \doteq 1/35$
C_{255}	$7/1024 \doteq 1/150$
C_{266}	$7/4096 \doteq 1/585$
C_{355}	$15/1024 \doteq 1/70$
C_{377}	$15/4096 \doteq 1/270$

It would probably be safe to ignore dominance and dominance types of epistasis and use parents in the first and second generations of selfing if the progenies were in at least the fifth generation. To use parents in the third generation progenies should be at least in the sixth. Thus, by maintaining pedigrees on S_0, S_1, S_2, and S_3

and selfing the progenies by bulk to at least the S_6, one could estimate $C_{0\infty\infty}$, $C_{1\infty\infty}$, $C_{2\infty\infty}$, and $C_{3\infty\infty}$ without very much error.

OTHER MATING DESIGNS OF RELATED MATES

The nested designs of the preceding discussion are obligatory with self fertilization. Any variation from these designs requires cross fertilization. Cross fertilization between unrelated mates, whether they be S_0, S_1, S_2, or S_3, and so on individuals or progenies, leads initially to non-inbred progenies and the designs with unrelated mates. If the progenies are not further inbred, the interpretation of the covariances of non-inbred relatives is appropriate. If the progenies are further inbred the appropriate interpretation of the covariances of inbred diploid relatives is explained on page 76.

There are, of course, many degrees in between the mating of unrelated mates and the mating of perfectly related parents, selfing. Some regular systems of matings, for example, are the classical ones given by Wright. A mating pattern could be worked out for crossing S_4 plants by mating S_4 plants from the same S_3, from different S_3 but the same S_2, and so on. These variations and the other regular systems of inbreeding will not be considered. Furthermore, it is believed that such systems have no real place in the estimation of genetic variances.

BACKCROSS DESIGNS

In designs making use of progenies from backcrossing to the two parents, the individual members of progenies cannot be considered to be random members of a single population because there is a distinct population of progenies for each of the two parents. Of course, the same is true for progenies in different generations of inbreeding, but the generations were separated in the discussion of self fertilization into an analysis of variance of each and an analysis of covariance between each pair for purposes of analysis. The same can be done for the backcross progenies. Let the first generation after the cross of two homozygous lines be designated as R_0. Progenies are produced by backcrossing n individual plants from any random mating generation, R_g, to each of the parent lines.

The expectations of mean squares and products are shown in Table 21 for a separate analysis of the progenies from each parent and a covariance analysis of the two sets of progenies and for a combined analysis of the progenies. This represents a general method of demonstrating the relationship between a combined analysis and separate analyses. There is, of course, more information available in the separate analyses than in the combined analysis. The error components of variance, for example, need not be assumed to be the same and separate estimates can be obtained. In a randomized experiment the error covariance, $\overline{\sigma}$, should be zero but may be estimated if there is reason to suspect that errors of progenies with the same R_g parent are correlated. Three covariances of relatives are available from the separate analyses. The combined analysis contains all of the information in the separate analyses pro-

TABLE 21.—BACKCROSS DESIGN—EXPECTATIONS OF MEAN SQUARES AND PRODUCTS.

Source	df	Expectations of mean squares or products		
		Separate analyses		
		Progenies of line 1	Covariance analysis	Progenies of line 2
Replications	k−1			
Rg parents	n−1	$\sigma^2+k\sigma^2_1$	$\bar{\sigma}+k\sigma_{12}$	$\sigma^2+k\sigma^2_2$
Error	(n−1)(k−1)	σ^2	$\bar{\sigma}$	σ^2
		Combined analysis		
Replications	k−1			
Lines	1			
Rg parents	n−1	$\sigma^2+k\sigma^2_{lb}+2k\sigma^2_b = \sigma^2+2k\sigma^2_{b'}$		
Lines x Rg	n−1	$\sigma^2+k\sigma^2_{lb}$		
Error	2(n−1)(k−1)	σ^2		

Let: C_{11} = Covariance of individuals from the same Rg parent and line 1.
C_{22} = Covariance of individuals from the same Rg parent and line 2.
C_{12} = Covariance of individuals from the same Rg parent but different lines.

Then: $\sigma^2_1 = C_{11}$, $\sigma_{12} = C_{12}$, $\sigma^2_2 = C_{22}$, $\sigma^2_{lb} = (C_{11}+C_{22})/2-C_{12}$
$\sigma^2_b = C_{12}$, $\sigma^2_{b'} = (C_{11}+C_{22}+2C_{12})/4$

vided the error variances are the same, errors are uncorrelated and $C_{11} = C_{22}$. Even if these relationships do not hold, the combined analysis may contain all the desired information, as would be true when only an average error and the sum or average of C_{11} and C_{22} are desired.

This design and the combined analysis in Table 21 corresponds to Comstock and Robinson (8) experiment III. They used the mean square expectation containing $\sigma^2_{b'}$, since they were only interested in interpreting $(C_{11} + C_{22} + 2C_{12})/4$ and $(C_{11} + C_{22})/2 - C_{12}$. Assuming only additive and dominance effects of genes, they found

$$\sigma^2_{b'} = \frac{1}{8}\Sigma\theta^2, \text{ and } \sigma^2_{bl} = \Sigma\Delta^2,$$

where θ and Δ may be identified from Tables 16 and 17. The same results are also available from Mather (30).

The extension to an epistatic model is almost completely unmanageable. The contributions of the epistatic terms to the variances depend on the distributions of the genes in the two parent lines. Hayman (19) discusses some of the difficulties in defining the effects when epistasis is allowed and these difficulties are magnified for the variances.

Unless one can safely assume only additive and dominance effects of genes this design is not believed to be useful in the estimation of genetic variances. In the covariances of relatives of the previous designs one could

at least have some opinion on the result of assuming a limited genetic model. That is, one was omitting positive terms, if any. Also, for many of the relatives, the coefficients of the epistatic terms were so small that no large error was made in assuming a restricted model, even if it were wrong. This does not appear to be the case for the backcross designs.

A general formulation of the covariances, C_{11}, C_{22}, and C_{12} will not be attempted since they are interpretable only for additive and dominance effects of genes.

LIMITED SAMPLES OR FIXED POPULATIONS

These are populations which are entirely contained in the sample. Most examples center around a set of inbred lines, their crosses, and possibly selfs of the crosses and backcrosses. With these populations many estimates and tests of hypotheses concerning effects of lines, interactions of lines, heterosis, and so on, with definite genetic implications, are available. All of these are phrased in terms of effects or comparisons of means as is appropriate for the interpretation of a fixed group of treatments or genetic entries. Quadratics are often used in the tests of hypotheses, and are essential for a composite hypothesis such as outlined by Hayman (17) for epistasis involving a set of inbred lines, their crosses, and selfs of the crosses. Many estimates of variances, although the variances are often of only a few quantities, are available: environmental variances of the lines, total genetic variance among lines, environmental variances of the crosses, variance of the average effects of lines in crosses, variance of the interaction effects of lines in crosses, or just total genetic variance among crosses, covariance of lines with cross progeny means, and so on. All of these variances and covariances can be estimated very accurately with enough experimentation when they apply strictly to the population of genotypes in the sample. The genetical and practical implications of the variances and covariances are not to be ignored.

The question arises as to whether a more general interpretation of the genetic variances of the entries in the experiment as to variances due to additive, dominance, and epistatic effects of genes can be made. From developments given pages 71 and 72 the genetic model must be limited to only additive and dominance effects of genes if gene frequencies can be assumed to be one half, and to only additive effects of genes if gene frequencies are not assumed to be one half. Furthermore, there is the absolutely necessary and much depended upon assumption that the genes are distributed among the lines at random. This actually means that the genes must be distributed among the lines so that the average product of their effects is exactly zero. It does not seem wise, then, to attempt to estimate components of genetic variance from a specific set of inbred lines, their crosses and with or without selfs of the crosses, and backcrosses.

Hayman (20) stresses that considerably more accuracy is obtained of estimates of variances when they are inferred strictly to the set of genetic material in the sample. This is very true for the estimates available from the sample, but for inference to another base of reference, such as additive and

dominance variances, there is an error of inference. This error can be determined only when an adequate sampling plan is devised. Hayman (20) further states that as many as 10 parents in design (AA) are required to supply useful estimates of genetic variances when the parents are considered to be a random sample. The only disagreement with this statement is that the number is generally far too conservative.

One often-asked question remains. Is it proper to use design (AA) progenies from a set of inbred lines and infer from estimates of variances to genetic variances in the random mating population which is wholly constituted from this set of lines? Again, there is the error of inference which is not easily evaluated. The answer is partially resolved in that if the number of lines are few the estimates of the variances are not reliable enough to make any strong inferences anyway.

LINKAGES

Linkages present two troublesome features in the estimation of genetic variances. Firstly, the base or reference population may not be in linkage equilibrium. Such is the case for populations which are genetic mixtures of two or more inbred lines, varieties or races, and which have not been randomly mated for several generations. Secondly, recombination values less than one half affect the covariances of some relatives, even though they can be assumed to be random members of a population in linkage equilibrium.

If non-inbred relatives are assumed to be in linkage equilibrium, linkages affect the covariances of those relatives, half sibs, full sibs, cousins, and so on which have common ancestors (Cockerham, 3). It also affects the covariances of those relatives for which one is an ancestor of the other except for parent and offspring. Correction of the results in this connection are given by Schnell (39). Linkages affect only the coefficients of the epistatic components and always increase the coefficients by an amount dependent upon the recombination values (no effect with free recombination).

Griffing (16) considers several maxima and minima for the average recombination value. He points out that one could use C_{po} and $C_{sA}(F_A=0)$ of Table 15 and the average recombination value to estimate σ^2_a and σ^2_{aa} free of linkage effects. This, of course, assumes the higher additive types of epistatic effects to be zero.

Inbreeding in the ancestors will reduce the effects of linkage on the covariances of non-inbred relatives in linkage equilibrium. There are no linkage effects, for example, if the ancestors are homozygous.

Most of the developments for linkage effects have been for gene frequencies of one half or for populations from the cross of two homozygous parents. It is in these populations that linkages are very important because the populations cannot be assumed to be in linkage equilibrium until after many generations of random mating. Mather (30) formulates the contributions of linkages for several generations with only additive and dominance effects of genes.

Comstock and Robinson (8) consider linkages for the backcross design of Table 21 and in another paper (35) for design (A/B), all with gene frequencies of one half and only dominance and additive effects of genes.

With a backcross design (Robinson *et al.* 37) for each of two different generations, Rg and Rg', of parents, one can test for the effects of linkage by comparing the components of the two experiments regardless of the genetic model, as long as gene frequencies have not changed during the generations of random mating. Hayman and Mather (21) consider linkages for additive and dominance effects in relation to two-factor epistatic effects.

The effects of linkages were studied by Gates *et al.* (13) when gene frequencies are one half and when progenies are developed by self-fertilization, such as in design $(S_{t''}/S_{t'},/S_t)$, for an additive and dominance model and for special epistatic models. Even if the S_0 generation is in linkage equilibrium, the S_1 is out of linkage equilibrium, and one is faced with the joint effects of linkage disequilibrium and recombination values of less than one half on the covariances of relatives. If the S_0 generation is the F_2 from a cross of two homozygous lines, then it is also out of linkage equilibrium for loci with recombination values less than one half. An attempt is made in Gates *et al.* (12) to account for linkage effects and estimate some genetic variances in this situation.

Only recently has a general and satisfactory formulation of linkages for several loci become available. Jones (25) formulates the linkage effects in the cumulants for generations from a cross of two homozygous parents. Schnell (38) developed a terminology for linkages slightly different from that of Jones, although it accomplishes the same purpose. This terminology allows him to formulate (39) the effects of linkage disequilibrium and of recombination values less than one half on all of the covariances of relatives including inbred ones. While this development is enlightening, the problem of properly accounting for the effects of linkages in the estimation of genetic variances still remains.

A certain amount of avoidance of linkage effects can be practiced. Several generations of random mating can be employed to reduce linkage disequilibrium in populations. Use can be made of the covariance of parent and offspring in linkage equilibrium which is not affected by linkages. The use of highly inbred parents in linkage equilibrium for the two-factor designs avoids linkage effects on the covariances of full sibs and half sibs. A procedure can be suggested which will avoid linkage effects on the covariances of full sibs and half sibs from non-inbred parents in linkage equilibrium, but too much effort is required for it to be generally practicable. To do this, each non-inbred parent is represented by its selfed progeny. Members of each selfed progeny are randomly mated for a few generations before making up the matings as outlined on page 66. If the progenies are fairly large a random gamete from the progeny should represent a random gamete from the original parent with free recombination.

While some linkage effects on the covariances of relatives can be avoided, it does not appear possible to bypass them entirely in the estimation of genetic variances.

ENVIRONMENTAL DESIGNS

The systems of matings used to produce the progenies were referred to as the mating design. For purposes of illustration, all the progenies of each mating design were considered to have been replicated in complete blocks in a single environment, i.e., a single location and year. However, the mating design is a method of producing the progenies. The manner in which the progenies are to be subjected to environments is the environmental design. For each mating design an environmental design must be superimposed. Considerations of the best environmental design are in part those generally discussed under the topic of the "design of experiments" and are too numerous to be included here. Only a few general observations will be made on the reduction of size of block and the extension to multiple environments.

Reduction in size of block

The number of progenies required for any of the complete mating designs in order to estimate the design components of variance, and of course the genetic components of variance, with even meager reliability, is very large. The larger the number of progenies the more land area is required for a complete block or replication. Increase in land area generally increases the environmental variance because of soil heterogeneity which also reduces the reliability of the components of variance per unit of land area. A solution to this paradox is to reduce the size of block or to use incomplete blocks. Other features, however, such as the distribution of degrees of freedom in the analysis of variance table, which are more pertinent to the reliability of the components of variance than the reduction in error variance, are involved in contrasting variations of the joint mating-environment design. Only some possibilities and a few don'ts will be presented.

One cannot accomplish anything by indiscriminantly throwing the progenies into just any incomplete block environmental design which may fit. Care must be taken that the incomplete block design allows one to estimate the desired components of variance unconfounded with environmental components of the design. It must be remembered that incomplete block designs were not developed from the standpoint of estimation of compounds of variance but for reliability of comparisons of means.

Incomplete confounding of groups of progenies with blocks may be employed. A design in which all of the progeny of each parent of design (AA) matings are placed in a separate block has been suggested.[2] This requires twice the number of progenies for a complete repetition. A possibility for design (AB) would be to place all of the progeny of each A parent in a separate block. This would introduce a block component of error in the mean square for the A parents but the other components could probably be estimated with more precision. These illustrations should sufficiently stress the point that incomplete block environmental designs must be specifically adapted to the mating design

[2]by C. E. Gates in privately distributed material.

if the desired components of variance or covariances of relatives are to be estimated more precisely.

A method of reducing the block size, and simultaneously increasing the number of parents for a fixed number of progenies which is applicable to all the mating designs for estimating components of variance, was put forth by Comstock and Robinson (8 and previously). This is complete confounding of progenies of sets of parents with environmental blocks and omitting those progenies of parents from different sets. A small number of parents are used as a set to make up the matings and their progenies are always put in the same block. The analyses are made within sets of progenies or blocks and pooled over blocks. The sacrifice is the degrees of freedom thrown away with blocks and the gains are the reduced error variance and the flexibility in distributing the degrees of freedom more evenly among the mean squares.

The incomplete mating designs discussed earlier are also methods of increasing the number of parents for a fixed number of progenies but not of reducing block size. Kempthorne and Curnow (29) consider some of the advantages and disadvantages of incomplete design (AA) which are generally extendable to other incomplete mating designs.

Extension to multiple environments

Just as components of genetic variance must be defined in terms of a population of genotypes they must also be defined in terms of a population of environments. This may be only for the microenvironmental variations of a single set of macroenvironmental conditions, such as was considered for purposes of simplicity in presenting the analyses of the designs. If one wishes, however, for the genetic variances to be appropriate for a broader range of macroenvironments, then they must be defined for this range of environments, and unbiased estimates can only be obtained from the inclusion of a sample of the environments. The translation of components of genetic variance from one population of environments to another meets with the same difficulties as it does from one population of genotypes to another and is readily accomplished only without genotype by environmental interactions. Recall that the translation of genetic variances from one generation of inbreeding to another required the non-existence of many gene interactions.

The plant breeder is generally forced to deal with environmental variations incidental to seasonal and yearly differences. He also, generally, is interested in fairly wide adaptation in space, thus, a range in locations. It should be stressed, however, that years and locations may be poor and insensitive characterizers of environmental conditions. Others such as soil moisture, fertility, temperature, and so on, although crudely classified, may represent sharper and more pertinent measures of environment.

Something might be gained by trying to group environments so that the gene environmental interactions are small within groups compared to that between groups. An example of such an attempt for several locations in Iowa

is given by Horner and Frey (22). A slightly different method of looking at the problem, and which in some circumstances may be useful, is to consider the covariances of relatives in different environments. For simplicity, consider only a single factor mating design of progenies such as unrelated full sib progenies, although the results may be easily generalized to include the other mating designs. At first consider only two environments, which might be locations or years. Expectations of mean squares and products for a separate analysis at each location, a covariance analysis between progenies of the two locations, and the combined analysis are given in Table 22. The analyses have the same

TABLE 22.—SEPARATE AND COMBINED ANALYSES OF PROGENIES IN TWO ENVIRONMENTS.

Source	df	Expectations of Mean Squares or Products		
		Separate Analyses		
		Environment 1	Mean Product	Environment 2
Replications	k−1			
Progenies	n−1	$\sigma^2+k\sigma^2_1$	$k\sigma_{12}$	$\sigma^2+k\sigma^2_2$
Error	(k−1)(n−1)	σ^2		σ^2
		Combined Analysis		
Environments	1			
Replications	2(k−1)			
Progenies	(n−1)	$\sigma^2+k\sigma^2_{ep}+2k\sigma^2_p$		
Prog. x Env.	(n−1)	$\sigma^2+k\sigma^2_{ep}$		
Error	(k−1)(2n−1)	σ^2		

C_{ii} = Covariance of full sibs in environment i.
C_{ij} = Covariance of full sibs in environment i with those in environment j.
$C_{ii} = \sigma^2_i$, $C_{ij} = \sigma_{ij}$, $C_{11} = \sigma^2_1$, $C_{12} = \sigma_{12}$, $C_{22} = \sigma^2_2$
$\sigma^2_{ep} = (C_{11}+C_{22}-2C_{12})/2$, $\sigma^2_p = C_1$.

pattern as that of the backcross progenies of Table 21 except we are now considering the covariances of relatives in the same and different environments. The relationship of the separate analyses to the combined analysis is readily deduced from the definitions at the bottom of Table 22. Robertson (34), using a slightly different form,

$$\sigma^2_{ep} = [(\sigma_1-\sigma_2)^2+\sigma_1\sigma_2(1-r_{12})]/2,$$

pointed out that the progeny by environment interaction component of variance could arise for two reasons, one being that the progeny components of variance were different in the two environments, and the other being a lack of a perfect correlation, r_{12}, of the progeny effects at the two environments. The extension to several environments is illustrated for the combined analysis in Table 23. Expressing the interaction component of variance in Robertson's (34) form,

$$\sigma^2_{ep} = \sum_{i<j} [(\sigma_i-\sigma_j)^2+2\sigma_i\sigma_j(1-r_{ij})]/l(l-1),$$

is just a generalization of the case for two environments.

TABLE 23.—COMBINED ANALYSIS OF PROGENIES IN l ENVIRONMENTS.

Source	df	Expectations of Mean Squares
Environments	$(l-1)$	
Replications	$l(k-1)$	
Progenies	$(n-1)$	$\sigma^2+k\sigma^2_{ep}+lk\sigma^2_p$
Prog. x Env.	$(l-1)(k-1)$	$\sigma^2+k\sigma^2_{ep}$
Error	$l(k-1)(n-1)$	σ^2

$$\sigma^2_{ep} = \sum_{i}^{l} C_{ii}/l - 2\sum_{i<j}^{l} C_{ij}/l(l-1), \qquad \sigma^2_p = 2\sum_{i<j}^{l} C_{ij}/l(l-1)$$

It is somewhat explanatory in this terminology to consider what is meant by the components of variance, σ^2_p and σ^2_{ep}. When the environments of the sample are assumed to be a random sample, then the progeny component of variance is the covariance of full sibs in different environments, and the progeny by environment component of variance is the difference between the covariance of full sibs in the same environment and in different environments. This concept can be extended easily to any complexity in the mating design and/or classification of environments. The covariances of relatives which are given genetic interpretations for a random sample of environments are of relatives in different or unrelated environments. It can also be pointed out what is meant by considering a specific or fixed set of environments. The covariances to be interpreted genetically are

$$C_{ii} = \sigma^2_i$$

for a single environment,

$$(C_{ii}+C_{jj}+2C_{ij})/4 = \sigma^2_{ep}/2+\sigma^2_p$$

for two specific environments, or

$$\sum_{i,j} C_{ij}/l^2 = \sigma^2_{ep}/l+\sigma^2_p$$

for a specific set of l environments.

This terminology also demonstrates the well known result that estimates of genetic variances from single environments will on the average be larger than those estimated from a random sample of environments in a combined analysis and by an amount equal to the interaction component of variance. A large interaction component of variance could be the result, but not necessarily so from previous considerations of σ^2_{ep}, of the genetic variances being larger at one environment than the other. The viewpoint has been put forward that one should hunt for an optimal set of environmental conditions for which genetic variances are largest. Others maintain that broad adaptation should be encompassed. Many of these considerations are too far afield and may be found in Falconer (10), Robertson (34), and Comstock (6).

The extension of the analyses of the designs to multiple classifications

of environments will not be exemplified here. For the inclusion of multiple classifications of environments reference is made to Matzinger and Kempthorne (31) for design (AA), and to Robinson *et al.* (36) for design (A/B). Extension to the other designs is straight forward.

CHOICE OF DESIGN

Choices among the designs for estimating genetic variances depend on many things, most of which are interdependent. A few of these are:

(a) the natural mode of reproduction and mating flexibilities of the species.
(b) the objective(s) in estimating genetic variances such as
    i. general interest in knowledge of gene action for quantitative characters.
    ii. making a choice among alternative selection and breeding procedures.
    iii. the prediction of response to selection.
(c) joint purposes such as estimating genetic variances and simultaneously selecting among progenies or evaluating hybrid combinations.
(d) reliability of the estimates.

Two approaches may be taken in the estimation of genetic variances. One is to assume a limited genetic model (Brim and Cockerham, 1; Horner and Weber, 23; and Robinson *et al.* 36). The model is restricted so that the number of components of genetic variance is at least as small as the number of estimates of distinct covariances of relatives. In case the number is smaller, the components of genetic variance are usually estimated by the least squares technique proposed by Mather (30) which can probably be improved upon by the maximum likelihood procedure of Hayman (18).

Another approach is to utilize estimating functions which contain either mostly additive variance, or mostly dominance variance or entirely epistatic variance (Cockerham, 4), the primary purpose being to obtain information on the relative amounts of these three variances. The breakdown of the genetic variance into additive, dominance, and epistatic components is probably sufficient for most purposes of the plant breeder. The further partitioning of the epistatic variance is necessary to show the contribution of the epistatic variance to the covariances of relatives, but the information conveyed by these partitions over and beyond the general interaction of non-alleles is not clear. The separation of all additive types of epistatic variance from the others is informative in that the others involve heterozygosity. The category of all dominance types of epistatic variance and other categories may be useful as our knowledge of the implications of epistatic partitions expands.

Generally, the plant breeder is primarily concerned about genetic variances because of their implications in choosing the most effective selection and breeding procedure. Some general comments on these implications may be found in Cockerham (5) and will not be repeated here. A few additional comments concerning the normally self-pollinating species may be helpful.

The designs of self-fertilization are the most appropriate for estimating additive and additive types of epistatic variance in homozygous or near homozygous populations. One need not be concerned about genetic variances with dominance in their nomenclature for a normally self-fertilizing species unless the species can be adapted to a selection and breeding procedure which utilizes heterozygosity. Often, normally self-fertilizing species do not exhibit much dominance or dominance types of epistasis (Brim and Cockerham, 1), but if one does and some may, a technique of accomplishing considerable cross fertilization should be found before focusing on these types of gene effects. The mating designs of unrelated mates are of course the most appropriate ones for estimating dominance and dominance types of epistatic variances.

All of the designs may be utilized as an integral part of a breeding and selection program. Those which require only one nursery season are the most practical from the standpoint of generation time. Robinson and Comstock (35) discuss the results of family selection in corn when the progenies conform to design (A/B). Other designs of unrelated mates could be employed, but design (A/B) is the easiest two factor mating design to adapt to non-inbred parents in corn and which allows the estimation of two components of genetic variance. The designs of self fertilization are of course the appropriate ones for selecting among progenies of self fertilization.

The problems in choosing among variations of a design, or between designs which accomplish the same purposes genetically, are mostly statistical. Kempthorne and Curnow (29) touch on most of these problems and illustrate the difficulties involved. The design which gives the most reliable estimates of components of variance is not easily pinpointed. One must first decide on the relative reliability desired for the estimates, and even then, the solution depends on the true values of the components of variance to be estimated (Gaylor, 14). The best general rule to follow is to employ the simplest mating and environmental design which gives the desired information.

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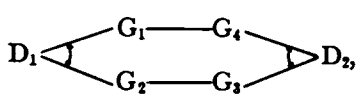
DISCUSSION

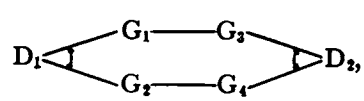
SEWALL WRIGHT: I have used path analysis since 1920 in deducing the correlations between relatives in additive systems. Accessory methods have been used to take account of dominance and interaction (optimum model). The method itself can, however, readily be extended to a large class of cases involving dominance and all sorts of interaction, including that between genotype and environment, by introducing the concept of joint paths (connections between variables that depend on concurrence of two or more *independent* single connections, four, for example, in the case of DD interaction). The value of the compound path coefficient for such a joint path is the produce of the elementary coefficients of *all* joined single paths. This still holds if there is only one variable in common in two joined single paths but the value is more complicated if there are two or more common variables, because of conditional probabilities.

The case of dominance gives a simple illustration (See Figure 1).

The four gametes, G_1, G_2, G_3, and G_4, may be connected in any ways in the pedigrees, subject to the above qualification. The dominance deviations are connected by a joint path



with coefficient $r_{14}r_{23}$, and a joint path



with coefficient $r_{13}r_{24}$. The total correlation between the relatives is thus:

$$r_{p_1p_2} = g_1g_2a_1a_2(r_{13}+r_{14}+r_{23}+r_{24})+d_1d_2(r_{13}r_{24}+r_{14}r_{23})+e_1e_2r_{E_1E_2}$$

The results are identical with those of Cockerham and of Kempthorne for all cases not subject to the qualification noted above.

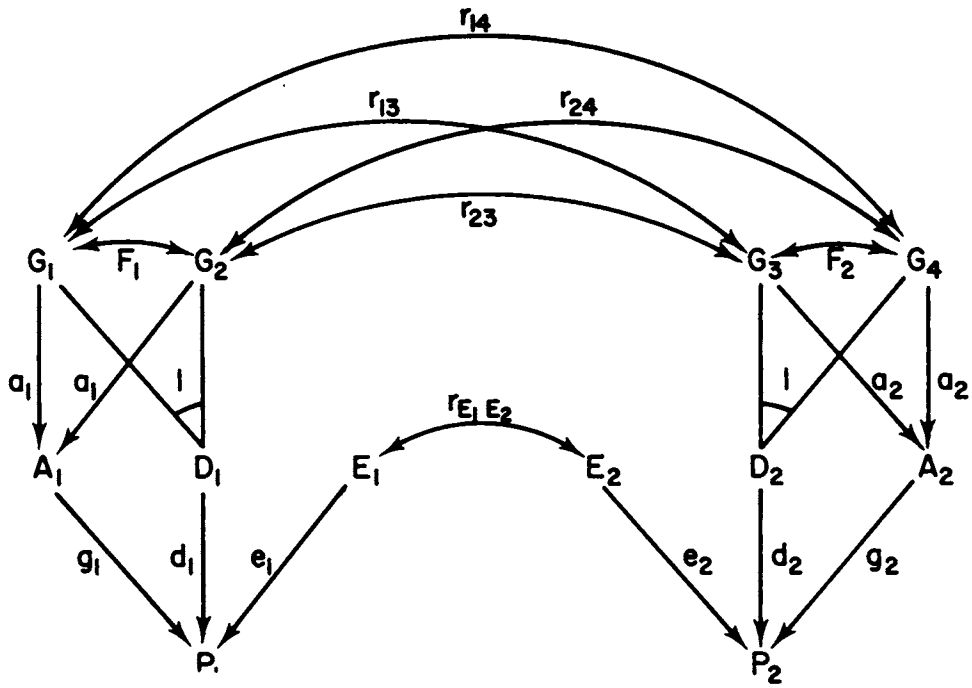


FIGURE 1. *Total correlation between relations by path coefficients.*

P_1, P_2 phenotypes of two relatives
A_1, A_2 additive genotypic deviations
D_1, D_2 dominance deviations
E_1, E_2 environmental deviations
$F_1(=r_{12})$, $F_2(=r_{34})$ inbreeding coefficients
r_{12}, r_{14}, r_{23}, r_{24} other gametic correlations
$r_{E_1E_2}$ environmental correlation
$a_1 = \sqrt{1/(1+F_1)}$, $a_2 = \sqrt{1/(1+F_2)}$
$g^2_1 + d^2_1 + e^2_1 = 1$, $g^2_2 + d^2_2 + e^2_2 = 1$

Biological Interpretation of the Genetic Parameters of Populations

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MY assignment in this symposium appears to be that of serving as a bridge to help span the chasm which often separates the devotees of statistical genetics and of plant breeding. An inherent hazard of this role is the fact that a bridge is likely to be trod upon by those on either bank.

Mathematicians are, in varying degrees, intellectual artists, entranced by the sheer beauty of logic expressed in symbols and intoxicated with the sense of power experienced in predicting the consequences of a given set of assumptions (even though hen-pecked at home!). Prime Minister Nehru recently[1] gently reminded scientists in India that the problem of his country was not to provide a paradise for intellectuals, but, with the help of science, to find the means of advancing 400 million people rapidly through 4 centuries of cultural development. The purpose of breeders is not to blow statistical bubbles of ever more intricate beauty, but to speed the evolution of plants and animals in directions which will benefit mankind. This requires harnessing the logic of mathematics to the realities of biology.

Mathematics, statistical or otherwise, is basically quantitative reasoning, expressed in shorthand symbolism. Now, it is awkward for anyone, and especially a scientist, to find fault with quantitative reasoning, as such. Our complaints must be directed to the very real difficulties in readily deciphering the several shorthands and to any inadequacies of the biological models employed. We must constantly be alert to the mirage of infallibility which so readily forms an unwarranted halo around the written symbols. The "queen of the sciences" can dazzle! Unfortunately, the chalk and pen convey no automatic warning of incomplete assumptions or fuzzy logic. The assurance needed can be provided only by meticulous comparison of the biological assumptions employed, whether by default *or* design, with the full array of pertinent biological knowledge, together with eventual experimental verification of predictive accuracy. Yet, it would be sheer folly to allow preoccupation with the hazards of mathematical expression of biological variables or parameters to blind us to the advances in understanding which have been and will continue to be pioneered in this fashion.

[1]Quoted in In Brief in Biol. AIBS 2(2):1 March, 1961.

Breeding is to genetics what engineering is to physics. The ancient art of plant and animal breeding has become the adolescent science of biological engineering. The term "adolescent" is used because "engineering" implies utilization of quantitative relationships among the variable ingredients or parameters in predicting results with reasonable accuracy. Of course, quantitative control of genetic change in plants and animals is a matter of degree. One can honestly say in the same breath: (a) that many truly remarkable feats of biological engineering have been accomplished and (b) that our comprehension of the parameters involved in deliberately induced genetic change is still very sketchy. Therein lies the continuing challenge!

ESSENTIAL FEATURES OF BREEDING THEORY

The fundamental nature of plant and animal breeding problems is almost infinitely complex, embracing the physical organization and transmission of genetic material, the biochemistry of gene duplication and of gene products influencing histogenesis, cell metabolism, morphogenesis, physiology, and behavior (34). Sewall Wright (36) has commented that, "Complete analysis of development of higher organisms nevertheless remains one of the most intractable problems of science." Although recognizing that theory of population genetics can to some extent bypass the levels of developmental and cellular biology, he (loc. cit.) emphasizes that "...We need a more adequate theory of quantitative genetics, based on generalizations at the level of physiological and developmental genetics, and also more understanding of the implications of population structures and ecological relations."

In general, the task of breeders is to utilize information on all pertinent components of performance for a suitable array of genotypes under an appropriate sample of environments in efforts to guide the generation of another array of genotypes capable of improved average performance, when both arrays are tested under some future, and only partially predictable, sample of environments. Hence it is clear that the quantitative parameters used in breeding work must take into account (a) the determinants of both variability and reproducibility of genotypes, (b) interactions of gene effects with each other and with environmental influences, and (c) the phenotypic and genetic relations among the significant components of performance, as defined by both natural and domestic selection.

The utility of any genetic parameter will be considered in terms of its probable contribution to the control of genetic change in performance (ΔG), recognizing that only appropriate breeding experiments provide acceptable confirmation.

COMPONENTS OF PHENOTYPIC VARIATION

Among the numerous parameters of interest, the most important are those which specify the amounts and kinds of genetic variation available for selection, simply because the response (ΔG) to a given selection differential ($\bar{s}$) is

determined directly by the regression of "true" breeding value (G') on observed phenotype ($b_{G'T} = \frac{\sigma_{G'}^2}{\sigma_T^2}$). The primes are used purposely, to remind us that not all components of the total genetic variability (σ_G^2) contribute in the same manner to selection response.

R. A. Fisher recognized long ago (12) that the total genetic variance could be subdivided into a portion due to the average effects of genes, another due to interactions of allelic gene effects (dominance), and still another due to interactions of non-allelic gene effects (epistasis). Wright (33, 35) also explored the contributions of specific types of gene interaction to the phenotypic correlations expected among relatives. More recently, several workers (18, 1, 21, 17, 19, and others) have developed the general theoretical expectations for further subdivision of the total genetic variance (σ_G^2) into portions:

σ_A^2, due to average effects of genes;

σ_{AA}^2, σ_{AAA}^2, etc., due to interactions among average effects of 2 or more non-allelic genes;

σ_D^2, due to interactions of allelic gene effects (dominance);

σ_{DD}^2, σ_{DDD}^2, etc., due to interactions of 2 or more non-allelic dominance effects;

σ_{DA}^2, σ_{DDA}^2, σ_{DAA}^2, etc., due to interactions between dominance and average effects of 2 or more non-allelic genes.

It is important to realize that the effect of any gene difference, and hence its contribution to genetic variance, is determined by the entire genotypic and environmental substrate in which the particular gene difference is expressed. Thus, the average effect of the same gene difference may vary considerably, for example, between highly inbred and crossbred populations, between differing environments, and especially between differing ways of measuring the effect (i.e., between traits, stages of development, or physiological functions).

Further, there is a growing awareness that, to the extent that gene effects do vary with the environmental situation, any sort of gene effect has sure meaning only for the sample of environment under which the effect was measured (5, 6, 8, 2, 3, 26, and 27). Simply stated, this means that selection of a group of genotypes because of their superior phenotype in one sample of environment is likely to mean less superiority and may even mean inferiority, of performance when the same total array of genotypes (or their progeny) are placed in another environment.

Contributions to Selection Response

If at this point you are inclined to ask, "So what?," it may be helpful to summarize the contributions of each of these components of total genetic variability to the regression of "true" breeding value on observed phenotype, for several different types of selection. In this summary (Table 1), it is specifically assumed

TABLE 1.—USEFULNESS OF DIFFERENT KINDS OF GENETIC VARIABILITY.

Portions of Total Genetic Variance σ_G^2	Selection for superior performance			
	Among clones (asexual reproduction), or F_{1s} (homozygous lines)	Among homozygous lines	Of progeny from crosses of complimentary non-inbred strains	Within a single segregating population
σ_A^2	All	All	All	All
σ_{AA}^2, σ_{AAA}^2, etc.	All	All	Part*	Part*
σ_D^2, σ_{DD}^2, σ_{DA}^2, etc.	All	(Missing)	*Part**	None
σ_{GE}^2	None	None	None	None

*Only to the extent that change in *gene frequency per se* from the selection increases the proportion of progeny benefited by the "joint" effect of two or more non-alleles.
**Depending upon *divergence* of gene frequencies at loci exhibiting varying degrees of dominance.

that all portions of the genetic variance except σ_{GE}^2 itself are free of bias from genetic-environmental interaction (i.e., refer to general adaptability over the range of environments under which the selection response is to be assessed). The σ_{GE}^2 is left in the table as one portion of the total genetic variance to emphasize the fact that it will be impossible to base selection at any given point in space and time on variation in performance under environmental circumstances precisely typical of those to be encountered by the population in the future. Hence, environmental interaction with those genetic variances which do contribute to selection response represents a source of temporary gain in adaptability to a given sample of environment that is lost when environment changes.

By definition, the variance from average gene effects (σ_A^2) contributes fully to selection response whatever the type of selection applied. The difficulty is in knowing what proportion of the total genetic variance (σ_G^2) within any given generation is due to gene effects which will not be altered by changes in the genotypic or environmental substrate in subsequent generations. In fact, the effective definition of σ_A^2 expands or contracts depending upon the magnitude of genetic-environmental interaction between generations.

Interactions between average effects of non-allelic genes (σ_{AA}^2, σ_{AAA}^2, etc.) contribute fully to response from selection among clones reproduced asexually, among homozygous lines, and among crosses of homozygous lines, for the reason that, except for mutation, no change in constitution of selected genotypes occurs between generations. In effect, interactions are "frozen" and become indistinguishable from average gene effects (σ_A^2).

In either selection within a non-inbred population or in progeny-test selection for improved performance of a strain-cross, only part of the σ_{AA}^2 variance contributes to selection response in the immediate progeny. Much of the superiority of selected parents in AA effects is due to the selected sample

of gametic combinations, which is dispersed by the meiotic processes of crossing-over and random assortment of chromosomes in gamete production and in the random recombination of gametes. This "decay" continues in subsequent generations at rates dependent upon tightness of linkage, until equilibrium proportions of gametes are reached, except as continued selection maintains the departure from equilibrium or as the proportion of favorable combination effects is increased by changes in the frequencies of the genes involved (24, 14, 7, and 8).

Genetic variances due to dominance and to non-allelic interactions involving dominance (σ_D^2, σ_{DD}^2, σ_{DA}^2, etc.) may be considered together because they behave somewhat alike in response to selection. They are fully utilized in selection among asexually reproduced clones or among F_1 crosses of homozygous lines, but are completely non-existent among the homozygous lines themselves. They do contribute to response from progeny-test selection for performance of a cross between non-inbred lines to the extent that selection is able to produce divergence in gene frequency and hence increase the proportion of heterozygotes in the cross at loci exhibiting some degree of dominance. However, response to selection for favorable interactions of non-allelic gene effects involving dominance (i.e., σ_{DD}^2, σ_{DA}^2, etc.) is subject to the same decay mentioned above for interactions of non-allelic average gene effects.

Selection within a single segregating population is powerless to utilize such variation, since there is no relationship between the dominance deviations (from average gene effect) of parent and offspring (i.e. the phenotypic difference between $\overline{Aa}$ and $\frac{\overline{AA}+\overline{aa}}{2}$ among parents produces no genotypic or phenotypic difference in their progenies).

Since the nature of the genetic variability available determines what type of selection will be most effective in producing genetic change, methods of estimating the components of genetic variance are a primary concern of breeders.

Experimental Demonstration of Genetic Variances

Other speakers (Cockerham, Kempthorne) will consider detailed methods of estimating components of the genetic variance. I wish only to present a few examples of simple experiments (Table 2) which I hope will help to illustrate the biological meaning and importance of the several types of genetic variation.

In plants, all components of the total genetic variance are included in the variation among clones or among F_1 crosses of homozygous lines (σ_X^2). Of course, the magnitude of the estimate of total genetic variance (σ_G^2) obtained in any given trial will depend upon the samples of clones or crosses studied.

If one adds to the same experiment the population of homozygous lines which produced the F_1 crosses, the genetic variance among the homozygous lines themselves would include only average gene effects and their interactions ($\sigma_P^2=\sigma_A^2+\sigma_{AA}^2+\sigma_{AAA}^2+$etc.). However, because heterozygotes are entirely missing, the genetic variance among unselected homozygous lines would be twice as

large as the variance among all crosses of those lines if there were no dominance $\left(\text{i.e., } \sigma_X^2 = \frac{\sigma_P^2}{2}\right)$. Hence, one can obtain one gross estimate of the importance of dominance plus the interactions involving dominance from

$$\sigma_X^2 - \frac{\sigma_P^2}{2} \cong \sigma_D^2 + \sigma_{DD}^2 + \sigma_{DA}^2 + \text{etc.}$$

This estimate measures the effect on genetic variance among F_1 crosses (or among clones or individuals in a randomly breeding population) of superimposing dominance upon an underlying model of no-dominance. This approach differs in definition

TABLE 2.—EXPERIMENT ILLUSTRATING MAJOR GENETIC PARAMETERS.

A. Design:

		Homozygous lines			All F_1 crosses		
		P_1	$P_2 \ldots$	P_m	X_1	$X_2 \ldots$	$X_{m'}$
Environments	E_1	n	n	n	n	n	n
	E_2	n	n	n	n	n	n
	.						
	.						
	.						
	E_k	n	n	n	n	n	n
		nk	nk	nk	nk	nk	nk

B. Analysis:

Source	DF	Expected Mean Square
Heterozygosity $(\bar{X} - \bar{P}) = H$	1	$\sigma_{\bar{R}}^2 + n\,\sigma_{E\bar{G}}^2 + n\,\bar{m}\,\sigma_{HE}^2 + n\,\bar{m}\,k\,\sigma_H^2$
Environments, E_i	(k−1)	$\sigma_{\bar{R}}^2 + n\,\sigma_{E\bar{G}}^2 + n\,\bar{m}\,\sigma_{HE}^2 + n(\bar{m}+m')\,\sigma_E^2$
$E_i \times H$	(k−1)	$\sigma_{\bar{R}}^2 + n\,\sigma_{E\bar{G}}^2 + n\,\bar{m}\,\sigma_{HE}^2$
F_1 's, X_i	m−1	$\sigma_{Rx}^2 + n\,\sigma_{EX}^2 + nk\,\sigma_Q^2$
$E_i \times X_i$	(m−1) (k−1)	$\sigma_{Rx}^2 + n\,\sigma_{EX}^2$
Within E_i X_i	km (n−1)	$\sigma_{Rx}^2 +$
Lines, P_i	(m′−1)	$\sigma_{R_\rho}^2 + n\,\sigma_{EP}^2 + nk\,\sigma_P^2$
$E_i \times P_i$	(m′−1) (k−1)	$\sigma_{R_\rho}^2 + n\,\sigma_{EP}^2$
Within P_i, E_i	km′ (n−1)	$\sigma_{R_\rho}^2$
Total	nk (m+m′)−1	

TABLE 2.—EXPERIMENT ILLUSTRATING MAJOR GENETIC PARAMETERS. (Continued)

C. Interpretations:

σ_P^2 includes *only* σ_A^2, σ_{AA}^2, σ_{AAA}^2, etc., (i.e., no dominance effects).
σ_X^2 includes $\sigma_{A'}^2$, $\sigma_{A'A'}^2$, $\sigma_{A'A'A'}^2$, etc. *plus* σ_D^2, σ_{DD}^2, σ_{DA}^2, etc.
but $\sigma_{A'}^2$ among X_i differs from σ_A^2 among P_i).
σ_H^2 includes only σ_D^2, σ_{DD}^2, σ_{DA}^2, etc. (i.e., all involving dominance effects).

$\left.\begin{array}{l} \sigma_{EH}^2 \text{ large} \\ \dfrac{\sigma_{EP}^2}{\sigma_P^2} > \dfrac{\sigma_{EX}^2}{\sigma_X^2}, \\ \sigma_{R_P}^2 > \sigma_{R_X}^2 \end{array}\right\}$ if inbred lines more sensitive than crosses to environmental influences.

Effective heritability in selection of crosses is:

$\dfrac{\sigma_X^2 + \sigma_{EX}^2}{\sigma_X^2 \sigma_{EX}^2 + \dfrac{\sigma_{R_X}^2}{n}}$ = for *local* adaptability, assuming complete control of future mean environment;

$\dfrac{\sigma_X^2}{\sigma_X^2 + \sigma_{EX}^2 + \dfrac{\sigma_{R_A}^2}{n}}$ = under *one* environment, for performance in *other* environments or general adaptability;

$\dfrac{\sigma_X^2}{\sigma_X^2 + \dfrac{\sigma_{EX}^2}{k} + \dfrac{\sigma_{R_X}^2}{nk}}$ = under average sample of environments, for general adaptability.

from that of partitioning directly the genetic variance observed among the F_1 crosses (1), to the extent that average gene effects and their interactions are altered by the average heterozygosity of the background genotype.

Another gross estimate of the importance of dominance plus all interactions involving dominance is available from the mean difference in performance between the homozygous lines and their crosses (i.e., $\bar{X} - \bar{P} = H$). This difference is due solely to the dominance deviations and their interactions arising from the increased heterozygosity of the crosses, since there is no change in gene frequencies and hence no change in the average gene effects and their interactions which would prevail in in the absence of dominance.

These two estimates of dominance contributions to genetic variance lead to a suggested *index* of *dominance* based on variances available from experiments such as the one shown in Table 2.

$$\frac{\text{Dominance Variance}}{\text{No Dominance Variance}} = \frac{2\left(\sigma_X^2 - \dfrac{\sigma_P^2}{2} + \sigma_H^2\right)}{\sigma_P^2} = \frac{\sigma_D^2 + \sigma_{DD}^2 + \sigma_{DA} + \text{etc.}}{\sigma_A^2 + \sigma_{AA}^2 + \text{etc.}}$$

This approach recognizes fully that genetic variance from dominance effects and their interactions is generated only by differences *in heterozygosity* among individuals or populations. It would seem rather near-sighted to ignore our old friend and constant companion, the inbreeding depression, in assessing the role of dominance and dominance interactions relative to that of average gene effects and their interactions.

Other experimental approaches are available for estimating the importance of interaction among non-allelic gene effects, independent of both average and dominance gene effects (8).

This same experiment provides a means of testing the idea that average phenotypic superiority of more heterozygous genotypes (i.e., dominance plus its interactions) is due to greater tolerance of environmental variations (20, 3, 5, and 8). This is another way of saying that highly inbred lines may be more sensitive to environmental variations because they are lacking many of the genes which the species has found useful in coping with variable environmental circumstances (Table 3). If this is so, then the ranking of the homozygous lines should change more between environments than the F_1 crosses $\left(\text{i.e., } \frac{\sigma_{EP}^2}{\sigma_P^2} \text{ larger than } \frac{\sigma_{EX}^2}{\sigma_X^2}\right)$. Also the average of all inbred lines should vary more among environments than the average of all crosses so that the advantage of the crosses over the inbreds is considerably greater in unfavorable than in favorable environments (i.e., σ_{EH}^2 large). Also, the random environmental variation among individual plants or plots of the same genotype should be greater for inbreds than for crosses (i.e., $\sigma_{R_p}^2$ larger than $\sigma_{R_x}^2$).

TABLE 3.—PHENOTYPIC EFFECTS, FOR DIFFERING ENVIRONMENTS OR TRAITS.

Genotypes	Environments				Mean
	1	2	3	k	
A_1A_1	+++	+	0	0	1.0 +
A_1A_2	++	+	++	+	1.5 +
A_2A_2	0	0	+++	+	1.0 +

It seems unreasonable on biological grounds to expect the kind of difference between the interaction of average and of dominance gene effects with environmental effects on the performance of F_1 crosses of inbred lines considered by Comstock (3), since both kinds of gene effects would be operating in the same genotypic background $\left(\text{i.e., } \frac{\sigma_{A\cdot E}^2}{\sigma_{A\cdot}^2} \text{ should equal } \frac{\sigma_{DE}^2}{\sigma_D^2}\right)$. However, only average gene effects and their interactions are operating in variation among homozygous lines and the more limited gene repertoire of homozygotes is a sound biological reason for expecting greater sensitivity to environmental hazards among inbreds than among crosses

$\left(\text{i.e., } \frac{\sigma_{EP}^2}{\sigma_P^2} \text{ larger than } \frac{\sigma_{EX}^2}{\sigma_X^2}\right)$. This illustrates further the biological inadequacy of attempts to estimate the relative importance of dominance and average gene effects solely by partitioning the variance among F_1 crosses of inbred lines or from comparing correlations among different sorts of relatives in the same population (31). One cannot ignore the fact that all dominance effects are activated solely by differences in heterozygosity, which are minor among different F_1 crosses but are major and the only factor responsible for inbreeding depression ($\bar{X}-\bar{P}$).

The significance of genetic-environmental interaction in selection response also can be illustrated readily from the experiment shown in Table 2. If selection among F_1 crosses of homozygous lines is directed towards general adaptability over a range of environments, of which the environments included in the experiment are a random sample, then the effective heritability of difference among crosses is:

$$b_{GX} = \frac{\sigma_X^2}{\sigma_X^2 + \frac{\sigma_{EX}^2}{k} + \frac{\sigma_{R_s}^2}{nk}},$$ except as σ_{EX}^2 is due to changes in scale between environments (29).

If selection among crosses is based upon performance in a single, randomly chosen, environment, then $k=1$ and at best σ_{EX}^2 behaves as a source of error not reduced by numbers tested per cross (n) within the test environment. At worst, it is conceivable that σ_{EX}^2 could be large and $\sigma_X^2 = 0$, or even that a negative genetic correlation could exist between performance of the same cross in different environments. In the latter case, selection for the genetic constitution which confers an advantage in one environment would produce a decline in performance in other environments; this possibility becomes quite plausible if the range of genotypes and of environments included in the analysis is sufficiently wide. To accommodate such a possibility, one need only substitute for

$$\sigma_X^2 = r_G \sigma_{X'}^2 = \sigma_{X_{ij}},$$

the covariance between phenotypes of the same cross in different environments and for

$$\sigma_{EX}^2 = (1-r_G)\,\sigma_{X'}^2, = (\sigma_{X'}^2 - \sigma_{X_{ij}}),$$

where $\sigma_{X'}^2$ is the genetic variance among crosses within the *same* environment.

The likelihood of negative r_G seems slight in the range of genotypes and environments of interest within a species, however occurrence of negative estimates for σ_X^2 or σ_P^2 in analyses of the type shown in Table 2 would suggest this possibility.

To the extent that future environments are controllable or predictable, existance of large σ_{EX}^2 would be strong reason to select for specific adaptability, since σ_{XE}^2 would then become usable genetic variability, the heritability being

$$b_{GX} = \frac{\sigma_X^2 + \sigma_{EX}^2}{\sigma_X^2 + \sigma_{EX}^2 + \frac{\sigma_{R_s}^2}{n}}, \text{ or } \frac{\sigma_{X'}^2}{\sigma_{X'}^2 + \frac{\sigma_{R_s}^2}{n}}$$

Correlation Among Components of Performance

Breeders are inescapably concerned in some degree with all of the performance characters which affect the economic utility of the plants or animals with which they labor. Now each characteristic of a given plant (or animal) is simply a different manifestation of the same genotype; the difference lies only in the method of measuring phenotypic expression of the genotype, including differences in anatomical locale, physiological function, stage of development, environmental influences, etc. In a very real sense, therefore, different traits may be considered as the same trait measured in different environments (11). The environmental difference commonly is large enough to change the scale of measurement drastically and to make the genetic and phenotypic correlation between different pairs of traits of the same individual vary from -1 to $+1$. A general diagram of the relationships between k traits of the same individual, or between expressions of the same trait in k environments is shown in Figure 1. Essentially, then, one can regard variability of total performance as the sum of the variances for individual traits or environments and the covariances between them.

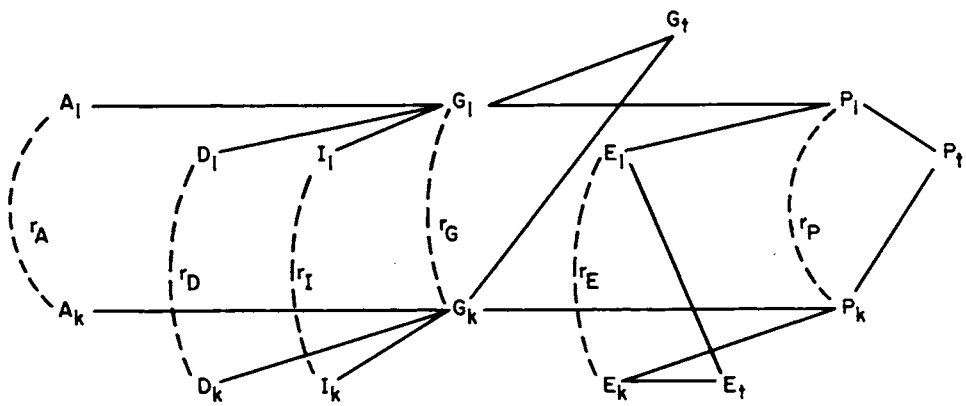

FIGURE 1. *Relationships of average (A) dominance (D) and inter-allelic interaction (I) gene effects, and environmental influences (E) for k different environments (or traits) to net adaptability (G_t) in performance (P_t) under the range of environments or of traits (E_t) sampled.*

The magnitude of correlations among traits (or environments) for the same genotype is significant in several respects. If selection for trait i alone produces genetic change ΔG_i, any other trait j will also be changed by $\frac{\Delta G_i}{\sigma_{Gi}} \cdot r_{Gij} \cdot \sigma_{Gj}$. Hence concern for the whole phenotype means concern with the r_G's. Also, construction of any index or total score intended to have maximum accuracy in predicting net breeding value (G_t) requires estimates of both the genetic and phenotypic correlations between each pair of traits (r_G and r_P in Fig. 1, Hazel, 15). It has been shown (16 and 9) that if selection is based on a total score for k different traits that are equally variable, heritable and important and if each pair of traits is equally correlated, the advantage of selecting for all k traits simultaneously ($\bar{s}_T$) over selection for one trait at a time ($\bar{s}_1$) would be

$$\frac{\Delta G_t \text{ from } \bar{s}_T}{\Delta G_t \text{ from } \bar{s}_I} = \sqrt{\frac{k}{1+(k-1)r_P}}, \text{ regardless of } r_G.$$

In this same case negative genetic correlations as large as $\frac{-1}{k-1}$ would reduce genetic gain to zero

$$\left(\text{i.e., } \Delta G_t \to 0 \text{ as } r_G \to \frac{-1}{(k-1)}, \text{ Dickerson } et\ al.\ 9\right).$$

OTHER GENETIC PARAMETERS

There are many parameters, in addition to the components of genetic variance and covariance which can be useful to the biological engineer. Only a few of these will be considered, and those only briefly, since my primary purpose has been to show that genetic parameters can have solid biological significance, if you speak the language!

The *selection differential* ($\bar{s}$) is the mean phenotypic superiority of selected parents over the population from which they were chosen. If the association between breeding value (G) and phenotype (T) is linear, the response from one generation of selection is $\Delta G = \bar{s}_T \cdot b_{GT}$. The selection differential often is expressed in standard deviation units $\left(\bar{i}_T = \frac{\bar{s}}{\sigma_T}\right)$, in which case $\Delta_G = \bar{i}_T \cdot r_{GT} \cdot \sigma_G$. The chief limitation of such prediction lies in uncertainty regarding the effective size of b_{GT} or r_{GT} and the assumption of linearity (8).

The potential size of the selection differential for a total score is governed by the intensity of selection possible, the ratio of numbers of parents selected to the total numbers measured (N′/N). The intensity of selection possible in turn is determined by the rate of reproduction, which might be defined as the reciprocal (N/N′) of the possible intensity of selection.

The *generation interval* (t) is the average age of parents when their progeny are produced. It is significant in expressing genetic change per unit of time as $\Delta G = \frac{\bar{s} b_{GT}}{t}$ (Dickerson and Hazel, 10).

Population size (N) is important as it relates to random loss of useful genes through inbreeding (22). However, the critical factor is the *effective population size* (4), as determined by intensity of selection and gross population size.

Intense selection (i.e., small N′/N) reduces ultimate limits of response to selection to the extent that it causes random loss of useful genes through inbreeding; naturally this effect is greater the smaller the effective population size (30).

Tightness of linkage between loci (c = cross-over incidence) is of interest because during limited periods of time in small populations, selection and inbreeding force linked genes to behave as a single gene, to a degree which depends upon intensity of selection and inbreeding and tightness of linkage (13 and 25).

Coefficients of inbreeding (f) and relationship, R, (32) have many uses, such as estimating the effect of pedigree inbreeding upon the amount and distribution of genic and genetic variances (23, 28, and 17), correcting time trends in performance for estimated inbreeding depression (9), and correcting performance of individuals or progenies for the effect of variation in level of inbreeding.

A number of other parameters, such as gene frequency (q), mutation rate (u), selective disadvantage of a genotype (s) are, of course, extremely useful in studies of individual loci and in theoretical analyses.

SUMMARY

Breeding is biological engineering. This implies utilization of quantitative relationships among the variables to predict results with reasonable accuracy. It involves using information on all pertinent components of performance, for a suitable array of genotypes, under an appropriate sample of environments, in efforts to guide the generation of another array of genotypes capable of improved average performance when both arrays are tested under some future and only partially predictable sample of environments.

Components of genetic variation are interpreted in terms of probable contribution to control of genetic change in performance. Simple experiments involving homozygous parental lines and their crosses are used to illustrate average gene effects, dominance effects and the non-allelic interactions of both, and methods of estimating the importance of each type of genetic variation.

Genetic-environmental interaction and genetic and phenotypic correlation among components of total performance are evaluated in terms of effectiveness of selection for general and special adaptability.

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Discussion: Some Comments on Quantitative Genetic Theories

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IN discussions of the relative merits of different approaches to quantitative genetics, I think that often too little account is taken of theory limitation. This leads to the implications that the theory is inadequate for certain situations. However, the theories may have been used under conditions for which they were not originally designed. Let me discuss briefly the place and function of the separate theories of evolution and quantitative genetics.

In the mathematical descriptions of evolution, associated with the names of Wright, Fisher, and Haldane, we are concerned primarily with changes of gene frequency from generation to generation. We then ascribe a selective advantage to the genotype and inquire how this selection, together with the forces of mutation, migration, and genetic sampling, can alter the gene frequencies in the population. Although theoretical treatment is generally applied to situations in which the genetic control of selective advantage is simple (no interaction between loci) this is not an inherent part of the theories. Wright, in particular, has stressed the importance of taking into account the interactions between genes at different loci. Hence, we ascribe selective advantages to genotypes and do not inquire as to why these genotypes have selective advantages. The population is then described at the gene level, and the same description applies to populations of Neurospora and to populations of elephants.

Genotypes, however, differ in their selective advantages because they differ in their effect on the development of the whole organism. Further, we may inquire into the relationships between the development of the organism and its selective advantage. Why do animals have a particular shape? Why is the gene action in one particular character different from that in another? This field has, in the context of natural selection, been extensively discussed by Rensch and Schmalhausen, and by Waddington in his recent book, THE STRATEGY OF THE GENES. Because in evolution we are dealing with a self-organizing system, we may expect that the relation of phenotype to selective advantage will, in the long run, affect the relation of the genotype to phenotype. Thus, the evolution of dominance and of canalisation are mechanisms by which selection against

deleterious genotypes succeeds in modifying the effect of the gene on the phenotype.

Most of us are interested in the relation between phenotype and selective advantage when applied to artificial selection in the population. Two schools of thought exist in theoretical quantitative genetics. If I may use names with offense neither to those mentioned, nor to those not mentioned, I will label the two different approaches as the Mather school and the Lush school. I would suggest that it is from lack of attention to the initial aims of these theories that some of the bitterest arguments have arisen.

Mather, in his approach to quantitative genetics, was primarily interested in questions of gene action. His theory, therefore, starts from a consideration of the effects of individual genes, and his experiments are set up with the intention of discovering things about the genes controlling quantitative variation. For instance, how many genes are controlling differences between inbred lines? To what extent can these differences be shown to be chromosomally inherited? To what extent are results affected by linkage? The experimental designs were basically directed at gene action and linkage and have to be evaluated from this point of view. In particular, I would stress that on the whole the experiments of the Mather group do not consider a random breeding population to which the results will be applied. In some cases, such an extrapolation to a random breeding population can easily be made, but in the main approach there has been no intention to do this.

The Lush school, on the other hand, has been primarily concerned with observations made on random breeding populations, with the descriptions of the relationships between different individuals in the population, and with the prediction of the response of the population to short-term changes in its "environment," using this term in the widest sense. This description is then given entirely in terms of variance components, and it must not be forgotten that it is in essence a static description of the population. It describes the population as it is at the moment, and cannot be expected to be an adequate description of the population as it will be after some generations of selection. The problem of the interpretation of these variance components, in terms of gene action, is an extremely difficult one, as we shall see later. In any population the variance is presumably due to many genes. We know neither the magnitude of the individual effects, the frequency of the alleles causing these effects, nor how the genes at different loci interact with one another. The model cannot deal accurately with some situations, and we then have to discard the variance component model and go back to a description of the variance of the population in terms of the individual genes concerned. The effect of inbreeding, for instance, can only be described under the very limiting assumption of completely additive gene action on the character concerned. In predicting the effects of selection we can merely say that the instantaneous rate of selection will be proportional to the additive genetic variation at any instant of time, but we have no good methods of predicting the changes of the additive genetic variance itself. Kimura has shown that in simple

cases the difficulty arises from the fact that the change of the second moment of the genetic variation with time under selection depends on the third moment, and so on.

A further consequence of the two approaches is that they have different "residuary legatees." By this I mean that they have different orders of preference for explanations of the response of the population to different changes in its situation. For instance, the Mather school tends to prefer a description of experimental results in terms of linkage rather than pleiotropy. On the other hand, the Lush school, on the whole, would prefer to explain surprising results in selection in terms of pleiotropy and only invoke linkage as the very final resort.

I think that there has been a very definite gap between the developments of Wright, Fisher, and Haldane on the one hand, and quantitative geneticists on the other. Only too rarely are the quantitative geneticists really aware that they are dealing with the effects of individual genes. They have to be content with a description of the situation in a population in terms of variance components. There is an extremely important equation which I think has tended to be overlooked on the United States side of the Atlantic. People are aware of it, but it appears infrequently in publication. This is the basic formula relating the effect of a gene on the character under selection to its selective advantage. This relationship was first discovered by Haldane some 20 years ago, and to my knowledge has been rediscovered by three or four people in the past decade, but still I can only point to one or two references to it in the literature. The formula then states that a difference of a unit on the scale of the character under selection corresponds to a selective advantage of $\bar{\imath}a/2\sigma$ where σ refers to the remaining variation. There is then a linear relationship between the effect on the metric scale and the selective advantage. It must be remembered, however, that this formulation strictly applies only to values of a/σ less than about $\frac{1}{2}$. There are several ways of deriving this formula, of which perhaps the simplest depends on the derivation of the regression of the frequency of the allele in question on the measurement of the metric character in individuals. This simple expression was first brought to my notice by Ralph Comstock about 4 years ago, but I still know of only one reference to it in the literature. (Falconer, 1, p. 205). I would like to sketch briefly the derivation with respect to an additive gene.

We write for the value of an individual $A_1 A_1$, $m\text{-}a + \zeta_{11}$, where ζ refers to the remaining variance, both genetic and environmental. We then have

	Frequency	*Gene Frequency*	*Measurement*
$A_1 A_1$	p^2	0	$m-a+\zeta_{11}$
$A_1 A_2$	$2pq$	$\frac{1}{2}$	$m+\zeta_{12}$
$A_2 A_2$	q^2	1	$m+a+\zeta_{22}$

from which we derive a covariance between gene frequency and the measurement of apq and a regression of gene frequency on measurement of $\frac{a\,pq}{\sigma^2_p}$. A selection

differential of $\bar{\imath}\sigma_p$ will lead to a gene frequency change of $\frac{\bar{\imath} a pq}{\sigma_p}$, which compared to the usual single gene expression of spq, gives $s = \frac{\bar{\imath} a}{\sigma_p}$. This formula is of great value in many situations in which we have to deal with selection processes where the variance component approach breaks down, and in which we have to go back to the individual genes.

I should like to touch briefly the problem of population size in selection, in particular, in reference to a paper of mine (3) to which Dr. Dempster has already referred. I might point out the basic ideas of the paper, which derives considerably from a paper by Kimura (2). Referring to a single gene with selective advantage in a population of size N, then the chance of this gene being fixed is dependent on Ns. This applies both to genes with additive effects on selective advantage and those showing a dominance recessive relationship. If we are selecting for a quantitative character, then the linear relationship between the effect of the gene on the character under selection, and its selection advantage (the proportionality being $\bar{\imath} / \sigma$) means that for all genes, in the absence of interaction between loci, the chance of fixation is proportional to $N\bar{\imath}$. It then follows that the final advance under selection of a population under artificial selection will be proportional to $N\bar{\imath}$, provided there is no interaction between loci. We can further say that for an additively acting gene the critical value of $N\bar{\imath}$ required in order to have a high chance of fixing this gene will be proportional to the reciprocal of $\frac{aq}{\sigma}$, where a is the effect of the gene and q is its frequency. At low values of $N\bar{\imath}$ we will therefore probably not succeed in fixing the desirable genes which in the initial population had either small effects or low frequencies, and as we increase $N\bar{\imath}$ we will fix more and more of these kinds of genes. The theory can also be extended to cover the chance of fixation of a deleterious recessive gene under inbreeding.

Perhaps the most interesting aspect of this theory is that it suggests a new experimental approach depending on the effect of an initial restriction in population size on the further advance possible under selection. As I mentioned earlier, it is extremely difficult to analyze the components of genetic variation and discover anything about the magnitudes or frequencies of the genes causing the response to selection. In the effect of an initial restriction of population size on possible further advance, we have a phenomenon which is dependent only on gene frequency and not on effect. Suppose we form sub-populations from an initial population, each sub-population being derived from a single pair mating in the first generation. In these sub-populations we have at each locus only four possible alleles, those in the two initial parents. If the response to selection from the base population was, in the main, due to genes at very low frequency, then

we will not get many of these genes in our sample of four alleles at each locus. The effect of this initial restriction on the limit of selection will therefore be greater than if the alleles contributing to the response in the initial populations were at frequencies around one half. We are currently carrying on some experimental work in Edinburgh with Drosophila along these lines.

The theory also deals with the relationship of intensity of selection to final advance with a given number of individuals measured each generation. If we select very intensively, we may increase the initial rate of progress at the expense of a decrease in the available genetic variation in subsequent generations. In other words, we may by chance have fixed genes in the early generations for which there were more desirable alternatives available. It turns out, as Dr. Dempster pointed out some years ago, that the optimum proportion selected to give maximum advance is one half. However, the curve of total advance as a function of proportion selected may be extremely flat-topped, so that the loss in total advance, in going from a 50 per cent to 20 per cent, or 10 per cent, selection may not be very great.

Finally, I would like to refer to a problem which concerns the breaking through of an existing plateau by the addition of new variation to the selected line, a problem which I gather greatly interests plant breeders at the moment. It is, of course, closely related to the effect of population size and selection intensity upon selection limits. The problem which particularly concerns me is the possibility that in my plateaued selection lines I may not have got, from my initial population, all the desirable genes that were available. How then do I go back to my initial population and sample it for new desirable genes to put into the selected line? Now, there are a fair number of variables in this problem which make it necessary to plan an extensive experimental analysis of it. One may list the questions as follows:

1. Should the first step be a reselection of the initial population for some generations?

2. After crossing to the selected line, will it pay to back-cross again to the selected line, for one or two generations?

3. After such crosses, will it pay to wait without selection for several generations for linkages to break up?

4. How intensely should one subsequently select?

As I see the problem from a theoretical point of view, we may be trying to pick just a few genes which in our base population are at low frequency, and put them into existing good chromosomes. If the genes in the initial population are of low frequency or have small effects, it may be preferable to start off with a period of selection of the initial population. The further question of whether one should wait for linkages to break up, and how intensely one should then select, seems a difficult one to answer theoretically. Obviously, if we immediately select very intensely, we stand a fair chance of merely reconstituting the selected line, which is a pointless thing to do. On the other hand, if we wait for many

generations to allow cross-overs to take place, we will finish with a jumbled mess of the desirable genes which are already available in coupling form in the selected line, but now are thoroughly mixed-up with the undesirable genes from the initial population. It may take us many generations to re-assort this. Furthermore, if our final selection is itself somewhat restricted for population size, we may in the process of re-assortment lose some of the genes which we had already fixed in our selected line.

I have myself carried out a small pilot experiment in this direction using *Drosophila melanogaster* and using as my plateaued line one which had been selected downwards for many generations and appears to have ceased to respond. I have only one replicate for each type of line and from my previous experience with Drosophila I would therefore hesitate to generalize from these results. I first of all crossed my initial population with the selected line. In the F_1 I started immediate low intensity selection (10 individuals out of 25 in each sex) on the one hand, and on the other hand, I allowed 5 generations of segregation before starting selection. In addition, I crossed the F_1 back to the selected line and again started to select immediately in one line and waited for four generations in another. In the final pair of lines, I back-crossed to the selected line once more, again selecting one line immediately and waiting several generations in the other. At the time of writing the line selected from the F_1 has had 15 generations of further selection downwards. The results are summarized briefly in Table 1.

TABLE 1.—THE AVERAGE VALUE FOR THE LAST FIVE GENERATIONS OF SELECTION IN THE ATTEMPT TO BREAK THROUGH A PLATEAU.

Origins	Gens. relaxed	Gens. selected	Mean
F_1	0	15	11.04
	5	10	11.82
1st backcross to selected	0	14	11.73
	4	10	12.62
2nd backcross to selected	0	13	11.30
	3	10	11.34
Selected line	-	—	11.26
Initial population	-	—	17.30

It will be seen that only the line selected from the F_1 has succeeded in breaking through the level of the initial line and this occurred at the sixth generation of selection. All the other five lines appear to be going to settle down at a position above the selected line. In all three pairs the line which has been selected straight away has advanced further than the line in which we waited for crossing-over to take place. But this is the only first of what will obviously be a long series of experiments and must not be taken too seriously.

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DISCUSSION

E. R. DEMPSTER: Are you satisfied that it is always most effective to cross the best replicates and throw the poor ones away? Isn't it possible that the best replicates are those in which selection has fastened on the few genes with large effects but in which the favorable genes with small effects, which may be more numerous and of equal importance with respect to ultimate limits, have been lost?

A. ROBERTSON: This is, of course, a question which ought to be answered experimentally but, speaking theoretically, I see no reason why we should have a smaller chance of fixing a gene with a small effect in a high replicate than we should in a low replicate. Presumably the selection pressure on a gene with a small effect will be slightly reduced if genes with major effects are segregating, but I would not expect this reduction to be large. However, we propose to go on and tackle this problem on some of our plateaued lines which have been selected with small population size.

R. E. COMSTOCK: Does relative adaptation of strains crossed to environment in which selection is to be done have a bearing on whether selection should be initiated immediately, or should it be deferred to allow opportunity for recombination?

H. F. ROBINSON: This concerns your suggestion of immediate and high pressure selection following crossing with diverse genetic stocks. I take issue with this and believe that several (?) generations of random breeding may be required to accomplish the recombinations that theory indicates should result.

A. ROBERTSON: To the questions of Dr. Robinson and Dr. Comstock, I think that in discussing the best procedure after having crossed exotic and "adapted" stocks the question of natural and artificial selection can be discussed in the same framework. Lumping together both kinds of selection, my own view is that probably there is some optimum degree of selection to which the cross population should be exposed in the early generations. I feel that it may be just as silly to select intensely straight

away as it is not to put on any selection pressure for, say, six generations. The natural selection which will occur in the environment of the "adapted" stock may, in itself be stronger than the optimum and any intense artificial selection superimposed on this will almost certainly lead merely to a return to the genotype of the "adapted" stock. I would then suggest to Dr. Robinson that the logical consequence of his approach would be to keep the cross for several generations in an environment which is intermediate in the parameters critical for survival and reproduction, between the environment native to the exotic stock and that of the adapted stock. Perhaps the best treatment of the cross material would be that suggested by Dr. Comstock—I think in reference to the pure exotic material. That is to say, that the cross should be brought into the commercial corn-growing environment by slow geographic transfer from the truly intermediate environment. This might provide just the degree of selection required to bring into the adapted stock the useful genes from the exotic stocks.

K. KOJIMA: Does the theory hold for genes with dominance, or epistatis? How do the effects of linkage come into your theory of selection limits?

A. ROBERTSON: The theory of selection limits which I have published recently was developed in terms of single genes, in a similar way as one can develop the variance approach to selection rates on the basis of single genes. As such the theory deals with additive action and with dominance but, of course, not with epistasis. To extend the theory to many genes we must put a summation sign in front of our expression. The critical question then becomes, Under what condition are we allowed to put this summation sign in front? I am thinking here particularly of the theory which shows that selection limits in a population are a function only of $N\bar{i}$. In general, the existence of epistasis will wreck this relationship, but there will be an exception to this in that epistasis of the purely scaler kind will not affect it. That is to say, provided there is a scale on which there is no epistasis and which is related in one-to-one fashion with our observed scale of measurement, then the final selection response in the population will again be a function only of $N\bar{i}$. The theory does not attempt to deal with linkage, but I would regard the importance of the theory in this respect as laying the foundation for a study of the effects of linkage on selection limits. We now know what to expect in theory if there is no linkage. We can then superimpose the effect of linkage—perhaps by Monte Carlo studies.

Discussion: Plant and Animal Improvement in the Presence of Multiple Selective Peaks[1]

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ON a short term basis, most variability appears to be additive especially after a change in the direction of selection such as is involved in a shift from natural to artificial selection. Many genes that have been favorable become unfavorable. If all variability were now additive, there would be just one best genotype toward which mass selection would tend to move the population, whatever the starting point, as far as the available gene pool permits.

On a long term basis, however, it is probably safe to say that there are always many selective peaks. Selection from a given initial gene pool tends to move the population to one of these, but it is not at all likely to be the highest. Having attained this, the stronger the selection, the more firmly the population is bound to it, apart from exceedingly rare favorable mutations. Further advance requires that the population move down somewhat from the peak it is on, and by some trial and error process work its way to a higher peak.

This multiplicity of selective peaks is a corollary of the multiple factor hypothesis and pleiotropy, a phenomenon that probably applies to all loci. Figure 1 is intended to represent the selective values *(W)* of genotypes on the hypothesis of four pairs of alleles with equal effects, no dominance, and selection directed toward an intermediate optimum. It may be noted that an intermediate optimum is to be expected for most characters, even though one or more are being consciously selected toward an extreme. It may also be noted that even if selection is directed toward an extreme, it is likely that most of the genes that are favorable in this respect will have pleiotropic effects that are unfavorable. These effects may be unimportant by themselves because of homeostasis, but as the number that are combined increases, homeostasis is likely to break down, leading to a situation essentially similar to that of characters which are in themselves selected toward an intermediate optimum. We may suppose that selection in Figure 1 is being directed toward ABCD as far as the primary character is concerned, but in combinations with three or four of these genes homozygous, unfavorable pleiotropic effects overweigh the primary favorable effects.

In either of these cases, there are six selective peaks. Each may be looked

[1]Paper No. 880 from the Department of Genetics, University of Wisconsin.

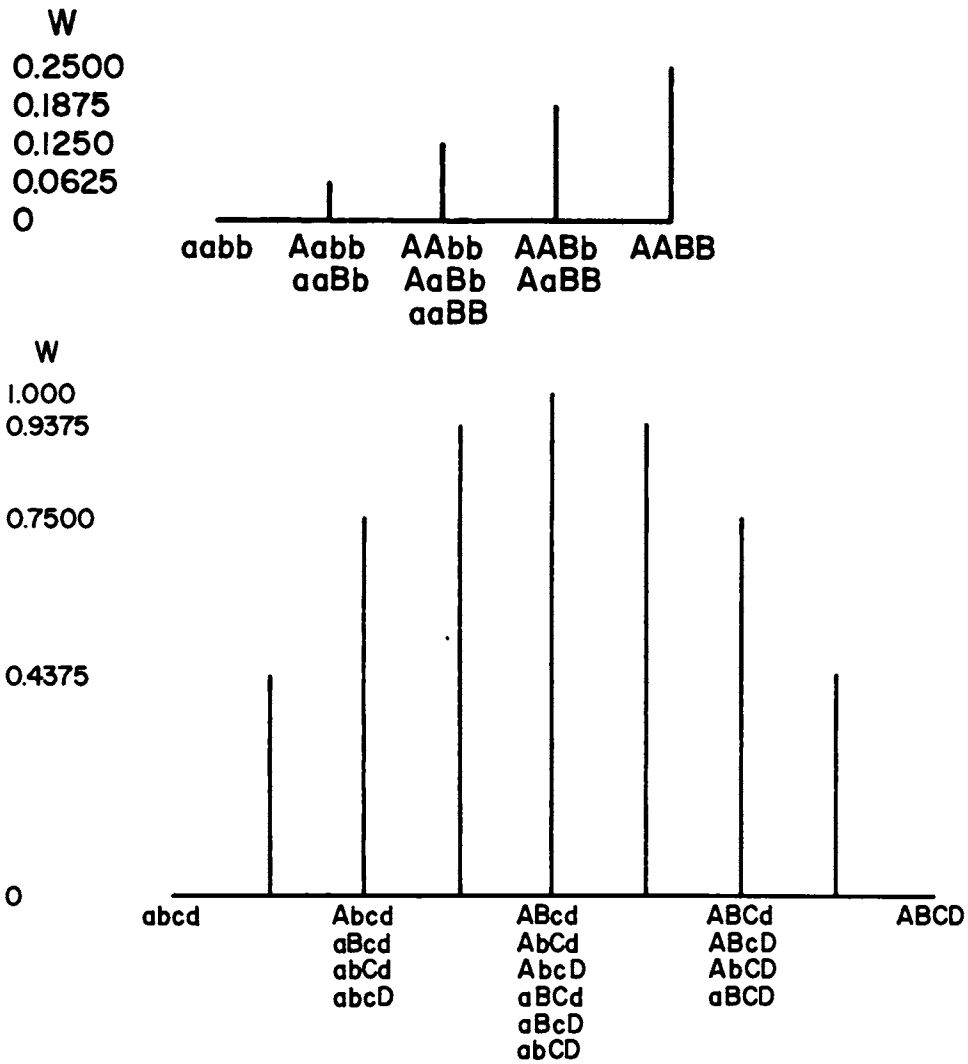

FIGURE 1. *Selective values (W) of genotypes in a system of four pairs of alleles with equivalent effects on a quantitative character assuming (in the upper figure) additive pleiotropic effects of A, B, and (in the lower figure) intermediate optimum with W declining as the squared deviation from the optimum. Note in (the lower figure) the occurrence of six selective peaks.*

upon as a more harmonious or more coadaptive system than those to the right or left in the figure. As far as the lower part of Figure 1 is concerned, these six peaks are all at the same level. It is assumed, however, that two of the loci have certain additive pleiotropic effects, indicated in the upper part.

Figure 2 shows the resulting selective values of the homozygous genotypes. Each of the six peaks is at two or four steps removed from each of the others. It is not necessary, however, to replace *bb* in *aabbCCDD* by *BB* before replacing

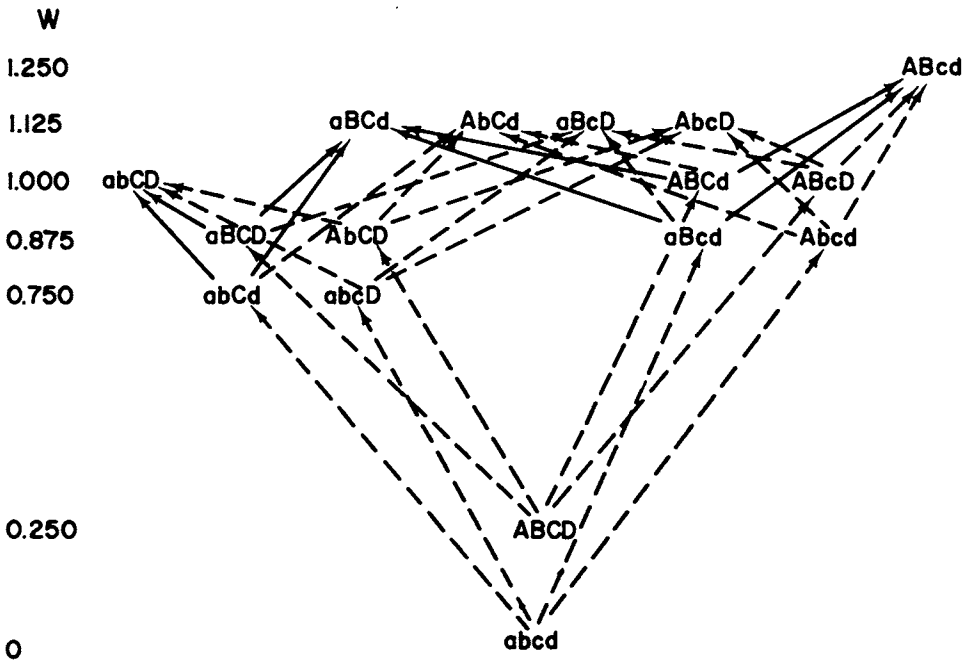

FIGURE 2. *Selective values, W, of 16 homallelic populations, based on an intermediate optimum with respect to quantitative effects of A, B, C, and D plus additive pleiotropic effects of A and B. Three peaks, considered separately, connected by solid lines.*

DD by *dd* in order to pass from *aabbCCDD* to *aaBBCCdd*. The population need shift very much less against the direction of selection if both gene replacements occur simultaneously.

Any system of frequencies at these loci can be represented by a point in 4-dimensional space, one dimension for each locus. Figure 3 represents two surfaces of this space, one in which *aaCC* is fixed but *B,b* and *D,d* vary with low selective peak at *aabbCCDD* ($\overline{W} = 1.00$) and high peak *aaBBCCdd* ($\overline{W} = 1.125$) separated by a shallow saddle ($\overline{W} = .99$). In the second surface, *BBdd* is fixed but *A,a* and *C,c* vary. Again there are two selective peaks, the low one being the same as the high one of the preceding surface and the high peak *AABBccdd* with $\overline{W}$ at 1.25. The intermediate peak is only one of the four at level 1.125 in the whole four dimensional field.

The calculations for Figures 3 and 4 are based on the selective values in Figures 1 and 2. The nonadditive components of $\overline{W}$ is given by $\overline{W} = C - [2\Sigma\alpha^2_i q_i(1 - q_i) + (M - 0)^2]$ in which C is a constant, q_i is the frequency and α_i the effect on the character of one of genes *A, B, C,* or *D, M* is the mean ($2\Sigma\alpha_i q_i$) and *0* the optimal grade.[2]

[2]Wright, S., 1935, the analysis of variance and the correlations between relatives with respect to deviations from an optimum. Jour. Genetics 30:243–256.

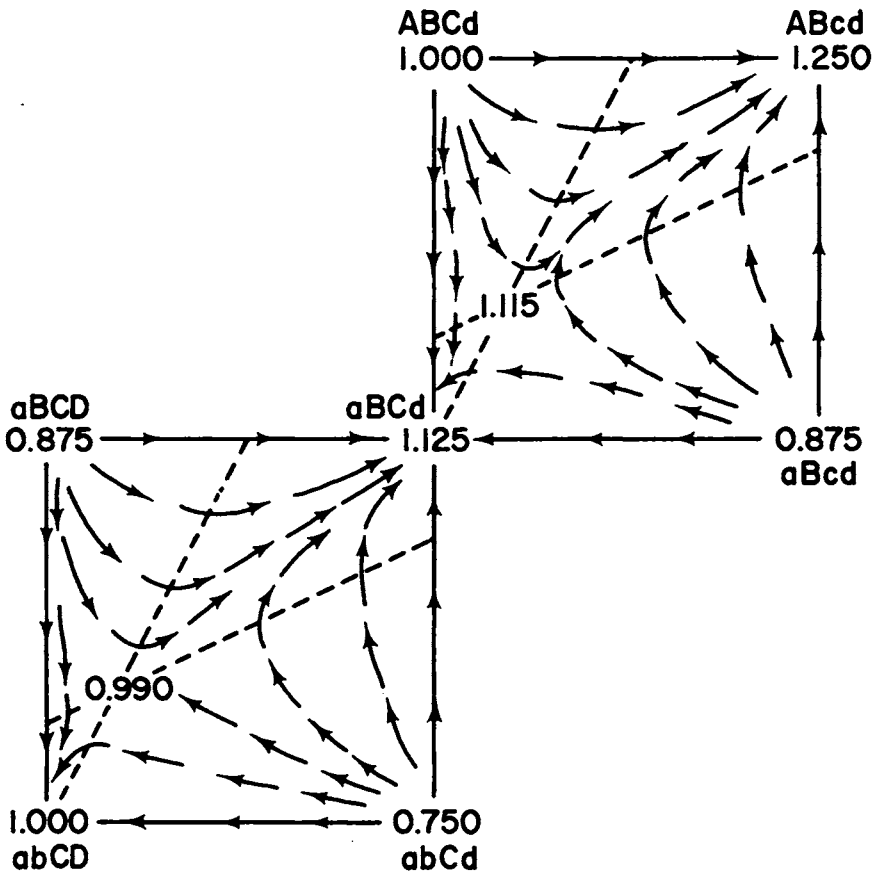

FIGURE 3. *Trajectories of gene frequency systems on surfaces of mean selective values on two faces of the 4-dimensional field.*

The directions in which populations tend to move under selection are indicated by arrows. We may assume that mutation pressure prevents any of the genes from being completely fixed. Thus, if for historical reasons the lowest peak is the best type at first, there is material available for further advance. Clearly, however, a further random process is necessary to move the population across a saddle toward one of the intermediate peaks. Figure 4 shows in profile the selective values along two paths from lowest to highest peak. The mean selective value of the population needs to be depressed only 8 per cent as much as would be involved in complete fixation of *aaBBCCDD* as a step toward *aaBBCCdd*. A relatively small amount of random drift due to bottlenecks in size of population, or from fluctuations in selection, can fairly easily move the population to a point at which the strong selection toward one of the intermediate peaks takes over.

If the process is occurring in a number of largely isolated subdivisions of

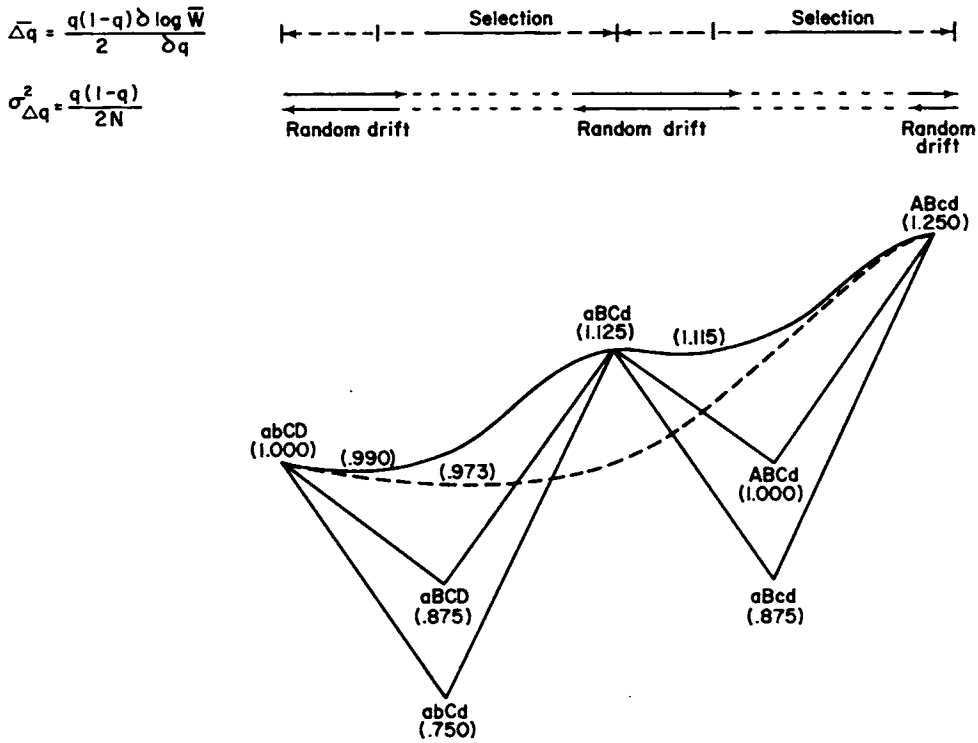

FIGURE 4. *Mean selective values of gene frequency systems along path of least depression from low peak abCD, through peak aBCd to high peak ABcd, and along path avoiding all four intermediate peaks.*

the population with genetic systems close to the low peak, some may be expected to reach each of the intermediate peaks. Small amounts of crossbreeding provide material for further random drift much more effectively than mutation. The coupled process, random drift and mass selection may then move populations to the highest peak. Selection between populations (by differential growth and crossbreeding) will carry the whole array of populations to the highest peak.

The process is, however, one that can apply only to pairs of alleles that differ very slightly in momentary selective value. The differences in the figures are, in fact, improbably great for this process to occur. On the other hand, an allele with momentarily strong selective disadvantage, but with effects that offer great promise if unfavorable side effects can be eliminated, may be utilized by means of coupled random drift and selection among minor modifiers as illustrated in Figure 5.

These figures present highly oversimplified models. Actually an enormously larger number of selective peaks is to be expected in a population of an organism that depends on harmonious systems of genes at each of a large number of aspects of fitness.

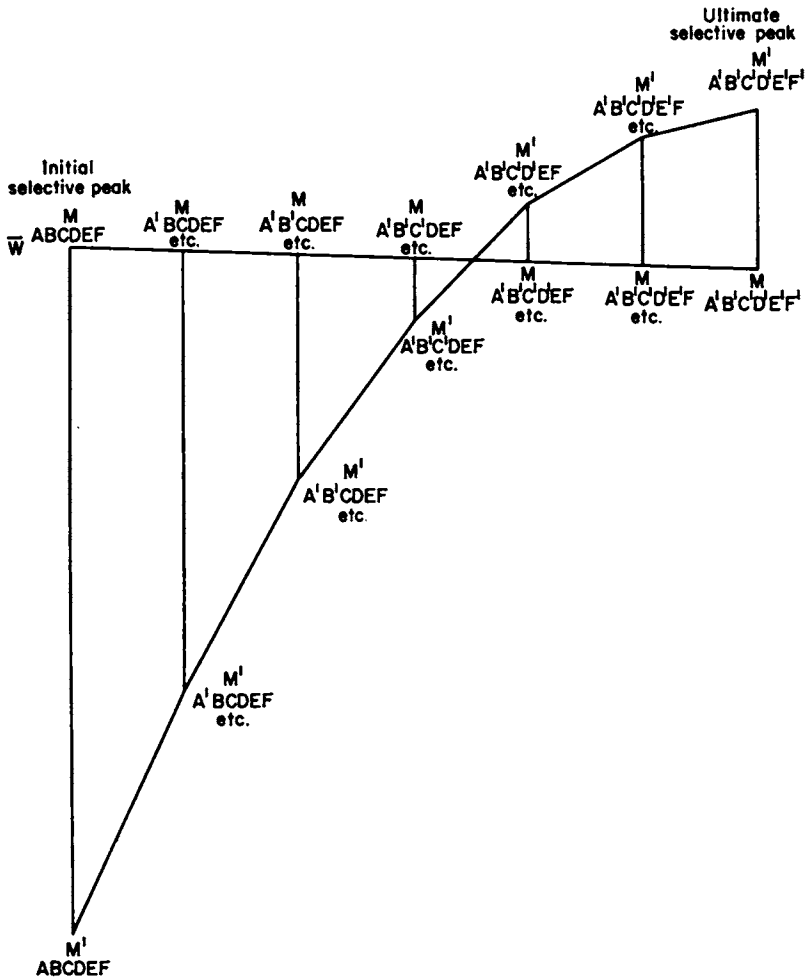

FIGURE 5. *M' is a major mutation with drastic net unfavorable effect in presence of ABCDEF, modifiers of M that are almost neutral. Unfavorable effects of M' are partially overcome by A', B', C', D', E' or F', resulting in net favorable effects of combinations with four or more of the latter. The higher selective peak may be attained locally by joint action of random processes and selection, and may spread through the species by interdemic selection.*

Any evolutionary process, including animal and plant improvement, requires coupling of a more or less random process to furnish raw material with a selective process. Random mutation coupled with mass selection is the ultimate process of this sort, but exploitation of the enormously amplified field of variability provided by recombination speeds up evolutionary change enormously, if it can be coupled with an adequate process of selection. This cannot be mass selection because recombinant types are broken down at once or almost at once, in spite of linkage, in the reduction division. There are only two effective methods. One of these is the coupling of predominant uniparental reproduction

(selfing or asexual reproduction) with selection among clones (obviously giving selection of genotypes as wholes) and sufficiently frequent crossing to give recombination. The other is subdivision of a crossbreeding species into small populations, sufficiently isolated to permit differentiation under the joint effects of random drift and intragroup selection, but coupled with intergroup selection.

DISCUSSION

A. ROBERTSON: Dr. Wright has produced some most interesting evidence on the existence of several adaptive peaks in the analysis of color pattern in guinea pigs. It seems to me important to ask to what extent may we be at an adaptive peak in our domestic plants and domestic animals. Now I would suggest that even though the plants and animals have been under some kind of selection for many generations, this does not mean that they have necessarily arrived at a plateau from which we can produce no immediate advance by selection. After all, our conditions of husbandry have changed so markedly for many of our domesticated species within the last hundred years that we may well expect still to have plenty of variation which can respond to straightforward selection, either in pure strains or in strain crosses.

Progress From Selection

W. L. BROWN, *Chairman*

Heritability

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THE concept of heritability originated as an attempt to describe whether differences actually observed between individuals arose from the differences in genetic makeup between the individuals or resulted from different environmental forces. Knight (14) defines heritability as "the portion of the observed variance for which difference in heredity is responsible." The concept of heritability is simple. Discrepancies arise when the definition is applied to breeding situations. For example, the nature of the genetic variability defined, the experimental units considered, and the inference population assumed will affect the heritability statement made for a character.

Heritability is used in both a broad and a narrow sense. For the broad sense the genotype is considered as the unit in relation to the environment. However, genes segregate and come together in new combinations exhibiting intra-allelic interactions (dominance) and inter-allelic interactions (epistasis). The differences between the actual effects of genes in combination and their average effect in the population are dominance and epistatic effects which are transmitted only in part. Thus, heritability in the broad sense considers total genetic variability in relation to the phenotypic variability, while heritability in the narrow sense considers only the additive portion of the genetic variability in relation to the phenotypic variability. As an example, a simply inherited character with complete dominance (such as flower color in the soybean) would have 100 per cent heritability in the broad sense and 67 per cent heritability in the narrow sense, while a character condition by complementary genes at two loci (such as green cotyledons in the soybean) would have 100 per cent and 27 per cent heritabilities, respectively. The experimental unit considered is the individual plant. Thus, heritability in the narrow sense expresses the fraction of the phenotypic differences between parents which one expects to recover in the offspring and is designed to give a practical interpretation to heritability.

Concepts of heritability and applications in the field of animal breeding have been discussed in detail by Lush (15, 16). The concepts of heritability are readily adaptable to quantitative genetic studies in animals. The unit for selection is the animal. Thus, heritability statements are based on the individual as the basic reference unit, and the extent of sampling which markedly affects

heritability statements in plants is not a factor in animal work. Adjustments are made when genetic variability is obtained from the mean of groups such as families, progenies, breeds, etc. Modes of reproduction are not a problem in animal work, and generally speaking, heritability in the strict sense is an acceptable definition which relates heritability to selection concepts.

Although the concept of heritability is readily adaptable to the description of genetic variability in animals, the study and resolution of the variability associated with the genotype by environment interaction is difficult. Further, maternal effects can create biases in heritability unless studies are properly designed. In general, heritability concepts relating genetic variability in animals are consistent with general definitions. In plant work, however, heritability concepts have not had the use or acceptance found in animal work. The purpose of this paper is to point out the reasons for this confusion and to unify heritability concepts for plant work.

DEFINITION FOR HERITABILITY IN PLANT WORK

Heritability statements will depend upon the restrictions one wishes to make for the definition and the basis (reference unit) which one uses to determine a measure. For quantitative measures in plant work, a plant, a field plot, replicated field plots in one environment, or replicated field plots in two or more environments may be considered as the reference unit, and each reference unit would affect the heritability statement made. To define heritability explicitly, one must first delineate a model characterizing the variability for a set of observations.

The observed value (phenotype) for a character (y), where $E[y]=0$, is visualized as comprising two additive parts, (a) that determined genetically which includes the additive portion (a_i) and nonadditive portions, dominance (d_i) and epistatic (i_i), of the genetic variability and (b) that determined environmentally which includes the total genotype by environment interaction ($(GE)_{ij}$) and a random error within environments (η_{ijk}). A phenotype is thus described by the model

$$y_{ijk} = a_i + d_i + i_i + (GE)_{ij} + \eta_{ijk}. \qquad \text{(i)}$$

Heritability in the strict sense would be

$$\sigma_A^2/[(\sigma_A^2 + \sigma_D^2 + \sigma_I^2) + (\sigma_{GE}^2 + \sigma_\eta^2)] \qquad \text{(ii)}$$

which is the idealized statement for heritability in which the plant is taken as the reference unit. Problems arise, however, in adapting this definition to practice. Measurements in plant work are frequently based on the total expression of individuals within a plot replicated within one or more environments. The plot may consist of progeny from open pollinated individuals, bulked progeny in advanced generation of selfing, progeny rows in a generation of selfing, clonal material, or other types of plant material. Statements may be based upon the

mean of plots replicated within one or more environments. Definition for heritability (ii) becomes lost in a maze of confusion. One then questions whether heritability for plant work could be defined as "the fraction of the phenotypic variability for a defined reference unit expected to be transmitted to the progeny (or propagules)." In the definition the reference unit for the *i*th genotype or composite of genotypes would be the mean of plots for the *j*, *k* environmental conditions. Heritability for a reference unit of *r* replications within *l* environments would then be

$$\sigma_g^2/[\sigma_G^2 + \sigma_{GE}^2/l + \sigma_e^2/rl] = \sigma_g^2/\sigma_y^2 \qquad \text{(iii)}$$

where σ_g^2 contains additive genetic variability and σ_G^2 the total genetic variability based on plot variability and breeding material.

"Heritability" defined in (iii) has had general acceptance by the plant breeders. The pertinent question, however, is whether (iii) defines heritability as originally conceived. To base the expression on a plot basis does not resolve the problem since a plot is a family of individuals. Further, genetic expectations depend upon the type of material used in the study. The need has justified a modification of heritability concepts for plant work. The expected genetic progress for a standardized selection differential of *s* is: $\Delta G = s(\sigma_g^2/\sigma_y^2)\sigma_y$. From the context of (iii), "heritability" expressed in selection concepts would be $H = \Delta G/s\sigma_y$ where the reference unit for the heritability statement would be the selection unit. The statement follows: " 'Heritability' is the fraction of the selection differential expected to be gained when selection is practiced on a defined reference unit." This concept of "heritability" is extremely useful. In practice, if the difference between the population mean and the mean of the selected group is, say, 6 bu/A and the heritability is .33, then the breeder would expect to gain about 2 bu/A by his selection. With a 5 per cent selection differential the expected genetic progress would be $2.06(H\sigma_y)$ as related to a breeding procedure and a reference unit (or sample).

Perhaps the term, heritability, should not be used for (iii) or for the ratio $\Delta G/s\sigma_y$ following from the definition. The term, relative expected progress, is descriptive and reflects the nature of the estimated parameter. However, the need for coining a new term is questionable. The concept ties relative genetic variability with selection concepts; however, the statistic is meaningless without proper ramifications of the genetic material and reference unit used for the statement.

IMPLICATIONS OF HERITABILITY STATEMENTS IN PLANT WORK

Examples can be found in the literature where heritability estimates were based on a single plot (or plant) or upon the average of plot yields, on the sampling of a single environment or upon two or more environments, and on a range of genetic material from F_2 plants to F_n progeny rows. Further, genetic variabilities inherent to crosses probably differ. Judgment must be used in evalu-

ating the information; however, as information from different sources becomes available, quantitative attributes can be characterized in concept as to ease of selection in a breeding program. For example, in soybeans the principal measurements can be ordered, seed yield <<(lodging, % protein) <(height, maturity, % oil, seed size) with respect to ease of selection. The principal characters in soybeans are quite highly heritable except for seed yield which has an H of about .35 in comparison with per cent protein and per cent oil which have ratios of about .60 and .70 respectively, based on two replications at two environments and F_3 line performance (11).

Heritability has value primarily as a method of quantifying the concept of whether progress from selection for a plant character is relatively easy or difficult to make in a breeding program. A plant breeder, through experience, can perhaps rate a series of characters on their response to selection. Heritability gives a numerical description of this concept. The position taken in this paper is that heritability statements should be unified with reference to a selection concept. In accordance with the proposed definition, $H = \Delta G/s\sigma_p$. The original analyses from Hanson *et al.* (8) were pooled for the three families reported. Each location-year was considered as a unique environment. The heritabilities were calculated in the context of (iii) and are given in Table 1. To consider selection

Table 1.—Heritability Analyses for Total Yield and Seed Yield Characters in Lespedeza Based on a Pooled Analysis of the Data Presented by Hanson et al. (8).

Reps/environment	Number environments	Heritability (%)	
		Total yield	Seed yield
1	1	14	19
2	1	21	27
2	2	35	43
2	4	52	60

Component	Total yield	Seed yield
δ_g^2	3,156	275
δ_{gE}^2	3,586	314
δ_p^2	16,316	847

$H = \sigma_g^2/[\sigma_g^2 + \sigma_{gE}^2/l + \sigma_p^2/rl]$

on the basis of a single plot or on the basis of a large number of sampled environments would be meaningless. However, to say that about 1/3 of the selection differential should be gained with 2 replications in 2 environments as the test unit would have interpretation in a practical breeding program for the improvement of total yield in lespedeza. Care should be taken in unifying the selection unit for a crop. For a standardized selection unit for a crop, one has a consistent definition for heritability.

HERITABILITY IN PLANT BREEDING

Since heritability has been considered in terms of selection concepts, one needs to define a genetic parameter which estimates the fraction of the phenotypic variability transmitted to the offspring. The basic definition is heritability in the strict sense, except that the mode of reproduction for a plant species and reference unit enters into selection concepts.

Designs for resolving genetic variability will be discussed in this symposium. Such designs designated as Design 1 (5) and Design 11 (18) are experimental plans to partition genetic variability. Heritability statements would be calculated from (ii) based on the genetic components estimated from the experimental design. The heritability statement would express the expected gain as a fraction of the selection differential when selection is practiced on heterozygous individuals.

The regression of offspring on parents has had considerable use. For progeny from an open-pollinated plant, heritability is twice the regression coefficient of offspring on parent. This statistic estimates heritability in the strict sense as based on a single plant unit. For progeny from self-pollinated individuals the regression coefficient of F_{n+k} on F_n, $n>1$, $k>0$, is relative expected progress. The regression coefficient measures directly the progress expected in the F_{n+k} (as a mean of the F_{n+k} reference sample) as a fraction of the selection differential applied in the F_n (as a mean of the F_n reference unit). Only the variability involving dominance in the offspring will bias the estimates of expected progress. When the progress is referenced to bulked row from F_2 plants in the n and $n+k$ generations of selfing, the covariance estimates σ_A^2, a dominance bias $(1/2)^{2n+k-4}\sigma_D^2$, a principal epistatic component σ_{AA}^2, and a negligible epistatic component involving dominance. The additive by additive component is taken as the principal epistatic component involving the additive scales. For the regression of a single plant progeny row from a parent progeny row on the parent progeny row, $n>2$ and $k=1$, the covariance estimates $[(2^{n-2}-1)/2^{n-3}]\sigma_A^2+[(2^{n-2}-1)/(2^{n-3})]^2\sigma_{AA}^2$, ignoring dominance bias. Although the covariance involving plant progenies from advanced generations will contain more genetic variability than advanced F_3 bulked rows, the regression coefficient is consistent with the use of heritability in this paper. The material upon which selection is practiced, however, is advanced progeny rows. The variability due to dominance is negligible and can be ignored, while the epistatic variability involving the additive scales has significance in selection when considering homozygous lines.

Although the regression approach is a straightforward technique for estimating heritability, genotype by environment interaction associated with the contraction or the expansion of the phenotypic scale can seriously bias the estimate of heritability and create conditions where heritability estimates greater than 1.0 may be obtained. Frey and Horner (6) have proposed the standard unit regression based on regression coefficient utilizing phenotypic measures expressed as standard deviates. The approach has merit only in that heritability estimates

are never greater than 1.0 and at least some of the genotype by environment interaction bias due to scale is removed.

For many species the yield of individually spaced plants is difficult to interpret since the measurement of concern is the totality of expression of individuals competing within an environment (plot). To resolve genetic variability based on the variability of individual spaced F_2 plants is questionable for many crops because (a) one cannot project the phenotypic expression of a genotype under space plantings to that expected for normal competing conditions for the crop unless the spaced condition is the normal competing environment and (b) estimates of environmental variability are not entirely reliable. The exceptions to these statements would involve measures such as disease ratings or data from such species as the fruit and nut crops or corn where space plantings used in the study is the normal state for production. However, the regression of F_3 progeny on F_2 plants measures heritability since the reference measure is the totality of individuals competing within a plot. Powers (21) has utilized parental and F_1 variability to estimate the environmental variability and the F_2 and the backcross genetic variability to partition genetic variability of individual plants. Warner (27) utilized the difference $2\ VF_2 - (VB_1 + VB_2)$ to obtain an estimate of the additive genetic variance which would be satisfactory if epistatic variability were negligible.

Estimates of genetic variances based on individual plant variability are extremely unreliable for species where interplant competition is a factor. Hinson and Hanson (10) reported on plant competition studies in soybeans. Four soybean lines were grown at 2, 4, 8, 16, and 32-inch spacings in pure stands and in a mixture of the four lines. Estimates of line variability (σ_{lp}^2) and of individual plant variability (σ_{Ip}^2) were available from the pure stands. Estimates of line variability with competition due to genetic types (σ_{lc}^2) and error between plants of the same genotype with competition (σ_{Ic}^2) were available from the mixed stands. The component estimates for seed yield per plant are given in Table 2. Competition due to genetic types doubled approximately the component estimates.

Heritabilities for seed yield per plant based on individual plant variability are given in Table 3, assuming that the four genotypes represent a random

TABLE 2.—PARTITION OF PHENOTYPIC VARIABILITY FOR SEED YIELD BASED ON INDIVIDUALLY SPACED SOYBEAN PLANTS WITH AND WITHOUT PLANT COMPETITION ARISING FROM GENETIC TYPES (10).

Spacing	σ_{Ip}^2	$(\sigma_{Ic}^2-\sigma_{Ip}^2)$	σ_{lp}^2	$(\sigma_{lc}^2-\sigma_{lp}^2)$
2	52.52	+.79	7.97	+24.05
4	93.30	+52.55	17.70	+49.10
8	253.50	+57.79	57.16	+228.00
16	530.04	+176.91	441.87	+191.92
32	1250.89	+1149.63	1240.08	+1225.10

TABLE 3.—HERITABILITY ESTIMATES FOR SEED YIELD BASED ON INDIVIDUALLY SPACED SOYBEAN PLANTS WITH ASSUMPTIONS FOR PLANT COMPETITION ARISING FROM GENETIC TYPES (10).

Spacing	No competition from genetic types	Competition from genetic types and σ_{Ic}^2	Competition from genetic types and σ_{Ip}^2
2	13	38	38
4	16	31	56
8	18	48	57
16	45	47	60
32	50	51	74

sample of genotypes from, say, an F_2 population. Heritabilities in the first column (assuming no plant competition due to genetic types) are larger than those expected for an F_2 population since the lines were selected. Heritabilities depend upon spacings and have questionable interpretation with respect to the yield of a genotype within a drilled row. The second column of heritabilities represents an experimental setup as proposed by Warner (27) where environmental plant variability is estimated from F_2 and backcross generations. The third column of heritabilities represents the more common situation where the environmental plant variability would be estimated from pure plant stands while total phenotypic plant variability contained variability arising from plant competition due to genetic types. For species such as soybeans where plant competition is a factor, the description of genetic variability based on individually spaced plants is meaningless.

For F_3 lines or F_3 lines advanced by selfing, the genetic variance for lines estimates $\sigma_A^2 + \sigma_{AA}^2$ in addition to a dominance bias which is considered negligible. The genetic variance for individual plant progeny rows in the nth generation of selfing ($n>2$) is $[(2^{n-2}-1)/2^{n-3}]\,\sigma_A^2 + [(2^{n-2}-1)/2^{n-3}]^2\,\sigma_{AA}^2$, again ignoring dominance. The expectations reflect the increase genetic variability between homogeneous lines and bulked lines and relative genetic variability estimates will be affected accordingly.

HERITABILITY AS RELATED TO MODE OF REPRODUCTION

If the objective of a heritability statement is to describe the advance within a heterozygous population where each selection operation is considered to be one of an infinite set of operations performed on the individuals of the population, then the statement desired is heritability in the strict sense based on the individual as the unit. The majority of the papers reporting heritability in plant work do not reflect this aspect of heritability. This section is designed to consider a few cases unique to the mode of reproduction of the plant and to interpret the heritability statements made. General groups will be considered and discussed. Examples will be noted by references which may be checked for procedure.

Heritability in cross-pollinated species.

Heritability statements for a population of heterogeneous individuals such as an open-pollinated variety of corn poses a genetic structure similar to that found in animal work. The unit is a plant which cannot be reproduced (except by clonal propagation in some species). The partitioning concept relates specifically to the respective entities of the population; however, one faces the dilemma of adapting plant variability to plot variability which is the basis for most selection practices. Robinson *et al.* (22) presented a heritability analysis based on individual plant variability for three populations in corn. The partition was based upon biparental matings as described by Comstock *et al.* (5). The analysis based on plant variability is given in Table 4. Heritability on a single plant basis would be $4\ \sigma_M^2/[\sigma_W^2 + \sigma_P^2 + \sigma_F^2 + \sigma_M^2]$ as reported by the authors. In terms of the heritability concepts developed in this paper, the fraction would reflect the selection gain when selection had been practiced on an individual plant basis. This concept, however, has limited value to the breeder unless he is concerned with simple mass selection.

TABLE 4.—COMPONENT ANALYSIS ON A PER PLANT BASIS FOR DATA OBTAINED FROM BIPARENTAL MATINGS (22).

Source of Variation	Expected Mean Square
Males	$\sigma_W^2 + p\,\sigma_E^2 + rp\,\sigma_F^2 + rpf\,\sigma_M^2$
Females w. males	$\sigma_W^2 + p\,\sigma_E^2 + rp\,\sigma_F^2$
Plot error	$\sigma_W^2 + p\,\sigma_E^2$
Plants w. plots	σ_W^2

p = no. plants per plot, r = no. replications, f = no. females/male
σ_W^2 = environmental plant component = $1/2\ \sigma_A^2 + 3/4\ \sigma_D^2$
σ_E^2 = =environmental plot component
$\sigma_F^2 = 1/4\ \sigma_A^2 + 1/4\ \sigma_D^2$
$\sigma_M^2 = 1/4\ \sigma_A^2$

Breeding procedures are based on plot tests. If heritability in the context of (iii) is acceptable, alternative forms can be considered. Heritability which defines the fraction of the selection differential gained with selection for superior biparental crosses is

$$\Delta_G/s\,\sigma_{\bar{y}} \text{ or } 2\sigma_M^2/[\sigma_W^2/prl + \sigma_P^2/rl + \sigma_{ME}^2/l + \sigma_{FE}^2/l + \sigma_M^2 - \sigma_F^2]$$

where the sampling of r replications of p-plant plots in l environments is considered (see Robinson *et al.* (22) for description of ΔG and Robinson *et al.* (23) for component structure with two or more environments). Similarly, relative selection potentials for the selection of males with biparental matings can be obtained by considering ΔG as defined by Robinson *et al.* (23). Methods of estimating genetic components (and hence heritability) from a diallel cross system can be obtained from Matzinger *et al.* (19) and from a cross system designated as

Design II by the authors from Matzinger *et al.* (18). Certainly, criticisms of the possible expressions for heritability in open-pollinated species are justifiable, yet heritability must be tied to selection concepts to have a usable interpretation.

Heritability in asexually reproduced plants.

In asexually reproduced plants, any combination of genetic factors which yields a superior genotype can be utilized through clonal propagation. Heritability in a broad sense would have meaning for asexually reproduced plants since all genetic variability is usable. A number of authors have estimated heritability based on the variability between available clones. The presentation by Keller and Likens (12) will serve as an illustrative example. The authors measured the variability between available clones of *Humulus lupulus.* Heritabilities based on single plots and replicated plots for sampled environments are given. The heritability statements made by the authors are in accord with definition (iii) considered in this paper and would be the expected proportion of the selection differential gained in identifying superior clones in a population of clones. Burton and DeVane (2) could have been quoted as an example for estimating heritability in asexually reproduced crops.

New genetic types through hybrid combination were considered by Morrow *et al.* (20) and Comstock *et al.* (4) working with the garden strawberry. Since genetic advance is measured by the potential clonal types which the system would produce, heritability in the broad sense as originally defined and referenced to an acceptable selection unit would be a meaningful statistic.

Heritability in self-pollinated species.

The majority of the heritability studies in self-pollinated species have been based on the analysis of F_3 line variability. Regression approaches also have had considerable use. The regression of bulked F_3 lines advanced to the F_{n+k} on F_n, $n>2$, $k>0$, measures, theoretically, relative expected progress similar to that estimated from an analysis of F_3 lines or F_3 lines advanced by bulking, when comparable sampling of environments are considered. Biases resulting from dominance are considered negligible. The line component contains a portion of the additive by additive epistatic variability; however, this epistatic variability is usable with respect to selecting superior homozygous lines. The estimate of heritability as defined in (iii) from F_3 line variability is straight-forward. The paper by Hanson *et al.* (8) from which the data in Table 1 were obtained will serve as an adequate format for this procedure. Procedures are detailed in the paper. There are many other good references which could be given.

As previously pointed out, genetic variance estimates based on individual plant progenies in the F_n generation ($n > 3$) or covariances involving such progenies differ from those expected when F_3 lines or F_3 lines advanced by bulking are considered. To argue that all variances should be adjusted so as to yield heritability in the strict sense begs the question of whether progress relative to a heterogenous F_2 population is the important criterion in contrast to progress relative to the homo-

zygous lines which a cross will produce. Heritability as defined in (iii) requires only $\Delta G/s\sigma_y$. Thus, heritability based on F_3 line performance refers to selection on an F_3 line basis. Heritability could be based on F_n plant progenies with a corresponding reference for selection. For either case, an estimate of the genetic variability among progenies (σ_g^2) and the phenotypic variability of progenies based on a mean of r replications in environments $\sigma_y^2 = (\sigma_g^2 + \sigma_{gE}^2/l + \sigma_e^2/rl)$, are required. Then $\Delta G = s\,\sigma_g^2/\sigma_y$ and $H = \Delta G/s\,\sigma_y$. With the assumption that the additive genetic variability represents the primary source of genetic variability, heritabilities based on types of generation material can be adjusted to a common basis by $H' = H/[k\,(1-H) + H]$ where H' is heritability in the reference generation, H is heritability as computed for the test material and k is the ratio of the additive coefficient in the test generation to the coefficient in the reference generation.

ADDITIONAL MEASURES FOR RELATIVE GENETIC VARIABILITY

In perusing the literature one notes that many authors have preferred to consider measures other than heritability to describe the relative genetic variability inherent in a character. Some authors have emphasized their estimates of variance components. The component estimates are the important results from a quantitative genetic study and must be presented whether or not the author wishes to discuss relative genetic variability.

The expected genetic advance (ΔG) for a reference unit was frequently used. The unit for selection requires a definition in the paper. ΔG as a per cent of the mean has been used to obtain comparable measures. The genetic coefficient of variation, Burton and DeVane (2), also has been used. However, converting to per cent of the mean to remove units of measure yields a statistic with questionable meaning. Five measurements in soybeans were selected to demonstrate this point (Table 5). The data were obtained from Johnson *et al.* (11) for the set

TABLE 5.—COMPARISON OF METHODS FOR EXPRESSING RELATIVE GENETIC VARIABILITY UTILIZING SELECTED SOYBEAN FIELD PLOT MEASURES (11).

Character	$\bar{X}$	ΔG†	$\Delta G/2.06\sigma_y$	$(\Delta G/\bar{X})100$	G.C.V.(%)
Yield (bu/A)	28.1	1.35	.25	5	5
Height (in.)	45.3	4.35	.61	10	6
Maturity (days)	59.7	3.22	.71	5	3
Lodging (score)	3.2	1.10	.73	34	20
Oil (%)	19.7	.68	.67	3	2

†Based on 5% selection differential.

referenced as population 1. The reference unit for selection is 2 replications at 2 environments, which represents an acceptable unit for selection in soybean breeding. The lodging measure is based on a score (1–5) where the range in readings is about twice the mean score while maturity is days from August 31. The reference point for maturity could have been taken as September 30, or some other date. Per cent oil, on the other hand, is a highly heritable character

with a relatively small range of observations. Neither the expected gain expressed as a per cent of the mean or the coefficient of genetic variation yield scales amenable for comparing relative genetic variability.

The units considered for selection must be defined. The reference unit for heritability as defined in (iii) would be the same as that considered for selection. Relative genetic variability statement would represent the fraction of the selection differential one expects to make through selection. Thus, a table giving the component estimates and the first three columns in Table 3 give the essential information for a set of quantitative genetic data.

Relative genetic sensitivity.

Considerable attention has been given to the problem of comparing measurement sensitivity (1, 3, 17, and 24). Hanson *et al.* (9) has attempted to combine measurement sensitivity concepts and genetic theory to obtain a statistic for comparing the gain or loss in sensitivity of selection when one transforms measurement scales. In developing the statistic (relative genetic sensitivity) the author forfeited some of the refinements developed for measurement sensitivity to obtain a simple statistic which was easy to calculate and to interpret. The statistic was not designed to replace heritability concepts but to augment the comparison of relative genetic variabilities when one modified the scales of measurement for a character. The development of the statistic will be considered in detail.

Consider an arbitrary scale (μ) reflecting the true genetic worth for any character. Then a mapping function $f(g_1)$ can be found to map the true genotypic scale (g_1) on μ. One is not concerned with regressing of g_1 on μ, rather, the scaling parameter between $f(g_1)$ and μ. With the assumption of an additive genetic model, the mapping function for any character becomes a linear function. The coefficients $b_{\mu 1}$ for μ on g_1 and $b_{\mu 2}$ for μ on g_2 are defined as scale parameters. The scale parameter can be defined as $b_{\mu i} = \sigma_\mu/\sigma_{gi}$, (26). Consider that one has a phenotypic observation and wishes to make a statement concerning the true relative genotypic value as measured on the scale μ. The genetic sensitivity (λ_1) would essentially be inversely proportional to the confidence increment in μ or $\lambda_1 = 1/\Delta t b_{\mu 1}\sigma_{\bar{y}1}$, $\sigma_{\bar{y}1}^2$, being the error variance of a mean and Δt the confidence interval in standard units. Two measures will have equal genetic sensitivity only if $\Delta t b_{\mu 1}\sigma_{\bar{y}1} = \Delta t b_{\mu 2}\sigma_{\bar{y}2}$ for any selected level of probability. Relative genetic sensitivity is defined as

$$\phi_{12} = \lambda_1/\lambda_2 = \{\sigma_{g1}^2\,\sigma_{\bar{y}2}^2/\sigma_{g2}^2\,\sigma_{\bar{y}1}^2\}^{1/2}.$$

With the assumption of independence between λ_1 and λ_2, test procedures have been developed involving statistics proportioned to λ_1^2, and λ_2^2, and the values necessary for tests of significance have been tabulated for cases with limited degrees of freedom (1, 24). However, the observations are correlated. For genetic variability studies where the degrees of freedom for progeny and error mean squares are usually large, an approximate standard error for ϕ_{12} can be calculated using the technique given by Kendall (13) and the asymptotic normal property of statistics estimated from large samples. An approximate standard error for ϕ_{12} is
$\phi_{12}\{(1-\rho_1^2)/n_1 + (1-\rho_2^2)/n_2 + H(2-H)/n_2\}^{1/2}/H$, where n_1 and n_2 are the degrees

of freedom for progeny and for error mean squares, respectively, H is the average heritability for the two characters, $H_i = r\sigma_{gi}^2/(r\sigma_{gi}^2 + \sigma_{\epsilon i}^2)$, and ρ_1 and ρ_2 are correlations involving the phenotypes and the error deviates, respectively.[1]

The definition of relative genetic sensitivity encompasses the concepts of measurement sensitivity and genetic theory. To have merit, the statistic must not only make biological sense but also be simple to use and easy to visualize. The statistic meets these requirements. If two measures are equally sensitive in identifying genetic differences, $\phi_{12} = 1.0$. One is thus interested in testing the deviation of an estimated ϕ_{12} from 1.0. σ_ϵ^2 is the measure of the reproducibility of a genotype within a population. Although for the reported study the population was within an environment, both $\sigma_{\epsilon i}^2$ and H can be defined for environments and involve the genotype by environment interactions. The value ϕ_{12} implies only that two measures have been equally sampled. $100\phi_{12}^2$ would be the number of environments (or replications) needed for measure criterion 2, expressed as a per cent of the number of environments (or replications) considered for measure criterion 1, to obtain equal sensitivity in the two measures for detecting genetic differences.

The statistic was used by Hanson *et al.* (9) to evaluate the conversion of certain primary measures in soybeans to energy measures. For example, per cent protein (X_1), per cent oil (X_2), and per cent residual (X_3) of the soybean seed were transformed to the proportion of the initial simple sugar carbons (p_i) associated with the respective seed fraction and the work lost in synthesizing the fraction. For demonstrative purpose the analysis of variances and covariances for protein (X_1) and proportion of carbon atoms associated with the protein complex (p_1) are given in Table 6. The phenotypic and error covariances required to estimate a standard error are also included in the table. The data were obtained from an F_3 line analysis. The relative genetic sensitivity of p_1 to X_1 $(\phi p_1 x_1)$ is $(.4907 \times .7250/.3926 \times .6967)^{1/2}$ or 1.14. The relative sensitivities are given in Table 7. Of primary concern in the study was the possible loss in sensitivity resulting from the transformation and the reduction in genetic variability for the transformed residual fraction. The increase of sensitivity for the transformed protein measure and essentially no change for the remaining fractions was pertinent information for the interpretation of the results.

TABLE 6.—ANALYSES OF VARIANCE AND COVARIANCE FOR PERCENT PROTEIN (X_1) AND PROPORTION OF SUGAR CARBONS ASSOCIATED WITH PROTEIN COMPLEX (p_1) IN SOYBEAN SEED (9).

Source of variability	Degrees of freedom	Σx_1^2	$\Sigma x_1 p_1$	Σp_1^2‡
Progenies†	3344	1.5101	+1.5305	1.6779
Error	3520	.7250	+.6915	.6967
σ_{gigj}		.3926	+.4196	.4907

†Progenies replicated twice, therefore $\hat{\sigma}_g^2 = (\text{M.S. Progeny} - \text{M.S. error})/2$.
‡p_1 coded by 10^{-2}.

[1]Two reasonable approximations were made to obtain a usable formula, (i) $V(\sigma_{gi}^2)/(\sigma_{gi}^2)^2 \leq 2[1/n_1 + 1/n_2]/H_i^2$ and (ii) H_1 and H_2 were replaced by H, the average of H_1 and H_2.

TABLE 7.—RELATIVE GENETIC SENSITIVITIES WITH APPROXIMATE STANDARD ERROR OF THE PROPORTIONATE MEASURE (p_i) AS COMPARED WITH THE PERCENT MEASURE (X_i) FOR THREE SOYBEAN SEED CHARACTERS (9).

Character	Relative genetic sensitivity (ϕp_{ixi})
Protein	1.14 ± .034
Oil	.97 ± .023
Residual	1.02 ± .033

TESTS OF SIGNIFICANCE FOR HERITABILITY

When the heritability statement is made with reference to the same number of replications and environments found in the study, then $F = 1/(1-H)$. From the statement, $P\{F>F_\alpha\} = \alpha$, then $P\{H<(F_\alpha-1)/F_\alpha\} = \alpha$, where F_α is the F value required in the study for significance at the α level of probability. The confidence statement for H requires the distribution of the ratio of a noncentral chi square to a central chi square. This distribution is known (25); however, the proper tabulations are not available. Graybill *et al.* (7) have developed a procedure for estimating confidence intervals for heritability. However, differences between heritabilities may be due to a number of factors which a confidence statement does not include.

DISCUSSION AND SUMMARY

Heritability in the broad sense or in the narrow sense or heritability based on single plants, on single plots, or on a sample (reference) of plots has been used to describe genetic variability in quantitative plant genetics. The need for standardization of the concept of heritability is evident, but the method may be subject to question. Arguments have been presented to support the need for a flexible definition. Further, heritability must represent a practical concept to have utility in plant breeding. Quantitative geneticists in plant work have little alternative but to consider heritability concepts in terms of selection concepts. Since expected genetic advance is $\Delta G = s\sigma_g^2/\sigma_y$, heritability was taken as $\Delta G/s\sigma_y$. In this respect heritability concepts in animal and in plant work are unified. Restricting the definition for heritability in the strict sense enabled the animal geneticists to achieve a consistent and usable statistic. To argue that these concepts should be applied directly to plant work is unreasonable. Modes of reproduction and methods for handling of plant material have created impossible situations. In plant work one concept for heritability should be adopted and this should be based on selection concepts as proposed in this paper. Questions on the use of terminology could be raised. An author may prefer to restrict the term heritability to the usage in (ii). The ratio, $\Delta G/s\sigma_y$ is a usable statistic. Actually the use of $\Delta G/s\sigma_y$ as found in Table 5 needs no terminology. Rather, it is the companion statistic to ΔG, expressing ΔG in relative measure. The point must be emphasized that the author has an obligation to present his estimates of variance components in addition to measures of relative genetic variability.

Considering heritability in terms of selection concepts has merit in that a consistent concept for heritability exists among plant breeders. The heritability statement must be prefaced by a statement of the material and selection unit upon which the heritability is based. For plant breeders working on a particular crop, this prefaced statement would not create confusion. The reference unit for selection and for the heritability statement would be identical. The problem is to identify an acceptable unit for selection. Most soybean breeders would accept 2 replications within 2 environments as a standard reference basis for selection in soybean work. Similar bases should be adopted for other crops. While heritability on a single plot basis has limited utility, heritability based on a large sample of environments and plots within environments would also have limited utility since heritability for any character can be made as close to 1.0 as desired by unlimited sampling.

The approach used in this paper was to present arguments relating heritability concepts to selection concepts in general classes of crops. Ramifications on techniques were covered by listing one or more references which would serve as examples. Heritability and selection advance were considered as two complementary concepts.

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DISCUSSION

P. ROBINSON: To calculate heritability and then to look for a practical interpretation is putting the cart before the horse. One should fully understand what heritability means, and what use can be made of it before calculating it. A non-restrictive definition of heritability would merely add to the present confusion. Would it not be better to aim in the other direction and make the definition of heritability more restrictive, e.g., to apply only in the narrow sense?

W. D. HANSON: One of my objectives in this presentation was to discuss the use and misuse of heritability by the plant geneticists. To make our definition for heritability more restrictive, e.g., to apply only in the narrow sense, would essentially eliminate it as a tool to the plant geneticists, for reasons which I have already discussed, unless you are willing to relax your definition of heritability in the strict sense. Heritability as defined in this paper is in line with current usage by plant geneticists. I have tied the concept to selection in an attempt to unify thinking. In this context, the

statistic has use in expressing relative expected gain in conjunction with expected progress and is extremely useful. I do not consider that I have put the cart before the horse by defining the parameter so that it would have applicability. Your criticism should be whether "heritability" as developed here should perhaps be called something other than heritability. The need for coining a new term is questionable.

E. R. DEMPSTER: In animal work, heritability is useful in helping the breeder to predict the relative advantages of different breeding procedures such as the relative weights to be put on individuals and families, the proportion of parents to carry over from one season to the next, etc. There must be similar problems in plant breeding such as the number of lines to be tested in relation to the number of replications, the intensity of selection in different generations, etc. rather than merely the gain one might get in a given generation with a certain breeding scheme. Perhaps heritability is not a good concept for plants, but isn't it possible that some parameters or combination thereof might be useful for these purposes? Presumably, I suppose, they would consist or be composed of some kinds of variance components. The speaker, however, has very lucidly discussed the difficulties that must be overcome in devising a satisfactory system in order to utilize such a set of parameters in making comparative predictions under the wide range of procedures and conditions with which the plant breeder has to deal.

W. D. HANSON: Heritability as developed in this presentation has and can be used to evaluate advantages of different breeding procedures, of sampling environments, etc. The basis for comparison would be relative gains for systems, attributes, etc.

H. F. ROBINSON: (1) Heritability on individual plant basis in corn should have meaning since we do deal with the crops on individual plant basis. (2) The major items of importance are the components of variance. Research worker must report these, apply as he wishes and as his judgment indicates would be of interest to his audience. *Be sure* to give the reader a clear and definite picture of what he did in computation of the quantities from the components of variance. We do need various bases for comparison of results from one study to another and one organism to another.

W. D. HANSON: I would like to underscore the importance of the points made by Dr. Robinson. I have dealt with expressions of relative genetic variability; however, the means and component estimates are the basic statistics which result from a quantitative genetics study. Heritability represents one of a number of ways which one can use the statistics to obtain genetic information.

Selection Index and Expected Genetic Advance

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THE selection index employed in plant and animal breeding refers usually to a linear combination of observations that is used to compute, for each individual available for choice, a criterion for selection. We shall call the mathematical description of this linear function the selection index, I, and a numerical value actually computed by an index from the observations on a particular individual, the selection criterion. For example, suppose that the records available on each of several dairy sires are y_1 = mean of 10 progeny, y_2 = dam's record. Then the index might be something like

$$I = .77(y_1 - \mu_1) + .08(y_2 - \mu_2).$$

If, for a particular sire, $y_1 = 450$, $y_2 = 500$, $\mu_1 = 460$, $\mu_2 = 480$, the selection criterion for this sire would be

$$.77(450 - 460) + .08(500 - 480) = -6.1$$

The selection index can be used for several different purposes, e.g.,

1. Selection on a single trait using information on the individual and certain of its relatives (5).
2. Selection on two or more traits using records made by the individual (3).
3. Selection on two or more traits using records on the individual and its relatives.
4. Selection of line-crosses using data in addition to that on the specific cross (4).

The first application of the selection index to plant breeding was by Smith (7), and the first to animals by Hazel (3). An excellent brief description of the method was given by Comstock (2). Cochran (1) presented many of the mathematical and statistical problems encountered in constructing indexes.

The foregoing publications and all others on the subject, so far as I am aware, have justified the procedure only for the case in which the information available on each candidate for selection is the same. More precisely, the N records and the underlying genetic value available on each individual are a random sample from some known (N + 1)-variate population. In actual practice, at least in animal breeding, this is seldom true. Rather, choices must be made among animals with different amounts of information. It does turn out, as will be shown in this paper, that the selection index procedure is in fact valid for the latter case.

SELECTION INDEX FOR THE EQUAL INFORMATION CASE

N records, say $y_1, \ldots, y_N$, are available on each candidate for selection. The breeding value of this individual is denoted by T. We shall deliberately not define breeding value at this time, but will do so later in the paper. $y_1, \ldots, y_N$, T are assumed to have an $(N + 1)$-variate normal distribution with variance-covariance matrix

$$\begin{bmatrix} C_{11} & C_{12} & \ldots & C_{1N} & t_1 \\ C_{12} & C_{22} & \ldots & C_{2N} & t_2 \\ \vdots & & & & \vdots \\ C_{1N} & C_{2N} & \ldots & C_{NN} & t_N \\ t_1 & t_2 & \ldots & t_N & g \end{bmatrix}$$

or in matrix notation,

$$\begin{bmatrix} & \cdot & \\ C & \cdot & t \\ \cdot \; \cdot & \cdot & \cdot \; \cdot \\ t' & \cdot & g \\ & \cdot & \end{bmatrix},$$ where C is an $N \times N$, non-singular matrix, t is an $N \times 1$ vector, and g is a scalar. The y's have means $\mu_1, \ldots, \mu_N$.

Construction of the Index

An index is wanted of the following form

$$I = b_1(y_1 - \mu_1) + \ldots + b_N(y_N - \mu_N).$$

Of all such linear functions which one is "best" in some sense? To answer this question we must define what we mean by best. A logical criterion would be that one which in the long run maximizes genetic progress, see, for example, Lush (6). Now the expected value of any particular T selected on the basis of such an index is

$$E(T|I) = \mu_T + b_{TI}(I - \mu_I)$$

$$= \mu_T + \frac{\sigma_{TI}}{\sigma^2_I}(I - \mu_I).$$

This is the well known formula for the regression of one variable on a second variable in the bivariate normal distribution. This is not true for other distributions, but may be a suitable approximation. Then the mean of the T's in a selected group is

$$E(\bar{T}|\bar{I}) = \mu_T + \frac{\sigma_{TI}}{\sigma^2_I}(\bar{I} - \mu_I).$$

If selection is strictly according to the index, $\bar{I} - \mu_I$ is equal to $\frac{z}{q}\sigma_I$, where z is the

ordinate of the unit normal distribution at the point of truncation, and q is the fraction of indexed individuals that is selected. Thus, the expected genetic progress in one cycle of selection on an index is

$$\frac{\sigma_{TI}}{\sigma^2_I}\frac{z}{q} - \sigma_I, \text{ which can be re-written as}$$

$$r_{TI}\frac{z}{q} - \sigma_T.$$

Since for any given population and intensity of selection $\frac{z}{q}\sigma_T$ is constant, the *b's* of the index should be chosen so as to maximize r_{TI}. Differentiating $\log r_{TI} = \log \sigma_{TI} - \frac{1}{2}\log \sigma^2_T - \frac{1}{2}\log \sigma^2_I$ with respect to $b_1, \ldots, b_N$, equating the partial derivatives to zero, and noting that

$$\sigma_{TI} = b_1\sigma_{y_1T} + \ldots + b_N\sigma_{y_NT}$$

$$\text{and } \sigma^2_I = b^2_1\sigma^2_{y_1} + 2b_1b_2\sigma_{y_1y_2} + \ldots + b^2_N\sigma^2_{y_N}$$

the following equations in the *b's* are obtained:

$$b_1\sigma^2_{y_1} + b_2\sigma_{y_1y_2} + \ldots + b_N\sigma_{y_1y_N} = \sigma_{y_1T}\frac{\sigma^2_I}{\sigma_{TI}}$$

$$b_1\sigma_{y_1y_2} + b_2\sigma^2_{y_2} + \ldots + b_N\sigma_{y_2y_N} = \sigma_{y_2T}\frac{\sigma^2_I}{\sigma_{TI}}$$

etc.

Since the magnitude of σ_I^2/σ_{TI} does not affect the proportionality of the *b's*, it has no effect on r_{TI} and can be chosen arbitrarily. For convenience let us choose the value, 1. Thus we have the above equations with σ_I^2/σ_{TI} deleted. In matrix notation the equations now are

$$Cb = t, \qquad (1)$$

where *b* is the N × 1 vector, $b_1, b_2, \ldots, b_N$, C is the variance-covariance matrix of the *y's*, and *t* is the vector of σ_{yT}'s. Note that these index equations are exactly like "normal" equations of multiple regression except that population variances and covariances appear in place of sample sums of squares and cross-products.

Expected Genetic Progress

With the *b's* determined, the expected genetic progress in one cycle of selection by truncation of a set of selection criteria can be computed from

$$r_{TI}\sigma_T\frac{z}{q}.$$

r_{TI} can be calculated conveniently by noting that

$$r^2_{TI} = \frac{(\sigma_{TI})^2}{\sigma^2_I \, \sigma^2_T} = \frac{\sigma_{TI}}{\sigma^2_T} \left(\text{since } \frac{\sigma_{TI}}{\sigma_I} = 1\right)$$

$$= \frac{b_1\sigma_{y_1T} + \ldots + b_N\sigma_{y_NT}}{\sigma^2_T}.$$

Also, we note that the expected value of a particular T, given the selection criterion, I_o, is

$$E(T \mid I_0) = \mu_T + \frac{\sigma_{TI}}{\sigma^2_I}(I_0 - \mu_I)$$

$$= \mu_T + I_0, \text{ since } \sigma_{TI}/\sigma^2_I = 1 \text{ and } \mu_I = 0.$$

Other Properties of the Selection Criterion

The selection criterion computed by the selection index has other properties of interest in addition to maximization of r_{TI} and of expected genetic progress.

1. $E(I - T)^2$ is minimum among all linear functions of the general form of the selection index. That is, the average value of the squared deviations of criteria from true breeding values is minimum. This is easy to prove by minimizing, for variations in b,

$$E(I - T)^2 = E[b_1(y_1 - \mu_1) + \ldots + b_N(y_N - \mu_N) - T]^2$$

$$= b_1^2\sigma^2_{y_1} + 2b_1b_2\sigma_{y_1y_2} + \ldots + b^2_N\sigma^2_{y_N} - b_1\sigma_{y_1T} - \ldots$$

$$- b_N\sigma_{y_NT} + \sigma^2_T.$$

When this expression is differentiated with respect to b's and the partial derivatives are equated to zero, the equations of (1) are obtained. Note that this property does not require the multivariate normal distribution, nor does the property maximization of r_{TI}. If the value of $E(I - T)^2$ is wanted for a particular index, it can be computed either by

$$\sigma^2_T - \sigma_{TI} = \sigma^2_T - (b_1\sigma_{y_1T} + \ldots + b_N\sigma_{y_NT}) \text{ or by}$$
$$\sigma^2_T(1 - r^2_{TI}).$$

A proof of these computing formulas is,

$$E(I - T)^2 = \sigma^2_I - 2\sigma_{TI} + \sigma^2_T$$

$$= \sigma^2_T - \sigma_{TI}, \text{ since } \sigma^2_I = \sigma_{TI}$$

$$= \sigma^2_T\left(1 - \frac{\sigma_{TI}}{\sigma^2_T}\right)$$

$$= \sigma^2_T\left(1 - \frac{(\sigma_{TI})^2}{\sigma^2_T \, \sigma^2_I}\right) \text{since } \frac{\sigma_{TI}}{\sigma^2_I} = 1$$

$$= \sigma^2_T(1 - r^2_{TI}).$$

It is also of interest to note that

$$\sigma^2_I = r^2_{TI}\sigma^2_T.$$

The proof of this is,

$$\sigma^2_I = \frac{(\sigma^2_I)^2}{\sigma^2_I} = \frac{(\sigma_{TI})^2}{\sigma^2_I} = \frac{(\sigma_{TI})^2}{\sigma^2_T \sigma^2_I} \sigma^2_T = r^2_{TI}\sigma^2_T.$$

2. $E(T|y_1,\ldots,y_N)$ = the selection criterion in the multivariate normal case. This comes directly from the well known result concerning the mean of a conditional distribution in the multivariate normal distribution. Thus, the average value of *T's* associated with a given set of *y's* is equal to

$$\mu_T + b_1(y_1 - \mu_1) + \ldots + b_N(y_N - \mu_N),$$

where the *b's* are exactly those of the selection index. Accordingly, we can state that the selection index procedure takes as the selection criterion the average value of all *T's* that are associated with *y's* equal to those on the individual that is a candidate for selection. Of course, this subset of *T's* shows variation, but less than the variation of *T's* in the entire population. From multivariate normal theory, this variance is

$$\sigma^2_T(1 - r_{TI}^2).$$

3. The probability of selecting the higher of a pair of *T's* is maximized. The proof of this is presented in the next section of this paper.

Unknown Means

What if the μ's are not known? In the equal information case any arbitrary values can be used, for it can be seen that

$$\begin{aligned} I &= b_1(y_1 - \mu_1) + \ldots + b_N(y_N - \mu_N) \\ &= b_1y_1 + \ldots + b_Ny_N - (b_1\mu_1 + \ldots + b_N\mu_N). \end{aligned}$$

Notice that the same function of the μ's appears in each selection criterion and consequently has no effect on ranking. This is not the case when the information is different from one individual to another.

SELECTION INDEX FOR THE UNEQUAL INFORMATION CASE

When two individuals have different information available for evaluating their breeding values, it is clear that different indexes are required. But then there is more than one r_{TI}, and it is obvious that the justification of the selection index method described in the preceding section no longer is valid. For example, suppose selection is from two kinds, A and B. All individuals in the A group have the same kind of information, and an index say I_A is used to discriminate among them; similarly for the B group, I_B is used for discrimination. Then the expected progress through selection on the basis of these two indexes is

$$(N_Ar_{TI_A}z_A + N_Br_{TI_B}z_B)/(q_AN_A + q_BN_B),$$

where N_A and N_B are the numbers of individuals available for selection in the two groups, $q_AN_A + q_BN_B$ is the number of individuals required to be selected, and z_a and z_b are ordinates of the unit normal distribution at the point of truncation. Maximization of this expression appears difficult since two sets of *b's*, q_A, and q_B must be determined. The difficulties multiply rapidly as the number of

different groups increases. Strangely enough this problem seems not to have been considered in previous discussions of selection.

Maximizing Probability of Selecting the Better of Two Individuals

The problem created by unequal information in the individuals considered for selection can be solved by finding a selection criterion which will maximize the probability of selecting the better of any two individuals. This method should then certainly maximize genetic progress. Suppose we have a set of records $y_1, \ldots, y_N$ available for choosing between individuals A and B with breeding values T_A and T_B. For example, y_1 might be the record on A, y_2 the record on the dam of A, and $y_3, \ldots, y_{12}$ the records on 10 progeny of B. The variance-covariance matrix of the y's is as before, C. The covariance between T_A and the y's is the vector, t_A and between T_B and the y's is t_B. T_A and T_B are assumed to have the same mean and can have any variance-covariance matrix we choose. These variables and the y's are assumed to follow the multivariate normal distribution. We want two indexes, one to compute a selection criterion for A and the second to compute a criterion for B.

$$I_A = b_1(y_1 - \mu_1) + \ldots + b_N(y_N - \mu_N),$$

$$I_B = b_1^*(y_1 - \mu_1) + \ldots + b_N^*(y_N - \mu_N).$$

Note that the same set of records is used for the two indexes, but some of the b's and b^*'s may be zero.

In order to maximize the probability of selecting the better of two T's the following probabilities must be as large as possible.

$$P(I_A - I_B > O \mid T_A - T_B > O),$$

$$P(I_A - I_B < O \mid T_A - T_B < O).$$

Now for any fixed value of $T_A - T_B$, say k, the distribution of $I_A - I_B$, is normal with mean

$$\mu_{I_A} - \mu_{I_B} + b_{I_DT_D}(k - \mu_{T_A} + \mu_{T_B}),$$

where $I_D = I_A - I_B$ and $T_D = T_A - T_B$. This mean then simplifies to $b_{I_DT_D}k$, since $\mu_{I_A} = \mu_{I_B} = 0$ and $\mu_{T_A} = \mu_{T_B}$. The variance of this conditional distribution is

$$(1 - r^2_{I_DT_D})\,\sigma^2_{I_D}.$$

The probabilities above can be maximized if we maximize the ratio of the mean to the standard deviation when k is positive and minimize this ratio when k is negative. Both of these can be accomplished if we maximize the ratio of $b_{I_DT_D}$ to the standard deviation, that is,

$$\begin{aligned} & b_{I_DT_D}/\sqrt{(1 - r^2_{I_DT_D})\sigma^2_{I_D}} \\ &= \frac{\sigma_{I_DT_D}}{\sigma_{I_D}\,\sigma^2_{T_D}} \Big/ \sqrt{(1 - r^2_{I_DT_D})} \\ &= \frac{1}{\sigma_{T_D}} \frac{r_{I_DT_D}}{\sqrt{1 - r^2_{I_DT_D}}}. \end{aligned} \tag{1a}$$

Since $\frac{1}{\sigma_{T_D}}$ is constant, maximization of (1a) is certainly accomplished by maximizing $r_{I_D T_D}$. But since $I_D = I_A - I_B$ is

$$I_D = (b_1 - b_1^*)y_1 + \ldots + (b_N - b_N^*)y_N$$
$$= \text{say } \beta_1 y_1 + \ldots + \beta_N y_N,$$

it is necessary now simply to solve the usual index equations (1) of the form

$$\beta_1 \sigma^2_{y_1} + \beta_2 \sigma_{y_1 y_2} + \ldots + \beta_N \sigma_{y_1 y_N} = \sigma_{y_1 T_D} = \sigma_{y_1 T_A} - \sigma_{y_1 T_B},$$

etc.,
or in matrix notation,

$$C\,\beta = t_A - t_B \text{ since } \sigma_{yT_D} = \sigma_{yT_A} - \sigma_{yT_B} = t_A - t_B.$$

Then, $\beta = C^{-1}(t_A - t_B)$

$$= C^{-1}t_A - C^{-1}t_B. \qquad (2)$$

Now, suppose we compute separate indexes for evaluating A and B as though A were to be ranked relative only to others with the same information and B relative to others with the same information, but different from A's. Using equation (1), we have

$$C\ b_A = t_A \text{ or}$$
$$b_A = C^{-1}t_A, \text{ and}$$
$$C\ b_B = t_B \text{ or}$$
$$b_B = C^{-1}t_B.$$

Now note that,

$$b_A - b_B = C^{-1}t_A - C^{-1}t_B,$$

which is exactly the same as β, see (2). Thus, we have proved that the usual selection index criteria are best for ranking regardless of unequal information.

Unknown Means

It was shown in an earlier section that lack of information concerning the μ's has no effect on ranking when all individuals have the same information. This is not true, however, with unequal information. In the case above, involving A and B,

$$I_A - I_B = (b_1 - b_1^*)(y_1 - \mu_1) + \ldots + (b_N - b_N^*)(y_N - \mu_N).$$

Clearly this difference, which we use in choosing between A and B, contains a function of the μ's, and if the μ's are unknown, the difference cannot be computed. One way out of this difficulty is to let

$$I = b_1 y_1 + \ldots + b_N y_N \text{ rather than}$$
$$b_1(y_1 - \mu_1) + \ldots + b_N(y_N - \mu_N),$$

and then to maximize r_{TI} subject to the condition that $E(I) = 0$. To illustrate, suppose y_1, y_2, y_3 are assumed to have a common mean, μ and we want an index,

$$I = b_1 y_1 + b_2 y_2 + b_3 y_3,$$

subject to E(I) = O. Now,

$$E(I) = E(b_1y_1 + b_2y_2 + b_3y_3)$$
$$= (b_1 + b_2 + b_3)\,\mu.$$

Consequently, E(I) = 0 if $b_1 + b_2 + b_3$ is required to equal 0. This condition must therefore be imposed on the selection index equations. Suppose the usual equations are

$$\begin{aligned} 20\,b_1 + \quad b_2 + \; 2\,b_3 &= 5 \\ b_1 + 25\,b_2 + \; 3\,b_3 &= 2 \\ 2\,b_1 + \; 3\,b_2 + 30\,b_3 &= 1. \end{aligned}$$

By augmenting these equations with a Lagrange multiplier, a, as follows, maximization of r_{TI} subject to $b_1 + b_2 + b_3 = 0$ is accomplished.

$$\begin{aligned} 20\,b_1 + \quad b_2 + \; 2\,b_3 + a &= 5 \\ b_1 + 25\,b_2 + \; 3\,b_3 + a &= 2 \\ 2\,b_1 + \; 3\,b_2 + 30\,b_3 + a &= 1 \\ b_1 + \quad b_2 + \quad b_3 + \; &= 0. \end{aligned}$$

The solution to these equations is $b_1 = .1077$, $b_2 = .0367$, $b_3 = -.0710$, $a = 3.0241$. This is in contrast to the following solution when μ is known, $b_1 = .2455$, $b_2 = .0690$, $b_3 = .0101$.

A second logical approach to the problem of unknown μ's is to use their estimates in the regular index. In the above example, the index would be,

$$I = .2455(y_1 - \hat{\mu}) + .0690(y_2 - \hat{\mu}) + .0101(y_3 - \hat{\mu}).$$

Now it turns out that if the estimators used are those obtained by maximum likelihood from the *y's* that were employed in the index, the index is actually the same as that derived by requiring E(I) = 0. Let us illustrate in the above example. The maximum likelihood (m.l.) estimator of μ is $k_1y_1 + k_2y_2 + k_3y_3$, where the *k's* are the solution to the following equations:

$$\begin{aligned} 20\,k_1 + \quad k_2 + \; 2\,k_3 + a &= 0 \\ k_1 + 25\,k_2 + \; 3\,k_3 + a &= 0 \\ 2\,k_1 + \; 3\,k_2 + 30\,k_3 + a &= 0 \\ k_1 + \quad k_2 + \quad k_3 \quad &= 1. \end{aligned}$$

The solution is $k_1 = .4246$, $k_2 = .3257$, $k_3 = .2497$, $a = -9.3169$.

$$\begin{aligned} \text{Then, } I &= .2455(y_1 - \hat{\mu}) + .0690(y_2 - \hat{\mu}) + .0101(y_3 - \hat{\mu}) \\ &= .2455\,y_1 + .0690\,y_2 + .0101\,y_3 - .3246\,\hat{\mu} \\ &= .2455\,y_1 + .0690\,y_2 + .0101\,y_3 - .3246(.4246\,y_1 + .3257\,y_2 \\ &\quad + .2497\,y_3) \\ &= .1077\,y_1 - .0367\,y_2 - .0710\,y_3, \end{aligned}$$

which is exactly the same as the index which requires E(I) = 0.

A general proof of the equivalence of these methods follows: The records available for evaluating an individual are the elements of an N × 1 vector, y, with variance-covariance matrix, C, and means $X\beta$, where X is a known $N \times p$ matrix and β is an unknown p × 1 vector. The covariance between T and y is the $N \times 1$ vector, t.

Then the usual selection index is

$b'(y - X\beta) = t'C^{-1}(y - X\beta)$, and if the m.l. estimators of β are substituted for β it becomes

$$t'C^{-1}(y - X\hat{\beta}).$$

The m.l. estimator is $\hat{\beta} = Ly$, where L, a p × N matrix, is the solution to

$$CL' + XA = 0$$
$$X'L' = I,$$

where A is a p^2 Lagrange multiplier, and I is a p^2 identity matrix (not the selection index). Solving these equations,

$$L' = C^{-1}X(X'C^{-1}X)^{-1}.$$

Therefore, $\hat{\beta} = Ly = (X'C^{-1}X)^{-1}X'C^{-1}y$.

Then the index $= t'C^{-1}[y - X(X'C^{-1}X)^{-1}X'C^{-1}y]$

$$= t'C^{-1}[I - X(X'C^{-1}X)^{-1}X'C^{-1}]y. \quad (3)$$

In the second method r_{TI} is maximized, subject to $E(I) = 0$. In this case b is the solution to the following equations

$$Cb + Xa = d$$
$$X'b = 0,$$

where a is a p × 1 Lagrange multiplier, and 0 is a p × 1 null vector. Solving these equations,

$$b = [I - C^{-1}X(X'C^{-1}X)^{-1}X']C^{-1}t,$$

and the selection index $= b'X$

$$= t'C^{-1}[I - X(X'C^{-1}X)^{-1}X'C^{-1}]y,$$

as in (3), thus completing the proof.

SETTING UP SELECTION INDEX EQUATIONS FOR ONE TRAIT

It is apparent from the preceding sections that the selection index method has very desirable properties at least in the multivariate normal distribution. But it must also be recognized that, strictly speaking, these properties exist only when the necessary population variances and covariances are known. Of course, the C matrix, the variance-covariance matrix of y's, can be estimated directly from an adequately large sample from the population of y's. In contrast, the covariance between T and the y's cannot always be estimated directly since T is sometimes unobservable. Therefore, quantitative genetic theory is then invoked to infer the value of such covariances. Also, on some occasions the elements of C are inferred from a combination of data and theory, if data alone are inadequate.

Coefficients of Left Hand Sides of Index Equations

Ideally one should like to have a very large sample from the N-variate population represented by the y's. Then the variance-covariance matrix can be estimated accurately enough that there need be no concern about the consequences of using an estimate of C rather than parameter values.

Computing C when all genetic variation is additive. In animal breeding the elements of C are sometimes estimated under the assumption that the model underlying the record on the *ith* animal is

$$y_i = \mu_i + g_i + e_i, \tag{4}$$

and that on the *jth* animal is

$$y_j = \mu_j + g_j + e_j,$$

where u_i and μ_j are fixed, g_i and g_j are additive genetic values of the two individuals, and e_i and e_j represent all other causes of variation. It is assumed that g_i, g_j, e_i, e_j, follow a multivariate distribution with all covariances zero except that between g_i and g_j, which is stated to be a $a_{ij}\sigma^2_g$, where a_{ij} is the numerator of Wright's (8) coefficient of inbreeding and σ^2_g is the population additive genetic variance (the initial population in case there has been inbreeding). The variance of y_i is assumed to be $\sigma^2_e+(1+F_i)\sigma^2_g$, where σ^2_e is the variance of e in the original population, and F_i is the inbreeding coefficient of the *ith* individual. These assumptions imply:

1. No selection since the period defining the initial population.
2. All genetic variance is additively genetic.
3. No covariance between additive genetic values and environmental values and no covariance between environmental values.

Then the C matrix for computing b's to use with single records on N individuals is

$$\begin{pmatrix} \sigma^2_y + F_1\sigma^2_g & a_{12}\sigma^2_g & \cdots & a_{1N}\sigma^2_g \\ a_{12}\sigma^2_g & \sigma^2_y + F_2\sigma^2_g & \cdots & a_{2N}\sigma^2_g \\ \vdots & \vdots & & \vdots \\ a_{1N}\sigma^2_g & a_{2N}\sigma^2_g & & \sigma^2_y + F_N\sigma^2_g \end{pmatrix}, \tag{5}$$

where $\sigma_y^2 = \sigma_g^2 + \sigma_e^2$ = variance of records in the initial population. It is sometimes convenient to write this matrix as

$$\sigma^2_y \begin{pmatrix} 1 + F_1h^2 & a_{12}h^2 & \cdots & a_{1N}h^2 \\ a_{12}h^2 & 1 + F_2h^2 & \cdots & a_{2N}h^2 \\ \vdots & \vdots & & \vdots \end{pmatrix}, \tag{6}$$

where h^2 = heritability in the narrow sense = σ^2_g/σ^2_y.

More than one record per individual. In animal breeding applications two or more records on the same trait of an animal are sometimes used in selection. Let us assume as an approximation that the correlation between two records on an animal is $(r + Fh^2)/(1 + Fh^2)$, where r is the correlation in the initial population between records on the same animal. This implies a model

$$y_{ij} = \mu + p_i + g_i + \acute{e}_{ij},$$

where $p_i + e'_i = e_i$ of the model in (4); p_i is permanent to the individual, its variance is σ^2_p, and it is not affected by inbreeding. All elements of the model are uncorrelated. Then,

$$r = (\sigma^2_g + \sigma^2_p)/\sigma^2_y.$$

Under these assumptions and when the y's refer to the means of n_1 records in the first individual, n_2 in the second, etc., the *ith* diagonal element of (6) is modified to

$$\frac{1 + (n_i - 1)r}{n_i} + F_i h^2, \text{ etc.} \tag{7}$$

When $n = 1$, the diagonal element simplifies to $1 + Fh^2$, as it should.

Using group means. Oftentimes we wish to use the mean of some group, such as a set of progeny or of sibs in the selection index. Under the same assumptions as already stated in this section, the diagonal of (6) corresponding to any group, say the *ith* is

$$\left[\frac{1 + (n_i - 1)r}{n_i} + F_i h^2 + (p_i - 1)a_{ii'}h^2\right]/p_i, \tag{8}$$

where n_i is the number of records on each member of the group,

p_i is the number of individuals in the group,

F_i is the inbreeding coefficient of each member of the group, and

$a_{ii'}$ is the intra-group numerator relationship.

The off-diagonal elements of (6) remain the same as though there were only one member in the group. This, of course implies, that every member of a group has the same relationship to any other individual whose record is used in the selection index. Note that when $p_i = 1$, the expression in (8) reduces to (7), and when $n_i = 1$ reduces to

$$[1 + F_i h^2 + (p_i - 1)a_{ii'}h^2]/p_i.$$

Use of Genetic Variance Components

In a population with no inbreeding and with the environment contributing nothing to covariance between records on different individuals it is easy to express covariances between relatives' records in terms of Wright's coefficient of relationship, dominance relationship, and components of genetic variance. These genetic components are,

1. Additive: variance due to single gene effects.
2. Dominance: additional variance due to allelic gene pairs.
3. Additive × additive: additional variance due to non-allelic gene pairs.
4. Additive × dominance: additional variance due to a single gene and an allelic gene pair,

and so on.

In general, let σ^2_{ij} refer to the variance due to the interaction of i non-

allelic genes and j allelic gene pairs. Given that there are q loci which contribute to the genetic variance of a trait, the total variance is

$$\sum_{i=0}^{q} \sum_{j=0}^{q} \sigma^2_{ij}, \qquad 1 \leq i + j \leq q.$$

Then, the covariance between two related individuals, is

$$\sum_{i=0}^{q} \sum_{j=0}^{q} a^i d^j \sigma^2_{ij}, \qquad 1 \leq i + j \leq q, \tag{9}$$

where a is the Wright coefficient of relationship between i and j, and d is the dominance relationship between them. The dominance relationship is computed as follows for individuals A and B.

$$A\begin{cases} C \\ D \end{cases} \qquad B\begin{cases} E \\ F \end{cases}$$

$$d_{AB} = \frac{1}{4}[a_{CE}a_{DF} + a_{CF}a_{DE}]. \tag{9}$$

To illustrate (9), a and d for non-inbred full sibs are $\frac{1}{2}$ and $\frac{1}{4}$, respectively. Thus, the genetic contribution to their covariance is

$$\frac{1}{4}\sigma^2_{01} + \frac{1}{16}\sigma^2_{02} + \frac{1}{64}\sigma^2_{03} + \ldots$$

$$+ \frac{1}{2}\sigma^2_{10} + \frac{1}{8}\sigma^2_{11} + \frac{1}{32}\sigma^2_{12} + \ldots$$

$$+ \frac{1}{4}\sigma^2_{20} + \frac{1}{16}\sigma^2_{21} + \frac{1}{64}\sigma^2_{22} + \ldots$$

etc.

Little progress has been made in estimating these genetic components, but if good estimates were available and if environmental covariances could be eliminated, the problem of setting up C for calculation of indexes would be completely solved for non-inbred populations. Apparently gene frequencies are required to determine the contribution of many of the components to covariance between relatives in inbred populations and, of course, these frequencies are not available for genes affecting most traits of economic importance.

Right Hand Side of Index Equations

The right hand sides of the equations are $\sigma_{y_1T}, \ldots, \sigma_{y_nT} = t$ and depend obviously on our definition of T. Three different definitions seem logical in animal breeding applications when selection is for the individual:

1. Future production of the individual.
2. Production of progeny of the individual.
3. Production of descendants of the individual.

(In plant breeding, selection is often among lines or line-crosses. We shall discuss our definition of T for these cases in a later section).

Future production on the individual. If T = future production and if it is assumed that all records on the individual have correlation, r (= repeatability), with each other, $\sigma_{yT} = r\sigma^2_y$ in a non-inbred population. If serial correlations exist, a different σ_{yT} must be assumed for first with second records as compared to first with third, etc. In any case σ_{yT} is always a covariance between actual records, and consequently the problem of setting up the right hand side of the index equations is exactly the same as that for the coefficient matrix on the left.

Progeny production. If selection for production of progeny is the main concern of the breeder, the covariances between y and T are simply covariances between records on particular relatives. For example, suppose y_1 is a record on the dam of the individual considered for selection, and y_2 is the mean of paternal sibs of the individual. Then,

σ_{y_1T} = covariance between grandam's and grandprogeny's records.
σ_{y_2T} = covariance between "half-aunt" and niece.

Descendants' production. If selection is for descendants, this is almost equivalent to selection for additive genetic value, for note that in a non-inbred population the covariances between an individual's record and its descendants' records are

$$\text{Progeny: } \frac{1}{2}\sigma^2_{10} + \frac{1}{4}\sigma^2_{20} + \frac{1}{8}\sigma^2_{30} + \ldots$$

$$\text{Grand progeny: } \frac{1}{4}\sigma^2_{10} + \frac{1}{16}\sigma^2_{20} + \frac{1}{64}\sigma^2_{30} + \ldots$$

$$\text{Great grand progeny: } \frac{1}{8}\sigma^2_{10} + \frac{1}{64}\sigma^2_{20} + \frac{1}{512}\sigma^2_{30} + \ldots$$

$$\text{Descendant } n \text{ generations removed: } \frac{1}{2^n}\sigma^2_{10} + \frac{1}{2^{2n}}\sigma^2_{20} + \ldots + \frac{1}{2^{in}}\sigma^2_{i0} + \ldots$$

Thus, it is obvious that after very few generations, the coefficient of σ^2_{10} is overwhelmingly large as compared to any of the other components. Consequently, we should be primarily concerned with additive genetic value, that is we can let T = additive genetic value. Then σ_{y_iT} is simply $a_{i\alpha}\sigma^2_{10}$, where $a_{i\alpha}$ is the relationship between the animal with the *ith* record and α, the animal being evaluated. Further, we note that the value chosen for σ^2_{10}, appearing as it does in all right hand members, does not affect ranking, and consequently is not needed to maximize progress through selection. If, however, we wish to estimate how much progress will, in fact, be made we do need to know either σ^2_{10} or h^2.

If we use $a_{i\alpha}\sigma^2_{10}$ as right hand sides of equations in conjunction with left hand coefficients of the form in (6), we can then divide both sides of the equations by σ^2_y and obtain selection index equations requiring knowledge only of relationships, inbreeding coefficients, h^2, and if repeated records are used, r.

Then, r_{TI} has a simple computing form,

$$r_{TI} = \sqrt{\frac{b_1\sigma_{X_1T} + \ldots + b_N\sigma_{X_NT}}{\sigma^2_T}}$$

$$= \sqrt{\frac{b_1a_{1_\alpha}\sigma^2_{10} + \ldots + b_Na_{N_\alpha}\sigma^2_{10}}{\sigma^2_{10}}}$$

$$= \sqrt{b_1a_{1_\alpha} + \ldots + b_Na_{N_\alpha}} \quad .$$

Let us illustrate these last simple procedures. We wish to construct an index based on the individual's record, y_1, and a record on each of the parents, y_2, y_3. Then the equations to be solved for b's, using the simplifying assumptions are

$$\begin{bmatrix} 1 & \frac{1}{2}h^2 & \frac{1}{2}h^2 \\ \frac{1}{2}h^2 & 1 & 0 \\ \frac{1}{2}h^2 & 0 & 1 \end{bmatrix} \cdot \begin{bmatrix} b_1 \\ b_2 \\ b_3 \end{bmatrix} = \begin{bmatrix} h^2 \\ \frac{1}{2}h^2 \\ \frac{1}{2}h^2 \end{bmatrix}.$$

The solution is $b_1 = h^2(2 - h^2)/(2 - h^4)$,

$$b_2 = b_3 = h^2(1 - h^2)/(2 - h^4), \text{ and}$$

$$r_{TI} = \sqrt{b_1(1) + b_2\left(\frac{1}{2}\right) + b_3\left(\frac{1}{2}\right)}$$

$$= \sqrt{\frac{h^2(3 - 2h^2)}{2 - h^4}} \quad .$$

As a second illustration, suppose we wish to select sires on the basis of the mean of p half-sib progeny. Then the index equations are

$$\frac{1 + (p-1)\frac{1}{4}h^2}{p} b = \frac{1}{2}h^2$$

$$b = \frac{2ph^2}{4 + (p-1)h^2},$$

$$\text{and } r_{TI} = \sqrt{\frac{ph^2}{4 + (p-1)h^2}}.$$

Alternative Computational Procedures

An interesting and sometimes useful variation on the selection index method is the following,

$$I = \gamma_1 \sigma_{y_1T} + \ldots + \gamma_N \sigma_{y_NT},$$

where γ's are the solution to the following equations,

$$\sigma^2_{1y}\gamma_1 + \sigma_{y_1y_2}\gamma_2 + \ldots + \sigma_{y_1y_N}\gamma_N = y_1 - \mu_1$$
$$\sigma_{y_1y_2}\gamma_1 + \sigma^2_{y_2}\gamma_2 + \ldots + \sigma_{y_2y_N}\gamma_N = y_2 - \mu_2,$$

It is seen that this procedure simply interchanges $(y_i - \mu_i)$ and σ_{y_iT} as compared to the conventional procedure. The advantage of this method is that if we wish to evaluate several individuals from the same set of records, we need to solve only one set of equations, for note that the right hand members are $y - \mu$, and these remain the same for all individuals to be evaluated from that set of records. In contrast, the usual method has on the right hand side σ_{y_iT}, which changes from one individual to the next, as T changes.

The proof of the identity of the two methods is very simple. In the usual method,

$$I = b'(y - \mu),$$

where b is the solution to

$$Cb = t, \text{ or}$$
$$b = C^{-1}t.$$

$$\text{Therefore, } I = (C^{-1}t)'(y - \mu)$$
$$= t'C^{-1}(y - \mu). \qquad (10)$$

In the new method

$$I = \gamma't,$$

where γ is the solution to

$$C\gamma = y - \mu.$$

$$\text{Therefore, } I = [C^{-1}(y - \mu)]'t$$
$$= (y - \mu)'C^{-1}t$$
$$= t'C^{-1}(y - \mu).$$

This is the same as (10) since a scaler is equal to its transpose.

If the μ's are unknown we can substitute their m.l. estimates in the right hand sides of these new equations or we can obtain identical results by letting the index $= \gamma't$, where γ is the solution to

$$C\gamma + X\alpha = y,$$
$$X'\gamma = 0,$$

and α is a $p \times 1$ Lagrange multiplier. The solution to γ is

$$[I - C^{-1}X(X'C^{-1}X)^{-1}X']C^{-1}y,$$

and the index is then $\gamma't = t'\gamma$

$$= t'[I - C^{-1}X(X'C^{-1}X)^{-1}X']C^{-1}y$$
$$= t'C^{-1}[I - X(X'C^{-1}X')^{-1}X'C^{-1}]y$$

which is the same as (3), the procedure described for maximizing r_{TI} subject to $E(I) = 0$.

Another interesting procedure, an expansion of which is useful in problems involving line crosses and in cases with unknown μ's, will now be described.

Let $y_i = \mu + g_i + e_i \qquad i = 1,\ldots,N$

We wish to rank according to *g's*, their variance-covariance matrix being *G*. The variance-covariance matrix of *e's* is *E*, and *g's* and *e's* are uncorrelated. Consequently, the variance-covariance matrix of *y's* is (G + E), and the covariance between *y* and *g* is *G*. Now it can be shown that the criteria for selection, say $v_1,\ldots,v_N$ = the vector *v*, are the solutions to

$$(I + EG^{-1})v = y - \mu \text{ or}$$
$$v = (I + EG^{-1})^{-1}(y - \mu). \tag{11}$$

To prove that this solution is identical to the conventional one we note that the criteria in the ordinary index procedure are

B'y, where B, an N × N matrix, is the solution to

$(G + E)B = G$, or

$B = (G + E)^{-1}G$.

Therefore, the criteria $= G'(G + E)^{-1}(y - \mu)$

$= G(G + E)^{-1}(y - \mu)$, since G is symmetric.

$= [(G + E)G^{-1}]^{-1}(y - \mu)$

$= (I + EG^{-1})^{-1}(y - \mu)$

= v shown in (11).

When $\mu = X\beta$ is unknown, the following procedure yields simultaneously the m.l. estimator of β and selection criteria based on maximizing r_{TI} subject to E(I) = 0. Also, the procedure is equivalent to substituting $\hat{\beta}$ = m.l. estimator for β in the usual index equation.

$$X'E^{-1}X\hat{\beta} + X'E^{-1}v = X'E^{-1}y$$
$$E^{-1}X\hat{\beta} + (E^{-1} + G^{-1})v = E^{-1}y. \tag{12}$$

The last of these equations can be written

$$X\hat{\beta} + (I + EG^{-1})v = y \text{ or}$$

$v = (I + EG^{-1})^{-1}(y - X\hat{\beta})$, where $\hat{\beta}$ is some estimate of β. This is the same *v* as above when $\hat{\beta}$ is substituted for β. To prove that $\hat{\beta}$ is the m.l. estimator of β, we note that the m.l. estimator of β is the solution to

$$X'(G + E)^{-1}X\hat{\beta} = X'(G + E)^{-1}y \text{ or}$$
$$\hat{\beta} = [X'(G + E)^{-1}X]^{-1}(G + E)^{-1}y. \tag{13}$$

When we eliminate v from (12), the following equations result

$$X'WX\hat{\beta} = X'Wy, \text{ where}$$
$$W = E^{-1} - E^{-1}(I + EG^{-1})^{-1}$$
$$= E^{-1} - [E + EG^{-1}E]^{-1}.$$

Consequently we can show that the solution to $\hat{\beta}$ in (12) is m.l. if we prove that $W = (G + E)^{-1}$, or that $(G + E)W = I$

$$(G + E)W = (G + E)[E^{-1} - (E + EG^{-1}E)^{-1}]$$
$$= GE^{-1} + I - (G + E)(E + EG^{-1}E)^{-1}$$
$$= GE^{-1} + I - GE^{-1} = I, \text{ thus completing the proof.}$$

In many applications of the above method the e's are uncorrelated and have common variance σ^2_e. That is, $E = \sigma^2_e I$ and $E^{-1} = \frac{1}{\sigma^2_e} I$.

Consequently, by multiplying each equation of (12) by σ^2_e we obtain

$$X'X\beta + X'v = X'y$$
$$X\beta + (I + \sigma^2_e G^{-1})v = y.$$

To illustrate, let y_1 = the record on individual, and y_2 and y_3 = records on parents. The mean of each y is μ. The model is the simple one of (4). Then,

$$X' = (1 \quad 1 \quad 1),$$
$$\sigma^2_e = (1 - h^2)\sigma^2_y,$$

$$G = h^2\sigma^2_y \begin{bmatrix} 1 & \frac{1}{2} & \frac{1}{2} \\ \frac{1}{2} & 1 & 0 \\ \frac{1}{2} & 0 & 1 \end{bmatrix}, \text{ and } G^{-1} = \frac{1}{2h^2\sigma^2_y} \begin{bmatrix} 4 & -2 & -2 \\ -2 & 3 & 1 \\ -2 & 1 & 3 \end{bmatrix}.$$

Then, the equations to be solved to evaluate these three individuals are

$$\begin{bmatrix} 3 & 1 & 1 & 1 \\ 1 & \frac{4-2h^2}{2h^2} & \frac{-2(1-h^2)}{2h^2} & \frac{-2(1-h^2)}{2h^2} \\ 1 & \frac{-2(1-h^2)}{2h^2} & \frac{3-h^2}{2h^2} & \frac{1-h^2}{2h^2} \\ 1 & \frac{-2(1-h^2)}{2h^2} & \frac{1-h^2}{2h^2} & \frac{3-h^2}{2h^2} \end{bmatrix} \cdot \begin{bmatrix} \mu \\ v_1 \\ v_2 \\ v_3 \end{bmatrix} = \begin{bmatrix} y. \\ y_1 \\ y_2 \\ y_3 \end{bmatrix}.$$

SELECTION INDEX FOR MORE THAN ONE TRAIT

The application of the selection index to selection for more than one trait requires only a simple extension of the principles described for one trait selection. In fact, if we define T properly, the techniques are exactly the same as in single trait selection. Suppose it is desired to select for breeding value with respect to s different traits and we denote the breeding values of these traits by $T_1, T_2, \ldots, T_s$. The records available for use in selection may be phenotypic observations on some or all of these traits in the candidates for selection or in their relatives.

One possibility for using a selection index on these several traits would be to construct selection indexes for computing a separate criterion for each trait on each individual and then to select on trait one only in the first generation, trait two in the second, and so on. This is called "tandem" selection. A second possibility would be to compute criteria as in tandem selection and then to select only those with all criteria equal to or higher than chosen minima. This is called selection by "independent culling levels." If, however, it is possible to assign to the traits relative economic values for increases of one unit, breeding value can then be defined as a weighted function of breeding values for the various traits. Thus, if the relative values are $v_1, v_2, \ldots, v_s$, the breeding value is defined as

$$T = v_1T_1 + \ldots + v_sT_s.$$

Employing this definition of T, the selection index equations, from the procedure of (1), have left members = C = the variance-covariance matrix of y's, and and the right members are elements of the N × 1 vector,

$$t = (\sigma_{y_1T}\ \sigma_{y_2T} \ldots \sigma_{y_NT})',$$

where $\sigma_{y_iT} = v_1\sigma_{y_iT_1} + \ldots + v_s\sigma_{y_iT_s}$.

Let t_1 = elements of vector of $\sigma_{y_iT_1}$,

t_2 = elements of vector of $\sigma_{y_iT_2}$,

etc.

Then, the right hand side of the selection index equations are

$$t = v_1t_1 + \ldots + v_st_s.$$

Consequently, the index equations are

$$Cb = t \text{ and}$$

$$b = C^{-1}t$$

$$= C^{-1}v_1t_1 + \ldots + C^{-1}v_st_s,$$

and the selection index is

$$b'y = v_1t_1'C^{-1}y + \ldots + v_st_s'C^{-1}y. \qquad (15)$$

An alternative procedure that leads to exactly the same result is to construct separate indexes for each trait and then to weight either these indexes or the sets of s criteria by the economic values, that is,

$$I = v_1I_1 + \ldots + v_sI_s.$$

The proof of the equivalence of these methods follows.

$I_1 = b_1'y$, where $b_1 = C^{-1}t_1$,

$I_2 = b_2'y$, where $b_2 = C^{-1}t_2$,

etc. Then,

$$I = v_1b_1'y + \ldots + v_sb_s'y$$

$$= v_1t_1'C^{-1}y + \ldots + v_st_s'C^{-1}y, \text{ which is the same as (15).}$$

This latter method has the distinct advantage that changes in relative economic values with time or differences from one location to another do not require construction of new indexes. For example, an extension worker who is

asked to advise dairymen on selection for both type and production realizes that the value of type relative to milk production is great for the breeder who capitalizes on show ring winnings by selling breeding stock but is of little or no value to the dairyman who sells only cull cows. The extension worker can, however, give this advice to all,

1. Evaluate animals for milk production with an index
   $I_m = b_1y_1 + \ldots + b_Ny_N$.
2. Evaluate the same animals for type with another index
   $I_t = \beta_1y_1 + \ldots + \beta_Ny_N$.
3. Weight the above two criteria computed for each animal by v_m and v_t.

The dairyman must decide for himself what values to use for v_m and v_t.

SELECTION OF LINES AND LINE CROSSES

The selection index method need not be restricted to selection of individuals, for exactly the same principles can be applied to discriminating among lines, line-crosses, or other genetic groups.

Selection of Groups for Top-Crossing

A certain number of genetic groups, inbred lines for example, are to be selected for top-crossing on some specified population. A test is performed in which q individuals are selected at random from the *ith* group and n_{ij} top-cross progeny of the *jth* individual from the *ith* group are observed. The following model is assumed:

$$y_{ijk} = g_i + p_{ij} + e_{ijk}, \tag{16}$$

g, p, and e are normally, independently distributed with means 0 and variances σ^2_g, σ^2_p, σ^2_e. We wish to maximize progress in $\bar{g}$ by using an index of the form,

$$I_i = b_{i1}\bar{y}_{i1.} + b_{i2}\bar{y}_{i2.} + \ldots$$

The C matrix has according to the model (16), the following elements:

$$\text{diagonals} = \sigma^2_g + \frac{1}{n^2_{i.}} \sum_j n_{ij}{}^2\sigma^2_p + \frac{1}{n_{i.}} \sigma^2_e$$

$$\text{off diagonals} = \sigma^2_g.$$

The right hand sides are all σ^2_g.

Selection of Single Crosses

A random sample of lines from some population is chosen for producing some or all of the possible single crosses. A random sample of n_{ij} progeny from the cross of line i by line j is observed. On the basis of these results a certain number of crosses is chosen for further testing or for commercial production. A simple criterion is the line cross mean, but if n_{ij} is small, this clearly is not a very accurate method. It seems logical to suppose that a better criterion could be

found by using also the mean of the reciprocal cross and the data from all other crosses in which either of the parental lines appears.

A simple model that is appropriate for some species is

$$y_{ijk} = g_i + g_j + s_{ij} + e_{ijk}.$$

The elements of this model are normally and independently distributed with means 0 and variances σ^2_g, σ^2_s, σ^2_e. It is assumed that reciprocal crosses are equal, except for sampling. Consequently $s_{ij} = s_{ji}$. The model also assumes either that the lines are homozygous or that only one progeny per parent is tested. The model can be expanded to incorporate less restrictive assumptions, but it suffices to illustrate the principles of index selection of crosses.

Selection for general combining ability. By definition, general combining ability refers to the relative value of the *g's*. Consequently $T_i = g_i$. A simple indexing procedure to evaluate the *αth* line is $I = b_\alpha \bar{y}_\alpha$ where $\bar{y}_\alpha$ is the mean of all observations on the *αth* line, and

$$b_\alpha = \sigma^2_g/\sigma^2_{\bar{y}_\alpha},$$
$$\sigma^2_{\bar{y}_\alpha} = \sigma^2_g + (\sigma^2_g + \sigma^2_s)[\sum_{j \neq \alpha} (n_{\alpha j} + n_{j\alpha})^2]/(n_{\alpha.} + n_{.\alpha})^2 + \sigma^2_e/(n_{\alpha.} + n_{.\alpha}).$$

If subclass numbers are unequal, a better index can be constructed by utilizing the data on all crosses rather than just those having the α line as a parent. Now the index is

$$I_\alpha = \sum_{i<j} b_{ij}\bar{y}_{ij}, \text{ where}$$
$$\bar{y}_{ij} = (y_{ij.} + y_{ji.})/(n_{ij} + n_{ji}).$$

To compute these *b*'s we use equations (1) where

$$\text{Diagonal element of C} = 2\sigma^2_g + \sigma^2_s + \sigma^2_e/(n_{ij} + n_{ji}), \tag{17}$$
Off-diagonal elements of C having one subscript in common $= \sigma^2_g$,
Off-diagonal elements of C having no subscript in common $= 0$, and
Right hand members = covariance between $\bar{y}_{ij}$ and g_α
$= \sigma^2_g$ if one subscript of $\bar{y}_{ij}$ is α
$= 0$ if neither subscript is α.

Selection for single cross performance. In this case T is the value of a single cross, which for the cross of α by γ is

$$g_\alpha + g_\gamma + s_{\alpha\gamma}.$$

A variety of procedures all leading to the same result can be used. The problem is quite analogous to selection for more than one trait since breeding value in the single cross is a linear function of underlying random variables *(g's* and *s)* while that for multiple trait selection is a linear function of breeding values for the several traits.

One method is to use the index,

$$\sum_{i<j} b_{ij}\bar{y}_{ij},$$

where $\bar{y}_{ij} = (y_{ij\cdot} + y_{ji\cdot})/(n_{ij} + n_{ji})$. Then the C matrix is the same as described above, (17). The covariances for the right hand side of equations (1) when the cross is, say $\alpha \times \gamma$, are

Covariance with $\bar{y}_{\alpha\beta}$: $2\sigma^2_g + \sigma^2_s$,
with $\bar{y}_{\alpha j}$, $\bar{y}_{i\alpha}$, $\bar{y}_{\gamma j}$, $\bar{y}_{i\gamma}$: σ^2_g, and
with all other $\bar{y}_{ij}$: 0.

This method is tedious since it requires as many solutions to the index equations as there are crosses to be evaluated. Consequently it is desirable to use instead the method described in an earlier section, in which y's and σ_{yT}'s are interchanged.

SOLUTION TO THE SELECTION INDEX USING LEAST SQUARES EQUATIONS THAT ARE APPROPRIATELY MODIFIED

Let the linear model for y, and N × 1 vector of observations be,

$$y = X\beta + Zu + e \tag{18}$$

X is a known N × p matrix of rank p.

β is an unknown p × 1 vector.

Z is a known N × r matrix of rank r.

u is an r × 1 vector having a multivariate normal distribution with means = O, and variance-covariance matrix = D, which is a non-singular, r^2 matrix.

e is an N × 1 vector having a multivariate normal distribution with means = O and variance-covariance matrix = R, which is a non-singular, N^2 matrix.

u and e are independently distributed.

We wish to estimate β by m.l. and to use these estimators, $\hat{\beta}$, in selection indexes of the form,

$$\hat{u} = B'(y - X\hat{\beta})$$

$\hat{u}$ is an r × 1 vector corresponding to u, but this does not necessarily imply that $\hat{u}$ is an estimator of u. Rather it is a set of criteria for selection.

B is an N × r matrix computed according to the principle of selection index construction.

According to the model, (18), the variance-covariance matrix of y is $A = R + ZDZ$, and the covariance between y and u is ZD, an N × r matrix. Consequently, the index equations are,

$$AB = ZD \text{ and}$$
$$B = A^{-1}ZD.$$

Therefore, $\hat{u} = DZ'A^{-1}(y - X\hat{\beta})$. (19)

The m.l. estimator of β can be found by solving the following equations

$$X'A^{-1}X\hat{\beta} = X'A^{-1}y \text{ or}$$
$$\hat{\beta} = (X'A^{-1}X)^{-1}X'A^{-1}y. \tag{20}$$

An alternative procedure that is often much easier requires setting up least squares equations to solve for β and u as though u were fixed and then adding D^{-1} to the lower r^2 submatrix of coefficients. The following equations result. This method was suggested by Henderson (4) in 1952.

$$\begin{aligned} X'R^{-1}X\tilde{\beta} + X'R^{-1}Z\tilde{u} &= X'R^{-1}y \\ Z'R^{-1}X\tilde{\beta} + (Z'R^{-1}Z + D^{-1})\tilde{u} &= Z'R^{-1}y \end{aligned} \tag{21}$$

We must now prove that $\tilde{\beta} = \hat{\beta}$ of (20) and that $\tilde{u} = \hat{u}$ of (19). To prove the former, we note that since in (21)

$$\tilde{u} = (Z'R^{-1}Z + D^{-1})^{-1}Z'R^{-1}(y - X\tilde{\beta}), \tag{22}$$

equation (21) can be reduced to

$$\begin{aligned} &X'W^{-1}X\tilde{\beta} = X'W^{-1}y, \text{ where} \\ &W = R^{-1} - R^{-1}Z(Z'R^{-1}Z + D^{-1})^{-1}Z'R^{-1}. \end{aligned}$$

Therefore, if $w = A^{-1}$, $\tilde{\beta} = \hat{\beta}$. We show that this is true by proving $AW = I$.

$$\begin{aligned} AW &= (R + ZDZ')[R^{-1} - R^{-1}Z(Z'R^{-1}Z + D^{-1})^{-1}Z'R^{-1}] \\ &= I + ZDZ'R^{-1} - Z(Z'R^{-1}Z + D^{-1})^{-1}Z'R^{-1} \\ &\quad - ZDZ'R^{-1}Z(Z'R^{-1}Z + D^{-1})^{-1}Z'R^{-1} \\ &= I + ZDZ'R^{-1} - Z(I + DZ'R^{-1}Z)(Z'R^{-1}Z + D^{-1})^{-1}Z'R^{-1} \\ &= I + ZDZ'R^{-1} - ZD(D^{-1} + Z'R^{-1}Z)(Z'R^{-1}Z + D^{-1})^{-1}Z'R^{-1} \\ &= I + ZDZ'R^{-1} - ZDZ'R^{-1} \\ &= I. \end{aligned}$$

In order to show that $\tilde{u} = \hat{u}$ we prove the following,

$$\begin{aligned} \tilde{u} &= (Z'R^{-1}Z + D^{-1})^{-1}Z'R^{-1}(y - X\tilde{\beta}), \text{ from (22).} \\ &= (Z'R^{-1}Z + D^{-1})^{-1}Z'R^{-1}AA^{-1}(y - X\tilde{\beta}) \\ &= (Z'R^{-1}Z + D^{-1})^{-1}Z'R^{-1}(ZDZ' + R)A^{-1}(y - X\tilde{\beta}) \\ &= (Z'R^{-1}Z + D^{-1})^{-1}(Z'R^{-1}ZDZ' + Z')A^{-1}(y - X\tilde{\beta}) \\ &= (Z'R^{-1}Z + D^{-1})^{-1}(Z'R^{-1}Z + D^{-1})DZ'A^{-1}(y - X\tilde{\beta}) \\ &= DZ'A^{-1}(y - X\tilde{\beta}) \\ &= \hat{u} \text{ of (19).} \end{aligned}$$

Thus, we have proved that if least squares equations are set up under the assumption that the random elements of the model, except for e, are fixed and then add the inverse of the variance-covariance matrix of the random elements, we can solve directly for the m.l. estimators of the fixed elements of the linear model and for criteria to use in selection. In many problems this method has distinct computational advantages over the conventional selection index method and over the usual m.l. estimation (weighted least squares) of the fixed elements of the linear model.

In most applications R is diagonal or better yet is $\sigma_e^2 I$, which greatly simplifies setting up (21). Also in some cases D also is diagonal, in the single cross example above, for instance. But if D is a large non-diagonal matrix, its inversion can be avoided if the following equations are written,

$$\begin{aligned} X'R^{-1}X\tilde{\beta} + X'R^{-1}ZD\tilde{v} &= X'R^{-1}y, \\ DZ'R^{-1}X\tilde{\beta} + (DZ'R^{-1}ZD + D)\tilde{v} &= DZ'R^{-1}y. \end{aligned}$$

Then, $\tilde{\beta}$ has the same value as in (21), and $\tilde{u} = D\tilde{v}$ has the same value as $\tilde{u}$ in (21). The proof of this is

1. Substitute $D^{-1}\tilde{u}$ for $\tilde{v}$ in (22).
2. Pre-multiply the last equation of (22) by D^{-1}.
3. Note that the resulting equations are identical to (21).

It is interesting to note that the lower r^2 submatrix of the inverse of the coefficients of the left side of (21) is the variance-covariance matrix of the deviation of $\hat{u}$'s from their respective u's. That is,

$$E(\hat{u} - u)(\hat{u} - u)'.$$

CONSEQUENCES OF USING PARAMETER ESTIMATES AND ASSUMING NORMALITY

Some of the unsolved problems of index selection are:

1. What are the consequences of non-normality on the efficiency of a selection index constructed as though y and T have the multivariate normal distribution when they actually have some other distribution?
2. What are the consequences of using variance and covariance estimates in place of parameter values on (a) the effectiveness of selection and (b) on prediction of genetic advance?
3. How should indexes be constructed to maximize genetic progress when either or both of the assumptions, normality and known parameters, do not hold?

The use of electronic computers, which are becoming increasingly available to plant and animal breeders, for sampling investigations of these problems appears promising. Work along these lines is in progress at Iowa State University, Cornell University, and probably elsewhere.

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Genotype-Environment Interactions

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INTRODUCTION

CONCLUSIONS about inheritance are inferred from data on phenotype. Appropriate interpretations depend, therefore, on our understanding of the composition of phenotypic variation.

We are all well aware that phenotype reflects non-genetic as well as genetic influences on development. Furthermore, the effects of genotype and environment are not independent. The phenotypic response to a change in environment is not the same for all genotypes; the consequences of variation in genotype depend on environment. This inter-play in effect of the genetic and non-genetic on development is what we call genotype-environment (GE) interaction.

An obvious and important effect of GE interaction is to reduce the correlation between phenotype and genotype with the result that valid inference becomes more complicated. This is true whether interest is focused on plant improvement procedures or on the mechanisms of inheritance.

The basic causes of GE interaction must be matters of physiology and biochemistry. Their analysis lies in the area of developmental genetics and will receive no further attention in this presentation. However, two related questions deserve brief consideration. Should explanations of GE interactions be sought? Is it likely that, by such explanations, statistical genetics will eventually be relieved of the problems presently posed by GE interaction? The respective answers in our opinion are (a) yes, and (b) no. Better understanding of causes is desirable and doubtless will prove significant in connection with plant improvement. However, unexplained interactions will always be with us. Future research will provide explanations for some but others will remain unexplained. Certainly, GE interaction will not be eliminated as a portion of the total problem to be dealt with in statistical genetics.

Aside from basic causes, the things worth knowing about GE interactions center around their magnitudes and the ways in which they impinge on genetic inquiries and genetic improvement efforts. A limited number of examples should suffice for illustration.

The plant breeder seeks genotypes that are high performing. Should he aim his program at development of varieties that will perform well in a broad spectrum of environments or at varieties highly adapted for special kinds of environments? The first alternative is favored by small GE interaction, the second by large. Whether environments can be characterized in advance is of course critical in this connection. A variety that is superior under very special conditions but only ordinary otherwise has little value if in advance of planting we cannot tell whether the special conditions will in fact prevail. However, criteria like length of season, moisture pattern history, soil type, and plans for fertilization provide bases for meaningful classification of environments prior to planting.

Should data on which selection will be based be collected at more than one location, in more than one year, or both? Here again the underlying issue is amount of GE interaction. The more interaction, the more will be gained by basing selection on performance measured over a larger sample of the kind of environments for which the eventual varieties are being developed.

A prime objective of quantitative genetic inquiry is magnitude of genetic variance as the basis for predicting genetic improvement in selection programs. The significance of GE interactions in this connection lies in their impact on reliability of estimates. Depending on kind of data employed, they may introduce upward bias. In any event they are the source of part of the random error of estimates. It is tempting to argue that no very exact information about size of genetic variance is really needed, since regardless of how large it may be the breeder must go ahead with his work; that while it would be nice to know in advance the progress likely to be achieved, what will actually be done would not be changed much anyway. General acceptance of this point of view would in our opinion be most unfortunate. First, over-estimation of genetic variance would in some cases lead to investment of time and effort not justified by the real potential for improvement of genetic stocks employed. Second, optimum procedure may vary significantly depending on magnitude of genetic variance. Third, there is danger that sound breeding programs may be adandoned prematurely or unwisely because of results that are disappointing relative to unwarranted expectations based on erroneous estimates of genetic variance. Finally, but of utmost importance, we are now at a critical point in evaluation of statistical genetic theory. Our present body of theory has great potential value as a source of guide lines in breeding practice. It will be most unfortunate if unwarranted doubts of its validity are allowed to accumulate. This could easily happen unless appropriate care is exercised regarding the evidence presented or accepted. In particular, basing expectations of progress on biased estimates of genetic variance will lead inevitably to discrepancy (on the average) between realized and expected response to selection.

The intent of the foregoing is not to argue that the breeder should obtain estimates of genetic variance for every genetic population employed in a breeding program—far from it. The cost of good estimates suggests that a

limited number of really good estimates be used for inference concerning generally similar materials.

Another major class of objectives in quantitative genetics involves the relative size of different genetic variances. The ratio of additive to dominance variance has been used as evidence concerning level of dominance, for example, Robinson *et al.* (13, 14) and Gardner and Lonnquist (7). Other issues that have been investigated in terms of genetic variance component ratios are importance of epistasis (e.g., see Comstock *et al.* 3), genetic differences between populations (e.g., see Moll *et al.* 11), and significance of linkage in quantitative inheritance (e.g., see Robinson *et al.* 13, and Gardner and Lonnquist, 7). Adequate precision in estimation of such ratios requires a somewhat higher order of accuracy in estimation of the individual variances than is usually needed for other purposes. In fact, the effort required for satisfactory unbiased estimates will generally be formidable. Most of you are aware that estimates from data collected in a single year and location are biased upward by GE interaction. However, for this very reason their coefficients of variation will be smaller. Further, if the bias involved is proportionately the same for variances to be compared, it disappears in the ratio estimate (1, 2). Briefly, reliable evidence concerning the ratios of genetic variances is much more expensive if it must be based on unbiased estimates of the separate variances. We see in this example a different facet of the complex of problems posed by GE interactions.

Further general discussion would serve little purpose. Let us turn now to more rigorous treatment of issues. Complete clarity can be achieved only if terms used are defined without ambiguity. Therefore, attention will be directed first to definitions.

THE MEANING OF ENVIRONMENT

We must first recognize that we use the word, environment, in two ways. We speak on the one hand of the environment of a single organism as opposed to that of another growing at the same time and in almost the same place and, on the other hand, of the environment associated with a general location and period of time. Specificity is absolute in the first case but not in the second. Distinction is sometimes achieved by prefix, micro- or macro-.

The environment of a single plant is made up of all the things, other than genotype of the plant, that affect its development. This includes physical and chemical attributes of the soil in which the plant grows; climatic variables (temperature, humidity, etc.) amount, distribution and quality of solar radiation; and the number and kind of biological organisms (pathogens, insects, etc.) to which the plant is exposed.

The complexity of environment is emphasized still more when we remind ourselves of the infinite variety of patterns in time (relative to the life span of plants) that is exhibited by many of the components of environment. For practical purposes the potential number of different single plant environments is infinite (even within a very restricted area) and the probability that two plants in the same field at the same time have had precisely the same environ-

ment is infinitesimal. It is this unique complex of forces in development that we call the micro-environment (of a single plant or organism).

We visualize on the other hand that organisms encounter a different class of environments in one area than in another, in one period of time than in another. The environments that are potential or realized within a given area and period of time are referred to collectively as a macro-environment. A macro-environment is in fact a population of micro-environments and differences between macro-environments rest in the fact that in terms of physiological consequence micro-environments are more alike within macro-environments than from one of the latter to another.

THE MODEL FOR PHENOTYPE

Searching discussion of any of the issues connected with GE interaction effects calls for concise advance specification of what we understand these effects to be. This is not provided by such common but ambiguous statements as "Let $(ye)_{ij}$ be the effect of interaction between the *ith* genotype and the *jth* environment."

Genotype environment interaction effects cannot be defined (or effectively discussed) without correlated definition of effects of genotype and environment. Hence, in the process of defining interaction effects, all of the effects visualized in some familiar models for phenotype will be considered.

Plant breeders, and population geneticists generally, are committed to the concept that genotypes vary in "value." In fact plant breeding revolves around a continuing effort to develop, discover, or identify genotypes that are in some way "superior" with reference to plant production purposes. It is logical therefore that a concise definition of the "value of a genotype" be provided that results in logical connection between "value" and effects. It is most convenient in fact to begin with definition of value of a genotype (or environment).

The value of a genotype rests in the phenotypic expressions that it evokes. These depend also on environment. However, there is no practical purpose to be achieved by assigning value to a genotype in terms of the associated phenotype in a specific micro-environment; a particular micro-environment has little chance of being encountered again. There appears little doubt that when the population geneticist speaks of the value of a genotype he means value (by the criterion of phenotypes evoked) with reference to a particular class or population of environments. And when he tries to compare the values of different genotypes or to measure variation in values of different genotypes, he is thinking of values that all pertain to the same population of environments.

The foregoing provides the guide lines for a set of formal definitions. Consider a population of n genotypes and another of m micro-environments. Let n and m be extremely large so that for practical purposes both populations may be assumed infinite. Now imagine a plant of each genotype grown in each environment to provide a phenotypic expression for each genotype in each environment. Let P_{kq} be any attribute of phenotype, e.g., plant height, associated

with the *kth* genotype in the *qth* micro-environment. The *mn* phenotypic values, *P's,* comprise a population that can usefully be visualized in terms of a two-way table (see Figure 1).

Environment	Genotype							Mean
	1	2	3		k		n	
1	P_{11}	P_{21}	P_{31}	. . .	P_{k1}	. . .	P_{n1}	X_1
2	P_{12}	P_{22}	P_{32}	. . .	P_{k2}	. . .	P_{n2}	X_2
3	P_{13}	P_{23}	P_{33}	. . .	P_{k3}	. . .	P_{n3}	X_3
.	.	.	.		.		.	.
.	.	.	.		.		.	.
.	.	.	.		.		.	.
q	P_{1q}	P_{2q}	P_{3q}	. . .	$P_{kq} = u + y_k + x_q + (xy)_{kq}$	. . .	P_{nq}	$X_q = u + x_q$
.	.	.	.		.		.	.
.	.	.	.		.		.	.
.	.	.	.		.		.	.
m	P_{1m}	P_{2m}	P_{3m}	. . .	P_{km}	. . .	P_{nm}	X_m
Mean	Y_1	Y_2	Y_3		$Y_k = u + y_k$		Y_n	u

FIGURE 1. *Tabular representation of a population of phenotypic values and the effects into which phenotypic value is divided.*

In accord with principles already discussed value of the *kth* genotype will be defined as

$$Y_k = \frac{1}{m} \sum_q P_{kq}$$

Effects are conventionally defined so that their population means are zero, and it is logical that value and effect of a genotype be perfectly correlated. Both result if the effect of the *kth* genotype is defined as

$$y_k = Y_k - u_Y$$

In like manner the value and effect of the *qth* micro-environment will be defined as

$$X_q = \frac{1}{n} \sum_k P_{kq} \text{ and}$$

$$x_q = X_q - u_x, \text{ respectively.}$$

Of course, $u_x = u_y$ and both equal u, the general mean of the population.

$$u = \frac{1}{mn}\sum_k\sum_q P_{kq} = \frac{1}{m}\sum_q\frac{1}{n}\sum_k P_{kq} = \frac{1}{n}\sum_k\frac{1}{m}\sum_q P_{kq}$$

If there were no GE interactions, i.e., if the difference between phenotypes evoked by any pair of genotypes in the same micro-environment were constant regardless of environment, P_{kq} would always equal $u + y_k + x_q$. Since differences between P_{kq} and $u + y_k + x_q$ result from GE interaction, the effect of interaction between the *kth* genotype and the *qth* micro-environment is logically defined as

$$(xy)_{kq} = P_{kq} - y_k - x_q - u.$$

Rearranging we obtain one of the familiar models for phenotype

$$P_{kq} = u + y_k + x_q + (xy)_{kq}. \qquad (1)$$

The definitions of the effects are arbitrary but intuitively appealing, and the authors believe them to be in conformity with the concepts of population geneticists generally. Moreover, they confer concise meaning on each effect in the model, a virtue that will facilitate clarity in further discussion.

Expression (1) does not recognize macro-environments but is easily extended to do so. The population of micro-environments pertinent to any genotype population in plant breeding will have dimensions of both time and space, i.e., the breeder is always interested in value of genotypes with respect to the micro-environments of a geographical area and a period of time extending into the future. A particular macro-environment, the *jth*, may be identified with a given time and location and will be comprised of the micro-environments that are potential therein. Its effect, f_j, is logically defined as the average of the effects of those micro-environments and the effect of interaction of the *kth* genotype with the macro-environment, $(fy)_{jk}$, as the average of the effects of interaction of the *kth* genotype with the micro-environments of the macro-environment.

$$f_j = \frac{1}{m_j}\sum_q x_{jq} \text{ and } (fy)_{jk} = \frac{1}{m_j}\sum_q (xy)_{jkq}$$

where m_j = number of micro-environments in the *jth* macro-environment. Expression (1) can now be rewritten as follows:

$$\begin{aligned} P_{jkq} &= u + y_k + x_{jq} + (xy)_{jkq} \\ &= \mu + y_k + f_j + (fy)_{jk} + (x_{jq} - f_j) + ((xy)_{jkq} - (fy)_{jk}) \\ &= u + y_k + f_j + (fy)_{jk} + e_{jkq}. \end{aligned} \qquad (2)$$

Here $e_{jkq} = (x_{jq} - f_j) + ((xy)_{jkq} - (fy)_{jk})$. In other words it is made up of (a) deviation of the effect of the *qth* micro-environment from the mean of such effects for the macro-environment and (b) the deviation of the effect of interaction between the *kth* genotype and the *qth* micro-environment from the mean of all these effects for the macro-environment.

Because populations of genotypes usually have a family structure, it is very frequently desirable that effects associated with families be included in

our models for phenotype. Let $\bar{y}_i$ be the effect of the *ith* family of genotypes and $(f\bar{y})_{ij}$ the effect of interaction between the *ith* family and *jth* macro-environment. They are logically defined as

$$\bar{y}_i = \frac{1}{n_i} \sum_k y_{ik} \text{ and } (f\bar{y})_{ij} = \frac{1}{n_i} \sum_k (fy)_{ijk}$$

where n_i = number of genotypes in the *ith* family.
We can now modify expression (2) as follows

$$P_{ijkq} = u + \bar{y}_i + f_j + (f\bar{y})_{ij} + e_{ijkq}, \tag{3}$$

where

$$\begin{aligned} e_{ijkq} &= (x_{jq} - f_j) + ((xy)_{ijkq} - (fy)_{ijk}) \\ &\quad + (y_{ik} - \bar{y}_i) + ((fy)_{ijk} - (f\bar{y})_{ij}) \\ &= (x_{jq} - f_j) + (y_{ik} - \bar{y}_i) + ((xy)_{ijkq} - (f\bar{y})_{ij}). \end{aligned}$$

THE MODELS AND THINGS STATISTICAL

Sums of effects

Because y_k and x_q of model (1) are defined as deviations from means it is obvious that their population sums, $\sum_k y_k$ and $\sum_q x_q$, should equal zero.

Next consider the (xy)'s of any single column in Figure 1, i.e. the interaction effects associated with a single genotype. From the definition of such effects, their sum for a column is

$$\sum_q (xy)_{kq} = \sum_q P_{kq} - m(u + y_k) - \sum_q x_q.$$

By the definitions of y_k and Υ_k

$$\sum_q P_{kq} - m(u + y_k) = 0.$$

Thus, $\sum_q (xy)_{kq} = \sum_q x_q$ = zero, and this is true for every genotype. By analagous procedure it can be shown that $\sum_k (xy)_{kq}$ = zero for every micro-environment.

Various other sums go to zero. These include, relative to model (2), $\sum_j f_j$, $\sum_j (fy)_{jk}$, $\sum_k (fy)_{jk}$, and $\sum_q e_{jkq}$; and relative to model (3), $\sum_i \bar{y}_i$, $\sum_i (f\bar{y})_{ij}$, $\sum_j (f\bar{y})_{ij}$, and $\sum_k \sum_q e_{ijkq}$.

Covariances of effects

In presenting models for phenotype, it is frequently stated as an assumption that variations of the several effects are mutually independent, i.e. that all covariances of effects are zero. Constraints imposed on covariances by the way in which effects are defined are worth noting.

Covariances of direct effects—These are uniformly zero when considered relative to the whole population or relative to the entire segment of the population associated with either a single genotype or a single environment. Consider x and y of model (1). Let $\sigma_{x.y}$ symbolize the covariance over the whole popula-

tion; ${}_k\sigma_{x.y}$, the covariance for the entire portion of the population associated with the *kth* genotype; and ${}_q\sigma_{x.y}$, the covariance for the entire portion associated with the *qth* micro-environment.[1] Thus,

$$\sigma_{x.y} = \frac{1}{nm}\sum_k\sum_q x_q\, y_k = \frac{1}{nm}\sum_k y_k \sum_q x_q = \text{zero},$$

$${}_k\sigma_{x.y} = \frac{1}{m}\, y_k \sum_q x_q = \text{zero, and}$$

$${}_q\sigma_{x.y} = \frac{1}{n}\, x_q \sum_k y_k = \text{zero}.$$

The key point in all cases is that every value of both $\sum_q x_q$ and $\sum_k y_k$ is zero. By similar algebra it is easily shown for model (2) that

$$\sigma_{t.y} = {}_j\sigma_{t.y} = {}_k\sigma_{t.y} = 0$$

and for model (3) that

$$\sigma_{t.\bar{y}} = {}_j\sigma_{t.\bar{y}} = {}_i\sigma_{t.\bar{y}}.$$

In all cases the subscript preceding σ identifies the segment of the population to which the covariance applies in the manner outlined for model (1). For example, the i of ${}_i\sigma_{f.\bar{y}}$ identifies this as covariance of f and $\bar{y}$ for the entire segment of the population associated with the *ith* family of genotypes.

Covariances of direct effects with interaction effects—With reference to model (1) consider the entire segment of the population associated with the *qth* micro-environment. For this segment the covariance of y with (xy) is

$${}_q\sigma_{y.xy} = \frac{1}{n}\sum_k y_k\,(xy)_{kq}.$$

There is nothing about this quantity that forces it to a particular value. However, its mean over all micro-environments is the covariance of y and (xy) for the entire population which we find must be zero.

$$\sigma_{y.xy} = \frac{1}{m}\sum_q {}_q\sigma_{y.xy} = \frac{1}{m}\sum_q \frac{1}{n}\sum_k y_k\,(xy)_{kq}$$

$$= \frac{1}{nm}\sum_k y_k \sum_q (xy)_{kq} = \text{zero}$$

because every value of $\sum_q (xy)_{kq}$ is zero.

Proceeding in much the same way it can easily be shown that ${}_k\sigma_{x.xy}$ need not be zero but that its mean over all genotypes is the covariance, $\sigma_{x.xy}$, for the whole population and is equal to zero.

[1]The dot between x and y in $\sigma_{x.y}$ is used to distinguish covariance of x and y from the standard deviation of (xy) which will be symbolized by σ_{xy}. This convention will be followed throughout.

With reference to models (2) and (3), it can be shown that $\sigma_{y.fy}$ and $\sigma_{\bar{y}.f\bar{y}}$ are zero but that for any single macro-environment ${}_j\sigma_{y.fy}$ and ${}_j\sigma_{.\bar{y}f\bar{y}}$ need not be zero.

Covariance of interaction effects—With reference to model (1), consider the (xy)'s associated with any pair of micro-environments, the qth and $q'th$. Covariance is

$$\sigma_{(xy)_{kq}(xy)_{kq'}} = \frac{1}{n}\sum_{k}(xy)_{kq}(xy)_{kq'}.$$

This covariance is obviously not constrained to zero, but its mean for all pairs of environments will be infinitesimal. For demonstration, consider the pairs of environments resulting if a particular environment, the qth, is paired with every other one. For these $(m-1)$ pairs the mean covariance is

$$\frac{1}{m-1}\sum_{q' \neq q}\frac{1}{n}\sum_{k}(xy)_{kq}(xy)_{kq'}$$

$$= \frac{1}{n(m-1)}\sum_{k}(xy)_{kq}\sum_{q' \neq q}(xy)_{kq'},$$

and since $\sum_{q}(xy)_{kq} = 0$, $\sum_{q' \neq q}(xy)_{kq'} = -(xy)_{kq}$.

Therefore, the mean covariance being considered becomes

$$-\frac{1}{n(m-1)}\sum_{k}(xy)^2_{kq} = -\left(\frac{1}{m-1}\right){}_1\sigma^2_{xy}$$

where ${}_q\sigma^2_{xy}$ is variance of interaction effects associated with the qth micro-environment. Finally, averaging over the m environments which might have been chosen as the constant one in pairing we obtain $-\left(\frac{1}{m-1}\right)\sigma^2_{xy}$ as the grand average for covariance between the (xy)'s of two micro-environments. It will be infinitesimal because m has been specified as very large. σ^2_{xy} symbolizes the variance of (xy)'s for the entire genotype-environment population and can easily be shown equal to $\frac{1}{m}\sum_{q}{}_q\sigma^2_{xy}$.

Similar demonstrations are possible for (fy) and $(f\bar{y})$ of models (2) and (3), respectively. Neither $\sigma_{(fy)_{ik}(fy)_{jk}}$ nor $\sigma_{(f\bar{y})_{ij}(f\bar{y})_{ij'}}$ is constrained to zero but on the average for all pairs of macro-environments both will approach zero (from the negative side) as the number of macro-environments in the whole environment population becomes large.

Covariance of e's with other effects in models (2) and (3)—It was noted earlier that $\sum_{q} e_{jkq} = \sum_{k}\sum_{q} e_{ijkq} =$ zero. Consequently, covariance of e with each other effect in

models (2) and (3) is zero both for the whole population and for the portion of the population associated with either any single macro-environment or any single genotype.

The operational model

Models presented so far have been offered as complements to definitions. They deal with the phenotypic values of individual plants (or other organisms) instead of the plot values frequently encountered in experimental data. They assume a single, somewhat idealized, class of macro-environments rather than the two-way stratification so frequently pertinent in practice. One or another of the three models will sometimes be appropriate to actual data, but more often the operational model will need to differ in some way from all of them. However, principles involved will not change.

The most common model in plant genetics and breeding is some variant of the following:

$$P_{ijkq} = u + \bar{y}_i + a_j + b_k + (ab)_{jk} + r_{jkq} + (\bar{y}a)_{ij} + (\bar{y}b)_{ik} + (\bar{y}ab)_{ijk} + e_{ijkq} \quad (4)$$

Here, $\bar{y}_i$ has the same meaning as in model (3), but in addition corresponds to y_i of models (1) and (2) when families involved are homogeneous genetically as in the case of clones, pure lines or F_1 crosses of pure lines,
a_j is the effect of the jth location,
b_k is the effect of the kth year,
$(ab)_{jk}$ is the effect of interaction between the jth location and the kth year,
r_{jkq} is effect of the qth replication at the jth location in the kth year,
$(\bar{y}a)$, $(\bar{y}b)$, and $(\bar{y}ab)$ are corresponding interaction effects, and
e_{ijkq} is a residual for the observation on the ith family in the qth replication at the jth location in the kth year.

The four effects, a, b, (ab), and r, represent a subdivision of the f of models (2) and (3). The three effects, $(\bar{y}a)$, $(\bar{y}b)$, and $(\bar{y}ab)$, represent the corresponding subdivision of the $(f\bar{y})$ of model (3) except that the interaction of family with the replication component of f is left a part of e.

Proof of analogies with earlier models in regard to covariances of effects is too tiresome to present. It will suffice to state that the same kind of things hold here. For example, ${}_j\sigma_{\bar{y},\bar{y}a}$ need not be zero. Its value is limited only to the range consistent with correlation between $\bar{y}$ and $(\bar{y}a)$ in the range, -1.0 to 1.0. On the other hand its average over all locations of the environment population must be zero. As one more example, $\sigma_{(\bar{y}a)ij(\bar{y}a)ij'}$, may vary from one pair of locations to another but its average for the whole population will be infinitesimal. Because the effect that would logically be symbolized as $(\bar{y}r)$ is contained in e, we cannot state that with respect to each replication, that the covariance of $\bar{y}$ with e is zero. However, this fact is judged to be relatively unimportant.

The other point to be recognized in connection with an operational model is that it represents an observed rather than a conceptual quantity. If model (3) were

employed as the basis for an expression to represent the population mean for a family in a specified macro-environment, we would end with

$$\bar{P}_{ij} = u + \bar{y}_i + f_j + (f\bar{y})_{ij}$$

The *e's* would drop out because $\sum_k \sum_q e_{ijkq} = 0$. In the operational case, the average or sum, as the case may be, of *e's* does not go to zero because individual phenotypic values contributing to any observed plot value are only a sample from the infinitude possible.

THE MODELS AND THINGS GENETICAL

The dependent nature of values and effects

It should be clearly obvious that the value of a genotype is not an inherent absolute quality of the genotype. The average of phenotypic expressions evoked by a genotype depends on the population of environments over which the average is taken. The breeder recognizes this when he states that a line, hybrid, or variety is well adopted for one category of environments (say, those of Southern Minnesota) but less well adapted for another (say, those of Northern Missouri).

In like manner, the value of an environment or class of environments depends on the genotype population with respect to which value is measured. For example, the environments of Iowa are far better when evaluated by performance of Iowa corn hybrids than when evaluated by performance of Texas corn hybrids.

It is apparent that similar statements could be made with reference to all effects in our models. In fact, each effect is conditioned by both the environment population and the genotype population. Clearly, no conclusions regarding genetic and phenotypic variation of quantitative traits can have much meaning without reasonably concise specification of the genotype-environment population to which they apply. And in this connection, *it is incumbent on the quantitative geneticist to remember that the environment populations that have operational significance to the plant breeder are always ones with dimensions in both space and time.*

The flux between genotypic variance and GE interaction variance

Since values and effects of genotypes depend on the environment population to which they apply, the same must obviously be true for associated variances. The interplay between genotypic and GE interaction variance when the reference population of environments is altered by constriction or expansion merits careful attention.

Consider a particular genotype population and a particular population of environments. The latter will be designated A. Let some segment of A be viewed as the jth macro-environment of A to be designated S. Either S or A may serve as a reference population of environments. Let y_i be effect of the ith genotype and $(fy)_{ij}$ the effect of interaction of the ith genotype with S when A is used. Let y_{si} be effect of the ith genotype when S is the reference population of environments. It follows from our definitions that

$$y_{si} = y_i + (fy)_{ij}.$$

Hence,

$$\sigma^2_{ys} = \sigma^2_y + 2_j\sigma_{y.fy} + {}_j\sigma^2_{fy}.$$

The average of ${}_j\sigma_{y.fy}$ over all macro-environments of A is zero, the same average for ${}_j\sigma^2_{fy}$ is σ^2_{fy}. Thus, on the average, we find

$$\sigma^2_{ys} = \sigma^2_y + \sigma^2_{fy}.$$

In other words, when the reference population of environments is made more homogeneous by constriction, genotypic variance is increased by incorporation of variance that was previously GE interaction variance. Going in the other direction, expansion of the reference population of environments will in general increase GE interaction variance at the expense of genetic variance. This suggests the limiting possibility of a genotype-environment population such that real variation in composition of genotypes is associated with no variance of genotypic values. An approach to this limit may in fact be anticipated as the result of continuing recurrent selection for value relative to a heterogeneous environment population.

This is the situation in which the breeder intent on further improvement might logically turn to selection aimed at varieties having special adaptations. The expression,

$$y_{si} = y_i + (fy)_{ij},$$

indicates that potential is increased by seeking special adaptation. The expression,

$$\sigma^2_{y_s} = \sigma^2_y + \sigma^2_{fy},$$

makes it clear that effective genetic variance is greater when selection is for value relative to a more homogeneous environment population. Attendant problems are (a) that of subdividing an original environment population so that the subdivisions are both clearly delineated and substantially more homogeneous and (b) the increased effort required because, in effect, a single breeding program would be replaced by several.

Effectiveness of selection

The breeder compares families (lines, hybrids, etc.) in a field trial to establish a basis for selection among them. He knows that the ones performing best are actually not that much better genetically, that if he were to compare the selected with the unselected families in a new trial, the observed mean difference would almost certainly be less than in the trial on which selection was based.

Gain to be expected from selection is commonly stated as

$$\Delta\bar{Y} = S\sigma^2_{\bar{y}}/\sigma^2_{\bar{p}} = k\sigma^2_{\bar{y}}/\sigma_{\bar{p}}$$

here S = selection differential in units of observation

k = selection differential as a multiple of $\sigma_{\bar{p}}$

$\sigma^2_{\bar{p}}$ = variance among phenotypic means of the kind used as the basis for selection, and

$\sigma^2_{\bar{y}}$ = variance of family effects as defined earlier.

The breeder who is not cowed by the sacred quality of symbols has been known to express doubts concerning the validity of this expression. He may insist that, given the same genetic population, so that $\sigma^2_{\bar{y}}$ does not vary, and the same selection intensity so that k remains constant, selection nevertheless may be much more effective in, say, one year than another even though $\sigma_{\bar{p}}$ is much the same from year to year. Why? Because there are unusual years (excessive rainfall, hot dry weather, adverse conditions for the normally most troublesome pathogens, etc.) in which the best performing families are not those that would have the best average performance in the area of concern, and because there are other very representative years in which the environment is very favorable for distinguishing families that would be best on the average.

This argument appears to have some biological substance. Let's review the situation. Consider a comparison of a sample of families in a particular macro-environment (which corresponds to the year basis of the breeders argument presented above). If we derive $\Delta\bar{Y}$ assuming ${}_j\sigma_{\bar{y}.f\bar{y}} = 0$, we obtain the usual expression. If we admit, as shown earlier we should, that ${}_j\sigma_{\bar{y}.f\bar{y}}$ need not be zero, we obtain

$$\Delta\bar{Y} = k\frac{(\sigma^2_y + {}_j\sigma_{y.fy})}{\sigma_{\bar{p}}}$$

and have a result that recognizes validity of the breeders argument. The covariance, ${}_j\sigma_{\bar{y}.f\bar{y}}$, may be negative or positive; hence $\Delta\bar{Y}$ will some years be less, some years greater. Because this covariance is zero on the average, the original expression is correct on the average (but only on the average). The merit of the more complete final expression is that it recognizes a source of variation in response to selection that hitherto has not been recognized in theory. This is important because it forces us to a more realistic view of the agreement to be expected between predicted and realized response to selection in short run experiments.

There is one other aspect of the matter that deserves some attention. If one were able to specify and provide an environment in which ${}_j\sigma_{\bar{y}.f\bar{y}}$ would be positive and large it would obviously be useful as one in which to compare genotypes. This, in effect, is what the breeder does when he selects for disease resistance on the basis of performance in a disease nursery. The disease nursery presents an environment that is atypical relative to general field environments but in which ${}_j\sigma_{\bar{y}.f\bar{y}}$ is believed to be positive and high.

Homeostasis

A more homeostatic genotype is, by definition (see Lerner, 10), one for which the variance of phenotypic values evoked in different environments is less. This is a matter of interest to the breeder because uniformity in the performance of a variety is desirable. It is not difficult to perceive how homeostasis at the level of production might occur. For example, a genotype resistant to a particular disease, other things being equal, would perform more uniformly over environments variable in regard to incidence of the pathogen or conditions affecting impact of the pathogen.

In terms of Figure 1, and model (1), the variance of phenotypic values associated with a specific genotype is that among *P's* within a column of the table which by our system of symbols is ${}_k\sigma^2_p$. Because $P_{kq} = u + y_k + x_q + (xy)_{kq}$ and $u + y_k$ is constant along any column, i.e. for any genotype,

$$
\begin{aligned}
{}_k\sigma^2_P &= \text{variance of } x_q + (xy)_{kq} \\
&= \sigma^2_x + 2_k\sigma_{x.xy} + {}_k\sigma^2_{xy}.
\end{aligned}
$$

Homeostasis implies variation in this quantity. By definition σ^2_x has only one value in any given genotype-environment population and therefore cannot contribute to the variation in question. However, both ${}_k\sigma_{x.xy}$ and ${}_k\sigma^2_{xy}$ may vary from genotype to genotype. A certain amount of variation in ${}_k\sigma^2_p$ could presumably result from variation in ${}_k\sigma^2_{xy}$ alone. However, the lower limit of ${}_k\sigma^2_p$ consistent with this explanation would be σ^2_x. To explain lower values would require that ${}_k\sigma^2_{x.xy}$ be negative and greater in absolute magnitude than $-\frac{1}{2}\,{}_k\sigma^2_{xy}$. Since ${}_k\sigma^2_{x.xy}$ must average zero for the whole population of genotypes, negative values must be accompanied in the whole population by counter-balancing positive values. Thus, while differential homeostasis has not been shown to require variation in ${}_k\sigma_{x.xy}$, any very considerable differences in homeostasis would certainly suggest such variation.

Single genotypes vs. families with regard to GE interaction variance

There are at least two reasons for interest in this matter. Uniformity of performance over different environments has been noted as a desirable attribute of varieties to be used in commercial production. A choice is sometimes presented. For example in the case of small grains use can be made of a single pure line or of a family artificially synthesized by mixing seed from a number of pure lines. There are doubtless other cases where such a choice is reasonable to consider. In another context, it is well known (and will be touched on later) that estimates of genetic variance that are possible from single plant data (as by comparison of F_2 and F_1 variance after a cross of pure lines) are biased upward by GE interaction variance. To supplement such estimates, outside information on magnitude of GE interaction variance would be useful. Must such outside estimates pertain specifically to single genotypes or will information obtained for families be equally good?

Somewhat more formally, the issue being discussed can be stated as follows: What can be asserted generally concerning the relative size of σ^2_{fy} and $\sigma^2_{f\bar{y}}$? The answer appears to lie in the fact that

$$(f\bar{y})_{ij} = \frac{1}{n_i}\sum_k (fy)_{ijk}$$

Because $(f\bar{y})$ is the average of a family of (fy)'s, its variance may confidentially be expected to be less.

Supporting evidence is presented by Sprague and Federer (15). They estimated two interaction variances, in our notation $\sigma^2_{\bar{y}a} + \sigma^2_{\bar{y}ab}$ and $\sigma^2_{\bar{y}b} + \sigma^2_{\bar{y}ab}$, for both single and double-crosses in corn. Estimates were consistently larger for single genotypes (single crosses) than for families (double crosses). Their results are summarized below

Estimates of	*Double crosses*	*Single crosses*
$\sigma^2_{\bar{y}a} + \sigma^2_{\bar{y}ab}$	1.54	4.37
$\sigma^2_{\bar{y}b} + \sigma^2_{\bar{y}ab}$	2.08	8.95

VARIANCE COMPONENT ESTIMATES

In plant genetics the most familiar source of variance estimates (and the one that will receive primary attention here) is data obtained in replicated field trials. The entries compared in such trials may be genetically homogeneous (clones, pure lines, etc.) or heterogeneous (double crosses, progenies by selfing from heterozygous parents, etc.).

The estimation procedure is now thoroughly familiar. It consists of computing an analysis of variance, setting mean squares equal to their expectations, and solving the resulting equations for parameters contributing to the expectations. Values obtained are of course estimates of the parameters rather than the actual true values of the parameters.

At this point it is well to remind ourselves that what we accept as the expectations of mean squares depends first of all on how we view the composition of the observations that make up our data; in the context of this paper, on our model for phenotype. This in turn should be unaffected by the scope of our data. We deceive ourselves if we shape our models to the dimensions of our data rather than to the problems on which we seek enlightenment through analysis of the data.

The problems of the plant breeder (and more generally of the population geneticist concerned realistically with evolution) demand that genotypic values and effects be defined with reference to an environment population that has dimensions in both space and time. This necessity should be recognized in our model for phenotype regardless of the dimensions of the data to be analyzed. Use of an appropriate model is our safeguard against misrepresentation of the information extractable from specific bodies of data.

Expectations of mean squares

Consider a typical trial in which n families are compared in a randomized block design with r replications at each of s locations in each of t years. Assume the same s locations each year. The composition of an observed plot value is reasonably represented by model (4). The form of the appropriate analysis of variance and the usually accepted expectations of its mean squares are well known (Table 1). Expectations are listed for only the mean squares that are useful in obtaining the estimates desired.

TABLE 1.—ANALYSIS OF VARIANCE FOR A TYPICAL "VARIETY" TRIAL.*

Variance source	d.f.	Mean square	Exp. of mean square
Years (Y)	(t−1)		
Locations (L)	(s−1)		
Y × L	(t−1)(s−1)		
Replications within Y and L (R)	ts(r−1)		
Families (F)	(n−1)	M_1	$\sigma^2_e + r\sigma^2_{\gamma ab} + rs\sigma^2_{\gamma b} + rt\sigma^2_{\gamma a} + rst\sigma^2_{\gamma}$
F × Y	(n−1)(t−1)	M_2	$\sigma^2_e + r\sigma^2_{\gamma ab} + rs\sigma^2_{\gamma b}$
F × L	(n−1)(s−1)	M_3	$\sigma^2_e + r\sigma^2_{\gamma ab} + rt\sigma^2_{\gamma a}$
F × Y × L	(n−1)(t−1)(s−1)	M_4	$\sigma^2_e + r\sigma^2_{\gamma ab}$
F × R	ts(n−1)(r−1)	M_5	σ^2_e

*Symbols for variances are all used as would be inferred from model (4) and the discussion that went with its presentation.

The analysis of Table 1 encompasses the cases where either s or $t = 1.0$ or where both equal 1.0. The difference in those cases is that a mean square will not be obtained for variance sources with degrees of freedom equal zero. For example, with data from only one year, $(t-1)$ = zero, and all mean squares for which $(t-1)$ appears in the listed degrees of freedom will be absent in the analysis.

It is obvious, and well known as well, that all five variances cannot be estimated separately unless both s and $t \geq 2$. Suppose $t \geq 2$, but $s = 1.0$. Then the relevant mean squares are reduced to the following:

Variance source	*Mean Sq.*	*Exp. of mean square*
Families	M_1	$\sigma^2_e + r(\sigma^2_{\gamma ab} + \sigma^2_{\gamma b}) + rt(\sigma^2_{\gamma a} + \sigma^2_{\gamma})$
F × Y	M_2	$\sigma^2_e + r(\sigma^2_{\gamma ab} + \sigma^2_{\gamma b})$
F × R	M_5	σ^2_e

Quantities that can be estimated are σ^2_e, $(\sigma^2_{\bar{\gamma}ab} + \sigma^2_{\bar{\gamma}b})$, and $(\sigma^2_{\bar{\gamma}a} + \sigma^2_{\bar{\gamma}})$. The only possible estimate of the genetic variance among families, $\sigma^2_{\bar{\gamma}}$, has expectation, $\sigma^2_{\bar{\gamma}} + \sigma^2_{\bar{\gamma}a}$, and is therefore biased upward by the amount of the genotype × location portion, $\sigma^2_{\bar{\gamma}a}$, of the GE interaction variance.

The extreme occurs when $s = t = 1.0$. Then the only quantities that can be estimated are σ^2_e and $(\sigma^2_{\bar{\gamma}} + \sigma^2_{\bar{\gamma}a} + \sigma^2_{\bar{\gamma}b} + \sigma^2_{\bar{\gamma}ab})$.

Unfortunately, the mean square expectations listed in Table 1 (and others like them) are so familiar and have been so long accepted that their justification is rarely reviewed. If it is assumed (1) that the variances of e, $(\bar{\gamma}ab)$, $(\bar{\gamma}a)$, and $(\bar{\gamma}b)$ are constant from one macro-environment to another and (2) that the various effects are mutually independent in their distributions (exhibit no covariances), then the expectations listed in Table 1 are correct. We have emphasized earlier that the second of these assumptions need not be true. Further, there is no rigorous justification for the first assumption. On the contrary, we know from experience that the variance of e (plot error variance) is variable from one experiment to another, i.e., from one macro-environment or set of macro-environments to another; and there is

nothing that compels the variances of the GE interaction effects to be homogeneous from one macro-environment to another.

Abandoning the foregoing assumptions let us examine the mean square expectations for data from a particular subset of years and locations. They will differ from those listed in Table 1 in two ways.

(a) Potential variation in all variances except $\sigma^2_{\bar{y}}$ must be recognized. Let ${}_{jk}\sigma^2_e$ be the variance of e for the jth location in the kth year. We then visualize an average of these for the entire population of macro-environments which can be symbolized as σ^2_e. In like manner let ${}_{jk}\sigma^2_{\bar{y}ab}$, ${}_{j}\sigma^2_{\bar{y}a}$, and ${}_{k}\sigma^2_{\bar{y}b}$ symbolize, respectively, the variance of $(\bar{y}ab)$ for a specific year-location, the variance of $(\bar{y}a)$ for a specific location, and the variance of $(\bar{y}b)$ for a specific year. Then in the expectations of Table 1 each variance except $\sigma^2_{\bar{y}}$ must be replaced by the average of the corresponding variances that pertains to the specific sub-set of years and locations, i.e.

$$\sigma^2_e \quad \text{is replaced by} \quad \frac{1}{st}\sum_j\sum_k {}_{jk}\sigma^2_e,$$

$$\sigma^2_{\bar{y}ab} \text{ is replaced by } \frac{1}{st}\sum_j\sum_k {}_{jk}\sigma^2_{\bar{y}ab},$$

$$\sigma^2_{\bar{y}a} \text{ is replaced by } \frac{1}{s}\sum_j {}_{j}\sigma^2_{\bar{y}a}, \text{ and}$$

$$\sigma^2_{\bar{y}b} \text{ is replaced by } \frac{1}{t}\sum_k {}_{k}\sigma^2_{\bar{y}b}.$$

Summation in each case is over the years and/or locations in which data were actually obtained.

(b) Various covariances of effects will appear in the expectations.

In order to make the full presentation as compact as possible, we will omit intermediate steps and show only the expectations of functions of mean squares that are routinely used as estimators of the several variance components. These functions are listed below:

Function	*Variance estimated*
$F_1 = (M_4 - M_5)/r$	$\sigma^2_{\bar{y}ab}$
$F_2 = (M_3 - M_4)/rt$	$\sigma^2_{\bar{y}a}$
$F_3 = (M_2 - M_4)/rs$	$\sigma^2_{\bar{y}b}$
$F_4 = (M_1 - M_2 - M_3 + M_4)/rst$	$\sigma^2_{\bar{y}}$

Their expectations for a specific subset of years and locations will be written first as follows:

$$E(F_1) = \frac{1}{st}\sum_j\sum_k {}_{jk}\sigma^2_{\bar{y}ab} + C_{1p},$$

$$E(F_2) = \frac{1}{s}\sum_j {}_j\sigma^2_{\bar{y}a} + C_{2p},$$

$$E(F_3) = \frac{1}{t}\sum_k {}_k\sigma^2_{\bar{y}b} + C_{3p}, \text{ and}$$

$$E(F_4) = \sigma^2_{\bar{y}} + C_{4p},$$

where each C_p is some quantity (positive or negative) due to covariances of effects having a specific magnitude for the pth subset of years and locations but variable in magnitude among such subsets.

Again in the interests of space, the complete composition of each C_p will not be given. The contributions of covariances of $\bar{y}$ with $(\bar{y}a)$, $(\bar{y}b)$, and $(\bar{y}ab)$; of covariances between the $(\bar{y}a)$'s of different locations; and of covariances between the $(\bar{y}b)$'s of different years to C_{2p}, C_{3p} and C_{4p} will suffice for our purpose. The composition of these C's with respect to the foregoing covariances are as follows:

$$C_{2p} = -\frac{2}{t(t-1)}\sum_k \sum_{k'<k} {}_{kk'}\sigma_{\bar{y}b\cdot\bar{y}b},$$

$$C_{3p} = -\frac{2}{s(s-1)}\sum_j \sum_{j'<j} {}_{jj'}\sigma_{\bar{y}a\cdot\bar{y}a},$$

$$C_{4p} = \frac{2}{t(t-1)}\sum_k \sum_{k'<k} {}_{kk'}\sigma_{\bar{y}b\cdot\bar{y}b} + \frac{2}{s(s-1)}\sum_j \sum_{j'<j} {}_{jj'}\sigma_{\bar{y}a\cdot\bar{y}a} + \frac{1}{s}\sum_j {}_j\sigma_{\bar{y}\cdot\bar{y}a} + \frac{1}{t}\sum_k {}_k\sigma_{\bar{y}\cdot\bar{y}b} + \frac{1}{st}\sum_j \sum_k {}_{jk}\sigma_{\bar{y}\cdot\bar{y}ab}.$$

It is well worth noting that every term represents an average of the covariance in question for the year-location subset in which data were collected. Consider the single term of C_{2p}. The summation is over all possible pairs of years in which data were collected. Whatever the value of t there are $\frac{t(t-1)}{2}$ ways of pairing them for covariance and the sum of the covariances is divided by that number. In like manner the third term of C_{4p} is the mean of the s covariances, ${}_j\sigma_{\bar{y}\cdot\bar{y}a}$, associated with the s locations in which data were collected.

Because of this the contributions arising from existence of these covariances

will tend to average out as the number of years and/or locations is increased. This should proceed rather rapidly for the terms involving double summations. For example, the number of covariances averaged in the single term given for C_{3p} is $s(s-1)/2$ which goes from 1 to 3 to 6 to 10 as s goes from 2 to 5.

The expectations of our four functions can now be rewritten as follows:

$$E(F_1) = \sigma^2_{ya} + \left[\frac{1}{st}\sum_j\sum_k {}_{jk}\sigma^2_{yab} - \sigma^2_{ya}\right] + C_{1p},$$

$$E(F_2) = \sigma^2_{ya} + \left[\frac{1}{s}\sum_j {}_j\sigma^2_{ya} - \sigma^2_{ya}\right] + C_{2p},$$

$$E(F_3) = \sigma^2_{yb} + \left[\frac{1}{t}\sum_k {}_k\sigma^2_{yb} - \sigma^2_{yb}\right] + C_{3p}, \text{ and}$$

$$E(F_4) = \sigma^2_y + C_{4p},$$

where σ^2_{yab}, σ^2_{ya}, and σ^2_{yb} are averages of the three interaction variances over the entire environment population with respect to which effects are defined. These averages, along with σ^2_y, are the quantities we reasonably seek to estimate.

Because ${}_{jk}\sigma^2_{yab}$, ${}_j\sigma^2_{ya}$, and ${}_k\sigma^2_{yb}$ average to σ^2_{yab}, σ^2_{ya}, and σ^2_{yb}, respectively, for the whole environment population and because all of the effect covariances contributing to the C's average to zero for the whole environment population, expectations for a *random* subset of years and locations, as distinguished from a *particular* (pre-chosen) subset, are what we wish them to be (in fact what the mean square expectations of Table 1 indicate them to be).

$$E(F_1) = \sigma^2_{ya} \qquad E(F_2) = \sigma^2_{ya}$$

$$E(F_3) = \sigma^2_{yb} \qquad E(F_4) = \sigma^2_y$$

The distinction between expectations for *random* and *particular* subsets of years and locations is a subtle one but important. The crux of the matter is that the terms which go to zero in expectations for a random subset represent errors of estimation to which we commit ourselves when we choose or specify a particular subset of years and locations in which the data are to be collected. The very best estimates available from data collected in a particular subset of years and locations, to be obtained by making number of replictions (r) and number of entries (n) very large, will still be subject to these errors. These errors are inherent to the years and locations in which a trial is conducted and cannot be modified by increasing dimensions of the trial within a given set of years and locations.

To review the whole issue very briefly, the potential variation (from one set of macro-environments to another) in estimate expectations reflects a kind of random variation in variance component estimates that is related in its average magnitude to the number of years and/or locations in which data for estimation are obtained rather than to the sheer number of degrees of freedom for mean squares employed (which can be increased by increasing n without

change in s or t). That such a component of error exists should come as no surprise but rather should seem reasonable. Suppose, for example, that the s locations in which data are collected happen to be very similar ones. In the extreme one can imagine them so similar that for practical purposes they are the same. Then the result would be as if there were rs replications at one location instead of r replications at each of s locations and it has already been shown that with data from but one location the estimate of family (genetic) effect variance will be biased (in error) upward by the genotype-location interaction variance.[1]

Existence of the kind of error discussed above cannot be doubted. Its magnitude is another matter and one that deserves attention in terms of experimental evidence.

Variation in estimates from different subsets of macro-environments

A study designed to provide preliminary evidence has been conducted at the North Carolina Agricultural Experiment Station by Dr. Robinson and his co-workers using half-sib families within an open-pollinated variety of corn. Seed for sixty families was produced using sixty random plants as pollinators and mating each to a large random sample of seed bearing parents. Seed produced was bulked by pollen parents (60 bulks). The sixty families have been compared in randomized block trials (2 replications) at each of 5 locations (central and eastern North Carolina) in each of five years (1955–59). Grain yield, measured as yield per 100 plants, is the trait for which results will be considered.

We will look at the data in two ways, stating at the same time that we are not sure of how it can best be used for the present purpose.

The data from each year-location were analyzed separately and from each of the 25 analyses an estimate of the "family" component of variance was obtained. Because each analysis involved data from only one year at one location, the quantity estimated was in all cases $(\sigma^2_{\bar{y}} + \sigma^2_{\bar{y}a} + \sigma^2_{\bar{y}b} + \sigma^2_{\bar{y}ab})$. Significant variation among

[1]For logical completeness it should be noted that our treatment has not been extended to terms that are variable by families or pairs of families. For example, for a specific pair of families there is a covariance, $_{ii'}\sigma_{y_a \cdot \bar{y}_a}$ which need not be zero though its average over all pairs of families in the population will be infinitesimal. As another example, $_i\sigma^2_{y_a}$, $_i\sigma^2_{y_b}$ and $_i\sigma^2_{y_{ab}}$ are all potentially variable from family to family. If consequences had been followed out it would have been shown that terms

like $\left[\frac{1}{n} - \Sigma_i \sigma^2_{y_a} - \sigma^2_{y_a}\right]$ and $\frac{2}{n(n-1)} \Sigma_n \Sigma_{n'<n} {}_{ii'}\sigma_{y_a \cdot y_a}$ belong in the expectations of various mean squares

for a *particular* sample of genotypes. Emphasis has not been directed at this class of refinements

because, for the usual case, n is large enough so that the coefficients of these terms $\left(\frac{1}{n} \text{ or } \frac{2}{n(n-1)}\right)$

are very small. The only situation in which they seem likely to be of more than trivial consequence is the rather unusual one where comparison of a small number of families in many macro-environments might be employed for estimation of genotype × environment interaction variances.

the estimates obtained would indicate either or both of (a) variation between the year-locations in one or more of the interaction variance components and (b) variation between the year-locations in one or more of the possible effect covariances. In 23 of the analyses the plot error variance ranged from 31.79 to 136.26 with an average of 73.79. This corresponded to a coefficient of variation of 15.4%. The other two sets of data exhibited high error variance (237.35 and 275.45) and therefore have not been used. The 23 sets of data used yielded estimates of the "family" variance component that averaged 11.11 and ranged from −3.94 to 52.00. Variance among the 23 estimates computed directly from the estimates was 180.10.

The question now is what variance of estimates is to be expected on the assumptions of homogeneity of the interaction variances and no covariances among effects. Such an "expected variance of estimates" was constructed in two ways:

(a) Ignoring differences in plot error variance observed in the 23 trials. In this case the average plot error variance for all 23 trials was taken as the real value of that parameter for all trials and the average of the estimates of "family" variance as the true value of $\sigma^2_{\bar{y}}$ plus the sum of the three interaction variances. In this case only one computation is involved since the variance would be the same for each estimate.

(b) Accepting for each trial the observed error variance as the true value of ${}_{jk}\sigma^2_e$ for the year-location of the trial. As in the first procedure the average estimate was accepted as the true value of the "family" variance. In this case a separate variance had to be computed for the estimate of each trial. These were then averaged to obtain one value applicable to variance among the 23 estimates.

The "expected variances" were computed first as if a different sample of families had been used in each of the separate trials. This result, however, is too high by the amount of variance anticipated as a consequence of sampling the genetic population (since the same sample of families was used in all trials so that the associated error was common to all estimates). This variance is $2\sigma^4_{\bar{y}}/59$ where $\sigma^2_{\bar{y}}$ is the "family" variance. The appropriate adjustment was approximated using as $\sigma^2_{\bar{y}}$, the average estimate of it obtained in another treatment of the data to be described below. Actually the adjustment turns out small so that the accuracy of the estimate of $\sigma^2_{\bar{y}}$ is not very critical. The "expected variances" by the two procedures were 106.45 and 132.81. Comparing with the observed variance of the estimates, F-values,1.69 and 1.36 were obtained. There is uncertainty concerning the appropriate point of entry to the F-table. However, accepting 22 as the degrees of freedom for variance of the estimates of family "effect" variance and 100 or more degrees of freedom for its expectation, F = 1.36 falls short of the 5% point while 1.69 exceeds it.

Actually it can hardly be argued that the observed variation among the trials in plot error variance was all explainable in terms of sampling. Accordingly, F = 1.69 must be considered too high. On the other hand the observed variation in plot error variance probably exaggerates the underlying true variation. Extremes regularly owe a portion of their extremities to sampling variation. Thus, F = 1.36 may be considered somewhat too low. Without further argument concerning niceties of the statistical test here applied, the authors are content with the conclusion that the

observed variation in estimates of $(\sigma^2_y + \sigma^2_{ya} + \sigma^2_{yb} + \sigma^2_{yab})$ from the 23 individual trials is sufficient to cast some doubt on the assumptions that effect covariances and interaction effect variances are uniform from one macro-environment to another.

The second thing done was to make 11 analyses, each of which dealt with data from a different pair of the 23 trials accepted as satisfactory with respect to plot error variance. The trials were paired so that for each analysis the two sets of data came both from different years and different locations. For example, one analysis involved data from location 2 in year 1 and from location 1 in year 2, another analysis involved data from location 4 in year 3 and location 3 in year 5, and so on. There were obviously a variety of ways in which the trials might have been paired within the restriction outlined. The actual pairing was done with no consideration to the data. The 11 analyses provided as many estimates of two quantities, $\sigma^2_{\bar{y}}$ and $(\sigma^2_{\bar{y}a} + \sigma^2_{\bar{y}b} + \sigma^2_{\bar{y}ab})$. Variance among estimates of $\sigma^2_{\bar{y}}$ would be increased by variation among macro-environments in covariance of $\bar{y}$ with $\bar{y}a$, $\bar{y}b$, or $\bar{y}ab$ or in covariance of any pair of interaction effects. Variance among estimates of $(\sigma^2_{\bar{y}a} + \sigma^2_{\bar{y}b} + \sigma^2_{\bar{y}ab})$ would be increased by variation among macro-environments in either variance of any interaction effect or covariance of any pair of interaction effects.

The 11 estimates of total interaction variance ranged from −8.65 to 20.58, the average being 5.72. The estimates of $\sigma^2_{\bar{y}}$ ranged from −10.81 to 15.71 and averaged 4.75. Approximate tests of significance were constructed along the general lines described for variation among estimates of family variances provided by the individual trials.

In the case of estimates of $\sigma_{\bar{y}}^2$, the observed variance among the 11 estimates was 51.33 and the two "expected variances" computed (one assuming no parametric difference in plot error variance from one pair of trials to another, the other accepting observed plot error variance as its real value for each pair of trials) were 38.77 and 37.41. The associated F-values from dividing observed variance of estimates by "expected variances" were 1.32 and 1.35. Neither comes very close to the 5% point for degrees of freedom, $n_1 = 10$ and n_2 taken even to be infinite, which is 1.88. On the other hand the observed variance was larger than the "expected variances".

In the case of estimates of $(\sigma^2_{\bar{y}a} + \sigma^2_{\bar{y}b} + \sigma^2_{\bar{y}ab})$ we might mention in passing that the complication of a common sample that was encountered in considering variation among estimates of family variance (those of $\sigma^2_{\bar{y}}$ plus interaction variance in the first instance and of $\sigma^2_{\bar{y}}$ in the second) was not involved. A new set of interaction effects can be assumed for each pair of trials. Here the observed variance of estimates was 60.08 and "expected variances" computed were 88.44 and 83.96. There is no suggestion of heterogeneity of the estimates.

The evidence here presented is encouraging. It fails to indicate that the random error in variance component estimates that is associated with macro-environments in which data for estimation is collected (and that has taken so much effort to describe) is very significant in magnitude. In this connection it should be noted that our treatment of these data was favorable to detection of the kind of error under discussion in the sense that estimates of which variance was considered were derived from data obtained in macro-environment sets of minimum size. On the other hand the data were unfavorable in the

sense that half-sib families provide, relatively speaking, little genetic and genotype-environment interaction variance to work with. It seems probable that more critical results would be obtained using a kind of family that is known to exhibit greater genetic variance. The authors feel that the issue deserves further attention and are happy to be able to say that data of the required type are presently being obtained at the North Carolina Experiment station.

It is probable that various workers already have data (collected for other purposes) from which at least some information on this issue might be extracted.

Sampling error of variance component estimates

Interest in the magnitudes of variance components leads naturally to questions concerning how well they can be estimated and the amount and kind of data required for estimates of sufficient accuracy. The type of error considered in the preceding two sections cannot be assessed with much confidence until more experimental evidence is available. In the meantime it is useful to know something about the sampling variance of estimates that is independent of covariances between effects. This can be viewed as a minimum variance to which something more is added if the sampling of macro-environments turns out to be consequence.

It is known (see for example, Kendall, 9) that if all contributing effects are normally distributed, the variance of a mean square is a function of its expectation as follows:

$$V(M) = \frac{2(EM)^2}{f}.$$

Here M symbolizes the mean square, EM its expectation and f the degrees of freedom associated with the mean square. From investigations by Comstock and Robinson (4) and Kelleher *et al.* (8) it appears that the normal distribution assumption may be satisfactory in relation to variances of metrical traits of plants.

The estimates of variance components are all linear functions of mean squares that are independent in their sampling errors. As a consequence, the variance of any estimate can be written as a function of the variances of the mean squares contributing to the estimate. The following procedure gives the correct result.

a. Write the function of mean squares that provides the variance component estimate.
b. Multiply the variance of each mean square by the square of its coefficient in the function.
c. The sum of these products is the sampling variance of the whole function.

Consider the estimate of σ^2_g in terms of the analysis and symbols of Table 1. The function providing the estimate is

$$(M_1 - M_2 - M_3 + M_4)/rst = \frac{M_1}{rst} - \frac{M_2}{rst} - \frac{M_3}{rst} + \frac{M_4}{rst}.$$

Accordingly, the variance of the estimate is

$$\frac{1}{(rst)^2}\left[\frac{2(EM_1)^2}{n-1}+\frac{2(EM_2)^2}{(n-1)(t-1)}+\frac{2(EM_3)^2}{(n-1)(s-1)}+\frac{2(EM_4)^2}{(n-1)(s-1)(t-1)}\right].$$

The same procedure yields expressions for the variance of any of the other estimates. For example, the variance of the estimate of $\sigma^2_{\bar{y}a}$ is

$$\frac{1}{(rt)^2}\left[\frac{2(EM_3)^2}{(n-1)(s-1)}+\frac{2(EM_4)^2}{(n-1)(s-1)(t-1)}\right].$$

To evaluate these expressions numerically one must assume values for the mean square expectations (which amounts to assuming values for the variance components) and for the numbers of families, locations, years and replications. As an example suppose 101 families are to be compared in 2 replications at each of 2 locations in each of 2 years ($n = 101, r = s = t = 2$). Assume further that $\sigma^2_{\bar{y}} = 20$, $\sigma^2_{\bar{y}a} = \sigma^2_{\bar{y}b} = \sigma^2_{\bar{y}ab} = 10$, and $\sigma^2_e = 50$. Then expectations of mean squares are obtained by substitution in expressions of table 1, and

$$EM_1 = 50 + 2(10) + 4(10) + 4(10) + 8(20) = 310,$$
$$EM_2 = EM_3 = 110,$$
$$EM_4 = 70, \text{ and } E(M_5) = 50.$$

Substituting in expressions for variances the following values are obtained.

Estimate of	*Variance*	*Standard Error*
$\sigma^2_{\bar{y}}$	39.13	6.3
$\sigma^2_{\bar{y}a}$	21.25	4.6
$\sigma^2_{\bar{y}b}$	21.25	4.6
$\sigma^2_{\bar{y}ab}$	27.62	5.3

One notes in the case of $\sigma^2_{\bar{y}}$ that a true value of 20 would be estimated with a standard error of 6.3. Obviously the estimate might turn out considerably different from the true value, possibly as high as 30 or as low as 10. The situation is still less satisfactory for the three interaction variances. Here true values of 10 would be estimated with standard errors about half as large (4.6 and 5.3). Obviously, one can go through the procedure with other values of n, r, s, or t to discover how more satisfactory estimates could best be obtained. Other things being equal considerations of the preceding sections make it obvious that choice should always favor higher values of s and/or t.

It should be noted that while what one computes as the variances of the estimates depends on values assumed for the variance components themselves, the ratios of standard error to quantity estimated does not change so long as the relative values assumed for variance components do not change. In the above example, if each variance component had been assumed twice as large each standard error would also have turned out twice as large. Another way of saying this is that for any fixed set of values for n s t and r, the coefficients of variation of the estimates depends on the relative rather than the absolute values of the variance components.

The impact of the foregoing is that we have the means to discover, in advance

of work aimed at estimation of variance components, quite a bit about the reliability of the estimates to be obtained. Computations of the kind outlined provide the basis for realistic planning of such investigations.

How much do we need to know about interaction variances

The fact that expected effect of selection is inversely proportional to $\sigma_{\bar{p}}$ and that $\sigma_{\bar{p}}^2$ can be logically viewed as

$$\sigma^2_{\bar{y}} + \frac{\sigma^2_{\bar{y}a}}{s} + \frac{\sigma^2_{\bar{y}b}}{t} + \frac{\sigma^2_{\bar{y}ab}}{st} + \frac{\sigma^2_e}{rst}$$

suggests that knowing the magnitude of each of the variance components is important. It is worth noting that this is not always so. The information that will contribute to ones purpose depends on the purpose. Consider an investigation aimed at learning whether observed response to selection agrees with prediction. What one needs are good estimates of $\sigma^2_{\bar{y}}$ and $\sigma^2_{\bar{p}}$. The latter can be estimated very well without separate estimates of its components. The estimate obtained comes directly from the actual phenotypic values on which selection is based in the course of the experiment. It is true that data adequate for satisfactory estimation of $\sigma^2_{\bar{y}}$ will also supply information about the interaction variance components but this is nevertheless not vital to the purpose of the work. This is worth keeping in mind so that in such a case emphasis in the design of field trials for variance estimation will be concentrated on minimizing the standard error of the estimate of $\sigma^2_{\bar{y}}$ without special regard to standard errors of other estimates available from the same data.

Let us consider another example in greater detail. Consider the situation where a breeder, for reasons that seem sufficient to him, has decided to conduct a recurrent selection program of a particular form and has chosen the genetic material to be used. He would reasonably wish to maximize progress per year but might feel that being able to predict rate of progress wasn't worth enough to justify the effort required to learn more about $\sigma^2_{\bar{y}}$ than could be inferred from reports by other workers. How much information on interaction variance does this breeder need as the basis for satisfactory decisions concerning the field tests on which selection will be based?

First consider $\sigma^2_{\bar{y}b}$, the year X family interaction variance. If it were zero or very small there would be nothing gained from testing in more than one year. In fact to do so would increase the time span of a cycle of the selection program and might easily result in less progress per year. Presumably, if $\sigma^2_{\bar{y}b}$ were large enough, it would pay to test over a two year period (possibly longer) as the basis for selection. How large would $\sigma^2_{\bar{y}b}$ need to be to make testing in more than one year profitable? Obviously, more is to be gained from the increase from one to two years than from any further increase. The contribution of $\sigma^2_{\bar{y}b}$ to $\sigma^2_{\bar{p}}$ is thereby decreased by half while increase from two to three year testing results in further decrease of only one-sixth of the original. Thus, it is reasonable to start by inquiring how large $\sigma^2_{\bar{y}b}$ would need to be to justify two year rather than one year testing. Recall that effect of selection is predicted as

$$k\,\sigma^2_{\bar{y}}/\sigma_{\bar{p}}.$$

Let length of cycle in the case of a one year test be symbolized as c. Then progress anticipated per year is

$$\Delta G_1 = \frac{k\sigma^2_{\hat{g}}}{c\sigma_{\hat{p}1}} \quad \text{for one year testing and}$$

$$\Delta G_2 = \frac{k\sigma^2_{\hat{g}}}{(1+c)_{\hat{p}2}} \quad \text{for two year testing.}$$

$\sigma^2_{\bar{g}}$ is not affected by the change from one to two years and assuming the same fraction of families will be selected in either case k will also remain the same. The ratio of progress per year for the two methods will then be

$$\frac{\Delta G_2}{\Delta G_1} = \frac{(c)}{(1+c)} \frac{\sigma_{\hat{p}1}}{\sigma_{\hat{p}2}}.$$

Thus, for $\Delta G_2/\Delta G_1 \geq 1.0$ it is necessary that $\sigma_{\hat{p}1}/\sigma_{\hat{p}2}$ be greater than $(1+c)/c$. The very maximum effect on $\sigma_{\hat{p}}$ from increase in t, the number of years tested, would occur if number of locations for testing and replications per location were so great as to make contributions to $\sigma^2_{\hat{p}}$ of variances other than $\sigma^2_{\hat{g}}$ and $\sigma^2_{\hat{g}b}$ approach zero. Then we would have

$$\sigma^2_{\hat{p}1} = \sigma^2_{\hat{g}} + \sigma^2_{\hat{g}b}$$

$$\sigma^2_{\hat{p}2} = \sigma^2_{\hat{g}} + \frac{\sigma^2_{\hat{g}b}}{2}$$

and $\frac{\sigma_{\hat{p}1}}{\sigma_{\hat{p}2}} = \sqrt{\frac{2(1+R)}{2+R}}$, where $R = \sigma^2_{\hat{g}b}/\sigma^2_{\hat{g}}$.

With R as large as 4.0, the value of $\sigma_{\hat{p}1}/\sigma_{\hat{p}2}$ would be only 1.29. This would be larger than $(1+c)/c$ only if $c \geq 4$. With $R = \frac{1}{2}$, the value of $\sigma_{\hat{p}1}/\sigma_{\hat{p}2}$ would be 1.095 and would be larger than $(1+c)/c$ only if $c \geq 11$. The only recurrent selection programs on which cycle length with one year testing (c) would be as great as 4 years are ones involving development of near homozygous lines as a prelude to the testing phase. Besides this, experimental evidence does not suggest that $\sigma^2_{\hat{g}b}/\sigma^2_{\hat{g}}$ is greater than one-half. Thus, the breeder would run no unjustifiable risk in deciding *without any experimental evidence of his own* regarding size of $\sigma^2_{\hat{g}b}$ that testing would be done in only one year.

Going on now to consideration of the other interaction variance components we find that, with one year testing ($t = 1$), $\sigma^2_{\hat{p}}$ reduces to

$$\sigma^2_{\hat{g}} + \sigma_{\hat{g}b} + \frac{\sigma^2_{\hat{g}a} + \sigma^2_{\hat{g}ab}}{s} + \frac{\sigma^2_e}{rs}.$$

Hence, to learn the effect of number of locations on $\sigma^2_{\hat{p}}$ requires estimates of only three quantities: $(\sigma^2_{\hat{g}} + \sigma^2_{\hat{g}b})$, $(\sigma^2_{\hat{g}a} + \sigma^2_{\hat{g}ab})$ and σ^2_e. These can be estimated from trials involving more than one location but only one year (see Expectations of Mean

Squares section), and in fact, it can be shown by methods outlined in the last preceding section that one year trials will be most efficient for estimation of these three quantities. If the breeder begins his program by testing at say three locations in one year, he will have initial estimates of the only kind he needs after his first cycle of testing and quite soon should have enough information to allow a near optimum decision concerning number of replications and locations to use in testing.

This example was not given to argue that comprehensive estimation of interaction variance components is never worthwhile. The purpose was to demonstrate that careful identification of questions to be answered together with logical use of theory available can in specific cases lead one to constructive simplification in over-all program planning.

Estimation of the relative size of two genetic variances

This problem arises in more than one context. However, regardless of the particular variances to be compared or the reason for comparing them the complication imposed by GE interaction effects is the same. Thus a discussion in terms of a particular example will suffice. The following will relate to the comparison of two specific variances for the purpose of obtaining information concerning the average level of dominance in gene action.

We have pointed out that genetic effects are functions of the specific environment population with respect to which they are defined. Furthermore, the genetic effects that have meaning for the plant breeder invariably pertain to an environment population that has dimensions in both time and space. To obtain unbiased estimates of variances arising from variation in these effects requires investigations that also have dimensions in both time and space, i.e. data on an appropriate complex of genetic families must be collected in more than one location and more than one year. On the other hand, the biased estimates available from data collected in a single year-location (macro-environment) will have, assuming any constant total amount of data, lower coefficients of variation.

The general situation can be stated more rigorously as follows. Let V_1 and V_2 be variances associated with effects defined relative to an environment population that is composed of the micro-environments potential in a geographical area and years extending into the future. Unbiased estimates i.e., estimates with expectations equal to V_1 and V_2, require data collected in more than one year and more than one location. However, biased estimates with expectations $V_1 + B_1$ and $V_2 + B_2$ can be obtained from data collected in a single macro-environment, one year and in one location. Moreover, for any constant amount of effort the biased estimates will have lower coefficients of variation. If it could be stated with confidence that

$$\frac{B_1}{B_2} = \frac{V_1}{V_2} \quad \text{so that} \quad \frac{V_1 + B_1}{V_2 + B_2} = \frac{V_1}{V_2},$$

the biased estimates would obviously be as satisfactory as unbiased estimates

for inference concerning the relative size of V_1 and V_2. Since unbiased estimates are far more costly, the issue outlined is extremely significant with respect to future work and progress in quantitative genetics. For this reason, the matter is deserving of the best understanding that can be brought to it.

Consider the approach in the investigation of level of dominance that was first described by Comstock and Robinson (5). While they referred to this approach as Experiment III it has, since then, been called Design III by most authors. (see for example, Gardner *et al.* (6), Robinson and Comstock (12), and Robinson *et al.* (13)). Details of the approach need not be outlined here. Instead, let us consider the composition of the two variances estimated.

The genetic material employed consists of two homozygous lines and a population in F_2 or beyond derived from crossing the two lines. Hence, apart from occasional mutation the alleles at any locus are limited to two which will be designated B and b. With respect to a single macro-environment let $\bar{B}\bar{B}$, $\bar{B}\bar{b}$ and $\bar{b}\bar{b}$ be the average genetic values (in the experimental genetic population) of individuals classified according to genotype at any single locus. Then let

$$x = \bar{B}\bar{B} - \bar{b}\bar{b} \text{ and}$$
$$h = \bar{B}\bar{b} - (\bar{B}\bar{B} + \bar{b}\bar{b})/2.$$

Averaging x and h over macro-environments of the entire environment population pertinent with reference to plant breeding problems yields $\bar{x}$ and $\bar{h}$. The variances of which relative values are sought are

$$V_1 = \Sigma\bar{x}^2 \text{ and } V_2 = \Sigma\bar{h}^2$$

where summation is over all loci. Let us consider the contribution of any single locus to unbiased and biased estimates, respectively. The contributions in the case of unbiased estimates are $\bar{x}^2$ and $\bar{h}^2$. In the case of the biased estimates made from data obtained in one macro-environment contributions of the single locus are x^2 and h^2. Averaging x^2 and h^2 over all macro-environments of the entire environment population yields

$$\bar{x}^2 + \sigma^2_x \text{ and } \bar{h}^2 + \sigma^2_h.$$

To summarize, the contributions of a single locus to unbiased estimates of V_1 and V_2 are $\bar{x}^2$ and $\bar{h}^2$ while contributions to biased estimates (from single macro-environment data) are on the average $\bar{x}^2 + \sigma^2_x$ and $\bar{h}^2 + \sigma^2_h$. Whether

$$\frac{B_1}{B_2} = \frac{V_1}{V_2}$$

depends then on whether

$$\frac{\sigma^2_x}{\sigma^2_h} = \frac{\bar{x}^2}{\bar{h}^2} \quad \text{or} \quad \frac{\sigma_x}{\bar{x}} = \frac{\sigma_h}{\bar{h}}.$$

In other words, the question becomes: must the coefficients of variation of x and h be equal in so far as their variations among macro-environments are concerned. The authors see no compelling reason for believing the answer to be yes; hence, they are dubious that relative size of genetic variances can be inferred with

complete assurance from single macro-environment data when the genetic effects of real interest pertain to a broader environment population.

Estimates from single plant data

The earliest studies of genetic variation in quantitative characters employed data on individual organisms (plants or animals), and this approach is still used frequently. GE interaction has particular significance relative to single plant methods.

Very often the plants are grown in a spacing that is abnormal relative to culture of the same plant for production purposes. This is done in some cases to enable easy separation of the parts of different plants and in others to minimize competition effects as a source of extraneous variation in performance. Unfortunately, there is no objective basis for translating results obtained with an unnatural spacing into information applicable to the normally imposed growing conditions for the plant. This is in reality a GE interaction issue. The difference in spacing makes the reference population of environments quite different from the one pertinent to the breeders problems. Briefly, genetic effects other than those of interest to the breeder are being investigated.

If special spacing were always involved, there would be little more to say except to note that though the approach offered little for the plant breeder, information provided could nevertheless mean something to the geneticist who is not concerned with whether what he studies has economic significance. However, there are plants like corn, tobacco and tomatoes with which studies of single plant behavior do not require special spacing.

Further discussion will be focused on the estimation of total genetic variation of a segregating population by the difference between the phenotypic variance of single plants of that population and the phenotypic variance of single plants having constant genotype. The most familiar example is the case where the variances among plants of two pure lines and/or the variance among plants of the F_1 between pure lines is subtracted from variance among F_2 plants to yield on estimate of total genetic variance in the F_2.

The first problem to be faced is that variance among plants of the same genotype (employed as an estimate of environmental variance) is usually obtained using only two or three genotypes. If the variability exhibited by plants of the same genotype differs from genotype to genotype by reason of differential homeostasis, the estimate obtained using only a few genotypes can hardly be taken as a reliable measure of the average intra-genotype variance for the segregating population. With plants that can be propagated asexually this problem can be circumvented by using numerous genotypes (from the very population being investigated) in the measurement of intra-genotype variance.

Another problem is posed by the fact that, using single plant data, only variances among plants grown in the same macro-environment can be employed. The result is that unless one is interested in genetic effects defined relative to the single macro-environment (effects which are not those pertinent to the

plant breeders problems) genetic variance and GE interaction variance always remain confounded. The point may be clarified using model (2),

$$P_{ijk} = u + y_i + f_j + (fy)_{ij} + e_{ijk}.$$

For plants raised in the same macro-environment but differing in genotype, $u + f_j$ is constant. Variance among them will be

$$\sigma^2_{(y\ +\ (fy))} + \sigma^2_e.$$

For plants of the same genotype and raised in the same macro-environment $y_i + (fy)_{ij}$ as well as $(u + f_j)$ will be constant. Variance among them will be only σ^2_e. The expectation of difference between estimates of these two variances will be, therefore,

$$\sigma^2_{(y\ +\ (fy))} \text{ instead of } \sigma^2_y,$$

as we would like it to be. It is now high time that the unavoidable bias of this sort of estimate of genetic variance be recognized by all workers. At the same time, the bias does not mean that such estimates have no value. If they are complemented by satisfactory estimates of the GE interaction variance by which they are biased (which for some materials are obtainable), their otherwise limited value can be considerably enhanced.

FINAL COMMENT

Because genetic facts are inferred from observations on phenotype, because selection is based on phenotype and because there is a potential contribution of genotype-environment interaction effects to phenotype of all quantitative characters, GE interaction is in some way involved in most problems of quantitative genetics and many problems of plant breeding. For this reason our discussion of GE interaction in relation to plant breeding and genetics has been varied in context. To attempt an item summary would run the risk on the one hand of over simplification and on the other of redundancy.

Rather than accept either risk we will close with the following brief statements. We have aimed first at identifying the most important issues connected with the fact of genotype-environment interaction. These have been discussed within one framework of definitions, terms, and symbols. In the hope of contributing to clarity, special attention has been given to definitions and their implications. Primary objectives have been (a) to clarify the ways in which GE interaction is involved in problems of quantitative genetics and plant breeding and (b) to demonstrate how logical considerations can contribute to understanding and, in some instances, to useful operational decisions. With one principal exception, experimental evidence has not been presented or discussed. In view of available evidence (not here reviewed) it has been assumed throughout that GE interaction is sufficient in the plant world so that all of its possible implications deserve attention.

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DISCUSSION

L. N. HAZEL: In your presentation you indicated that the expectation of the family × environment interaction covariance over a population of families and environments is not zero. Can you explain this more fully?

R. E. COMSTOCK: I hope I didn't say exactly what you've quoted me as saying. A brief review may clarify things. Consider a population of families with reference to just two environments. For each family-environment combination there is an interaction effect. In total we have a bivariate distribution, one effect for each family in each of the two environments, as many pairs of effects as there are families. The covariance between pair members in this bivariate distribution needs not be zero and indeed would not be exactly zero except by rare chance.

On the other hand there is a covariance like that just described for every pair of environments in the environment population. If there are M environments in the population, there would be $\frac{M(M-1)}{2}$ of these covariances and their average would approach zero so closely that for practical purposes it can be said to be zero.

Thus, the answer is that the expectation of covariance of family × environment interaction affects associated with any two specific environments is rarely zero, but the expectation of this covariance for the whole population of environment pairs is essentially zero.

W. D. HANSON: If one has only 2 locations in 2 years and since you do not have an adequate sample of locations or years, would you care to comment on the feasibility of treating the data as 4 environments?

R. E. COMSTOCK: I don't believe I'd do that. It would lead to a single estimate of GE interaction variance for which the expectation would be somewhat less than the sum of the three kinds of interaction variance and would leave some fraction of the family × year and family × location interaction variances confounded with family variance in the expectation of what would be used as an estimate of family variance.

I doubt that there would be compensating advantages to be gained from the procedure. For example, the contribution to the estimate of family variance from covariances of family effects with interaction effects would be unchanged.

L. H. PENNY: The relatively larger L × Y × V interaction as compared to the L × V and Y × V interactions may be explained in part by the large effects of stress periods at certain stages of plant development. Studies conducted by Agricultural Climatologists in Iowa indicated that a moisture stress at silking time, even though of short duration, may have a large effect upon the yield of corn.

R. E. COMSTOCK: Your suggestion makes sense to me. The greater size of the L × Y × V interaction variance has to be due to one or more aspect of environment for which the pattern of variation among locations differs from year to year. This seems likely to be the case for timing of stress periods relative to physiological stage of plants.

GLENN W. BURTON: The lack of location × genotype interaction has very great significance to the plant breeder because it means that in general a variety bred and tested in one of the locations will give a similar performance in the other locations sampled and if good may be recommended throughout the area. It also suggests that within the area sampled perhaps only climatic variations need be adequately sampled during the testing program.

R. E. COMSTOCK: I am in general agreement, but would still urge caution with respect to generalizing that location × genotype interaction will always be small. As a boy I happened to live very close to a line of distinct change in soil type involving quite sharp differences in drainage, acidity and organic content. I cannot believe that between the two sides of that line there would not have been considerable location × genotype interaction. I think acceptance of the idea that location-genotype interaction is small should be conditioned by ones knowledge of the area in question.

C. O. GARDNER: Since data reported for self-fertilized crops indicate that σ^2_{GY} and σ^2_{GL} are both very low and perhaps zero and σ^2_{GLY} is large and the same thing has been reported in corn by Robinson, can't 2 locations in each of two years be treated as 4 independent environments? This would reduce the magnitude of the standard errors of the components as follows:

$$V(\sigma^2_{GLY}) = \frac{2}{r^2}\left(\frac{M^2_{GLY}}{3(g-1)} + \frac{M^2_E}{f_E}\right) \text{ instead of } \frac{2}{r^2}\left(\frac{M^2_{GLY}}{(g-1)} + \frac{M^2_E}{f_E}\right)$$

$$V(\sigma^2_G) = \frac{2}{(lyr)^2}\left(\frac{M^2_G}{(g-1)} + \frac{M^2_{GLY}}{3(g-1)}\right) \text{ instead of}$$

$$\frac{2}{(1ry)^2}\left(\frac{M^2_G}{(g-1)} + \frac{M^2_{GL}}{(g-1)} + \frac{M^2_{GY}}{(g-1)} + \frac{M^2_{GLY}}{(g-1)}\right)$$

of course, if σ^2_{GL} and σ^2_{GY} do not equal zero, this would not be true.

R. E. COMSTOCK: If you have seen enough evidence to conclude with assurance that the year × genotype and year × location interaction variances are inconsequential in magnitude it would be logical to proceed as you suggest for the reason you've outlined.

My own inclination would be to stick with the conventional analysis. In the first place, I'd want to get whatever further information was possible concerning relative size of the three interaction variances. Second, the analysis you suggest biases the estimate of genetic variance by a fraction (one-third, I believe, when there are two locations and two years) of whatever year × genotype and location × genotype variance there might really be. I do not like to risk bias in estimating genetic variance unless the gain in variance of the estimate is going to be considerable. In this case, I believe you will find if you investigate further that the variance of the estimate of genetic variance would not usually be much reduced. This is because most of it comes from your $M^2_G/(g-1)$ term.

Vector Analysis Applied to Crop Eugenics and Genotype-Environment Interaction

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A VECTOR may be thought of as a directed force. It has both magnitude and direction. The angle between vectors is derived from the relationship $r = \cos \theta$, where r equals the correlation coefficient between the two sets of data comprising the two vectors in question. In addition, the terminus of a vector may be considered as a locus in space. For example, in Cartesian coordinates the symbol (4, 6) has come to mean 4 units of x and 6 units of y. Likewise (4, 6, 7) would mean 4 units of x, 6 of y, and 7 of z and for multi-dimensional space the symbol (4, 6, 7, 12...k) is an uniquely located point in n space.

The value r^2 has been used for many years to measure the degree of determination of one set of data by another (Wright, 14). In 1958, a vector representation of biological fields of force based on the degree of determination was developed by Grafius and Kiesling. Since then, a more comprehensive model has been developed to include n-space, Grafius and Kiesling (5). In these models the degree of determination was used as a cosine of the angle between two vectors. Empirically, good agreement was obtained between the observed and the total possible degree of determination but it is now known that this agreement was only a very close approximation. Recently, Robert Morley Jones suggested certain changes which make the agreement precise. His suggestions were to let r equal the cosine of the angle between two vectors and to write a vector in two-space as the function of cosecants. These changes have been incorporated in the present paper. The revision makes very little difference in practical results but the model is now aesthetically much more satisfying.

Multi-dimensional vector space has been used in the field of psychology, Thurstone (12) and in the field of genetics, Wright (15). However, the approach here is thought to be distinct, and for present purposes, more direct.

Mathematical considerations

We define the magnitude of a vector as the average magnitude of its elements

so that, for example, $|\bar{a}| = \frac{1}{n} \sum_{i=1}^{n} a_i = 1.$

We define a vector $\bar{g}$ in orthogonal 3 space (Fig. 1A) as

$$k\,\bar{g} = \bar{a}\cos\alpha + \bar{b}\cos\beta + \bar{c}\cos\gamma.$$

The vector $\bar{g}$ might represent the relative yield values of a set of varieties. If $\bar{a}$, $\bar{b}$, and $\bar{c}$ are composed of the relative yield values from the same varieties grown under different conditions, then it follows that $\bar{g}$ may be estimated from $\bar{a}$, $\bar{b}$, and $\bar{c}$ if the angles α, β, and γ are known. These angles are obtained from the relationship $r_{\bar{g}\bar{a}} = \cos\alpha$, $r_{\bar{g}\bar{b}} = \cos\beta$, etc.

Suppose that α and β are known but vector $\bar{c}$ is not. Further, that $\bar{a}$ and $\bar{b}$ are not orthogonal. The degree of determination of $\bar{g}$ may be obtained by reflecting $\bar{g}$ perpendicular to the plane so that the shadow falls at $\bar{g}'$ in Figure 1B. From spherical trigonometry it can be shown that $\cos^2 q = \cos^2\alpha/\cos^2\Theta$. It can also be shown that $\cos^2 q = r^2_{\bar{g}\bar{g}'}$. To find $\bar{g}'$ we write $k\bar{g}' = \bar{a}\csc\Theta + \bar{b}\csc\phi$, and since $\bar{g}'$ has a magnitude of 1, k is found to equal $\csc\Theta + \csc\phi$ and

$$\bar{g}' = \frac{\bar{a}\csc\Theta + \bar{b}\csc\phi}{\csc\Theta + \csc\phi}.$$

If the variances of $\bar{a}$ and $\bar{b}$ are markedly different, then the proportions of $\bar{a}$ and $\bar{b}$ should be divided by the standard deviations of $\bar{a}$ and $\bar{b}$, respectively.

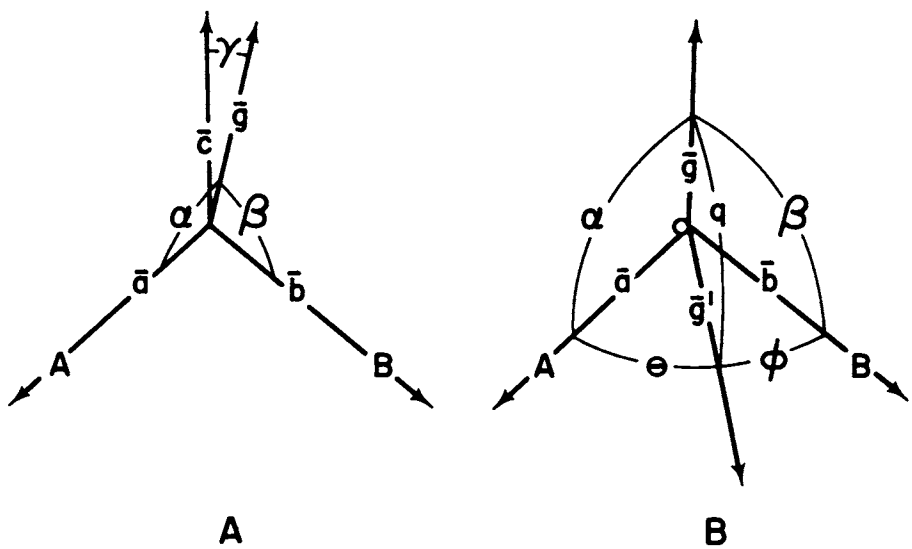

FIGURE 1. *1A, orthogonal 3-space. IB, spherical triangle where $\bar{g}$ is projected onto the AOB plane. The vectors $\bar{a}$, $\bar{b}$, $\bar{c}$ are of unit length with their origin at zero. The letters α, β, Θ, γ, and q, represent angles.*

APPLICATIONS IN CROP EUGENICS

H. V. Harlan *et al.* (6) stated the problem, "The writers have made hundreds of crosses at various times over a period of years, but always there was a lurking feeling that some other cross might have been better. There was little known about the value of varieties as parents and there were too many to choose from." We will bend vector analysis towards this end.

In self-fertilized crops, in the absence of epistasis, the mean for any trait of the unselected progeny after selfing will approach the mid-parent. Throughout this paper epistasis will be used to mean the various interactions of additive and non-additive effects (1, 2). Where these epistatic interactions are demonstrably due to the phenotypic multiplication of component parts, as in yield in small grain (8, 2, 13), they can be minimized or removed by ignoring the complex trait and measuring the components.

The problem of selecting the best parents is not restricted to self-fertilized crops. In the case of corn, Jenkins (7) suggested a solution based on single cross and top cross testing which is being used not only in corn but in many other crops where a hybrid is the desired end product. In crops such as rye, many of the forage crops and, in some cases, corn, synthetic varieties comprised of a number of selected lines are substituted for hybrid varieties *per se*. While it is common practice to try to evaluate characters in addition to yield by means of polycross or top cross tests, the attempt is usually restricted to only a few traits. In addition there is usually no attempt to control the proportions of each genotype so as to produce a maximum approach to an ideal.

In the present model we attempt to demonstrate that, not only is it possible to handle a number of traits simultaneously, but the existing methods of selecting parents in self-fertilized crops and of selecting parents and/or recombining lines in cross-fertilized species fall short of what could be achieved.

Superficially this problem appears extremely difficult, as several economic characters must be considered at one time and the prediction of the most favorable "blend" of germ plasm from several parents is most perplexing. Actually, a solution may not be difficult as it appears possible to create progenies so that the means for a number of traits are tightly clustered around an ideal.

The model is based on quantitative gene action. Complex characters such as yield, lodging, and quality have been broken up into their component parts to minimize epistatic interaction. The characteristics of the entire genotype are described by a vector which in turn is to be compared with an imaginary ideal. It is assumed that at least part of the variation of each trait is genetic and that the observed mean is the best estimate of the true mean.

The materials consist of data for 13 traits for 18 varieties of barley grown in standard replicated micro-plots at East Lansing, Michigan. The traits are listed in Table 1. The data for each trait were converted to a percentage of the mean of the population so that the mean value for each trait was 1.00. The "ideal" in Table 1 is an imaginary variety possessing an optimum value for each trait. This optimum is not necessarily the absolute optimum, since this may not be attainable, but it may be an optimum for the set of parents being investigated in a given environment. If a single ideal cannot be decided upon, several ideals may be written. After the crosses have been made the populations can be tested by growing the bulk populations for each ideal to see which is more nearly suitable. Thus, the ideals can be subjected to a statistical test to determine which of several is best.

TABLE 1.—RELATIVE PERCENTAGE VALUES FOR 13 TRAITS FOR A SET OF 19 BARLEY VARIETIES. A SAMPLE OF EIGHT VARIETIES PLUS AN IDEAL AND A RANGE OF ACCEPTABILITY IS PRESENTED HERE.

	C.I. Numbers									
Traits[1]	*5105*	*2947*	*7149*	*6969*	*9537*	*9548*	*9549*	*10,000*	*Ideal*	*Range*
X	107.5	84.3	81.4	74.1	82.8	106.1	117.7	107.5	118.0	±20.4
Y	96.0	92.5	111.7	97.7	109.9	113.4	94.2	94.2	100.0	±10.0
Z	104.0	97.0	102.0	101.7	98.7	101.0	102.0	109.8	107.7	± 6.2
F	94.9	90.9	83.0	59.3	130.4	122.5	114.6	102.8	115.0	±15.2
Height	101.8	111.1	108.0	98.8	92.6	98.8	98.8	108.0	93.0	± 8.4
Date Headed	117.6	88.2	117.6	73.5	132.3	73.5	102.9	73.5	118.0	±28.4
Mildew	83.3	111.1	111.1	111.1	55.6	27.8	27.8	83.3	27.8	±13.9
Color score	98.1	102.4	101.3	100.3	97.0	100.3	98.1	100.3	101.3	± 1.2
Extract	96.1	99.2	101.5	101.0	100.0	100.3	98.9	101.5	102.4	± 2.0
Diastatic Power	86.4	99.6	106.3	112.9	79.2	81.8	77.7	89.9	102.2	±12.5
Barley Nitrogen.	95.7	107.4	94.4	97.4	97.0	98.3	98.3	105.7	82.6	±15.8
β amylase	91.4	98.0	105.2	113.7	78.0	82.1	75.6	96.4	105.7	±11.6
α amylase	64.1	103.9	108.0	106.5	61.1	84.0	87.4	93.4	103.1	±27.3

[1]Reading down in order, the traits are: heads/unit area, kernels/head, av. kernel weight, force a culm will resist. The remainder are self-evident. Low values for mildew indicate resistance. The quality data are through the courtesy of Dr. A. D. Dickson and Dr. R. G. Shands.

Since each trait was not of equal economic importance, the data were weighted on the basis of a range of acceptability. A trait which was acceptable for only a narrow range was weighted most heavily. This weighting is a matter of judgment and the weighting formula is arbitrary. The formula used in weighting was $T' = 1.00 + \Delta T/10R$, where T' = the weighted trait, 1.00 is the mean, ΔT is the change in T measured from a mean of 1.00 and R is the range in values over which a strain could vary and still be acceptable. The coefficient of R is an arbitrary constant.

As an example, the weighted value of X for Cl 5105 in Tables 1 and 2 is

$$T' = 1.000 + \frac{(1.075 - 1.000)}{10 \times (.408)} = 101.8\%.$$

Other methods of weighting are no doubt possible and the best one is that which gives, as a final result, the best fit to an ideal variety.

The next step after weighting is to calculate the correlation coefficients between the parental lines and the ideal. In Table 3, only four lines have a strong positive correlation with the ideal. In general, negative relationships are undesirable although negative vectors can be added to positive ones to increase the relationship with the ideal, providing the base angle between the putative parents is wide enough.

The intercorrelations among the four vectors picked in Table 3 are given in Table 4.

TABLE 2.—WEIGHTED RELATIVE PERCENTAGE VALUES FOR 13 TRAITS FOR A SET OF 19 BARLEY VARIETIES. A SAMPLE OF EIGHT VARIETIES PLUS AN IDEAL IS PRESENTED HERE. WEIGHTING IS ON THE BASIS OF THE RANGE OF ACCEPTABILITY.

	C.I. Numbers								
Traits[1]	5105	2947	7149	6969	9537	9548	9549	10,000	Ideal
X	101.8	96.2	95.4	93.7	95.8	101.5	104.3	101.8	104.4
Y	98.0	96.2	105.8	98.8	105.0	106.7	97.1	97.1	100.0
Z	103.2	97.6	101.6	101.4	99.0	100.8	101.6	107.8	106.2
F	98.1	96.7	94.4	86.6	110.0	107.4	104.8	100.9	104.9
Height	101.1	106.6	104.8	99.3	95.6	99.3	99.3	104.8	95.8
Date Headed	103.1	97.9	103.1	95.3	105.7	95.3	100.5	95.2	103.2
Mildew	94.0	104.0	104.0	104.0	84.2	74.2	74.2	94.0	74.2
Color Score	92.1	110.0	105.4	101.2	87.5	101.2	92.1	101.2	105.4
Extract	90.2	98.0	103.8	102.5	100.0	100.8	97.2	103.8	106.0
Diastatic Power	94.6	99.8	102.5	105.2	91.7	92.7	91.1	96.0	100.9
Barley Nitrogen	98.6	102.3	98.2	99.2	99.0	99.5	99.5	101.8	94.5
β amylase	96.3	99.1	102.3	105.9	90.5	92.3	89.4	98.4	102.5
α amylase	93.4	100.7	101.5	101.2	92.9	97.1	97.7	98.8	100.6

[1]Reading down in order, the traits are: heads/unit area, kernels/head, average kernel weight, force a culm will resist. The remainder are self-evident. Low values for mildew indicate resistance.

TABLE 3.—SIMPLE CORRELATION COEFFICIENTS FOR 13 TRAITS OF 18 VARIETIES VERSUS AN IDEAL VARIETY.

	C.I. Number								
	5105	2947	7149	6969	9187	9190	9538	9537	9548
Ideal vs.	+0.1438	−.3072	−.2094	−.2870	−.0632	−.0879	−.3309	+.4783	+.7974
	C.I. Number								
	9549	9551	9554	9555	9999	10,000	10,001	9545	10,002
Ideal vs.	+.7523	−.6558	−.5406	−.1865	−.7585	+.4649	−.0645	−.0119	−.0130

TABLE 4.—INTER-CORRELATIONS AMONG FOUR POSITIVE VECTORS.

	C.I. Number			
	9537	9548	9549	10,000
9537 = $\bar{a}$	+1.0000	+.6949	+.7561	+.1996
9548 = $\bar{b}$	+.6949	+1.0000	.+8707	+.5520
9549 = $\bar{d}$	+.7561	+.8707	+1.0000	+.5727
10,000 = $\bar{e}$	+.1996	+.5520	+.5727	+1.0000

The maximum degrees of determination of the ideal by the progeny from the six possible crosses are given in Table 5. Notice the proportions of each line required to get the maximum. In the first two crosses, even an approximation to the exact proportions is impossible. In others, one can recognize either simple crosses or single backcrosses. These proportions were calculated as follows:

Let CI 9548 = $\bar{b}$ and CI 10,000 = $\bar{e}$ be coplanar vectors and let the cosine between them be 0.5520 as in Table 4. Then the maximum similarity between the progeny means and the ideal is obtained when the resultant of the coplanar vectors coincides with the shadow cast perpendicular to the plane by the ideal vector. Then, from spherical trigonometry and from a figure similar to 1B let

$$\tan \Theta = \frac{\cos \beta - \cos \alpha \cos \gamma}{\cos \alpha \sqrt{1 - \cos^2 \gamma}}, \text{ where } \gamma \text{ equals angle AOB.}$$

As in Figure 2 let $\bar{b}$ = CI 9548 and $\bar{e}$ = CI 10,000. Hence, from Tables 3 and 4

$$\tan \Theta = \frac{0.4649 - (0.7974)(0.5520)}{(0.7974)\ (\sqrt{1 - 0.3047})} = 0.0372.$$

Now, $k\bar{g}' = \bar{b} \csc \Theta + \bar{e} \csc (\gamma - \Theta)$ or

$$g' = \frac{26.90\ \bar{b} + 1.23\ \bar{e}}{26.90 + 1.23} = 0.956\ \bar{b} + 0.044\ \bar{e}.$$

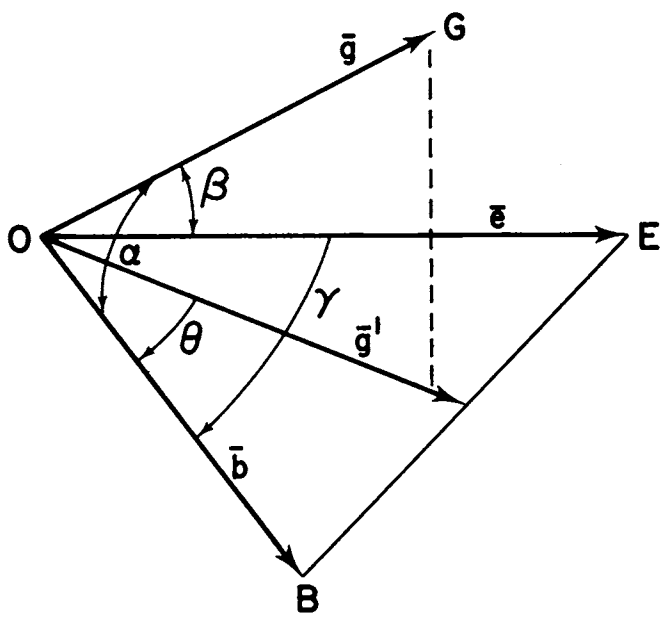

FIGURE 2. *The two coplanar vectors $\bar{b}$ and $\bar{e}$ represent the putative parents C.I.9548 and C.I.10,000, respectively. The vector $\bar{g}$ represents the theoretical ideal. The vector $\bar{g}'$ is as close as one can come to the ideal with these two parents.*

This suggests that several backcrosses might be in order. However, the convergence is very slow after the first backcross as shown in Table 5. After one backcross most of the possible degree of determination of $\bar{g}$ by $\bar{g}'$ has been attained. To construct the first backcross vector we proceed as follows, using the data in Table 2:

$$g'_1 = 0.75\ (1.015) + 0.25\ (1.018) = 101.6\%$$
$$g'_2 = 0.75\ (1.067) + 0.25\ (0.971) = 104.3\%$$
$$\vdots$$
$$g'_{13} = 0.75\ (0.971) + 0.25\ (0.988) = 97.5\%.$$

TABLE 5.—THE DEGREE OF DETERMINATION OF THE IDEAL BY THE PARENTS AND THE EXPECTED INBRED PROGENIES OF VARIOUS CROSSES. THE THEORETICAL DEGREES OF DETERMINATION ARE AFTER WRIGHT (14) AND ARE THE MAXIMUM POSSIBLE WITH THESE PARENTS. THE ACTUAL ARE PRACTICAL SUBSTITUTES FOR THE THEORETICAL.

Parent or Cross	Equations for Degree of Determination		Degree of Determination	
	Theoretical Maxima	Practical Proportions	Theoretical	Actual
CI 9537 = $\bar{a}$				0.23
9548 = $\bar{b}$				.64
9549 = $\bar{d}$				.57
10,000 = $\bar{e}$				.22
$\bar{a} \times \bar{b}$	$1.17\bar{b} - .17\bar{a}$	$.25\bar{a} + .75\bar{b}$	0.65	.59
$\bar{a} \times \bar{d}$	$1.18\bar{d} - .18\bar{a}$	$.25\bar{a} + .75\bar{d}$	.59	.52
$\bar{a} \times \bar{e}$	$.51\bar{a} + .49\bar{e}$	$.50\bar{a} + .50\bar{e}$	.37	.35
$\bar{b} \times \bar{d}$	$.71\bar{b} + .29\bar{d}$*	$.50\bar{b} + .50\bar{d}$	.65	.64
$\bar{b} \times \bar{e}$	$.96\bar{b} + .04\bar{e}$	$.75\bar{b} + .25\bar{e}$	.64	.63
$\bar{d} \times \bar{e}$	$.93\bar{d} + .07\bar{e}$	$.75\bar{d} + .25\bar{e}$	.57	.56
$(\bar{a} \times \bar{e}) \times (\bar{b} \times \bar{d})$		$1/8\bar{a} + 1/8\bar{e} + 3/8\bar{b} + 3/8\bar{d}$		.61

*This approximates a backcross ratio but since the angle between $\bar{a}$ and $\bar{d}$ is $\cos^{-1}$ 0.8707 = 29.5°, and since a shift of 10° in theta only reduces the information by 3%, a straight cross is the best practical solution.

It has been noted that the rate of convergence is small in the foregoing cross. Intuitively, one should expect this to be true since one could move $\bar{g}'$ in figure 1B a few degrees to the right or left without materially changing q. As a rule of thumb, a shift of ten degrees will reduce the degree of determination by three percent.

In some cases negative relationships were found. For example, in the cross of $\bar{a} \times \bar{b}$ (Table 5), Θ was found to be 53.7° which meant that $\bar{a}$ and $\bar{g}'$ were 53.7° apart whereas $\bar{a}$ and $\bar{b}$ were only 46.0° apart. Hence, $\bar{g}'$ lay 7.7° beyond $\bar{b}$. This problem was resolved algebraically by considering $\bar{b}$ as the resultant of $\bar{g}'$ and $\bar{a}$. Whence, $\bar{b} = \dfrac{\bar{a} \csc 53.7° + \bar{g}' \csc 7.7°}{\csc 53.7° + \csc 7.7°}$, and $\bar{g}' = 1.17\bar{b} - 0.17\bar{a}$, which is of course an impossible result. A backcross to $\bar{b}$ gave the expected result shown in Table 5. This value was

obtained by actually constructing the hypothetical population vector from the equation $\bar{g}' = 0.75\bar{b} + 0.25\bar{a}$ and then calculating $r^2_{\bar{g}\bar{g}}$, to get the degree of determination, Table 5. The cross $\bar{a} \times \bar{d}$ presents a similar problem.

In the remaining four crosses, the actual and theoretical maxima are quite close. It should be pointed out that according to theory the magnitude of the vectors should not deviate greatly from the magnitude of the ideal, but in this problem the variety magnitudes do deviate from the ideal. However, the close agreement between the actual and expected maxima for the last four crosses in Table 5 leads one to conclude that minor deviations from a mean length of unity are not serious. The expected degree of determination was calculated by path coefficients after Wright (14) and Grafius and Kiesling (4).

From Table 5 one might conclude that the best cross would be either $\bar{b} \times \bar{d}$ or $\bar{b}^2 \times \bar{e}$. In some cases, however, it may be desirable to create populations having a broader genetic base to take advantage of linkage recombinations and wider ranges of parental values. The multiple cross in Table 5 has the advantage of possessing at least one parental value for each trait within the acceptable range for each trait. For example, the hypothetical progeny mean for diastase falls outside the ideal $\pm$ the range in Table 1. Inspection of Table 1 shows that of the four parents, $\bar{a}$, $\bar{b}$, $\bar{d}$, and $\bar{e}$, only $\bar{e}$ falls within the range of acceptability. Recombination plus selection might be expected to move the mean of the *selected* progeny towards a more favorable value in any of the crosses in Table 5, but one might have greater confidence where one of the parents was known to have fallen in the acceptable range, especially where linkage was involved.

The detrimental effects of lines $\bar{a}$ and $\bar{e}$ were minimized by a single backcross to either *b* or *d*, Table 5. Accordingly, an optimum multiple cross was $(\bar{a} \times \bar{e}) \times (\bar{b} \times \bar{d})^2$ which gives a degree of determination of 0.61, closely approaching the theoretical maximum. In this case $\bar{g}' = 1/8\ \bar{a} \times 1/8\ \bar{e} + 3/8\ \bar{b} + 3/8\ \bar{d}$.

Up to this point, the estimates of degree of determination have been based on weighted data. If the weights were properly chosen, the comparison of the various expected progeny means with the ideal should be fairly close after transferring back to unweighted data. The results from three hypothetical crosses are shown in Table 6. It would appear that the weighting was adequate, as the means are within the range of acceptability for most traits and deviate greatly only for diastatic power and β-amylase. The strongest selection pressure would thus be needed on these two traits.

CROSS-FERTILIZED SPECIES

In cross-fertilized species the problem does not differ greatly from the foregoing. The procedure is the same, but the predicted parental influence is based on topcross or polycross data. In other words, the progeny means are estimated through topcross or polycross tests. Since this is an accepted procedure, little need be said in its defense except to add that specific combining ability effects due to epistasis will be minimized wherever possible through the use of the components of complex multiplicative traits such as yield.

Where an F_1 or similar hybrid is the desired end point, vector analysis can

TABLE 6.—EXPECTED PROGENY MEANS FROM THREE HYPOTHETICAL CROSSES AS COMPARED TO THE IDEAL, BASED ON ACTUAL RATHER THAN WEIGHTED DATA.

Measure	$\bar{b} \times \bar{d}$	$\bar{b} \times \bar{e}$	$(\bar{a} \times \bar{e})(\bar{b} \times \bar{d})^2$	Ideal	Range
X	111.9	106.8	107.7	118.0	±20.4
Y	103.8	103.8	103.4	100.0	+10.0
Z	101.5	105.4	102.2	107.7	± 6.2
F	118.6	112.6	118.1	115.0	±15.2
Height	98.8	103.4	99.2	93.0	± 8.4
Date Headed	88.2	73.5	91.9	118.0	±28.4
Mildew	27.8	55.6	38.2	27.8	±13.9
Color Score	99.2	100.3	99.0	101.3	± 1.2
Extract	99.6	100.9	99.9	102.4	± 2.0
Diastatic Power	79.8	85.9	81.0	102.2	±12.5
Barley Nitrogen	98.3	102.0	99.1	82.6	±15.8
β Amylase	78.9	89.2	81.0	105.7	±11.6
α Amylase	85.7	88.7	83.6	103.1	±27.3

[1]Reading down in order, the traits are: heads/unit area, kernel/head, av. kernel weight, force a culm will resist. The remainder are self-evident.

still make an important contribution. For not only is it possible to consider several traits at one time, but, using four inbred lines, hybrids may be created which in theory are superior to the double cross—and at very little added expense. As an example, the cross $(\bar{a} \times \bar{e})(\bar{b} \times \bar{d})^2$ in Table 5 can be shown to be superior to $(\bar{a} \times \bar{e})$ $(\bar{b} \times \bar{d})$. The data in this case are for barley, but a similar situation could be visualized for corn.

Once estimates of the contribution of each potential parent have been obtained, the problem is identical to that of the self-fertilized species. The unique departure from traditional use of this information lies in the treatment of several traits simultaneously and according to their independent contribution to the ideal.

MULTI-DIMENSIONAL VECTOR SPACE

In the previous example oblique axes were used as they occurred. In the present case it is intended that orthogonal basis vectors be constructed from known vectors. The use of orthogonal vectors permits a direct solution to the vector problem.

The data consisted of 14 vector sets. These sets were composed of the relative yields of 22 varieties of oats grown under 14 different environments. Replicated plots 12 by 14 feet in area, with the center two drill rows harvested for yield, were used as sources of the data. The yield data from each location were converted into per cent of the location mean so that the mean length of each vector was 100 per cent or 1.00.

Five locations were picked from a total of 14 as being distinct (Table 7). Note that the vectors are almost orthogonal with the exception of the plot grown in Tuscola County in 1956.

TABLE 7.—VALUES OF r^2 REPRESENTING THE ANGLE BETWEEN FIVE VECTORS. THE BAR INDICATES r WAS NEGATIVE.

Location[1]	Major Variable	$I_{E'55}$	$I_{L'55}$	$T_{'52}$	$T_{'56}$	$I_{L'56}$
$I_{E'55}$	cool nights	1.0000	$\overline{0.0020}$	$\overline{0.0694}$	0.2724	0.0032
$I_{L'55}$	hot nights	$\overline{0.0020}$	1.0000	0.0019	$\overline{0.1273}$	0.0844
$T_{'52}$	drought	$\overline{0.0694}$	$\overline{0.0019}$	1.0000	$\overline{0.1089}$	$\overline{0.0599}$
$T_{'56}$	lodging	0.2724	$\overline{0.1273}$	$\overline{0.1089}$	1.0000	0.0119
$I_{L'56}$	rust	0.0032	0.0844	$\overline{0.0599}$	0.0119	1.0000

[1]I and T stand for county. Subscript E and L stand for early and late planting. The subscript numbers indicate years.

It should be pointed out that the late planting in 1956 for Ingham County was infested with both race 202 of leaf rust *Puccinia coronata* (Pers.) Cda. and race 7 of stem rust *P. graminis avenae* Erikson and Henn. In the two comparisons where this was important, in Ingham and Lenawee counties in 1957, leaf rust was more severe than stem rust and in addition both race 216 and race 202 of leaf rust were present. Hence, this comparison is not as clear cut as would be desirable. Nevertheless, the presence of "rust" was clearly detected by the system.

Since the vectors in Table 7 are not orthogonal, largely because of T_{56}, they must be moved about until they are orthogonal, or approximately so. The easiest way to do this is to use the Gram Schmidt orthogonalization process, Murdock (9) which holds one vector constant and moves the others to orthogonal positions around it. There is merit in this scheme, but it was decided to avoid selecting any one vector but instead to move all vectors to orthogonal positions by an iterative process. It was arbitrarily decided to use r^2 values in the iterative process. This would tend to avoid abrupt changes in the position of any vector.

Referring to Figure 3, let A, B, and C be the observed vectors and let them be moved in such a way as to become orthogonal. Further, let the angle between A and $B = \alpha$, between B and $C = \beta$, and between A and $C = \tau$. Using matrix algebra and multiplying rows into columns, we find

$$\begin{vmatrix} A_i & B_i & C_i \end{vmatrix} \cdot \begin{vmatrix} p_a & -\cos^2\alpha & -\cos^2\tau \\ -\cos^2\alpha & p_b & -\cos^2\beta \\ -\cos^2\tau & -\cos^2\beta & p_c \end{vmatrix} = \begin{vmatrix} a_i & b_i & c_i \end{vmatrix}$$

where

$$a_i = A_i p_a - B_i \cos^2\alpha - C_i \cos^2\tau,$$
$$b_i = -A_i \cos^2\alpha + B_i p_b - C_i \cos^2\beta, \text{ and}$$
$$c_i = -A_i \cos^2\tau - B_i \cos^2\beta + C_i p_c.$$

The p values are scalars to maintain a unit length for the derived vectors $\bar{a}$, $\bar{b}$ and $\bar{c}$. Thus,

$$p_a = 1 + \cos\alpha + \cos\tau,$$
$$p_b = \cos\alpha + 1 + \cos\beta, \text{ and}$$
$$p_c = \cos\tau + \cos\beta + 1.$$

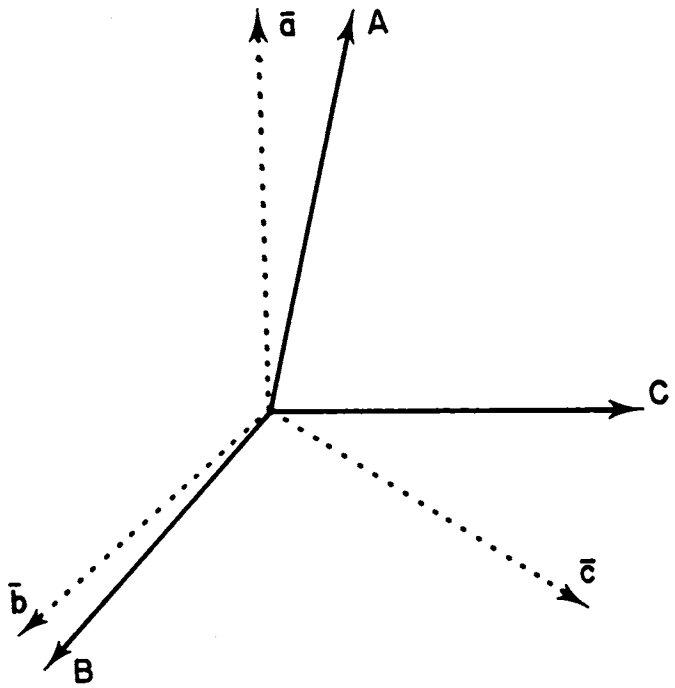

FIGURE 3. *Since the vectors will not ordinarily be othogonal, i. e., $r \neq O$, it may be necessary to move vectors.*

As a numerical example for the five vector set in Tables 8 and 9, let the angle between I_{55} and $I_{L55} = \alpha$, and the angle between I_{55} and $T_{52} = \tau$ and so on, then

$$a_i = A_i p_a - B_i \cos\alpha - C_i \cos\tau - D_i \cos\delta - E_i \cos\epsilon.$$

In this case, using r^2 values from Table 7,

$$p_a = 1 + \cos\alpha + \cos\tau + \cos\delta + \cos\epsilon$$
$$= 1 - 0.0020 - 0.0694 + 0.2724 + 0.0032 = 1.2042.$$

TABLE 8.—ORIGINAL VECTORS WHERE I AND T REFER TO INGHAM AND TUSCOLA COUNTIES, RESPECTIVELY, AND THE SUBSCRIPT NUMBERS REFER TO THE YEAR. THE SUBSCRIPT L REFERS TO LATE PLANTING. DATA ARE YIELDS IN PER CENT OF THE LOCATION MEAN.

Variety	Location				
	I_{55}	I_{L55}	T_{52}	T_{56}	I_{L56}
Ajax	101.8	115.6	93.2	108.6	122.8
Beaver	119.5	97.9	91.2	109.6	116.6
Cherokee	93.9	110.3	109.1	81.6	98.4
Clarion	105.0	109.9	97.8	87.8	115.6
Clintafe	102.7	119.6	83.9	99.3	88.6
Clinton	96.1	109.5	105.0	90.5	90.5
.	.	.	.	.	.
.	.	.	.	.	.
.	.	.	.	.	.

TABLE 9.—DERIVED VECTORS $\bar{a}$, $\bar{b}$, $\bar{c}$, $\bar{d}$, AND $\bar{e}$.

Variety	$\bar{a}$	$\bar{b}$	$\bar{c}$	$\bar{d}$	$\bar{e}$
Ajax	99.3	114.0	97.3	109.5	121.9
Beaver	120.0	97.8	96.7	103.3	116.7
Cherokee	98.3	107.6	104.4	84.7	98.3
Clarion	109.2	106.6	98.3	86.7	115.4
Clintafe	102.4	119.5	87.2	99.4	85.5
Clinton	98.3	108.6	101.9	93.0	89.7
.	.	.	.	.	.
.	.	.	.	.	.
.	.	.	.	.	.

Hence, from Table 8,

$$a_1 = (1.018)(1.2042) - (1.156)(-0.0020) - (.932)(-0.0694) - (1.086)(0.2724) - (1.228)(0.0032) = 99.3\% \text{ and}$$

$$a_2 = (1.195)(1.2042) + (.979)(-0.0020) + (.912)(0.0694) - (1.096)(0.2724) - (1.166)(0.0032) = 120.0\% \text{ as is shown in Table 9.}$$

A similar procedure was followed for $\bar{b}$, $\bar{c}$, $\bar{d}$, and $\bar{e}$. When the correlation coefficients between these vectors were calculated the vectors were still not orthogonal and so the process was repeated using $\bar{a}$, $\bar{b}$, $\bar{c}$, $\bar{d}$, and $\bar{e}$ vectors to derive a basis set of $\bar{a}'$, $\bar{b}'$, $\bar{c}'$, $\bar{d}'$, and $\bar{e}'$. These vectors were approximately orthogonal as shown in Table 10.

TABLE 10.—VALUES OF r^2 FOR THE SECOND CYCLE DERIVATION BASIS VECTORS $\bar{a}'$, $\bar{b}'$, $\bar{c}'$, $\bar{d}'$, $\bar{e}'$. THE BAR OVER THE NUMBERS INDICATES AN ANGLE GREATER THAN 90°.

Vector	$\bar{a}'$	$\bar{b}'$	$\bar{c}'$	$\bar{d}'$	$\bar{e}'$
$\bar{a}'$	1.0000	0.0047	0.0000	0.0036	0.0000
$\bar{b}'$	0.0047	1.0000	$0.\overline{0036}$	0.0162	0.0167
$\bar{c}'$	0.0000	$0.\overline{0036}$	1.0000	$0.\overline{0002}$	0.0016
$\bar{d}'$	0.0036	$0.\overline{0162}$	$0.\overline{0002}$	1.0000	0.0060
$\bar{e}'$	0.0000	0.0167	0.0016	0.0060	1.0000

The squared correlation coefficients between the orthogonal basis vectors and the data from the nine remaining locations are given in Table 11. Note that the total degree of determination (R^2), as contrasted to the sum, is always slightly lower. This is caused by the basis vectors not being exactly orthogonal. The total degree of determination (R^2) was calculated after Wright (14) and Pearson (10) as $R^2 = 1 - \frac{\Delta}{\Delta_{xx}}$ where Δ is the determinant of the 6 × 6 matrix of correlation coefficients between

TABLE 11.—VALUES OF r^2 BETWEEN THE BASIS VECTORS $\bar{a}'$, $\bar{b}'$, $\bar{c}'$, $\bar{d}'$, AND $\bar{e}'$ AND THE NINE LOCATION VECTORS, WHERE I, K, L, AND T REPRESENT INGHAM, KALAMAZOO, LENAWEE, AND TUSCOLA COUNTIES, RESPECTIVELY. THE BASIS VECTORS $\bar{a}'$, $\bar{b}'$, $\bar{c}'$, $\bar{d}'$, AND $\bar{e}'$ REPRESENT THE MAJOR VARIABLES COOL NIGHTS, HOT NIGHTS, DROUGHT, LODGING, AND RUST[1], RESPECTIVELY.

Vector	I_{52}	K_{52}	L_{52}	T_{55}	K_{55}	I_{56}	K_{56}	I_{57}	L_{57}
$\bar{a}'$ cool nights	0.0229	$0.\overline{0095}$	0.0273	0.0123	0.2267	0.1452	0.0804	$0.\overline{0009}$	0.0366
$\bar{b}'$ hot nights	0.0413	0.2686	0.4176	$0.\overline{0003}$	$0.\overline{0821}$	$0.\overline{0827}$	$0.\overline{1871}$	0.0995	0.0413
$\bar{c}'$ drought	0.2168	0.0532	0.0195	$0.\overline{1437}$	$0.\overline{1578}$	$0.0\overline{359}$	$0.\overline{0379}$	$0.\overline{1351}$	$0.\overline{2061}$
$\bar{d}'$ lodging	$0.\overline{0409}$[2]	$0.\overline{0751}$	$0.\overline{0271}$	0.0361	0.2620	0.1696	0.4206	0.1036	0.0857
$\bar{e}'$ rust	$0.\overline{0354}$	$0.\overline{0101}$	0.0027	0.0352	0.0613	0.0921	0.0145	0.1798	0.3518
Sum	0.3573	0.4165	0.4942	0.2276	0.7899	0.5255	0.7405	0.5189	0.7215
Calculated determination	0.3438	0.3905	0.4722	0.2026	0.7491	0.5009	0.6837	0.4807	0.6426

[1]See text.
[2]The bar above the numbers indicates an angle greater than 90°.

the location being compared and the five basis vectors, and Δ_{xx} is the determinant based on the correlation matrix of the five basis vectors alone.

A description of the environment at the nine locations is given in Table 12. The environmental factors setting the pattern, as measured by the degree of determination, are marked with an asterisk. Of necessity, these patterns are mutually exclusive. Apparently a moderate departure from normal cannot be seen in the pattern of varietal performance when accompanied by a violent departure in some other category, as for example, the effects of drought and temperature for Lenawee County, 1952.

TABLE 12—.ENVIRONMENT AT NINE LOCATIONS IN MICHIGAN WITH REGARD TO THE MAJOR VARIABLES DEGREE NIGHTS, DROUGHT, DIFFERENTIAL LODGING, AND RUST[1].

Location	Degree Nights[1]		Rainfall[2]			Lodging	Rust[3]
			May	June	July		
Ingham Co.	1952	167	+1.88	−2.08*	0.00	Light	Light
Kalamazoo Co.	1952	209*	−0.55	−1.41	−0.67	Light	Light
Lenawee Co.	1952	330*	+1.04	−2.50	−0.72	Light	Light
Tuscola Co.	1955	58	+1.20*	−0.52	−0.58	Medium	Light
Kalamazoo Co.	1955	130*	−1.87	−0.32*	−0.04	Medium*	Light
Ingham	1956	123*	+1.85	−1.57	+0.41	Medium*	Light
Kalamazoo Co.	1956	193	−0.05	−0.52	−0.32	Heavy*	Light
Ingham Co.	1957	141	+1.42	−0.49	+5.27*	Heavy*	Heavy*
Lenawee Co.	1957	207	−1.23	−0.74	+0.02*	Heavy	Heavy*

[1]Degree nights are the cumulative total degrees above 60° for the growing season based on U.S. Weather Bureau minimums.
[2]Departures from normal.
[3]Rust refers to joint effects of races 202 and 216 of leaf rust and race 7 of stem rust. Leaf rust caused the most damage in 1957 in Ingham county. The effects of leaf rust and stem rust were more nearly equal in Lenawee Co.
*Factors setting pattern for the location as measured by the degree of determination in Table 11.

The squared correlation coefficients in Table 11 and the basis vectors $\bar{a}'$, $\bar{b}'$, $\bar{c}'$, $\bar{d}'$, and $\bar{e}'$ can be used to estimate the nine vectors. For example, from Table 11 and 13:

$$K_{55i} = \frac{a'_i\sqrt{(0.2267)} + (200 - b'_i)\sqrt{(0.0821)} + (200 - c'_i)\sqrt{(0.1578)} + d'\sqrt{(0.2620)} + e'\sqrt{(0.0613)}}{P}$$

where P is the constant to adjust the average length of K_{55} to 1.00. It will be noted that $200 - \bar{b}'_i$ and $200 - \bar{c}'_i$ were used in place of $\bar{b}'_i$ and $\bar{c}'_i$. This is necessary because the angles exceed 90° and are negative. It is required to make the angles positive. This can be done by changing the direction of the basis vectors momentarily by subtracting the individual values from twice the mean. Thus, a value of 120 becomes 80 and so on. The correlation between this new vector and the original basis vector is −1.00. Hence the correlation of this new vector with K_{55} is the same as for the original basis vector with its sign changed. An example is given based on Tables 11 and 13.

TABLE 13.—YIELD DATA IN PER CENT OF THE LOCATION MEAN FOR THE DERIVED BASIS VECTORS. COLUMNS 2 AND 3 ARE 200—b'_i AND 200—c'_i, RESPECTIVELY.

Variety	a'	200–b'	200–c'	d'	e'
Ajax	99.2	86.3	102.5	109.4	122.2
Beaver	120.4	102.6	103.2	102.9	117.2
Cherokee	98.3	92.7	95.6	84.9	98.3
Clarion	109.3	94.1	101.6	86.6	116.0
Clintafe	102.3	80.3	102.6	100.1	84.6
Clinton	98.3	91.3	98.1	93.4	89.3
–	–	–	–	–	–
–	–	–	–	–	–
–	–	–	–	–	–

$$K_{55}\ \text{Ajax} = \frac{0.992(0.4761) + 0.863(0.2865) + 1.025(0.3972) + 1.094(0.5119) + 1.222(0.2476)}{0.4761 + 0.2865 + 0.3972 + 0.5119 + 0.2476} = 103.6\%$$

$$K_{55}\ \text{Beaver} = \frac{1.204(0.4761) + 1.026(0.2865) + 1.032(0.3972) + 1.029(0.5119) + 1.172(0.2476)}{1.9193} = 109.1\%.$$

The estimated K_{55} vs K_{55} gave a correlation of 0.86. The closeness of agreement is a function of the degree of determination shown in Table 11. In the case of T_{55} this value is rather low, but in the other eight cases the degree of determination would probably be acceptable to a biologist engaged in crop testing.

It is not claimed that the five basis vectors are an exact representation of temperature, drought, lodging, and so on, but merely a close approximation of these

effects. As such, they can be used to predict relative varietal performance. For example, if weather records and field observations led one to conclude that lodging and high night temperature were the major variables affecting the performance pattern, these observations could be used in prediction. Suppose further that the two environmental variables were judged to be equally important by competent observers, then an estimate of varietal performance could be made using 50 per cent of $\bar{b}'$ and 50 per cent of $\bar{d}'$.

DISCUSSION

The intent in this paper has been to present a vector method for use on biological material which would be both versatile and objective. The versatility of the tool is obvious, but the objectivity has not been argued. The vectors, the angles between them, and the degrees of determination are completely objective. The objectivity of the ideal vectors, of planes of force, or of basis vectors has not been established. The argument relies on the establishment of general agreement.

In the construction of an ideal vector several experienced persons could perhaps reach an agreement on an ideal, but in the event that no agreement could be reached, several ideals could be constructed and then approximated in actual crosses which could be tested in a controlled experiment. Thus, an ideal could have a large degree of objectivity. This particular experiment has not yet been performed but it would seem to be very worthwhile.

Under a devastating attack by a pathogen, universal agreement will be readily reached among biologists that the influence of the pathogen on yield is a highly important environmental variable. Thus, the fact that a location (A) had a severe epiphytotic could be considered an objective conclusion.

Shown a nursery (B) which was not infested with the pathogen in question, the biologists would all agree on this observation but they might not agree that the disease was the most important environmental variable differentiating A from B. Hence the assumption that the major point of difference between A and B was due to the disease, i.e. the establishment of the disease plane or basis vectors, is subjective and not a point on which universal agreement could always be reached. The chances of universal agreement may be enhanced by careful choice of locations and greatly enhanced by controlled replicated experiments where the pathogen is controlled in half of the plot and allowed to parasitize the other half. At this point, the method appears to be objective, the objectivity being reduced to the degree that the designation of the basis vectors or force planes depends upon the opinion of the individual biologist.

In many seasons, the number of major variables may be too large to establish basis vectors. Seasons will occur, however, from time to time, which are characterized by hot nights, stem rust, drought, or lodging, and sets of data from these seasons will be extremely useful in determining the impact of environment on the genotype. Subsequent observations should help to establish or reject the validity of the basis vectors.

The eugenics model is predicated upon the assumption that it is possible

to predict progeny means for both self-fertilized and cross-fertilized species. Linkage is no barrier to the model as the *means* are independent of linkage in the absence of epistasis. Linkage will, however, tend to prevent the occurrence of a perfect variety within the population.

Epistasis will confuse the estimates of progeny means and it is proposed to minimize this effect by the use of the components of complex traits such as yield, lodging resistance, and quality. In support of this assumption, experiments with barley, Grafius (2); oats, Luedders (8); and wheat, Whitehouse *et al.* (13); indicate that troublesome epistatic interaction effects for yield can be removed by dealing with the components of yield and that the mid-parent does furnish a good estimate of the unselected progeny means, in an F_5 generation, for example. There is no intent to ignore the work on natural selection within bulk populations. In many cases these effects are slow in appearing and are often beneficial to man, Suneson (11). If the effects are large and occur quickly, then natural selection must be considered. It was not considered in the present model.

It is recognized that the correlation coefficient is a test for pattern and that it is theoretically possible for a variety to have a +1 correlation with the ideal and not have the means for each trait within the acceptable range. However, when the restriction is applied that each vector approach the magnitude of the ideal, this is not possible. When the mean values of the various vectors deviate greatly from the ideal, then care should be taken to prevent selecting such a parent. Under these conditions it is best to calculate the expected values before making the cross.

In the case of cross-fertilized species, the topcross and polycross tests are accepted methods for predicting progeny performance. The use of components of complex traits, such as yield in corn, should improve the precision of these tests through the elimination of the component interaction as an unknown variable.

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It is a pleasure to acknowledge the contribution of Drs. R. L. Kiesling and M. W. Adams as sections of this paper have appeared under joint authorship.

DISCUSSION

R. E. COMSTOCK: By earlier statements, you indicate that genetic variance as well as "approach to ideal" is important. Have you given any attention to how much "approach to ideal" you can afford to give up in return for a given amount of genetic variance?

If I understand, you assume additivity so that the attributes of a cross will be midway between parents crossed. Is this correct? Then if I understand further, you are looking for a cross such that deviations of cross from ideal multiplied by economic values weights and summed over traits is minimized. Cannot these summed weighted deviations be worked up arithmetically and compared for different crosses? This might not be as efficient, but I'm asking to clarify what you are trying to do. You see, I am having trouble recalling my trig.

J. E. GRAFIUS: In the case of selection for one trait, the answer to your question could be arrived at by means of the expected genetic gain. In the case of many characters, some of which may be correlated and some of which may have intermediate optima, I am no longer sure that a large genetic variance is desirable for all traits. In fact, for many traits the ideal may be an optimum and no further charge desired. In this case zero genetic variance would be welcome wherever the population mean and the ideal were the same. In other traits, the ideal is merely a modest request for progress, and selection pressure in the presence of genetic

variance could isolate individuals superior to the ideal for this trait. It would be logical to expect that the angle between parental vectors would, in general, give some indication of the expected genetic variance in the unselected progeny. One use of this assumption would be to select parental pairs which would contribute a low average variance to the population but which had a relatively wide difference for two or three traits for which the ideal was not at an optimum. As an example of such traits, in barley there appears to be a relationship between seed size and modification in malting which imposes a ceiling on seed size and many parental strains are in the neighborhood of this optimum. On the other hand, increases in tiller number and head size are desirable.

The statement in the second part of your question is correct and one can use the sum of squares of the deviations as a measure of the approach to an ideal. We went further and used trigonometry to get the proportions of each parent. For reasons which will be stated in answer to Dr. Sewall Wright's statement, we did not want a least squares solution for the proportions of each parent.

E. R. DEMPSTER: Is the primary purpose to (1) obtain something close to the ideal by crosses and at the same time (2) create variability to permit eliminating the particular deviation still remaining by selection?

J. E. GRAFIUS: Yes.

D. R. KNOTT: Will not the usefulness of your parents depend on whether they carry the same or different plus genes for a particular character and if so, how is this taken into account?

J. E. GRAFIUS: In general, those parental vectors which lie closest together will have the greatest tendency to have the same plus genes. It is, of course, possible to get the same degree of determination of the ideal from parental vectors lying 90° apart as from a pair lying 0° apart. Whether or not one wants the greatest total genetic variance for all traits is, I think, questionable. My reasoning is given in my answer to Dr. Comstock.

KEN-ICHI KOJIMA: If you intend to use vector methods to find combinations and proportions of varieties which would come close to the projection of an ideal, and if you want to start to select from it toward the ideal, I should think you would have to give a proper consideration to gene interactions, linkages and pleiotropy in finding the combinations and proportions. Can you comment on it?

J. E. GRAFIUS: Once the population is created, then the standard selection principles apply. Our objective was to create populations with means as close as possible to an ideal. Linkage and just sheer numbers of genes will prevent getting a perfect variety but recurrent selection should be a powerful tool towards this end. In some cases several generations of random

mating may be necessary before starting selection. In regard to pleiotropy, the influence of gene background, negative physiologic correlations, etc., our degree of ignorance is admittedly high. Therefore, we suggest starting with the *vin ordinaire* of all plant breeders, the standard variety and attempting minor but significant modifications in it. Since the model exists there can be no argument that it cannot exist. If progress towards the ideal plateaus, then we must write a new ideal, accepting the progress made and modifying our demands toward a new goal in a feedback type operation. Of course, one can use the vector method for the wild jumps too, but with less certainty as to whether the model is biologically possible with the existing gene pools.

H. F. ROBINSON: You use components of yield to eliminate epistatic effects, you say. Do you have epistasis in yield, and if so, what is your evidence for epistatic effects being absent in yield components?

J. E. GRAFIUS: If epistasis is used to mean the interactions of the various additive and non-additive effects, then epistasis exists in yield. It has been demonstrated in several crops by Jinks (Genetics, 1955); in wheat by Whitehouse, Thompson, and Ribeiro (Euphytica, 1958); in barley by Grafius (Agron. Jour., 1959); in oats by Luedders (M.S. Thesis, Mich. State Univ., 1960); in flax by Manner (Hereditas, 1958); and in tomatoes by Powers (Heterosis, 1952) and by Williams (Nature, 1959) to mention a few. In general, the components of complex characters such as yield have been predictable on the basis of the mid-parent in self-fertilized crops whereas yield itself is either less predictable, or not predictable at all. This kind of treatment ignores the classic type of epistasis. I am sure that it exists but so far it has not been a major deterrent to prediction.

I cannot handle the classic type of interaction and if the primary purpose is to look for this then some other tool such as the Diallel is more appropriate. At present, I can see no reason why favorable epistatic reactions of the classic type should be less frequent in a cross chosen by the vector method than in a random choice of parents.

In the case of cross-fertilized organisms, the parent is evaluated on the basis of its performance in test crosses. The use of components of yield in corn for example, should isolate that part of the specific combining ability which is due to component interaction.

HENRY E. SCHAFFER: In several crosses, the cross decided on had a lower percentage of the total degree of determination than did one of the parents. Does this indicate that the cross is not as good as the better parent?

J. E. GRAFIUS: It indicates that the best parental vector more nearly resembles the ideal than the unselected progeny vector. Selection pressure within the progeny, however, may isolate individuals which are superior to the

best parent. The cross must be made to supply the genetic variability on which selection can act.

F. H. W. MORLEY: Could one achieve a similar result by the use of an index? Varieties with the highest correlation with the ideal, and the minimum with each other, might yield the best combinations, especially if optima were intermediate.

J. E. GRAFIUS: I believe the answer to your question is covered in my answer to Dr. Comstock.

J. A. NELDER: Is not the scaling of the dimensions of the vector by using the ranges closely similar to using a loss function for a variety with components x_i from the ideal μ_i given by $L = \Sigma\lambda_i (x_i - \mu_i)^2$? If so, it might be better to consider a general quadratic loss function $L = \Sigma\lambda_{ij} (x_i - \mu_i)(x_j - \mu_j)$ allowing correlations between deviations. Thus, given two parent vectors, the best vector in their plane is that which minimizes L.

J. E. GRAFIUS: No comment. I am not familiar with the procedure.

SEWALL WRIGHT: It seems to me that the particular problem considered by Dr. Grafius can be attacked most simply by the method of least squares. The problem, as I understand it, is to find the proportions, P_A, P_B- - -P_K, in which a given set of strains, A, B,- - -K, should be combined so that the averages for each of a large number of characters will approximate as closely as possible a set of ideal values, I_1, I_2- - -I_n. It is assumed that the number of characters, n, is larger than the number of strains. Let μ_{Ai} be the mean of character i in strain A, etc. We can write n observation equations:

$$\begin{aligned}
P_A\mu_{A1} + P_B\mu_{B1} \text{ ———— } P_K\mu_{K1} &= I_1 + \Delta\ (1)\\
P_A\mu_{A2} + P_B\mu_{B2} \text{ ———— } P_K\mu_{K2} &= I_2 + \Delta\ (2)\\
P_A\mu_{An} + P_B\mu_{Bn} \text{ ———— } P_K\mu_{Kn} &= I_n + \Delta\ (n).
\end{aligned}$$

These equations may be given appropriate weights (w). They yield K simultaneous linear (normal) equations to solve for the desired proportions, P_A, P_B - - - P_K.

$$\frac{\partial}{\partial P_A} \Sigma w\Delta^2\ (i) = 0$$

$$\vdots$$

$$\frac{\partial}{\partial P_K} \Sigma w\Delta^2\ (i) = 0.$$

J. E. GRAFIUS: For two parents both methods will achieve the same proportions of parents. We chose not to use the least squares method for several reasons.

First of all, Adams and I first visualized the problem as a vector problem and a useful method for creative thinking should not be lightly discarded.

Secondly, while the two methods will give the same result originally we do not always choose to use the least squares result as it is unnecessarily precise. For example, in one cross the least squares proportions were .96$\bar{b}$ to .04$\bar{e}$ whereas it could easily be shown by the vector method that .75$\bar{b}$ + .25$\bar{e}$ will give 97 per cent of the possible degree of determination without driving the genes of the non-recurrent parent to extinction.

In the third case, one will frequently find parents with strong positive correlations with the ideal but with negative coefficients in the least squares solution. Using vectors one can calculate the positive proportions of each parent needed to give a given degree of determination of the ideal.

Finally, the vector method is a visual method and one may calculate the proportions of parents by means of a sphere, protractor, and dividers.

Discussion: Statistics and Plant Selection

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PLANT breeders are interested in two kinds of characters—those which can be measured on individuals, and those which cannot. The applicability of population analysis techniques must depend in large measure on this elementary classification.

CHARACTERS WHICH CAN BE MEASURED ON INDIVIDUALS

The procedures developed by population geneticists and applied by animal breeders are generally applicable here, and many extensions and refinements of analyses and inference become possible through replication, the use of selfing, top-crossing, the diallel, and simultaneous tests in different environments. I think it is fair to comment that these possibilities have seldom been adequately exploited. However, I am not sure that criticism is as justified as it might seem to be.

In the first place the vast majority of "non-competing" characters include disease resistance, or very broad adaptive characters such as maturity time. Frequently, these are simply inherited, with one or few identifiable genes or, if polygenic in nature, selection is rapidly effective in bringing the mean within desired limits. Moreover, the material in which such characters are being examined or selected seldom constitutes a readily definable population. Hence, the concepts of heritability are not applicable except in a very loose sense.

Plant breeders concerned with such situations have, on occasions, exhibited symptoms of guilt because they have not been able to present estimates of heritability. They have not always realized that the glib usage of such terms is a frank admission that we are unable to define the effects of single genes. Heritability and related concepts offer at best an empirical description of certain population attributes which may be useful in planning and prediction. At times, there seems to be a real danger of losing perspective, of letting the procedures and the estimates become an end, and not a means to an end.

With certain characters expressed by individuals which constitute definable populations, the concepts developed by animal breeders may well apply. In such individuals and populations the use of heritability in the broad or the

narrow sense, selection indices, prediction of progress, and the estimation of genotype-environment interactions may be both possible and profitable.

I must emphasize that considerable effort devoted to examination of the reliability of records from spaced plants, as indicators of performance in commercial plantings, may be a useful precaution in the early stages of a selection program. A comparison of several genotypes at different stand densities would be an obvious experimental approach.

In this context Dr. Hanson's discussion on heritability is indeed timely. In plant lines, or families, which can be replicated, heritability may be made to approach 1.0 by increasing the number of replications, locations, and years. This has been well appreciated by animal breeders who have become accustomed to discuss heritability of individual record, multiple records, or family means and have usually been able to switch readily from one to the other. Plant breeders have not always defined their terms clearly and have seldom followed through to the application of their estimates in selection procedures. Unless the unit of measurement such as the individual, the average at a location, or the plot mean, is stated precisely the use of an estimate must be ambiguous.

I am not in full agreement with Hanson's suggestion that heritability should be used only in connection with response to selection. Indeed, the term has been used in so many senses, and so loosely, that we are forced either to discard it, or to define it on each occasion it is used. The term has some appeal on historical grounds, and is descriptive and functional when we apply it to ratios involving genotypic and environmental parameters. Few of us use it so often that the inclusion of a precise definition in each publication would seem unreasonably repetitive.

CHARACTERS WHICH CANNOT BE ASSESSED ON SINGLE PLANTS

Material which is physiologically adjusted and is resistant to diseases and pests can usually be improved only by selection for characters which are affected by competition, and other components of the environment, to such an extent that lines can be ranked only if material is put through its paces in tests resembling commercial conditions. Many avenues for exploitation of the techniques of quantitative inheritance are immediately closed. Measurement of the individual becomes impossible or meaningless. However, techniques which make use of averages (e.g., $\bar{F}_1$'s, polycrosses, $\bar{F}_2$'s, $\bar{B}\bar{C}$, $\bar{P}$arents) may still be available if the problems of seed production are not too formidable. I do not propose to explore such techniques here, but again must support Hanson's plea for precise definition in the use of the term "heritability."

Genetic theory may sometimes be used to predict progress from selection for this kind of character. Thus, selection of parents on the basis of performance of their polycross progeny will result in an amount of progress which might be predicted because the individuals in any polycross plot are half-sibs. The variance among polycross entries may then be taken as approximately $\frac{1}{4}\sigma^2_A$, where σ^2_A is the additive genotypic variance, if the original parents can be regarded as

a random sample, which is mating at random with the other members, and is derived from a random mating population in equilibrium. Even if these assumptions are not wholly valid, predictions of progress may still be reasonably accurate provided departures from the required conditions are not drastic.

However, I think the means of plots containing numerous different though related genotypes should not be regarded uncritically as the mean of the appropriate genetic class. The individuals in the plot compete with one another and the mean yield may be influenced more by the most vigorous individuals than by the general average of the group.

Selection indices may be used for the evaluation of plot means just as for the performance of an individual. As far as I am aware the same elegant modifications described by Henderson for individuals may be adapted to groups of plants divided into genetic categories at any levels. No assumptions about populations are required unless one wishes to make some statement about the heritability of an index.

The estimation of genotype by environment interactions demands some form of replication of genotypes. This may be accomplished on the individual level by clonal propagation, or by the use of families. Many adaptations are obvious and need not be considered further here. The inferences which can be made about populations are, however, far from obvious, apart from the mere detection of such interactions. The sensitivity of genotypes to environment may depend largely on the level of heterozygosity. Thus, the presence of genotype-environment interactions in a sample of inbred lines may not indicate that such interactions are present, or equally important, in F_1's; and *vice versa*.

While there are limitations to the application of the techniques of statistical genetics to improvement of characters expressed only in competing populations, and this fact must be recognized, there are some areas in which refinements may be an important practical possibility.

Firstly, I was delighted to hear Dr. Nelder speak of the possible alliance of growth analysis and statistical genetics. My own studies have shown genetic differences in relative growth rate, net assimilation rate, and the rate of development of leaf area index. If these attributes are determinants of economic value, as they almost certainly are in forage crops, growth analysis offers a powerful tool for increased efficiency of selection.

Secondly, I think we plant breeders have been rather overawed by statisticians who tell us that we need some impressively large number of replicates to demonstrate differences of a certain size. Acceptance of this viewpoint has, by restricting our selection differentials, probably done almost as much to hinder progress as the more refined designs have helped. The optimum number of replicates may be determined by techniques such as those of Rojas and Sprague (4). I suspect that, at least in the initial stages of selection, the optimum number of replications at any location will be closer to one than to three; that more locations should be included, and that some partitioning of interactions by orthogonal contrasts would help to clarify the sources of interactions. Comstock's paper outlines the basis for evaluation of different programs.

The use of genotypic correlations may be applied to plot as to individual yields. It may well be that, although the phenotypic correlation between two characters is zero, by partitioning the genetic and environmental portions are found to be opposite in sign. Apart from the biological interest in such situations, the use of environmental correlations to correct for environmental variation and of genotypic correlations to aid selection might be profitable. The phenotypic correlations frequently published can seldom be interpreted in terms of genetic and environmental effects, but this need not be so.

In this conference there has been little or no mention of selection for intermediate optima. Yet, the necessity of keeping certain characters within an acceptable range is one of the greatest problems of the plant breeder. Certain selection index approaches (1 and 2) are calculated to select for one or more characters while holding others constant. Intermediate optima may be included in the methods used by Dr. Grafius, but in general this field invites further exploration and development.

The experimental estimation of genotypic parameters may be rather discouraging. As Comstock emphasized, the variance of the estimates is frequently so large that confidence in even the first digit of a heritability estimate is seldom justified. Fortunately, the picture is a little brighter than it seems.

It so happens that the optimum strategy in selection does not vary greatly except with quite large variations in heritability, e.g. Morley and Heinrichs (3). We are therefore interested in knowing whether genotypic variation is large, medium, or small. If genotypic variation is small, one might well call off the breeding program and look for more expressed variability by introduction, mutation, or the removal of some genetic or environmental bottleneck. If it is large, one might well proceed with a selection program, confident that worthwhile gains will be obtained. In the middle part of the range a decision may be postponed, or a compromise strategy developed.

Since estimates usually need not be highly accurate if relatively simple schemes are to be examined, there seems to be little point in setting up a large experiment to obtain them. A regular breeding program may frequently, indeed usually, provide a source of estimates, or, at the cost of a little inefficiency, it may be slightly altered for that purpose.

There is a need for more work to define the accuracy required for decisions on breeding schemes, especially where σ_A^2 is small but non-additive genotypic variance is appreciable. The presence of non-additive genotypic variation is a necessary, but by no means a sufficient, indication for the exploitation of heterosis rather than of σ_A^2. The decision to be taken should depend on the progress which can be achieved from a given investment, and this will very frequently be determined as much by the biological characteristics of the material, especially the mode of reproduction, as by the genotypic parameters. However, if both types of programs are practicable, a high level of accuracy of estimates may be required.

This argument underlines the fact that plant breeders cannot regard estimates of genotypic parameters as an end in themselves. Rather, the estimates

serve as a basis for evaluation of breeding programs within the limits imposed by the biology of the material. The objectives in estimation of parameters in plant breeding will often differ from those in population or physiological genetics. In these fields slight alterations in parameters may have considerable evolutionary or physiological significance. Therefore, large experiments may be necessary, and the experimental material should be selected with that in mind.

This discussion has tended to emphasize certain difficulties because I think the usual approach, which is to avoid or ignore them, has not been in the best interests of plant breeding, perhaps not of statistical genetics. Let me conclude, however, by stating firmly that I believe there are many applications of statistical genetics to plant breeding which could be made right now. Many more need to be developed, but if the job is left with the animal breeders we will lag a long way behind. It is our task to overcome the difficulties ourselves, not to rely too much on others. If the contributors to this symposium have been predominantly animal breeders, this has probably been because insufficient plant breeders have taken the trouble to develop statistical genetics in their own field.

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Genetic Parameters-Experimental Estimates and Their Applications

F. W. SCHNELL, *Chairman*

Estimates of Genetic Parameters in Cross-Fertilizing Plants and Their Implications In Plant Breeding[1]

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THE ultimate objective of the plant breeder is to produce "strains" or "hybrids" that are superior in some way to those already in commercial production. To accomplish this, he must devise a breeding program which will allow him to produce and reproduce genotypes that represent somewhere near optimum combinations of genes for a particular area. Information of a statistical nature concerning the variation that exists in the breeding population is of fundamental importance in planning such a program. The breeder should know not only what portion of the total variation among plants is a direct result of genetic differences but also the nature of the genetic variation that exists. In addition, a knowledge of the magnitude of the genotype × environment interaction variance is needed, and the relationships among the various characters which are important in the development of a new variety must be understood. When information on these points is available, the breeder can decide which of the numerous breeding procedures is most likely to succeed.

The genetic parameters which are useful to the plant breeder may be listed as follows:

1. Additive genetic variance (σ^2_A), which results from the additive effects of the genes at all segregating loci.
2. Dominance variance (σ^2_D), which results from intra-allelic interaction of genes at segregating loci.
3. Epistatic variance which results from inter-allelic interaction of genes at two or more segregating loci and which is divisible into additive × additive (σ^2_{AA}), additive × dominance (σ^2_{AD}) and dominance × dominance (σ^2_{DD}) for the two-locus situation and into additive × additive × additive (σ^2_{AAA}), etc. for three or more loci.
4. Average degree of dominance or ratio of dominance variance to additive genetic variance.
5. Genotype × environment interactions which may be divided into addi-

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tive gene effects × environment and non-additive gene effects × environment.

6. Genotypic correlations among quantitative characters of importance for the particular crop.

The purpose of this paper is to summarize some of the estimates of genetic parameters obtained for quantitative characters studied in cross-fertilizing plants. Numerous reports have appeared in the literature; however, many of the experiments have not been well planned to yield useful data. As a result, they are inconclusive or limited in their interpretation and application.

METHODS USED TO ESTIMATE GENETIC PARAMETERS

The estimation of genetic parameters has been accomplished by analysis of variance and regression techniques applied to data collected on various kinds of parents and their progenies. Most experiments have involved randomized complete block designs or slight modifications of such designs. The components of variance and covariance and parent-offspring regression coefficients have been estimated and interpreted in view of their genetic expectations based on the particular genetic model assumed. Environmental variation among plants within plots has been estimated by use of genetically uniform material such as clones, F_1 single crosses, or homozygous lines.

Many published findings are based upon parent material and one or more kinds of progenies grown in randomized complete block or split-plot designs. In other experiments special designs have been used to obtain information of a genetic nature. Four of the most extensively used mating systems will be mentioned. Designs I, II, and III proposed by Comstock and Robinson (11, 12) and the diallel cross first analyzed with statistical genetic techniques by Sprague and Tatum (59) have been very useful in gaining information on the kinds and amounts of genetic variation in specified populations.

Design I involves mating randomly chosen pollen parents (males) to randomly chosen seed parents (females) to produce half-sib and full-sib progenies. Design II involves a set of randomly chosen parents divided into two groups (preferably equal). Progenies are produced by mating all members of one group (males) to all members of the other group (females). This design is excellent for multiflowered plants or for inbred lines. Design III involves mating randomly chosen F_2 or more advanced generation plants back to both of the parent inbred lines producing pairs of backcross progenies. The diallel cross involves all possible matings among a set of randomly chosen parents. Reciprocal crosses and the parents may also be included in the test with the crosses. Design II is a form of the diallel cross. Progenies produced in all four of these designs are generally grown in randomized complete blocks. The analyses of variance in their simplest forms are presented in Table 1. These analyses indicate that the genotype component of variance cannot be estimated independently of the genotype × environment interaction component when a single test is conducted. Only by testing over locations and years can unbiased estimates be obtained.

TABLE 1.—ANALYSES OF VARIANCE OF PROGENIES (OR PARENTS) TESTED IN r REPLICATIONS IN A RANDOMIZED COMPLETE BLOCK DESIGN IN A SINGLE ENVIRONMENT.

Source of variation	d.f.	Mean Square	Parameters Estimated
a. Parents or progenies of any kind:			
Replications	(r−1)		
Progenies	(g−1)	M_1	$\sigma^2 + r(\sigma^2_{GE} + \sigma^2_G)$
Error	(r−1)(g−1)	M_2	σ^2
b. Design I:			
Replications	(r−1)		
Males	(m−1)	M_1	$\sigma^2 + r(\sigma^2_{fe} + \sigma^2_f) + rf(\sigma^2_{me} + \sigma^2_m)$
Females in males	m(f−1)	M_2	$\sigma^2 + r(\sigma^2_{fe} + \sigma^2_f)$
Error	(mf−1)(r−1)	M_3	σ^2
c. Design II:			
Replications	(r−1)		
Males	(m−1)	M_1	$\sigma^2 + r(\sigma^2_{mfe} + \sigma^2_{mf}) + rf(\sigma^2_{me} + \sigma^2_m)$
Females	(f−1)	M_2	$\sigma^2 + r(\sigma^2_{mfe} + \sigma^2_{mf}) + rm(\sigma^2_{me} + \sigma^2_m)$
Males × females	(m−1)(f−1)	M_3	$\sigma^2 + r(\sigma^2_{mfe} + \sigma^2_{mf})$
Error	(mf−1)(r−1)	M_4	σ^2
d. Design III:			
Replications	(r−1)		
Lines	1	M_1	
Males	(m−1)	M_2	$\sigma^2 + 2r(\sigma^2_{me} + \sigma^2_m)$
Males × lines	(m−1)	M_3	$\sigma^2 + r(\sigma^2_{mle} + \sigma^2_{ml})$
Error	(2m−1)(r−1)	M_4	σ^2
e. Diallel Cross:			
Replications	(r−1)		
General combining ability	(m−1)	M_1	$\sigma^2 + r(\sigma^2_{se} + \sigma^2_s) + r(m-2)(\sigma^2_{ge} + \sigma^2_g)$
Specific combining ability	[m(m−1)/2] − m	M_2	$\sigma^2 + r(\sigma^2_{se} + \sigma^2_s)$
Error	(r−1){[m(m−1)/2] − 1}	M_3	σ^2

The symbols used in Table 1 are believed to be self-explanatory, but the components of variance are defined as follows:

σ^2_G = total genetic variance among progenies (or parents).
σ^2_{GE} = the genotype × environment interaction variance.
σ^2_m = genetic variance among males.
σ^2_{me} = male genotype × environment interaction variance.
σ^2_f = genetic variance among females mated to the same male.
σ^2_{fe} = female genotype × environment interaction variance.
σ^2_{mf} = male genotype × female genotype interaction variance.
σ^2_{mfe} = male genotype × female genotype × environment interaction variance.
σ^2_{ml} = male genotype × line genotype interaction variance.

σ^2_{mle} = male genotype × line genotype × environment interaction variance.
σ^2_g = general combining ability variance.
σ^2_{ge} = general combining ability × environment interaction variance.
σ^2_s = specific combining ability variance.
σ^2_{se} = specific combining ability × environment interaction variance.
σ^2 = variance among plots within replications and equals

$\frac{\sigma^2_w}{k} + \sigma^2_b$ when the plot values analyzed are means of k plants. σ^2_w is the variance among plants within plots and σ^2_b is the environmental variance among plots within a replication. Individual plant data are frequently not taken.

The assumptions involved in deriving the mean square expectations and the genetic interpretations for Designs I, II, and III are given by Comstock and Robinson (12) as follows:

1. Random choice of individuals mated for production of experimental progenies.
2. Random distribution of genotypes relative to variations in environment.
3. No non-genetic maternal effect.
4. Regular diploid behavior at meiosis.
5. No multiple alleles.
6. No correlation of genotypes at separate loci. This implies no linkage among genes affecting the character studied or that, if linkages exist, the distribution of genotypes is at equilibrium with respect to coupling and repulsion phases.
7. No epistasis, i.e., the effect on variation in genotype at any single locus is not modified by genes at other loci.
8. For estimating degree of dominance, gene frequencies of one-half at all loci where there is segregation (not necessary for Design III).

Under these assumptions the genetic components of variance estimated in the designs in Table 1 have the following interpretations:

Design	*Component of variance*	*Genetic equivalent*
General design	σ^2_G	$\sigma^2_A + \sigma^2_D$ for parents; $1/4\ \sigma^2_A$ for polycross progenies.
Design I, III	σ^2_m	$1/4\ \sigma^2_A$
Design I	σ^2_f	$1/4\ \sigma^2_A \times 1/4\ \sigma^2_D$
Design III	σ^2_{ml}	σ^2_D
Diallel Cross Design II	σ^2_g σ^2_m	$\frac{(1+F)}{4}\ \sigma^2_A$ where F is the coefficient of inbreeding.
Diallel Cross Design II	σ^2_s σ^2_{mf}	$\left(\frac{1+F}{2}\right)^2 \sigma^2_D$

GENETIC PARAMETERS IN CORN

The most extensively studied cross-pollinating crop is corn (*Zea mays* L.). The ease with which corn can be crossed or self-pollinated, the large number of progenies that can be produced, and the relative ease with which quantitative characters can be measured make corn an ideal plant for statistical genetic studies and for evaluating breeding procedures. The most extensive work reported on corn has been done at the North Carolina Experiment Station under the direction of Dr. H. F. Robinson and Dr. R. E. Comstock, but considerable work has also been done at other institutions.

The results of research using the designs mentioned have appeared in a number of publications. Reports will not be discussed in detail, but an attempt has been made to summarize the most important results, together with some interpretations. Of primary importance are the data on grain yield, but most authors have presented data on other quantitative characters as well.

Estimates of additive genetic variance for grain yield obtained utilizing Designs I and III on F_2 hybrid populations and open-pollinated varieties are summarized in Table 2. Individual estimates are subject to considerable random variation, so only means for each hybrid or variety are given. The estimates appear to be relatively stable within groups of similar material. The F_2 hybrids and varieties of the Southern prolific dent types do not differ appreciably in the magnitude of additive genetic variance; however, the variety average is slightly higher. Likewise, the one Cornbelt hybrid examined gave estimates comparable to Southern prolific hybrids. Estimates obtained from Cornbelt varie-

TABLE 2.—MEAN ESTIMATES OF ADDITIVE GENETIC VARIANCE OBTAINED IN STUDIES OF CORN POPULATIONS.

Kind of Population	Reference	Population	Single environment		Two or more environments	
			No. of estimates	$\hat{\sigma}^2_A$	No. of estimates	$\hat{\sigma}^2_A$
F_2 Hybrid (unselected)	15	(NC34 × NC45)F_2	4	.0031	—	—
	15	(CI21 × NC7)F_2	7	.0031	2	.0018
	15	(NC33 × K64)F_2	4	.0036	2	.0013
	15	(NC16 × NC18)F_2	1	.0070	—	—
	24	(M14 × 187-2)F_2	6	.0042	3	.0029
Open-pollinated variety (unselected)	15	Jarvis	4	.0044	3	.0033
	15	Weekley	4	.0044	2	.0015
	15	Indian Chief	2	.0032	1	.0014
	39	Krug	4	.0097	2	.0080
	39	Hays Golden	4	.0066	2	.0046
	39	Lancaster	4	.0082	2	.0078

ties are somewhat larger; however, it is recognized that these estimates may be somewhat biased due to non-random mating under Nebraska climatic conditions (See reference 39). Estimates obtained in the second year were believed to be less biased and were somewhat lower; however, only the mean is shown.

One point apparent from data in Table 1 is that all estimates based on experiments conducted in a single environment are biased upward. This is because the male component of variance arises not only as a result of additive genetic effects alone but also as a result of the interaction of additive genetic effects with the particular environment in which the experiment is conducted. The amount of bias appears to be nearly 50 per cent. Estimates based on experiments conducted in two or more environments are much more realistic, although these may be slightly biased because they are, with one exception, estimated from experiments at only one location (2 years) or in only 1 year (2 locations). Not all interactions with environments can be separated from genotypic effects.

The relationship between dominance variance and additive genetic variance in hybrid populations has been used to gain information on the average degree of dominance of genes influencing yield and other quantitative characters. The average degree of dominance which has been estimated in several experiments involving F_2 hybrids is presented in Table 3. Most of these estimates indicate the average degree of dominance to be in the over-dominance range; however, it was recognized from the outset that such estimates could result from repulsion phase linkages of genes in the partial to complete dominance range. Comstock and Robinson (12) have provided the theoretical evidence on this point. Experimental evidence indicating linkage bias has been provided by Comstock, *et al.* (15), Gardner and Lonnquist (24), Robinson, *et al.* (55) and Lindsey.[2] This evidence has been obtained by making simultaneous estimates in F_2 hybrids and in advanced generations obtained by random mating. Several generations of random mating will permit the breaking of linkage groups, and the hybrid populations should approach equilibrium with respect to linkage phases. The most extensive results evaluating the effect of linkage on estimates of average degree of dominance are summarized in Table 4. The results clearly indicate that linkage bias is a factor in estimates obtained from early generation hybrids and that the average degree of dominance of genes determining grain yield is in the partial dominance range. This does not exclude the possibility that overdominance may exist at some loci, but it does not appear to be as important as Hull (29, 30) suggested.

Hull (30) calculated parent-offspring regressions in a diallel cross and then calculated the second order regression of the parent-offspring regression coefficients on the parent line means. Solving of the second order regression function for the case where the parent-offspring regression is zero provides an

[2]Lindsey, M. F. The effect of linkage bias on estimates of genetic variance and the average degree of dominance for genes influencing quantitatively inherited characters in the F_2 and advanced generations of a hybrid population of corn. Ph.D. Thesis, North Carolina State College. 1960.

TABLE 3.—ESTIMATES OF ADDITIVE GENETIC AND DOMINANCE VARIANCE, THE RATIO $\hat{\sigma}_D^2/\hat{\sigma}_A^2$, AND AVERAGE DEGREE OF DOMINANCE ($\hat{a}$) OBTAINED FOR THE F_2 GENERATION OF HYBRID POPULATIONS.

Population	Publication	Design[1]	Years	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_D/\hat{\sigma}^2_A$	$\hat{a}$
CI21 × NC7	52	I-1-1	47	.0064	.0045	.70	1.19
	23	III-2-1	50–51	.0017	.0028	1.65	1.81
	23	III-1-2	51	.0018	.0040	2.22	2.14
	15	III-1-1	56	.0019	.0022	1.16	1.52
	[2]	III-1-1	57	.0015	.0015	1.00	1.41
	[2]	III-1-1	58	.0022	.0052	2.36	2.19
	[2]	III-1-1	59	.0039	.0035	.90	1.34
			Means	.0028	.0034	1.21	1.56
NC34 × NC45	52	I-1-1	47	.0019	.0176	9.26	4.30
	15	III-1-1	55	.0060	.0057	.95	1.38
	15	III-1-1	56	.0018	.0042	2.33	2.16
	15	III-1-1	56	.0027	.0042	1.56	1.77
			Means	.0031	.0079	2.55	2.26
NC33 × K64	23	III-2-1	50–51	.0022	.0019	.86	1.31
	23	III-1-2	51	.0022	.0028	1.27	1.58
			Means	.0022	.0024	1.09	1.48
NC16 × NC18	52	I-1-1	47	.0070	.0036	.51	1.01
M14 × 187-2	24	III-2-2[3]	54–56	.0079	.0012	.15	.56
	24	III-1-2	55	.0014	.0018	1.29	1.59
	[4]	III-1-2	59	.0010	.0026	2.60	2.27
			Means	.0036	.0019	.53	1.37

[1]The design number indicates the type of design, the number of years, and the number of locations.
[2]Data reported by M. F. Lindsey, 1960, Ph.D. Thesis, N. C. State College.
[3]One location in 1954 and a different location in 1956. Only 2 tests involved.
[4]Unpublished data of C. O. Gardner and J. H. Lonnquist, University of Nebr.

TABLE 4.—COMPARISON OF ESTIMATES OF AVERAGE DEGREE OF DOMINANCE OBTAINED IN THE F_2 GENERATION WITH THOSE IN MORE ADVANCED GENERATIONS (INDIVIDUAL EXPERIMENTS POOLED).

Generation	Population	
	CI21 × NC7[1]	M14 × 187-2[2]
F_2	1.68	1.98
F_4	—	1.04
F_8	1.24	.72
F_{12}	1.09	—
F_{16}	—	.62

[1]Summarized by Lindsey, M. F., 1960, Ph.D. thesis, North Carolina State College.
[2]Data of C. O. Gardner and J. H. Lonnquist, University of Nebraska.

estimate of the expected line mean where the regression surface is level and heritability is zero. For 17 negative trends found in 25 sets of data, estimates of the expected line mean were near or within the range of the data. Degree of

dominance estimated for nine sets of data varied from 1.41 to 2.25. The lines were all highly selected and only F_1 and F_2 hybrid yields were studied. Hull interpreted these data to support the hypothesis of overdominance, and he advocated a system of recurrent selection for specific combining ability for corn improvement.

Rumbaugh and Lonnquist (57) reported on a set of diallel crosses advanced from the F_1 to the F_5 by inbreeding. The regression of means on level of heterozygosis and the regressions of progeny means on the constant parent for each level of inbreeding were studied. Also a graphic method employed by Jinks (31) and Allard (3) was used. The data were interpreted to indicate that non-additive effects were relatively unimportant compared to additive effects and that partial dominance of genes prevailed. There were some indications that overdominance may exist. Since four of the lines were selected for high general combining ability and four for low, the results are not too surprising.

The use of the diallel cross in plant breeding to evaluate specific combining ability of lines or clones was common long before the theory was developed. Sprague and Tatum (59) were the first to estimate the components of variance for general and specific combining ability. They found that when lines had been previously tested and selected for yield potential, the component of variance due to specific combining ability ($\hat{\sigma}^2_D$) for grain yield was relatively larger than that due to general combining ability ($1/2\hat{\sigma}^2_A$). Thus, dominance and epistatic effects were concluded to be much more important than additive gene effects. When the lines were relatively unselected, the opposite was true. Rojas and Sprague (56) analyzed diallel crosses that were tested over more than one location and more than one year. Variance due to specific combining ability was consistently greater than that due to general combining ability. Matzinger, *et al.* (42) reported on a diallel experiment involving 10 S_1 lines considered to be unselected for yield. With this level of inbreeding $\hat{\sigma}^2_g$ estimates 1/4 σ^2_A and $\hat{\sigma}^2_s$ estimates 1/4 σ^2_D in the absence of epistasis. Ratios of $\hat{\sigma}^2_D/\hat{\sigma}^2_A$ calculated from data of Rojas and Sprague were .48 and .58 compared to a ratio of 8.67 reported by Matzinger, *et al.*

Estimates of average degree of dominance cannot be obtained directly in open-pollinated varieties. On the other hand, indirect evidence is provided by the ratio $\hat{\sigma}^2_D/\hat{\sigma}^2_A$, which is given in Table 5. The value of this ratio calculated from averages in the case of F_2 hybrids given in Table 3 is over three times as large as it is for open-pollinated varieties.

TABLE 5.—ESTIMATES OF ADDITIVE GENETIC AND DOMINANCE VARIANCE AND THE RATIO $\hat{\sigma}_D^2/\hat{\sigma}_A^2$ REPORTED FOR GRAIN YIELD IN CORN VARIETIES BY ROBINSON, *et al.* (54).

Variety	No. of tests	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_D/\hat{\sigma}^2_A$
Jarvis	6	.0030	.0005	0.17
Weekley	6	.0037	.0018	0.49
Indian Chief	2	.0023	.0010	0.35
	Means	.0030	.0011	0.37

If multiple alleles were not present in the varieties studied, values of $\hat{\sigma}^2_D/\sigma^2_A$ for a single locus can be calculated for different degrees of dominance, and different gene frequencies. These values as presented by Robinson, *et al.* (54) are as follows:

Degree of Dominance	*Gene Frequency*				
	.5	.6	.75	.9	.99
.8	.32	.44	.66	.89	.27
1.0	.50	.75	1.50	4.50	49.50
1.5	1.12	2.20	13.50	10.12	.20
2.0	2.00	5.33	∞	2.00	.08

It is unreasonable to believe that the average gene frequency is anywhere near .99; hence, these data on varieties must be interpreted to indicate the average degree of dominance to be in the partial dominance range.

Estimates of additive genetic variance and dominance variance for characters other than yield have been reported for hybrid populations and varieties by several authors (15, 23, 24, 39, 52, 54). However, because of the biases that may be involved from linkage in hybrid populations and from non-random mating in Cornbelt varieties studied at Nebraska, only the results of Robinson, *et al.* (54) with Southern prolific varieties are presented in Table 6. Additive genetic variance is somewhat greater than dominance variance for all characters reported, but the latter is important in height characters and ear diameter.

Some attempt has been made to assess the importance of epistasis in yield of corn. Sentz *et al.* (58) studied the relationship between degree of heterozy-

TABLE 6.—ESTIMATES OF ADDITIVE GENETIC VARIANCE, DOMINANCE VARIANCE, AND THE RATIO $\hat{\sigma}_D^2/\hat{\sigma}_A^2$ REPORTED FOR CHARACTERS OTHER THAN YIELD IN THREE OPEN-POLLINATED VARIETIES BY ROBINSON, *et al.* (54).

Population	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_D/\hat{\sigma}^2_A$	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_D/\hat{\sigma}^2_A$
	Date of flowering			No. of ears		
Jarvis	4.3	.08	.02	.046	.0008	.02
Weekley	7.5	(−2.76)	—	.059	(−.0277)	—
Indian Chief	4.1	(−1.33)	—	.034	(−.0160)	—
	Plant height			Ear height		
Jarvis	36.4	8.2	.22	16.4	9.7	.59
Weekley	30.8	7.3	.24	29.6	4.1	.14
Indian Chief	33.8	(−1.6)	—	29.6	(−8.2)	—
	Ear length			Ear diameter		
Jarvis	.16	.02	.11	.0047	.0015	.32
Weekley	.31	(−.01)	—	.0072	.0024	.33

gosis and the performance of quantitatively inherited characters in corn. Theoretical considerations indicate that a linear relationship is expected when loci effects are independent but that it should be curvilinear if epistasis is important. By using five levels of heterozygosis in two sets of material, they found curvilinear relationships to exist, and they interpreted the results to indicate the existence of non-allelic gene interactions for the quantitative characters yield, ears per plant, ear length, ear diameter, maturity, plant height, and ear height. Bauman (6) reported evidence which he also interpreted to indicate the existence of epistasis for yield, ear height, and kernel row number.

Comstock, *et al.* (15) reported on work with open-pollinated varieties. They used Design I and have attempted to estimate genetic variability among individuals within families. Single cross hybrids between random inbred lines of the same variety have been used to estimate environmental variation among individuals. The genetic variance among individuals within families estimates $1/2\ \sigma^2_A + 3/4\ \sigma^2_D$ in the absence of epistasis. Hence, if $\sigma^2_{w_g}$ is the genetic variance among individuals, $\hat{\sigma}^2_{w_g} = 3\hat{\sigma}^2_f - \hat{\sigma}^2_m$. The authors found that the variance which could be attributed to epistasis was not more than 1/10 the total genetic variance, but the results were not conclusive.

The relative magnitude of the interaction variance due to additive gene effects × environments compared to that of non-additive gene effects × environments is of interest. Gardner, *et al.* (23) assumed that they were essentially proportional to the variances of the genetic effects themselves. Work at North Carolina (15) suggests that the interaction involving non-additive genetic effects is smaller than that associated with additive genetic effects. Rojas and Sprague (56) found the opposite to be true, and data of Matzinger, *et al.* (42) were inconsistent in this regard. Data collected at Nebraska have also been inconsistent. The original assumption of proportionality may be valid but should be further checked.

With the kind of estimates that have been obtained, expected gain from various kinds of selection programs can be calculated. Expected progress in a single generation or cycle is a function of heritability and the selection differential, where the latter is the difference in means between the selected group and the entire group from which it was selected. Heritability must be calculated according to the units involved in selection. Robinson, *et al.* (52), utilizing data from F_2 hybrids, predicted a gain of 16 per cent in grain yield by selecting the biparental progenies among the highest yielding 5 per cent. Likewise, they predicted a gain of 11 per cent by an ear-to-row breeding technique. In a later paper (54) these same authors reported data on open-pollinated varieties which indicated that additive genetic variance was great enough that intra-variety selection should be rather effective. If a recurrent selection procedure similar to the one used by Lonnquist (40) was followed, they predicted the improvement in yield to be 15 per cent, 12 per cent, and 13 per cent for the varieties Jarvis, Weekley, and Indian Chief, respectively.

In a later report, Comstock, *et al.* (15) provided data on progress realized

from selection. Selection was based on grain yield among full-sib families in Design I studies. These results are presented in Table 7. The general agreement between observation and prediction is excellent. Gardner (22) utilized genetic variance studies made on the variety Hays Golden and predicted a gain of 3.5 to 4.5 per cent per generation by mass selection based on the grain yield of individual plants. Results of five generations of mass selection are summarized in Figure 1. An average gain of 3.8 per cent per generation has been realized in this experiment.

TABLE 7.—OBSERVED YIELD INCREASES (% OF MEAN) RESULTING FROM SELECTION COMPARED TO PREDICTED GAINS BASED ON GENETIC VARIANCE STUDIES REPORTED BY COMSTOCK, *et al.* (15).

Population	Cycle of Selection	Predicted Increase		Observed Total Increase
		One Cycle	Total	
NC34 × NC45	1st	4.0	4.0	11.1
	2nd	.3	4.3	−12.6
CI21 × NC7	1st	9.7	9.7	5.1
	2nd	5.1	14.8	11.3
Jarvis	1st	15.5	15.5	11.1
Weekley	1st	10.9	10.9	11.0
Indian Chief	1st	8.5	8.5	8.3

Data from the variety Krug collected at two locations in 1957 indicate that recurrent selection as practiced by Lonnquist (40) should result in a gain of 10.7 per cent in the first cycle of selection. However, he reported gains of 41.6 per cent in a very low-yielding test at one location in 1947 and 17.7 per cent in relatively high-yielding tests conducted at two locations in 1948. Later tests involving the second cycle synthetic and the variety Krug indicate that the original estimates of gain are undoubtedly too high (41, 44).

Genotypic correlations among quantitative characters in corn were reported by Robinson, *et al.* (53). Characters most highly correlated with yield were number of ears per plant (.82), ear height (.48), and plant height (.38). No important negative correlations were noted. The use of phenotypic and genotypic variances and covariances in constructing a selection index and the expected gain from selection based on the use of an index were discussed. Increased gains of as much as 30 per cent might be expected by use of an index rather than selecting on a basis of yield alone. An index of yield, ears per plant, and plant height was the most efficient.

CONCLUSIONS FROM CORN RESEARCH

The data on yield in corn suggest the following conclusions:

1. Additive genetic variance has been shown to exist at least in moderate amounts even in adapted open-pollinated varieties. This idea is supported by direct estimates and perhaps more important by selection studies. Realized gains

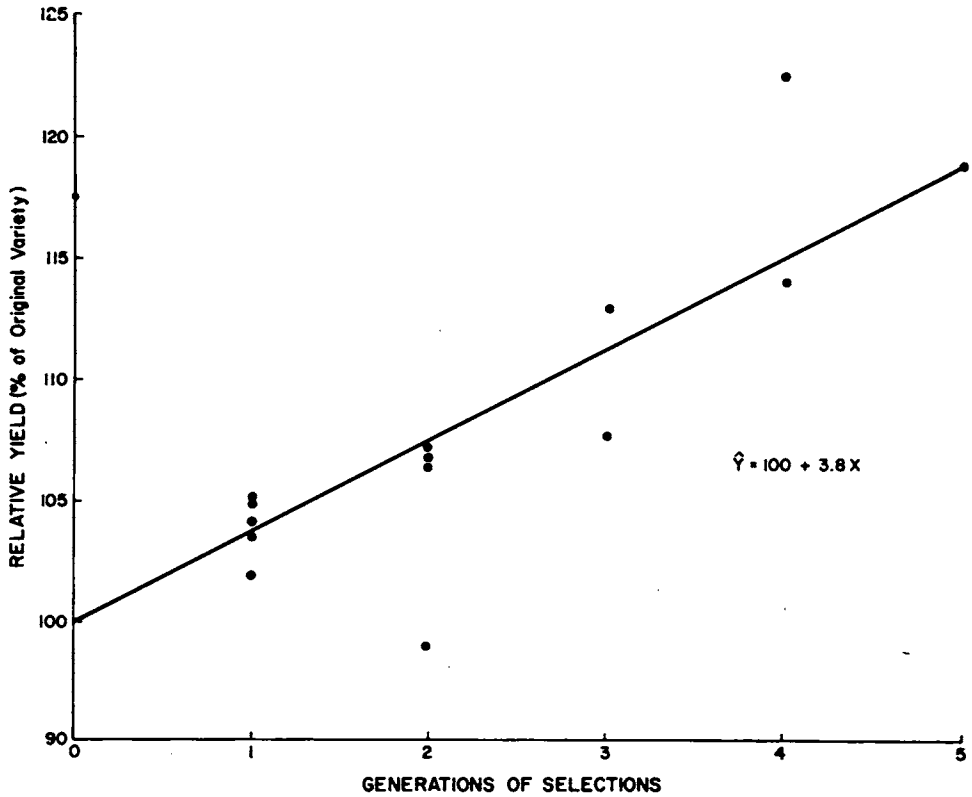

FIGURE 1. *Effect of mass selection on grain yield in the Hays Golden variety of corn reported by Gardner (22).*

from selection have been in good agreement with predicted gains based on genetic parameters estimated. Some increase in yield should be possible by any of the mass selection techniques providing environmental variations are held to a minimum.

2. The magnitude of the dominance variance indicates that dominance exists at some loci and probably at a majority of the loci involved. Dominance is believed to be in the direction of the more favorable gene. Estimates of average degree of dominance in the over-dominance range obtained with F_2 hybrids appear to have been biased upward as a result of linkage of genes that are only partially or completely dominant. Likewise, results from F_1 and F_2 hybrids of highly selected lines analyzed by Hull's regression technique may have been biased by linkage and epistasis. Overdominance may exist at some loci, but it is not believed to be of major importance in heterosis in corn. Results reported can be interpreted without resorting to overdominance.

3. Although the data are limited and inconclusive, epistatic variance does not appear to be of any great magnitude in the total genetic variance of corn

populations. On the other hand, epistatic combinations of genes in inbred lines may be of importance in contributing to heterosis in the F_1 hybrid.

4. Genotypic effects vary with environment thus contributing to relatively large genotype × environment interactions. Any estimates of genetic parameters based upon tests conducted in a single environment are likely to be seriously biased. Data on the relative magnitudes of additive genetic effects × environments and non-additive genetic effects × environments are inconclusive.

5. Further information is needed on the various genetic parameters estimated. Additional evidence on the overdominance issue and particularly on epistasis is needed. Selection experiments in open-pollinated varieties must be continued and investigations are needed to determine the effects of selection on the various genetic parameters in such varieties. Genotypic correlations among quantitative characters in open-pollinated varieties and their use in a selection index would be of considerable interest.

6. The magnitude of the non-additive genetic variance, the possibility that overdominance may exist at some loci, our meager knowledge about epistasis, and the fact that inbred line hybrids today are much superior to any other material lead one to conclude that hybridization will continue to receive the most attention in corn breeding programs in the years immediately ahead. Some use may be made of mass selection or recurrent selection for general combining ability in early generations of selection to increase the frequency of desirable genes in populations prior to inbreeding. Reciprocal recurrent selection as proposed by Comstock *et al.* (14) is a breeding procedure that theoretically has an excellent chance of success and one that is likely to be used considerably in the next decade. Crosses of inbred lines extracted from varieties modified by a few generations of reciprocal recurrent selection should be considered.

Data reported by numerous authors on characters other than yield indicate that additive genetic variance is larger than dominance variance and heritabilities tend to be higher than that for yield. Relatively high heritabilities have been observed for plant and ear height and maturity measures, but those for ear measurements have been relatively low. Dominance of some genes is believed to exist for all characters measured. Epistasis has been reported for a few of the characters.

GENETIC PARAMETERS IN ALFALFA

Many of the results of plant breeding research with corn have been found to be applicable to alfalfa. This is indeed fortunate because corn studies are much easier to conduct than similar studies in alfalfa. On the other hand, alfalfa does have some advantages over corn. Individual plants (clones) can be reproduced by stem cuttings allowing one to observe several plants of the same genotype. However, this does necessitate the assumption of no important variance in performance among clones due to differential reaction to vegetative propagation. The high degree of self sterility in alfalfa causes difficulty in inbreeding but is an advantage in producing crosses in isolated blocks. When

one considers the estimation of genetic parameters utilizing statistical genetic techniques, there is one important difference in the two crops. Alfalfa is generally considered to be an autotetraploid, although many qualitative characters have been found to be inherited in a diploid manner, and quadrivalent pairing at meiosis has not been evident in the majority of cells examined. Hanson (26) reported that less than 10 per cent of the cells contained one or more quadrivalents, although an earlier report by Grün (25) indicated 40 per cent had one or more. Genetic studies of qualitative characters indicate that both disomic and tetrasomic inheritance exist (19, 50, 60, and 62). There is very little evidence to indicate whether polygenes controlling quantitative characters in alfalfa behave in a disomic or tetrasomic manner and possibly both types of inheritance are operating.

The statistical genetic theory applicable to polyploids is much more complex than in the case of diploids; consequently, it has received relatively less attention. Genetical expectations are not the same and they vary with different kinds of polyploids. Segregation may occur on a chromosome or on a chromatid basis and one has the additional complication of double reduction.

Since it is not known whether polygenes controlling yield and other quantitative characters in alfalfa behave in a disomic or tetrasomic manner, extensive breeding studies will have to be conducted along with the development of the theory of polyploids to gain an understanding of the genetic situation in this crop. Comstock and Robinson (13) pointed out that it can be shown that in polyploids there are circumstances in which intra-allelic gene interaction would contribute greatly to the genotypic variance among half-sib families (polycross progenies). They suggested that the covariance between the half-sib families and parent clones appears to be a more satisfactory basis for estimating variance resulting from average gene effects in polyploids. Later work by Kempthorne (36, 37) indicates that for a single segregating locus the parent-offspring covariance is equal to $\sigma^2_A/2 + \sigma^2_D/6$ and the covariance among half-sib families (variance among polycross progenies) is $\sigma^2_A/4 + \sigma^2_D/36$. This indicates that additive genetic variance estimated from polycross progenies would provide the least biased estimate of additive genetic variance. Dessureaux (17) has discussed the theory of the diallel cross applied to the single locus, two allele autotetraploid model with random mating and random chromosome segregation.

Kehr and Gardner (35) investigated the variety Ranger to determine the kinds and amounts of genetic variation in forage yield present and to assess the possibilities and methods of improving the variety. Randomly chosen plants derived from certified seed of Ranger alfalfa were used. Replicated tests involving solid stands of a number of clones and their polycross progenies were established. The genetic variance among clones and among polycross progenies and the genetic covariance between parental clones and their polycross progenies were estimated. Forage yields were recorded in tons per acre, and the results interpreted under the assumptions listed for diploids are summarized following.

Based on performance in single 10-foot rows in four replications over a

2-year period the heritability estimates and predicted gains were nearly identical for the two experiments. Estimates of additive genetic variance calculated as twice the parent-offspring regression and as four times the polycross progeny component of variance were similar and were averaged to calculate heritability. It was concluded that an appreciable amount of additive genetic variance exists in the variety Ranger and yield increases of about 8.5 per cent might be expected to result from one cycle of selection if the clones among the highest-yielding 10 per cent were saved and recombined. The large amount of non-additive genetic variance present, however, suggests that other breeding systems might be more rewarding.

Experiment		Genetic variances			Ratio	Heritability (progeny mean)	Predicted gain from selection
		Total	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$	$\hat{\sigma}^2_D/\hat{\sigma}^2_A$		%
Non-irrigated	1955–56	.104	.035	.069	1.97	.25	8.8
Irrigated	1956–57	.289	.104	.185	1.78	.28	8.5

Additional information on forage yield from a six-clone diallel cross was reported by Kehr (34). Although the number of clones is far too few to provide data with any degree of precision, the results which can be calculated from his data are in general agreement with results reported by Kehr and Gardner (35) for the variety Ranger. Additive genetic variance and dominance variance can be estimated as $4\hat{\sigma}^2_g$ and $4\hat{\sigma}^2_s$, respectively, assuming diploid inheritance and no epistasis. These estimates are $\hat{\sigma}^2_A = .0108$ and $\hat{\sigma}^2_D = .0732$; the ratio $\hat{\sigma}^2_D/\hat{\sigma}^2_A$ is 6.8, which is understandable since the clones used were highly selected for general combining ability. Heritability based on progeny means estimated as

$$H = \frac{\sigma^2_A}{\sigma^2_g + \sigma^2_s + \frac{\sigma^2_{gr}}{r} + \frac{\sigma^2_{sr}}{r} + \frac{\sigma^2_{gy}}{y} + \frac{\sigma^2_{sy}}{y} + \frac{\sigma^2}{ry}},$$

where $r = 6$ replications and $y = 2$ years would be 30.7 per cent in contrast to Kehr's estimate of 58 per cent. When calculated for four replications, heritability would be 26.3 per cent, a figure directly comparable to the estimates of 25 and 28 per cent in the two experiments reported by Kehr and Gardner (35). Kehr calculated heritability using components of genetic variance among crosses and of the interactions of crosses with replications and years. With diploid inheritance and no epistasis, the numerator of his heritability ratio estimates $5/14\ \sigma^2_A + 1/4\ \sigma^2_D$. The formula which he used is appropriate only for the single crosses tested assuming they could be reproduced and used commercially. Interactions of general combining ability and specific combining ability with years were .0033 and .0017, respectively.

Morley, *et al.* (45) report data from which one can calculate the ratio $\hat{\sigma}^2_D/\hat{\sigma}^2_A$ to be 1.25 for summer production and .15 for winter production in Australia. Some F_1's in the diallel cross were completely dormant; hence, variation in winter production was discontinuous resulting in relatively high estimates of additive genetic variance.

Morley and Heinrichs (46) and Heinrichs and Morley (28) utilized a modification of an analysis given by Kempthorne (37), which is essentially Design I, to analyze genotypic variation in the creeping-root character and winter hardiness in alfalfa. The population studied originated from *Medicago falcata* L. × *Medicago media* Pers. crosses which formed the basis of the very hardy Canadian variety Rambler. Genetic variation of the creeping-root character was found to be predominantly additive, but heritability was only about 20 per cent. In the case of winter hardiness, less than half the genotypic variance was additive indicating that the character might not respond readily to mass selection. The genotypic correlation between winter hardiness and creeping-root was 0.38. In view of the natural and artificial selection for winter hardiness which must have been especially severe over many generations in the parents of the original material, it is not surprising that additive genetic variance for this character is low. Selection for creeping-root had not been extensive; hence, considerable additive genetic variance still exists. This agrees with findings of Sprague and Tatum (59) with regard to inbred lines of corn previously selected and those previously unselected for yield. Some system of progeny testing along with mass selection was suggested as a suitable breeding procedure.

Elling, *et al.* (21) report data on percentage of winterkill in Minnesota which indicates that additive genetic variance was 18.3 times larger than non-additive, which is in direct contrast to the results obtained in Canada. The difference is in the populations sampled. Clones used by Elling, *et al.* originated in several states, some of which have mild winters.

Adams (1) reported on a root-proliferation trait in alfalfa, which is assumed to be the same character as creeping-root. He utilized clones and their intercross families and found unexpectedly large genetic variances among clones and among plants within intercross families suggesting large non-additive variances relative to additive, but he did not draw any definite conclusions.

Carnahan, *et al.* (10) utilized 14 promising clones from 8 different states in a diallel cross and studied seedling vigor and fall growth habit in the year of establishment. Studies were conducted simultaneously in several states. Kehr (34) reported on fall growth habit and also on spring growth habit and rate of recovery after cutting. These results are summarized below:

	Carnahan, *et al.*		Kehr		
	Seedling vigor	Fall growth habit	Fall growth habit	Spring growth habit	Rate of recovery
$\hat{\sigma}^2_A$	6.44**	4.44**	.212*	.071	.444*
$\hat{\sigma}^2_D$	1.20**	.68**	.163*	.956**	.326**
$\hat{\sigma}^2_D/\hat{\sigma}^2_A$	.19	.15	.77	13.51	.74

* significant at the .05 level of probability.
**significant at the .01 level of probability.

Additive gene effects appear to be more important than non-additive effects for the characters such as seedling vigor, fall growth habit, and rate of recovery, while non-additive effects predominate in the case of spring growth habit. The diverse sources of germ plasm could account for the low ratios noted by Carnahan, *et al.*

Adams and Semeniuk (2) studied leafspot reaction in alfalfa. They found that almost all of the genetic variance was additive. However, additive genetic variance was virtually exhausted in one generation of selection. Dessureaux (16) reported high heritability of tolerance to manganese toxicity estimated from parent-progeny regression. In crosses between widely divergent parents, differing in only one or a few genes, such results can be expected.

GENETIC PARAMETERS IN FORAGE GRASSES

Much of what has been said about alfalfa also applies to many of the forage grasses. Many, although not all, are polyploids and a high degree of self sterility is common. The degree of ploidy, however, may be much higher than the tetraploid level and may vary considerably even within a single species. For example, Nielsen (48) reported chromosome numbers observed for 50 switchgrass plants collected from an area extending from Wisconsin and Montana south to Arkansas and Arizona. A polyploid series of 18, 36, 54, 72, 90, and 108 somatic chromosomes was found to exist. Some grasses are probably autopolyploids and others allopolyploids. From the standpoint of statistical genetics, allopolyploids behave somewhat as diploids.

One of the earliest reports on a statistical approach to the genetics of grasses was that of Burton (7), who worked with pearl millet, a diploid annual. Estimates of heritability and genotypic correlations among characters based on total genetic variance were presented. In a later paper, Burton (8) indicated that, on the average, 55.9 per cent of the total genetic variance in forage yield was non-additive and 44.1 per cent was additive. This report was based on a series of Design II studies conducted with inbred lines over an 11-year period. The increase in forage yield of a synthetic variety released by Burton in 1950 was only 33.5 per cent of that realized from a "hybrid" (first generation synthetic) released in 1958. The hybrid exceeded the check variety by 51.7 per cent.

Research on switchgrass, a native tall prairie grass which shows considerable promise as a forage grass in the Great Plains, has been done at the Nebraska Experiment Station by Newell and Eberhart. Seed from numerous strains (single plant or group of plants at a single site) was collected from fields and along roadsides throughout Nebraska and Northern Kansas. Plants grown from such seed represent a random sample of switchgrass plants available for initiating a breeding program in the area. The first step in such a program should be to get a basic understanding of the kinds and amounts of genetic variation that exist in the sample collected. With such knowledge an efficient breeding program can then be planned. Two papers (20, 47) have been published on this work. In one, total genetic variance among 31 strains collected was estimated for 7 characters. Heritability (in a broad sense), and expected gain from selection

TABLE 8.—ESTIMATES OF GENETIC VARIANCES AND HERITABILITY FOR QUANTITATIVE CHARACTERS IN SWITCHGRASS REPORTED BY NEWELL AND EBERHART (47).

Character Measured	Forage type[1]	Genetic variances			$\hat{\sigma}^2_D/\hat{\sigma}^2_A$	Heritability	
		Total	$\hat{\sigma}^2_A$	$\hat{\sigma}^2_D$		Parent-offspring regression	Realized
Leaf height	1	24.2	17.0	7.2	.42	.24	.46
	2	21.4	64.1	—	—	1.37	1.32
Plant height	1	82.2	81.0	1.2	.01	.63	.75
	2	74.1	104.1	—	—	1.17	1.33
Seed yield	1	76.0	22.1	53.9	2.44	.14	.09
	2	48.9	43.5	5.4	.12	.65	.40
Total yield	1	.0462	.0144	.0318	2.21	.18	.40
	2	.0196	.0259	—	—	.52	.91

[1] 1 = small blue-green type and 2 = medium-tall blue-green type.

were calculated. In a second experiment, 113 clones selected from the better collections derived from over 100 sources were used. Additive genetic variance estimated as twice the parent-progeny covariance, total genetic variance estimated from the variance among parent clones, and heritability estimated as twice the parent-offspring regression and from realized gain in progenies of promising clones are presented for four characters in Table 8. The relatively large amounts of additive genetic variance observed might be expected in material which has undergone so little selection. However, high estimates in type 2 are attributed to non-random mating of parent clones. The amount of bias that exists is unknown, so the relative importance of additive and non-additive genetic effects is not clear. Estimates in type 1 seem realistic and may be relatively unbiased. Observed gains realized in progenies were in excellent agreement with predicted gains based on total genetic variance in parent clones. Genotypic correlations among seven quantitative characters, some of which are negative, were reported. No attempt was made to utilize the data in a selection index.

Heritability estimates in sand bluestem by Kneebone (38), who used analysis of variance and parent-offspring regression techniques, were as follows:

Estimation procedure	Plant ht.	Stem diameter	% leaf	% protein in leaves
From clone component of variance	.80	.42	.56	.51
From progeny component of variance	.80	.26	.57	—
From parent-progeny regression	.53	.28	−.02	—

Substantial progress in altering plant height should be possible by selection. Altering diameter would be more difficult but may be unimportant since a high plant population could provide complete ground cover regardless of the diameter of individual plants. Actual gain of the best-rated clone for each character as determined by progenies from open-pollinated seed was 19.8 per cent shorter height, 13.0 per cent greater diameter, and 9.1 per cent leafier. These values were close to one-half the gain predicted from clones which is what would be expected, since there was no control of the pollen parent. This suggests that much of the genetic variation must be additive. A similar conclusion can be drawn from the close agreement of heritability estimates from progeny performance with those from clone performance.

Studies have been reported on bromegrass by a number of workers. Hawk and Wilsie (27), McDonald, *et al.* (43), and Nielson and Kalton (49) used parent-offspring regressions as measures of heritability. Estimates for forage yield varied from .22 to .34. Estimates of .43 for plant height and .32 for spread were reported by McDonald, *et al.* (43), and estimates of .32 for seed yield, .67 for seed weight, .83 for fertility index, and .38 for panicle number were reported by Nielson and Kalton (49). The latter authors also reported genotypic correlations of .75 for seed yield and panicle number, .59 for seed yield and fertility index, and .04 for seed yield and seed weight. Timothy, *et al.* (61) tested five clones, their polycross progenies and F_1 diallel crosses. General combining ability was concluded to be more important than specific combining ability for forage yield and seed yield. The reverse was true for plant height. The clones were said to be selected for contrasts in these characters.

Kalton, *et al.* (33) and Kalton and Leffel (32) studied genetic variation in orchardgrass. The first paper reported estimates of heritability in a broad sense made from clones and their S_1 progenies. Panicle number and yield were low in heritability. Spring vigor, leafiness, and plant height were intermediate. The second paper involved a diallel cross of 11 clones. Heritability on a plot basis was estimated using the formula

$$H_1 = \frac{2\hat{\sigma}^2_g}{2\,\hat{\sigma}^2_g + \hat{\sigma}^2_s + \hat{\sigma}^2_e} \times 100.$$

The authors refer to the paper of Rojas and Sprague (56) and it appears that their intent was to express additive genetic variance as a fraction of total phenotypic variance. When homozygous lines are used, the components σ^2_g and σ^2_s are equal to $1/2\ \sigma^2_A$ and σ^2_D, respectively, with disomic inheritance in the absence of epistasis; however, when non-inbred parents are used the same components are equal to $1/4\ \sigma^2_A$ and $1/4\ \sigma^2_D$. Hence, the estimate

$$H_2 = \frac{4\hat{\sigma}^2_g}{4\,\hat{\sigma}^2_g + 4\,\hat{\sigma}^2_s + \hat{\sigma}^2_e} \times 100$$

might be more appropriate for what the authors had in mind. The two estimates are shown below for the data presented:

Character	H_1	H_2
Spring vigor	15.1	22.9
Disease score	37.6	36.2
Bloom date	52.6	71.0
Panicle No. (2 yrs.)	42.3	57.3
Green forage yield (2 yrs.)	21.1	28.4

The interaction of general effects and specific effects with years were about equal for forage yield, but in the case of panicle number, the interaction of general effects with years was much greater.

Baltensperger and Kalton (5) estimated total genetic variance and heritability in a broad sense in reed canarygrass. Heritabilities were 25.8 per cent for hay vigor, 47.6 per cent for bloom date, 66.0 per cent for leaf width, and 73.1 per cent for leafiness. Genotypic correlations were found to be 0.58 for leafiness and hay vigor and 0.15 for leafiness and leaf width.

In tall fescue Burton and DeVane (9) estimated heritability using total genetic variance. The estimates reported were .40 and .45 for forage yield and .34 for seed yield.

Dewey and Lu (18) reported on genotypic correlations among components of crested wheatgrass seed production. Genotypic and phenotypic correlations were in excellent agreement. Important negative correlations existed between fertility and seed size, $r = -.71$, and between fertility and plant size, $r = -.66$. Seed size and plant size were positively correlated, $r = .53$. All genetic correlations between seed yield and other characters measured were positive.

CONCLUSIONS FROM ALFALFA AND FORAGE GRASS RESEARCH

The data on alfalfa and forage grasses suggest the following conclusions:

1. The data reported are far less extensive than those reported for corn and in most cases experiments have not been planned to yield genetic information about a larger population than the one tested.

2. In one alfalfa variety, additive genetic variance for forage yield was approximately one-third of the total genetic variance and heritability was about 25 per cent on a progeny mean basis. In another, variation in the creeping-root character was largely additive but heritability was only about 20 per cent. For most characters other than yield, additive genetic variance was greater than non-additive.

3. Results with forage grasses appear to be similar to those in alfalfa. Additive genetic variance constitutes somewhat less than half the total genetic variance in the case of forage yield and heritability appears to be approximately 20 to 30 per cent.

4. No critical comparisons of actual gains and predicted gains based on

statistical genetic theory were found. Predictions based on total genetic variance were in reasonably good agreement with actual gains, however.

5. The results obtained with alfalfa and several forage grasses are in general agreement with the more extensive investigations conducted on corn. Therefore, breeding systems which allow one to utilize the non-additive genetic variance as well as the additive would appear to be more promising than those which do not. The use of advanced generation synthetics which has been common in alfalfa and forage grass work has permitted some progress, but the use of F_1 hybrids or first generation synthetics would be preferable if the mechanics of seed production can be solved. Burton's work with pearl millet verifies this. Also, the use of reciprocal recurrent selection is to be highly recommended if the mechanics of making test crosses can be solved.

GENERAL CONCLUSIONS

The application of statistical genetic theory to plant breeding experiments has added materially to our knowledge of the types of gene action involved in the inheritance of quantitative characters in cross-fertilizing plants. For many years plant breeders have recognized the significance of specific and general combining ability, which are directly related to non-additive and additive genetic effects, respectively. However, only in recent years has information become available on the relative amounts of variation due to these two kinds of genetic effects and their interactions with environments. Most breeders have divided genetic variance into additive genetic variance and dominance variance, realizing that epistasis may be important, giving rise to bias in the estimates reported. Development of the statistical genetic theory may now make possible unbiased estimates of all three kinds of genetic variance.

Our knowledge of heterosis has also been increased through statistical genetic studies. Evidence obtained in corn genetic research and selection studies indicates that partial to complete dominance of genes influencing yield is far more important than overdominance in heterosis of yield in corn. On the other hand, the existence of overdominance cannot be completely ruled out on the basis of present information.

There is a distinct need for well-designed experiments applying statistical genetic theory to plant breeding research. Many reports involve the application of statistical genetic techniques as an afterthought. While some of the material used in diallel crosses or in parent-progeny studies does represent some population about which the breeder wishes to make some inferences, in many cases the material is highly selected for one reason or another and conclusions must be limited to the particular material studied. Such results can be misleading if not interpreted properly. The calculations made have not always been clearly stated, and incorrect procedures are believed to have been followed in some instances.

Experiments involving only a few clones and their progenies with inadequate replication are of little practical value from a statistical genetic viewpoint. The magnitude of the standard errors applicable to the genetic parameters esti-

mated are so large that the estimates have little meaning. A few well-designed experiments with adequate precision that yield unbiased estimates of genetic and environmental variances would be far better than many small, poorly-planned ones.

Genotype-environment interactions are an important factor in yield and other characters. Genetic variance estimates based on data from a single environment are undoubtedly biased upward. Experiments involving either perennial or annual crops must be repeated over time and space. The question concerning the relative magnitude of the variances due to the interactions of additive and non-additive gene effects needs to be resolved. The determination of the number of environments needed to adequately measure genotype response in a breeding program is dependent upon such knowledge.

The availability of high-speed digital computers at many universities now makes possible the processing of large masses of data in a relatively short time. Estimates of components of variance and covariance and their use in calculating genotypic and phenotypic correlations and selection indices has become much more feasible. More plant breeders should give consideration to the use of a well-constructed selection index in choosing their breeding material.

Along with the use of more refined experiments to provide the kind of data needed and faster computing equipment to analyze data, more thought needs to be given to the genetic interpretations, the implications, and the limitations of each individual experiment as well as of all experiments as a group. There is a definite need to utilize biochemical, physiological, and cytological approaches along with statistical methods in seeking a basic understanding of the inheritance of quantitative characters.

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DISCUSSION

H. L. CARNAHAN: Most parents used in typical breeding programs are not representative of the total population of a species. Do estimates of genetic variance components from such selected parents have any general applicability?

C. O. GARDNER: Estimates of genetic variance components obtained from experiments involving a group of highly selected parents and/or their offspring do not have general applicability. Interpretation generally must be limited to the particular material tested since such material does not represent a sample from some larger population. A plant breeder would rarely, if ever, be using parents representative of the total population of a species. He might, however, have several segregating populations with which he could work and he has the potential of producing many more. The problem of the plant breeder is to choose foundation stocks, develop genetically variable populations, to make selections, and to develop varieties or hybrids that represent somewhere near optimum combinations of genes. Genetic information on the segregating populations is needed to indicate which populations promise the greatest possibility of success and to provide a basis for determining the best breeding procedure.

R. E. COMSTOCK: The question of utilizing reciprocal recurrent selection (RRS) is viewed a little differently by plant and animal breeders. The cattle breeders make considerable use of individual performance as a basis for selection. RRS is a progeny test system which has some inherent inefficiency when genetic variance is high. Thus, when the animal breeder considers RRS, he thinks of two things: (a) The possible disadvantage of a progeny test system on the one hand, and (b) the possible advantage of selecting for combining ability on the other hand. However, the corn breeder is usually using a progeny test system anyway and as a result has only one issue in mind when he considers RRS.

C. H. HANSON: In connection with your mass selection experiment in corn, Dr. Dudley and I will discuss at the forthcoming workshop on polyploids the results of seven cycles of mass selection in alfalfa, as well as the accompanying shifts in means and genetic variances within cycles. The selection was done at Raleigh, N. C. for disease and insect resistance in unselected material. Under the conditions of this experiment, mass selection appeared to be quite effective.

H. F. ROBINSON: Dr. Falconer has raised the question as to the need for RRS procedure in corn. If σ^2_A is of major importance, RRS may still have an important role to play. The few loci that may give overdominant or epistatic expressions very well could be of sufficient importance to justify use of RRS. Results from intercrossing of lines (S_8) all from within Jarvis

variety indicate special combinations may be important and may be superior, partially due to non-additive effects. One F_1 cross among lines within Jarvis gave heterosis of 30 per cent.

C. H. HANSON: I am inclined to feel we should be more specific as to circumstances when comparing the effectiveness of different selection procedures. For improving unselected material in the early stages of a breeding program, mass selection may be as good as any procedure we have. This would be consistent with relative large estimates of additive variance being obtained.

L. H. PENNY: Could the estimates of genetic variance obtained from Corn Belt open-pollinated varieties of corn in Nebraska have been larger than those obtained from open-pollinated varieties in North Carolina because of differences in environments in which the estimates were obtained rather than because of real differences in the amount of genetic variability in the varieties?

C. O. GARDNER: If we assume that in each case the varieties were evaluated in their region of adaptation, I do not see how differences in environments could be a factor. In each case, we were attempting to obtain unbiased estimates of genetic variances with environmental variances eliminated.

R. H. RICHARDSON: With an excess of negative σ^2_D ($> 1/2$ where $\sigma^2_D = 0$), including significant reduction due to fitting dominance, of what value are your estimates of $\sigma_D{}^2$ other than in showing there are serious biases in the estimates and in their use in arguments involving average degree of dominance and overdominance?

C. O. GARDNER: The estimates of σ^2_D and σ^2_A obtained in open-pollinated varieties at Nebraska are presented to emphasize the need for extreme care in planning and conducting experiments of this kind to avoid any bias. However, I believe they also indicate that considerable additive genetic variance exists in these varieties even though we don't know the exact amount. My conclusions concerning average degree of dominance are based primarily on data from Design III studies where biases could not be a factor.

DAVID D. RUBIS: You have considered variety × location × years interaction. How important is date of planting as an environmental component? In the southern states where such crops as corn and soybeans may be planted over a period as much as 6 to 8 weeks, it is of interest to know if the same variety selected at an early date of planting will also be the best variety when planted at a late date. In other words will there be a significant V×L×D interaction. What evidence is available as to the importance of date of planting as an important variance component? In the northern states where years may be different due to early season

versus late season, etc., using date of planting may result in more information from a single year's experiment as to genotype × environmental-interaction. Do you think this may be so? Comments please.

C. O. GARDNER: In some situations I am sure that a genotype × date of planting interaction or a genotype × location × date of planting interaction will be significant. However, I do not know how they will compare on the average with genotype × year, genotype × location, and genotype × year × location interactions. In our corn genetic studies in Nebraska, where our tests are all conducted under irrigation. I do not think that variation in date of planting within the recommended range of dates would result in a sizable genotype × date of planting interaction. On the other hand, if irrigation was not practiced, variation in rainfall pattern might have a significant effect. This might be worth checking but I doubt that varying dates of planting would be a suitable substitute for testing at different locations and in different years.

E. B. SNYDER: In some cross-bred tree species, there is a big growth depression on selfing. However, because trees are surrounded by collateral relatives, the genotype of an individual is to be, say, 10 per cent inbred. If this is the usual situation, could we expect an improvement and, if so, would it be less than expected if the maximum heterozygote were produced?

C. O. GARDNER: The question is not entirely clear but I interpret it to be:

1. If we collect from the "best" trees in natural populations to produce a new generation of trees, could we expect improvement?
2. Would hybridization result in greater improvement than mass selection or selection based on progeny tests?

I know of no information on the kinds and amounts of genetic variation or on the relative amounts of genetic and environmental variation in tree populations. However, the breeding principles which have been developed in other cross-fertilizing species of plants are likely to apply. Based on information on corn, I would expect to make improvement by selecting seed of superior individuals to produce my next generation. Unless overdominance is important, there would be no point in attempting to synthesize the "maximum heterozygote." Information on corn leads me to believe that overdominance is not of major importance in heterosis. One still might consider a hybridization program in order to capitalize on any non-additive genetic variation that exists; however, there is no assurance that such a program would be more successful than mass selection or selection with some form of progeny testing.

JOHN BARBER: Given certain basic information about forest trees (specifically loblolly pine, *Pinus taeda* L.), what suggestions can you offer toward establishing a program of forest tree breeding?

C. O. GARDNER: The suggestions that I would make would depend upon the basic information given. I doubt that such information is already available so the first step would be to initiate a program to obtain information which would allow you to plan an efficient forest tree breeding program. You would need to know something about the kinds and amounts of genetic and environmental variances, the correlations among the various characters of importance, and the relationship between juvenile characters and mature characters. A considerable span of years might be involved in gathering such information, but someone needs to get such work started or the information will never be available. In the meantime I would assume that cross-fertilizing forest tree species behave in somewhat the same way as other cross-fertilizing plants. I would assume that both additive and non-additive genetic variances exist, and if I had sufficient funds, I would initiate both a selection program and an inbreeding and hybridization program. I would start by harvesting seed from what you consider to be the best trees in natural populations. I would establish an experiment which would allow me to measure the between and within family variances (Cuttings might be used to measure environmental variances within and between plots.) Data should be collected in the seedling stage and periodically until the trees reach maturity. As soon as the trees reach the reproductive stage you could recombine the best ones based on seedling vigor, rate of growth, etc. to form a new population. By using one of the mating designs discussed you could get valuable genetic information. I would start an inbreeding program by trying to self-fertilize some of the best trees in natural populations, and I would test the lines in hybrid combination after 2 or 3 generations of selfing.

A thorough knowledge of animal breeding as well as plant breeding would be of value to the forest tree geneticist. The use of a selection index to predict the mature value of a tree from seedling and juvenile data should be investigated.

Experimental Estimates of Genetic Parameters and Their Applications in Self-Fertilizing Plants[1]

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BREEDING methodology in the naturally self-fertilizing organisms has developed primarily by empirical methods with little attention directed towards assessing particular types of gene action or magnitudes of genetic variances in various populations. Evidence that success has been achieved in many cases is obvious from the performance of new released varieties in most plants. It appears, however, that the most significant improvement has been achieved for characters with relatively simple inheritance, such as transfer of disease resistance or other qualitative characters from one variety or species into another.

Progress in selection for quantitative characters has been achieved much more slowly. It is possible that this has resulted from a slower development of breeding principles for the complexly inherited characters. In recent years, the progress in improvement of quantitative characters has been enhanced by the accumulation of bits of information on population variability in many of the self-pollinated crops.

In the present paper an attempt is made to review information available in the literature relative to the following objectives:

1. Present estimates of genetic variances from some of the naturally self-fertilizing (or mostly self-fertilizing) crops. Since it is impossible to present all published data, only representative estimates from some of the species will be given. The estimates will be related to the type of gene action predominant in these species.
2. Evaluate the stability of different generations, i.e., pure lines, crosses, and segregating populations, over a wide range of environmental conditions.
3. Relate the estimates available to improved efficiency in varietal development and evaluation of self-fertilized crops.

GENETIC PARAMETERS IN RESTRICTED SAMPLES

Experiments for estimation of genetic variability in self-fertilized plants have been primarily of two types. In most of the experiments various generations

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of material arising from the cross of two pure lines are evaluated where gene frequency of segregating loci is assumed to be 0.5. The other design which has been used in a number of crops is the diallel cross.

From segregating generations of crosses of two pure lines

Following the method of Mather (28), estimates of genetic parameters have been obtained in a number of species. Some basic assumptions used in the experiments are no epistasis and frequencies of alleles at each locus are 0.5 through all generations (no selection). Under these assumptions, it is possible to express genetic variances in two quantities, D and H. D as defined by Mather and Vines (30) "depends on differences between individuals distinguished by being homozygous for the two allelomorphs of the various genes, while H depends on the departure of the heterozygote from the mean of the two comparable homozygotes."

Many different characters for practically all of the self-fertilized crops have been studied in a number of crosses. To try and make any general statements concerning the relative magnitude of D and H would be futile since within a single experiment, different crosses give widely diverse estimates for the same character. For example, in two crosses of barley, estimates of D and H for number of ears are shown in Table 1 (42). In one population evidence was for most of the variation arising from dominance effects and in the other population only variance arising from additive effects was observed. Therefore, no attempt will be made to review all of the estimates of genetic variance obtained in every crop.

TABLE 1.—ESTIMATES OF GENETIC PARAMETERS FOR EAR NUMBER IN BARLEY FROM TAKAHASHI *et al.* (42).

Population	D	H
1	1.34 ± .19	22.25 ± .69
2	8.85 ± .07	−2.05 ± .24

In most of these experiments, the estimation of D and H was accomplished without obtaining component estimates of epistasis, genotype × environment interaction, or linkage effects. Instead, in many instances, an attempt was made to assess the magnitude of these factors as they contribute to error in estimates of D and H and to remove any bias which was contributed by them. Scaling tests for fitting D and H are applied to the data to detect the deviations due to epistasis and genotype × environment interaction on the original scale of measurement. Where these deviations are significant, a transformation of the original data is attempted to remove the non-additiveness of genetic effects among loci without affecting dominance relationships and to make genotypic effects independent of environment.

The choice of an appropriate scale has not been easy in most experiments. For example, in Power's data on locule number in tomato, reported by Mather (28), a scale which was adequate for one cross was inadequate in another, and a scale used for a cross in one year was inadequate in the next.

There is also evidence that certain types of epistasis may not be easily scaled out by a transformation. For example, Ryder (39) found that the significant estimates of the statistics A, B, C, and D of Mather (28) for seed size in lima beans were changed very little by the use of a logarithmic transformation. From these tests, together with a comparison of observed means with theoretical genetic models, he concluded the presence of some type of complementary epistasis for this character. From the variance component analysis, it appeared that the estimate of H was biased by this epistasis.

In other cases, where scaling tests suggest that a transformation has been satisfactory, there still remains evidence of epistasis or genotype x environment interaction. Hadley (12) applied scaling tests for plant height in sorghum on parental, F_1, F_2, and F_3 generations. Although there was no evidence of epistasis, there was indication of genotype x environment interaction. The use of a logarithmic transformation appeared to be an improvement over the original scale. The estimates of D and H are presented in Table 2. The inclusive estimates were obtained by a least squares solution from estimates of F_2 variance, V_{F_2}; variance of means of F_3 progenies, $V_{\bar{F}_3}$; covariance of F_3 mean and F_2 parental measurement, W_{F_2/F_3}; mean variance of F_3 families, $\bar{V}_{F_3}$; and two environmental variances, E_1 and E_2. The exclusive estimates were obtained from the same data with the exception that $\bar{V}_{F_3}$

TABLE 2.—ESTIMATES OF GENETIC PARAMETERS FOR PLANT HEIGHT IN SORGHUM FROM HADLEY (12).

	Scale in inches		Scale in log inches	
	Inclusive	Exclusive	Inclusive	Exclusive
D	84.9** ± 13.2	84.9	.0124* ± .0042	.0121
H	19.3 ± 42.2	19.3	.0110 ± .0142	.0122

*Significant difference at 5% level.
**Significant difference at 1% level.

was omitted from the computations. The test of linkage is the homogeneity test of D and H in the two groups of material. Results of the analysis of variance gave no indication of linkage and the estimates of D and H were similar for inclusive and exclusive estimates in both transformed and untransformed data. The mean square for residual interaction, however, was significant suggesting that the original scaling tests did not detect epistasis present, or that the transformation was inadequate in removing interaction of genotype and environment completely.

A study by Mather and Vines (30) is one of the most extensive uses of this method for obtaining the relationship between genetic components and assessing the influence of epistasis, genotype × environment interaction, and linkage. Plant height and date to flowering were measured in first and second backcross, parent, F_1, F_2, F_3, and F_4 generations in *Nicotiana rustica*. Scaling tests indicated that advanced generations were not in agreement with expectations from the parents and F_1; however, since the results of scaling tests were variable from year to year, the estimates of variances were obtained from untransformed

data. From a combined analysis of data for two years, there was evidence of interaction of genes for inheritance of plant height, and these interactions varied in the different years with little evidence of linkage. For flowering time there was evidence of linkage but no evidence of interaction.

More recently, estimates of epistatic parameters have been presented in several crops by Hayman (17). By comparing means of different generations, estimates of interaction between additive effects, between additive and dominance effects, and between dominance effects were obtained. In the Danmark × Johannisfeuer tomato cross, there was interaction between dominance effects for mean number of locules per fruit. In a cross between two wheat varieties, negative heterosis for per cent shattering in F_1, but positive heterosis in F_2, F_3, and backcrosses was thought to reflect the interaction between dominance effects which was estimated. In one cross of *Nicotiana rustica* varieties there was interaction between additive effects and between additive and dominance effects. In another cross interactions existed between additive and between dominance types.

Another source of bias in estimates of D and H is interplant competition described by Sakai (40). From a cross of two rice varieties, estimates of D and H were obtained for panicle number ignoring competition effects, and also by adding a competition effect to the model. The estimates of D, H, and X, the competition effect, are shown in Table 3. The competition effect is the largest component in the model where it is estimated and the relative importance of additive and dominance effects are reversed in the two models with the large apparent estimate of dominance no longer existing when the competition term is included in the model.

TABLE 3.—ESTIMATES OF GENETIC PARAMETERS FOR PANICLE NUMBER IN RICE FROM SAKAI (40).

Component	Mather's Method	Sakai's Method
D	−4.61 ± 4.35	4.81 ± 3.24
H	46.82 ± 13.92	0.97 ± 14.92
X		7.92 ± 2.35

Diallel cross.

The diallel cross has probably been the most popular single design for assessing quantitative variability in self-pollinated crops. In this section, results will be cited for experiments where inferences are made within a given set of lines. These methods were developed by Hayman (15) and Jinks (21) following the earlier development by Mather.

Jinks (21) observed heterosis for plant height, early flowering, and leaf length from an 8-parent diallel of *Nicotiana rustica* evaluated for 2 years. Incomplete dominance was indicated for flowering time; however, the observed heterosis and large estimates of dominance for plant height and leaf length appeared to result from some type of gene interaction.

Other evidence of non-additivity of gene effects has been obtained by this procedure. Allard (2) found evidence of dominance and epistasis of the complementary type for increased seed size in lima beans. Estimates of epistatic effects were obtained by Hayman (16) from mean comparisons of *Nicotiana rustica*, and selection was proposed for complementary epistasis and against duplicate epistasis. Whitehouse *et al.* (43) found interaction for yield in a 4-parent diallel in spring wheat. Gene action for the components of yield appeared to be primarily additive and a logarithmic transformation removed the interaction for yield. Johnson and Aksel (24) in several diallel experiments in barley suggested overdominance for yield with an association between high yield and an excess of recessive genes.

From the preceding experiments little generalization can be done. There is ample evidence that epistasis, genotype × environment interaction, and linkage may all be biasing estimates of D and H. Since the relative bias to D as compared to H is not known, it is difficult to determine the relative magnitude of additive and dominance variances.

More recently, procedures have been developed to estimate relative amounts of additive, dominance, and epistatic variances and to compare these with estimates of genotype × environment interaction. The remainder of the paper will be devoted to presenting estimates of these parameters in different crops.

ESTIMATES OF GENOTYPE × ENVIRONMENT VARIANCES

A measure of the relative stability of genotypes under a wide range of environmental conditions is necessary in determining efficient breeding procedures. Variety tests repeated over years and locations help in determining efficient allocation of experimental material to evaluate varieties over a range of environmental conditions. Studies for the estimation of genetic variances are often repeated in different environments to obtain a measure of the stability of the genetic effects. In most cases, genetic variances are estimated with respect to an average over environments. The estimates of genotype × environment interaction give some idea of the magnitude of bias from estimating genotypic components in single experiments.

In studies evaluating the importance of genotype × environment interactions, different types of genetic material have been subjected to a range of environments. A common experiment has been to consider the environments as defined by locations and years. Since data are available on many crops for this procedure and since the implementation of breeding programs must usually fit within this framework, some results of these studies will be given. Many other types of environmental variables could fit into a similar framework.

The model assumed is

$$y_{ijkl} = \mu + v_i + y_j + l_k + (yl)_{jk} + (vy)_{ij} + (vl)_{ik} + (vyl)_{ijk} + r_{jkl} + e_{ijkl},$$

where y_{ijkl} is the yield of the genetic material in the experiment in the *lth* repli-

cate in the *kth* location in the *jth* year; μ is a common mean of all entries over all replicates, locations, and years; v_i is a measure of the average genotypic effect of the *ith* entry; y_j is the average effect of the *jth* year; l_k is the average effect of the *kth* location; $(yl)_{jk}$ is the average interaction of the *jth* year with the *kth* location; and the other interactions have the appropriate meaning designated by the corresponding subscripts. In most experiments, the entries, years, and locations are considered random variables. In certain cases only tests of significance of mean squares due to various sources of variation are made; in others, estimates of components of variance associated with the model are obtained.

In Table 4, estimates of genotype and genotype × environment interaction variances are presented for yield of several crops. Miller *et al.* (32) compared 15 varieties of cotton at 9 locations in North Carolina for 3 years. For yield, σ^2_{vy} and σ^2_{vl} were small and nonsignificant; however, σ^2_{vyl} was significant, being greater than one-half the magnitude of the variety component. For other agronomic traits, the first order interactions were significant but were smaller than the second order interactions and were a small fraction of the variety variance.

TABLE 4.—COMPARATIVE ESTIMATES OF GENOTYPE x ENVIRONMENT INTERACTION VARIANCES FROM VARIETAL EVALUATIONS.

Component	Cotton[1] Lint Yield	Tobacco[2] Leaf Yield	Soybeans[3] Seed Yield	Soybeans[4] Seed Yield
σ^2_v	.028	40719**	.194*	1.901**
σ^2_{vy}	.001	1990	1.307	.938*
σ^2_{vl}	.002	100	.881	−.083
σ^2_{vyl}	.016**	7002**	2.773**	3.037**
σ^2	.063	20913	7.800	6.070

[1]Miller *et al.* (32).
[2]Jones *et al.* (25).
[3]Unpublished data of C. A. Brim, Crops Research Division, ARS, USDA and North Carolina State College, Group VI Maturity.
[4]Unpublished data of C. A. Brim, Crops Research Division, ARS, USDA and North Carolina State College, Group VII Maturity.
*Significant difference from zero at 5% level.
**Significant difference from zero at 1% level.

Similar results were obtained by Jones *et al.* (25) for tobacco. Seven varieties were compared at five locations in three years. From nine agronomic and chemical characters only one significant estimate of σ^2_{vy} and one of σ^2_{vl} were obtained. Significant estimates of σ^2_{vyl} were obtained for seven of the characters; however, in most cases this component was a small fraction of the genetic variance.

Brim[2] compared soybean varieties in different maturity groups. In Group VI material evaluated at three locations in North Carolina from 1954 to 1956, the only significant interaction component for yield was σ^2_{vyl}. Group VII mate-

[3]Unpublished data of C. A. Brim, Crops Research Division, ARS, USDA and North Carolina State College.

rial was evaluated at four locations during the same period. In this study the variety × year component was significant in addition to the variety × year × location.

In all three crops, σ^2_{vyl} was the primary genotype × environment component, and variety × location was very small. The importance of the second order interaction, however, varied among the crops. In tobacco it was only about one-sixth of the magnitude of the variety component but in cotton it was over one-half of this component. The estimates of the plot error and interaction components in the two soybean experiments are of the same order of magnitude. In comparison to the average differences among varieties, the interactions in Group VI are much larger than in Group VII. In the Group VI material the range in genetic diversity was very narrow with most of the varieties having a common pedigree. In Group VII, the varieties were isolated from widely different parentage.

Nei (35) compared performance of 32 rice varieties in Japan at a single location for 2 years. Significant variety × year interaction was obtained for culm length, ear length, and ear weight per plant but not for number of ears or ear weight per stem. For ear length the interaction component was about one-third that of the genotypic component, whereas, for the other characters it was a lesser fraction in comparison to the genotypic variance.

Forty-nine chemical and physical and 3 agronomic characters of tobacco were compared for 6 tobacco varieties at 5 locations for a 3-year period by Collins *et al.* (5). Of the 52 estimates of each of the genotype × environment interaction components there were no significant estimates of σ^2_{vl}, 6 of σ^2_{vy}, and 4 of σ^2_{vyl}.

Estimates of similar components are presented in Table 5 where the genetic material is early generation random lines from the cross of two pure line varieties or strains. Ten characters were evaluated in cotton by Miller *et al.* (33) in random F_4 and F_5 lines from two populations evaluated in successive years. Of the 20 estimates of each genotype × environment component, significance was shown for only 3 line × year, 2 line × location, and 3 line × year × location components. Even where interactions were significant, they were small in relation to the genotypic components except for lint yield (Table 5) and bolls per plant in population 1. In an earlier study Al-Jibouri *et al.* (1) evaluated F_3 progenies of an interspecific cross of cotton at two locations and found the progeny × location interaction was a small proportion of the phenotypic variance, varying from 1 per cent for lint strength to 16 per cent for yield.

Similar estimates obtained by Brim[3] in soybeans for two populations, each arising from crossing two pure lines, are shown in Table 5 for seed yield. The estimates are averages of components obtained from random F_3, F_4, and F_5 lines from these crosses evaluated at two locations for 2 years. A number of F_4 and F_5 lines from random F_2 plants of soybeans were evaluated by Johnson *et al.* (23) at

[3]Unpublished data of C. A. Brim, Crops Research Division, ARS, USDA and North Carolina State College.

TABLE 5.—COMPARATIVE ESTIMATES OF GENOTYPE x ENVIRONMENT INTERACTION VARIANCES FROM RANDOM F_3, F_4, AND F_5 PROGENIES.

Component	Cotton[1] Lint Yield		Soybeans[2] Seed Yield		Lespedeza[3]	
	Pop. 1	Pop. 2	Pop. 1	Pop. 2	Total Yield	Seed Yield
σ^2_v	6.85	5.15	5880	5588	2639	215
σ^2_{vy}	−1.65	0.46	753	2731	1553	94
σ^2_{vl}	−2.32	−0.99	39	614	592	23
σ^2_{vyl}	7.05**	0.89	1061	656	2210	233
σ^2	28.72	22.74	12562	17783	16360	819

[1]Miller *et al.* (33).
[2]Unpublished data of C. A. Brim, Crops Research Division, ARS, USDA and North Carolina State College.
[3]Hanson *et al.* (13).
**Significant difference from zero at 1% level. F tests were applied to cotton data only.

several locations for 2 years. Since data from each location were not available for each year, a combined analysis of all data was not possible. Analyses of subsets of the data suggested that performance at a single environment was inadequate for yield, but plant height, seed weight, and oil per cent were more consistent from one environment to another.

Three populations of lespedeza, each arising from crosses of pure lines with wide agronomic differences were compared by Hanson *et al.* (13). Random F_3 and F_4 progenies were evaluated at two locations for 2 years. The estimates of genotypic variance and of genotype × environment interaction were similar for the three populations and only averages of the estimates are shown in Table 5 for total vegetative yield and seed yield. For both characters, the three-factor interaction is the largest interaction component and is almost as large as the genotypic variance.

Any broad inferences with respect to all self-pollinated crops is impossible as the estimates have varied considerably, but the information presented suggests several trends. In most experiments where genetic material is grown in a limited area of adaptation, there was little genotype × location interaction. This is not to be unexpected since past experimentation has allowed most researchers to make realistic subdivisions within a geographical area. A modification in the evaluation of experimental material can be made if genotype × location is a large component by restricting the evaluation to a subset of the original locations. Horner and Frey (19) obtained estimates of the variety × location interaction from nine locations for 5 years in oats. Subdivision of the area into 2, 3, 4, and 5 subregions reduced the variety × location component by 11 per cent, 21 per cent, 30 per cent and 40 per cent, respectively, from that of all nine locations.

Of greater significance apparently is the genotype × year × location interaction. As suggested by Miller *et al.* (32) and Jones *et al.* (25), each individual experiment is unique and the environmental conditions differentiating these experiments are not necessarily related to the year or location grouping. It is

interesting to note that the predominance of the second order interaction was fairly general in different crops whether yield was vegetative, lint, or seed. If this relationship is as general as it now appears, a simplification in evaluation studies might be satisfactory. If a sample of locations in different years was not required to be in the same immediate area, it would often simplify obtaining good plot land for experimentation. The analysis would then just involve genotypes and environments with no distinction made between years and locations. This procedure would also facilitate the combined analysis of experiments when an experiment at one location in one year fails.

Although one must be cautious of minimizing the importance of genotype × environment interaction, it should be emphasized that *a priori* it need not be a limiting factor in evaluating genetic material. From the estimates cited its importance varied among crops. As the genetic diversity of the material under evaluation increases the magnitude of genotype × environment interaction becomes less important relative to genotypic differences.

In the naturally crossbreeding species there has been considerable evidence that homozygotes are less stabilized against environmental differences than heterozygotes. This has been interpreted by some to be a function of heterozygosity *per se* and by others to be related to the effects of past forces of natural selection.

Information is also available in self-pollinated crops comparing pure lines with hybrid material as they respond to changes in environment. If hybrid material was better buffered, it would lend support to the heterozygosity *per se* hypothesis. On the other hand, if pure lines showed greater phenotypic stability, it would be evidence that during the course of evolution of self-pollinated crops some internal buffering mechanism had been developed and would suggest that any deviation from the normal breeding procedure of a crop causes it to lose its buffering ability.

A few examples will be sufficient to illustrate the pattern. In 1912 Hayes (14) found F_1 variability slightly greater than the average of the parents for six cases and less than average in five cases for different characters in crosses of *Nicotiana tabacum*. Lower environmental variances in hybrids than in parents of *Primula sinensis* were obtained for style length and anther height by Mather (29).

From a cross of two *Triticum vulgare* varieties, Palmer (36) presented estimates of parent and F_1 variances for the components of yield and yield itself shown in Table 6. The designations are

e = number of ears per plant
n = mean number of grains per ear
g = mean weight of one grain
en = number of grains per plant
ng = mean weight of grain per ear
eng = weight of grain per plant.

TABLE 6.—PARENT AND F_1 WITHIN PLOT VARIANCES IN WHEAT FROM PALMER (36).

Character[1]	Cross 7	Dreadnought	F_1
e	1.30	2.00	.76
n	32	38	42
g	18	11	40
en	2258	2319	1067
ng	.11	.07	.18
eng	6.60	8.28	5.84

[1]See text for description of characters.

The variances of the two parents differed for *e*, *g*, and *ng*. For the three individual yield components, the F_1 variance was lower than either parent for *e*, slightly higher than both parents for *n*, and considerably higher than both parents for *g*. The combination of characters reflect the individual component variances with total weight, *eng*, showing less variation in F_1 than in parents. In another cross of *Triticum vulgare*, Copp and Wright (6), the within plot variance for average kernel weight was higher in F_1 than in either parent.

In a *Nicotiana rustica* diallel test Jinks and Mather (22) found no difference between the parents and F_1 hybrids for within plot variances for leaf length and capsule number. For plant height, the F_1 families differed in variance with no difference among parents or no average difference between parents and F_1 hybrids. For flowering time, both parents and F_1's vary within themselves but again there is no average difference between parent and F_1 variability. Using a diallel analysis there was evidence of average partial dominance for low within plot variance for flowering time.

No differences were found between parents and F_1 hybrids for stability to environmental variation in *Lycopersicum esculentum* by Williams (46). For most characters the average F_1 variances were between the parental variances. In individual crosses for some characters the F_1 variability was similar to the most variable parent and in others, similar to the least variable parent.

There is probably a good reason for the fact that uniformity is not the same in different characters of a particular crop. Increased variation in one character is often accompanied by decreased variability in another. For example, similar grain yield in small grain may be associated with considerable variation in number of tillers, number of seeds per head, or weight per seed. This mechanism of adjustment allows the plant to perform well for yield in many environments. For this reason, one must be cautious of measurements of variability in a single character as a criterion of stability of an organism.

From these data and many others, it would appear that the stability of an individual with respect to environment is not related to its homozygous or heterozygous state, but is specific for a particular character in each cross, and would seem to be related to the genotype of the individual. The implications of this situation are important, but perhaps unfortunate. If there is considerable heterogeneity of within plot variances among pure lines, this fact must be taken into

account when estimating genetic variances. If this is an "inherited" trait, any segregating populations will be mixtures of individuals with different environmental components.

One word of caution about these results should be given. Most papers refer to the varieties as pure lines, and as such assume no genetic variability within a line. In most cases no information is given on the number of generations of selfing in each variety.

VARIANCES OF GENERAL AND SPECIFIC COMBINING ABILITY

In studies of diallel crosses, information has been used in two ways. First, the studies may be used to characterize crossing relationships among a group of varieties or lines with the goal of identifying crosses which would be expected to be good source material for selection. Secondly, they have been used to obtain information concerning a base population of which the material in the test is only a sample. Attempts at clarification of the theory involved in these two uses have been given by Griffing (11) and Hayman (18).

The subdivision of the analysis of diallel crosses into variances of general combining ability (σ^2_g) and of specific combining ability (σ^2_s) requires no genetic assumptions as the subdivision is purely statistical. The use of the estimates and their interpretation does, however, require genetic assumptions.

Gilbert (10) has reviewed many of the diallel crosses in the literature and presented estimates of mean squares for general and specific combining ability. Certain limitations in each of the experiments make it difficult to estimate components of σ^2_g and σ^2_s. On inspection there appears to be an effect of both general and specific combining ability for the following data: Allard (2), seed size in lima beans; Jinks (21), plant height in *Nicotiana rustica;* Currence *et al.* (7), yield of tomatoes; Powers (37), yield of tomatoes; and an 18 × 18 diallel for flowering date in tomatoes. The inability to solve for components makes it difficult to assess the relative importance of each.

Estimates of σ^2_g and σ^2_s were obtained in soybeans by Leffel and Weiss (27). Both were important for yield, date of flowering, height, oil content of seed, iodine number of oil, and seed quality with σ^2_g being much larger than σ^2_s for maturity, flowering, and seed size.

Components of variance for both σ^2_g and σ^2_s were found to be significant for flowering time in an F_1 and F_2 diallel cross of *Trifolium subterraneum* L. by Davern et al. (8). However, the estimate of σ^2_s was only a small fraction of σ^2_g and there was no evidence of heterosis. With the same species, Morley (34) reduced an estimate of σ^2_s for germination percentage by removing one of the parents from the diallel. The genetic variance remaining was σ^2_g; the parent removed apparently contained genes which showed interaction in crosses to the other parents.

Often the estimates of σ^2_g and σ^2_s are used for the further estimation of components of genotypic variance relative to some population. Although easiest interpretation results when the source material is a random mating population,

often the diallel is made among varieties in which case the estimates refer to a hypothetical population from which these varieties may have been obtained. An example of the latter case will be given to show some of the inferences which can be drawn. These data were obtained in the tobacco genetics program at North Carolina State College representing cooperative work of the author and Dr. T. J. Mann.

Eight varieties representing most of the acreage planted to flue-cured tobacco in the United States at the time of initiation of the study were crossed in all possible crosses, including reciprocals. A single F_1 plant of each cross, excluding reciprocals, was self-pollinated to obtain the F_2 generation.

The experimental material was evaluated at Clayton and Rocky Mount, North Carolina in 1958 and 1959. A replicated split-plot design was used in all experiments. In 1958 the parental varieties and the 56 F_1 families were evaluated with each whole plot consisting of two parents, the F_1, and reciprocal F_1 from these two parents. In 1959 a whole plot consisted of a common F_1 and F_2 family.

Significant differences were detected among the eight varieties for all of the characters studied indicating the presence of genetic variability in the population for all characters. Comparisons of reciprocal F_1 hybrids gave no evidence of reciprocal differences for any of the characters, and data for reciprocals were combined within each family.

In Table 7 overall mean comparisons of the parent, F_1, and F_2 generations are presented. The heterosis values were obtained from 1958 data and are expressed as per cent increase of the F_1 hybrids above the average of the parents. Inbreeding depression estimates were obtained from 1959 data and are expressed as per cent F_2 reduction below F_1 performance.

Significant, although small, amounts of heterosis were obtained for

TABLE 7.—AVERAGE PERCENT HETEROSIS FROM MID-PARENT AND PERCENT F_2 DEPRESSION FROM F_1 FOR AGRONOMIC AND CHEMICAL CHARACTERS OF TOBACCO.[1]

Character	Heterosis $\frac{F_1-MP}{MP}$	Depression $\frac{F_1-F_2}{F_1}$
Yield	1.16**	3.49**
Plant height	2.17**	1.80**
% nicotine	−1.50	−1.22
% nornicotine	0	0
Leaf length	0.60	0.38
Leaf width	1.46*	1.64**
Value/cwt	0.64	1.32**
No. of leaves	−0.50	−0.17
Days to flower	−1.20**	−1.59**
Leaf axil suckers	3.73**	1.94

[1]Unpublished data of D. F. Matzinger and T. J. Mann, North Carolina State College.
*Difference between generations significant at 5% level.
**Difference between generations significant at 1% level.

increased vegetative leaf yield, earlier days to flower, taller plant height, wider leaves, and more leaf axil suckers. No heterosis was observed for a quality index measured as value per 100 pounds, number of leaves, leaf length, per cent nicotine, and per cent nornicotine. All of the characters exhibiting heterosis gave a depression of F_2 below F_1, except leaf axil suckers. Value per 100 pounds was the only character showing inbreeding depression in the absence of heterosis.

The constancy of heterosis for a specific variety in all crosses was tested by the source of variation arising from (parents vs. F_1) $\times$ family. Significance for this component would indicate that the degree of heterosis for a particular character was very largely determined by the specific parents crossed. Such differential response of parents and F_1 for the different varieties was detected for yield and plant height, but none of the other characters.

Estimates of genetic variability and genotype $\times$ environment interaction for the 10 characters obtained from the diallel analysis of F_1 data at the 2 locations in 2 years are shown in Table 8. Variance component estimates are given for σ^2_g, σ^2_s and all interactions of general and specific effects with environments; e.g., σ^2_{gy} is the component associated with the interaction of general combining ability effects with years.

The estimates of σ^2_g were significant for all characters, but none of the estimates of σ^2_s were significant. If one now makes the assumption that these estimates apply to a base population of which the parents used in the diallel may be considered a sample, the expectation of σ^2_g and σ^2_s can be expressed as components of genotypic variance.

The following model has been described by Kempthorne (26) for defining genotypic variance in terms of additive, dominance and epistatic effects:

$$\sigma^2_G = \sigma^2_A + \sigma^2_D + \sigma^2_{AA} + \sigma^2_{AD} + \sigma^2_{DD} + \text{etc.},$$

where σ^2_A is the variance of the total additively genetic values,

σ^2_D is the variance of the total dominance contributions,

σ^2_{AA} is the variance of the epistatic contributions of the type additive $\times$ additive from all pairs of loci, and the other epistatic contributions are designated by their subscripts.

Assuming gene frequency of 0.5, two alleles per locus, and additivity among loci, the relationship between Mather's D and H and the above model is $\sigma^2_A = (1/2)$ D and $\sigma^2_D = (1/4)$ H. Components of σ^2_g and σ^2_s can be expressed in the model as follows:

$$\sigma^2_g = (1/2)\ \sigma^2_A + (1/4)\ \sigma^2_{AA} + (1/8)\ \sigma^2_{AAA}$$
$$\sigma^2_s = \sigma^2_D + (1/2)\ \sigma^2_{AA} + \sigma^2_{AD} + \sigma^2_{DD} + (3/4)\ \sigma^2_{AAA} + \sigma^2_{AAD} + \sigma^2_{ADD} + \sigma^2_{DDD}$$

for three segregating loci. With more loci the coefficient of higher order additive type epistasis terms decreases in σ^2_g and increases in σ^2_s.

The generation mean relationships and genetic variances are quite consistent with each other. Small values for the estimates of σ^2_s for all characters is an indication of no dominance or epistasis, and consequently the significant estimates of σ^2_g for these characters are estimates of $(1/2)\sigma^2_A$. The small amount of

TABLE 8.—ESTIMATES OF VARIANCE OF GENERAL AND SPECIFIC COMBINING ABILITY AND INTERACTIONS WITH YEARS AND LOCATIONS IN A DIALLEL OF *Nicotiana tabacum*.[1]

Component	Yield	Plant height	Nicotine	Nornicotine	Leaf length	Leaf width	Value/cwt	No. of leaves	Days to flower	Leaf axil suckers
σ^2_g	23,581**	19.0**	.17**	.00066**	.808**	1.42**	1.68**	.821**	1.414**	1.045**
σ^2_s	−1,074	.9	.01	.00000	−.131	−.13	−.03	−.023	.194	.382
σ^2_{gy}	115	3.0	−.03	.00007	−.231	.08	−.11	.255**	.337	.164
σ^2_{sy}	1,122	0.5	.00	−.00009	−.314	.99	.23	−.016	−.495	−.587
σ^2_{gl}	−637	0.6	−.02	−.00002	−.246	−.02	.19	−.009	.084	−.099
σ^2_{sl}	39	1.3	−.01	.00005	.363	.18	.42	.101	−.017	−.827
σ^2_{gyl}	1,201	3.3	.05**	−.00001	.296	.01	.25	.001	.008	.132
σ^2_{syl}	268	−1.3	.00	.00014	−.033	−.69	.46	.070	.459	.065

[1]Unpublished data of D. F. Matzinger and T. J. Mann, North Carolina State College.
**Significant difference from zero at 1% level.

heterosis and inbreeding depression is further evidence of the relative importance of additive genetic effects in this material.

Six genotype × environment interaction components were estimated for each of the 10 characters. Only 2 significant estimates were obtained of the 60 possible, σ^2_{gy} for number of leaves and σ^2_{gyl} for per cent nicotine. Growing conditions were considerably different in the four experiments. For example, the range in yield of all F_1 families was from 1,679 pounds per acre at Clayton in 1959 to 2,126 pounds per acre at Rocky Mount the same year. In spite of these mean differences there was little interaction of genotypes with years or locations. It is interesting that both of the significant interaction components are interactions involving additive genetic effects; however, in comparing all of the estimates there is little evidence that additive, dominance, or epistatic effects exhibit differential interaction with environment. Instead, one would probably conclude that this is additional evidence for the relatively small amount of genotype × environment interaction in tobacco.

ESTIMATION OF EPISTATIC VARIANCE

From the sample estimates presented from a number of self-pollinated crops, there was considerable evidence of bias from epistasis. It is unfortunate that the amount of data comparing quantitative estimates of epistasis with additive and dominance variances is so limited. Several experiments have been designed to yield estimates of σ^2_A, σ^2_D, and σ^2_{AA} under the assumption of no dominance types of epistasis.

Horner and Weber (20) presented an expression for designating genotypic variances and covariances of types of relatives for the model of σ^2_A, σ^2_D, and σ^2_{AA}, two alleles per locus, no linkage, and a gene frequency of one-half. They showed that

$$\text{Cov (k;n,n')} = \left(\frac{2^{k-1}-1}{2^{k-2}}\right)\sigma^2_A + \left(\frac{2^{k-1}-1}{2^{n+n'-4}}\right)\sigma^2_D + \left(\frac{2^{k-1}-1}{2^{k-2}}\right)^2\sigma^2_{AA},$$

where Cov *(k;n,n')* is the genotypic covariance of progenies in the *nth* generation tracing to particular genotypes in the *kth* generation with progenies in the *n'th* generation from the same genotypes in the *kth* generation. Thirty variances and covariances for maturity date in soybeans were available to estimate the above genetic components. The estimates presented in Table 9 show that most of the

TABLE 9.—ESTIMATES OF ADDITIVE, DOMINANCE, AND ADDITIVE x ADDITIVE EPISTATIC VARIANCES FOR MATURITY DATE IN SOYBEANS FROM HORNER AND WEBER (20).

Model	σ^2_A	σ^2_D	σ^2_{AA}	R^2
σ^2_A	10.92			.9623
$\sigma^2_A + \sigma^2_D$	10.85	1.43		.9625
$\sigma^2_A + \sigma^2_D + \sigma^2_{AA}$	11.06	1.07	−.10	.9627

variance is accounted for by additive effects, although the estimate of σ^2_D is decreased by adding σ^2_{AA} to the model.

From these data and some additional generations, Gates *et al.* (9) tested for the presence of linkage. Significant linkage effects were obtained for yield, plant height, and flowering time with repulsion types predominant for plant height and coupling types for flowering time. No linkage was observed for maturity, time of flowering to maturity, seed weight, oil percentage, or lodging.

Estimates of variances from two soybean crosses were obtained by Brim and Cockerham (4) for nine characters. Significant estimates of σ^2_A were obtained for all characters in both crosses. In Table 10 estimates of the components of genotypic variance are presented for those characters which exhibited significant estimates of either σ^2_D or σ^2_{AA}. In population I the only significant estimate other than σ^2_A was of σ^2_{AA} for per cent protein. In population II there were significant estimates of σ^2_D for fruiting period and unthreshed weight and of σ^2_{AA} for maturity, height, and per cent oil. Multiple correlation coefficients indicated that the percentage of the sum of squares accounted for by dominance variance alone was low in both populations for all characters, varying from 0.4708 to 0.6020. By fitting either σ^2_A or σ^2_{AA} alone all R^2 values were above .90, although R^2 for fitting σ^2_A alone was always higher than when fitting σ^2_{AA} alone.

TABLE 10.—ESTIMATES OF GENETIC COMPONENTS OF VARIANCE IN TWO SOYBEAN CROSSES EXTRACTED FROM BRIM AND COCKERHAM (4.)

Character	Population	σ^2_A	σ^2_D	σ^2_{AA}
Protein, %	I	.34 ± .07	.02 ± .17	.26 ± .08
Fruiting period	II	4.26 ± .43	2.39 ± 1.04	−.03 ± .47
Maturity	II	4.90 ± .57	1.89 ± 1.39	1.54 ± .63
Height	II	14.5 ± .9	2.8 ± 2.2	2.9 ± 1.0
Unthreshed wt.	II	.28 ± .03	.29 ± .08	−.05 ± .04
Oil, %	II	.17 ± .02	−.07 ± .05	.06 ± .02

VARIANCE ESTIMATION AND SIMULTANEOUS SELECTION OF PURE LINES

In many experiments work has been directed towards simply estimating types of variance present in crosses among commercially available varieties or in some instances in interspecific crosses. When considering the material only in the test, practical application is directed towards the choice of material in which to continue further work. In the experiments aimed at estimating population structure, theoretical gains expected in the average of the selected group in the next generation under various alternative breeding procedures are compared and some method, usually the one suggesting the most gain for the attributes under selection, is chosen and put into operation. In successive cycles the observed gains are compared with predicted as a check on the genetic theory. Such a procedure is designed to yield a superior performing population, and one from which material can be selected at each cycle for varietal development. If

the design employed in estimating variances contains only crossbred material, such as a diallel, little information is available on the performance of selfed lines. Then, separate material must be evaluated to go into a varietal development program.

For use in tobacco a combination design has been utilized, designated as a simultaneous selfing and diallel test crossing design. The design incorporates genetic variance estimation together with early generation evaluation of selfed progeny. The design is most easily accomplished by multi-flowered plants and those which yield a large number of seeds per cross. In crops with a limited number of seeds per plant, the parents can be selfed for one generation and bulked crosses made among the progeny rows.

The material used as parents arises from any inbred generation of a cross of two homozygous lines. Random selection of parental plants used in the design is important if any inferences are to be made regarding the population from which they were obtained and in predicting gain to be expected from selection.

The design is illustrated in Figure 1. Eight plants are chosen as parents, four being designated as male parents (numbered 1–4) and four as female parents (numbered 5–8). All possible crosses are made between the two groups of parents giving 16 full-sib families designated C_{ij}. This is a type of diallel cross where the parents on one side of the diallel table are different from those on the other side. At the same time, each of the parent plants is selfed to give eight selfed progeny families, designated X_i. This represents one set of the material. A number of these sets are obtained, each tracing to a different random group of eight parent plants.

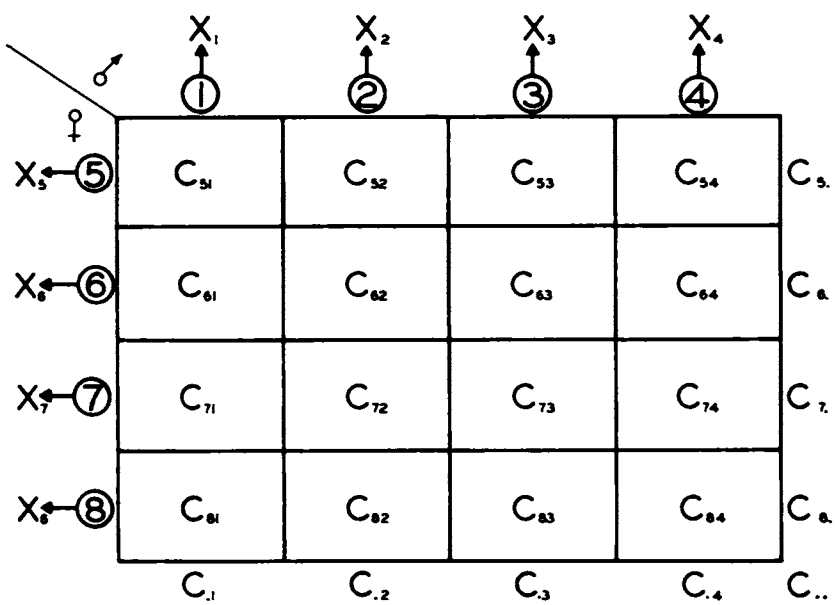

FIGURE 1. *Simultaneous selfing and diallel test crossing design.*

Several alternatives are available in the evaluation of the material in the next generation. Either the crossbred progeny or the selfed progeny can be evaluated in replicated tests, or both groups of material incorporated into the same test. If only the full-sib families are evaluated, estimates of additive genetic and dominance variances can be obtained. If the inbred families are also included in the test, an estimate of the additive × additive epistatic variance can be obtained in addition to additive and dominance variances.

Often the primary objective of genetic variance estimation is to predict the amount of gain from selection when following different breeding procedures. The method of predicting gain depends upon: (1) material evaluated, (2) material selected, and (3) the material to be evaluated in the next cycle. In the present design predicted gain can be on the basis of data from full-sib families, inbred progenies, or a combination of both.

If just full-sib families are evaluated, gain can be predicted for several situations. First, one can predict the gain in the next generation from identifying the superior full-sib families, replanting these families from remnant seed and intercrossing to form a new population. Secondly, the full-sib families can be used as a progeny test, and the gain predicted from random mating the parents (or their selfed progeny) of the superior full-sib families. That is, the identification of the superior parental plants is on the basis of their mean crossbred performance to the others, designated $C_{i.}$ and $C_{.j}$. If the selfed families are evaluated in the test in addition to the full-sib families, a joint selection procedure can be utilized using both kinds of information in the selection gain predictions.

The major purpose of the controlled design is in the estimation of population variability and its relationship to change in mean population level. In addition to this, however, much information is obtained concurrently on potential varieties. If the major portion of the variance is additive or additive × additive type of epistatic variance, the breeder can identify his superior inbred families and continue inbreeding to homozygosity. Even if the inbred families are not evaluated in the test, if the variance is primarily of the additive type, that is, if the parents have a high degree of general combining ability, superior selfed families can be identified on the basis of their crossbred performance. If there should be a large amount of dominance variance, superior full-sib families could be identified and carried on in varietal development with the development towards specific combinations in F_1 hybrids. Thus, at the end of each cycle, information is available on population variability as it relates to further progress in the population as well as the identification of superior families to incorporate into a varietal development program.

Using this design the components of genotypic variance were obtained in a cross of two varieties of *Nicotiana tabacum* by Matzinger *et al.* (31) as shown in Table 11. Both crossbred and selfed material arising from F_2 parental plants were evaluated. Plant height was the only character showing heterosis with the F_1 as tall as the high parent. Estimates of σ^2_A larger than their standard errors were observed for yield, plant height, number of leaves, leaf width, per cent

TABLE 11.—ESTIMATES OF GENETIC COMPONENTS OF VARIANCE IN A TOBACCO CROSS FROM MATZINGER *et al.* (31).

Character	σ^2_A	σ^2_D	σ^2_{AA}
Yield	170*	39	45
Value	11.1*	8.6*	−0.3
Days to flower	17.9	85.6*	−1.2
Plant height	4.74*	1.31	4.26*
Number of leaves	7.61*	6.35*	0.65
Leaf length	0.23	−0.75	0.62*
Leaf width	0.69*	−0.59	−0.02
Number of suckers	4.9	18.0*	−4.7
Nicotine	0.177*	−0.052	0.003
Total alkaloids	0.192*	−0.059	0.004

*Variance component estimate larger than its standard error.

nicotine, and per cent total alkaloids. Value, days to flower, number of leaves, and number of suckers exhibited dominance variance and σ^2_{AA} was obtained for plant height and leaf length.

The selection goal in this population is to incorporate the high yield level of one parent with the high alkaloid level of the other. The genetic correlation between these two characters was −0.54. A selection scheme favoring selection of the top yielding full-sib families and intercrossing from remnant seed was suggested to raise yield and allow for recombination between genes governing yield and alkaloid production.

An example of the use of this design where only the crossbred material is evaluated was the cross of Dixie Bright 244 × Coker 139,[4] both varieties which are low in per cent total alkaloids. All genotypic variance for alkaloid appeared to consist of σ^2_A, suggesting that the marginal mean of four crosses tracing to an F_2 plant would be a good measure of the worth of that F_2 individual. The highest F_2 plant was identified and remnant selfed seed planted. One random F_3 plant was selfed and in 1959 this material in the F_4 generation was compared with the original parents. The alkaloid contents were Dixie Bright 244—1.60 per cent, Coker 139—1.52 per cent, and the F_4 family—1.87 per cent. In 1960, two F_5 lines of this family were evaluated with one having about the same alkaloid as the previous generation and the other showing an increase. Thus, it would appear that characterization of the genetic structure of a population and selection for desired characters in pure line varieties can proceed concurrently.

IMPLICATIONS IN PLANT BREEDING

A major decision to be faced by the breeder of self-pollinated plants is whether to develop homozygous varieties or to find specific desirable hybrid combinations as varieties. Probably the most basic comparison in quantitative characters is that of parental vs. F_1 hybrid performance. Ashton (3) summarized

[4]Unpublished data of D. F. Matzinger and T. J. Mann, North Carolina State College.

evidence of heterosis for wheat, oats, barley, sorghum, rice, cotton, tobacco, tomato, egg plant, and soybeans. From his estimates, it is evident that the occurrence of heterosis of F_1 relative to mid-parent is widespread in self-pollinated plants with every crop showing heterotic response for some character. In many, although not all, of the species, F_1 performance above superior parent was obtained for some character. Expression varied depending upon the specific parents crossed with greater hybrid vigor often arising from interspecific hybrids than intervarietal crosses.

In most of the early work on varietal crosses interest in heterosis was on the commercial use of F_1 hybrids. Two criteria required for their successful use are ease of obtaining crossed seed and a sufficient increase in superiority of crossbred progeny to offset increased seed cost. The mechanical problem of commercial production varies among the self-pollinated species. The number of seed obtained per cross varies from a low percentage of pollinations yielding seed, and then only a single seed per cross in oats, for example, to almost complete success of pollination with several thousand seeds per cross in tobacco. In certain of the crops, such as sorghum and tomatoes, incorporation of male sterility has aided in obtaining large amounts of crossed seed. In cotton, gametocides are being developed as an aid in crossing. It is quite probable that the problem of large scale crossing could be solved even in small grain. For example, Wiebe (44) showed how a recessive gene for male sterility and a recessive gene for resistance to a phytocide can be used to produce hybrid seed in barley.

Since the problem of crossing can be circumvented, the main criterion for the use of F_1 hybrids would seem to be the magnitude of superiority of the crossbred families. In almost every crop, investigators have at some time proposed wide scale use of F_1 hybrids because of superiority for a particular character. The influence of the hybridization procedures in corn seems to have caused the breeder of self-pollinated crops to make a special effort to utilize similar procedures.

In spite of the literature proposing use of F_1 hybrids the problem will be disposed of quickly by the fact that in almost every case homozygous lines have been isolated equal to the F_1 or even surpassing it. An example of transgression was given by Smith (41) for crosses among varieties of *Nicotiana rustica*. The F_1 hybrids generally were taller with larger but fewer leaves when compared to mid-parent and in certain instances the F_1 exceeded the superior parent. By inbreeding and selection, strains were obtained which transgressed the best parent or F_1 for these characters.

A crop presently being grown as F_1 hybrids on a commercial scale is the tomato. Powers (38) indicated it should be possible to isolate homozygous lines from a cross of Porter $\times$ Ponderosa, where the F_1 is superior to the high parent for weight per locule, which would equal, if not exceed the F_1 hybrid. As a critical test of this issue, Williams (45) chose two F_1 hybrids of tomato which were used commercially in England because of early crop yield superiority over the best available homozygous varieties. Performance of selected F_4 lines comparable

to the hybrids suggested that lines could be isolated in homozygous state equal to the hybrids.

The isolation of pure lines equal to hybrid combinations from which they have been derived is supported by the predominance of additive genetic variance reported in this paper for many self-pollinated plants. Also, the lack of a consistent pattern of environmental stability for pure lines vs. F_1 hybrids would cause one to question the argument often expounded favoring commercial use of F_1 hybrids because of greater environmental stability until information on each specific situation is obtained.

Commercial utilization of heterosis would seem to be limited to those cases where an F_1 gives immediate superiority for some desired character, resulting from a combination of desirable traits from the two parents, until selection in segregating generations gives the same or a superior product. In certain instances the isolation of pure lines may be somewhat more difficult. As the number of genes determining the inheritance of a particular character becomes large and if tight repulsion linkages predominate, a large population size will be necessary to recover desired types. In interspecific crosses, sterility may impose an immediate limitation; however, methods of overcoming such barriers are well known in many crops. In most cases, however, the product resulting from a direct interspecific cross is of limited commercial use because of undesirable traits contributed by one of the species. Such a limited role of the temporary use of F_1 hybrids would seem to reduce the amount of effort a breeder would wish to spend developing hybrids. Efficiency of breeding procedures is then related to the amount of genetic variance present in various populations.

For the plant breeder estimates of genetic and environmental parameters are of importance primarily as they relate to an improved variety by selection. Knowledge gained from quantitative genetic studies helps in making decisions which will increase the efficiency of a breeding system and may not suggest any drastically new procedures. Although selection is beyond the scope of this paper and is treated by Manning, Penny *et al.*, Griffing and Langridge, and Kojima and Kelleher in this volume, a few comments are presented as they relate specifically to self-pollinated plants.

The amount of dominance variance present in many of the experiments is questionable because of bias in the estimation in practically all designs. Where σ^2_D and σ^2_{AA} have been estimated, there is some evidence of each in certain instances. Often, however, many of the significant estimates of σ^2_D and σ^2_{AA} are negative. The predominant type of variance in these extensive studies seems to be σ^2_A. Whether this is a general phenomenon resulting from the evolutionary history of naturally self-pollinating organisms is still unknown.

The predominance of σ^2_A together with the fact that pure lines have been isolated equal to F_1 hybrids from which they were derived would seem to favor development of breeding systems utilizing σ^2_A. Since heterosis has been observed in most crosses, it will be of interest to determine if a large portion of the non-

additive variance estimated for some characters is of the additive × additive types.

If variance is primarily additive, one can compare the expected gain from selection at various levels of inbreeding. Brim and Cockerham (4) compared expected progress from selecting the superior 5 per cent of the progenies of soybeans from F_2, F_3, F_4, F_5, and F_∞ parents for yield, per cent protein, and per cent oil. The gain in expected progress by selecting in inbred material increased with selfing, but at a decreasing rate. They suggested inbreeding parents to the F_3 or F_4 generation before evaluating progenies.

Where σ^2_{AA} makes up a large portion of the genotypic variance, breeding systems will probably change very little from those used when variance is all σ^2_A. Homozygous genotypes will still be desired; however, it now becomes more important that selection must not be too severe in early stages of a breeding program as opportunity must be allowed for the desirable epistatic combinations to come together. Linkage complicates the problem and if linkages are predominately of the repulsion type, a generation of intercrossing to increase opportunity of recombination may become important.

LIMITATIONS AND NEEDS

A survey of the reported estimates of genetic parameters in self-pollinated plants points up a number of drastic limitations of the estimates available. To merely state that additional estimates are needed before more general statements of interpretation can be made would be inadequate. Most of the studies which have been conducted would seem to be limited to a test of various genetic models and a measure of the ability of an experimentor to obtain adequate estimates.

The most serious limitation in the past seems to be the inefficiency of the design used. In many cases proper experimental field design was not used and interpretations are questionable. In other instances, where an apparently adequate field design was employed, the estimates still have excessively large standard errors. To attempt to obtain information about the action of genes in quantitative characters by phenotypic observations would be a large enough problem with good design estimates, but with poor estimates it is almost an impossibility. It would be desirable to decide on the types and generation of material which would give maximum information from a given number of plots, rather than decide upon an easy crossing system and work out the analysis after the experiment is completed. The justification often given for not estimating any epistatic components is that until methods are refined to yield better estimates of σ^2_A and σ^2_D, little hope could be given for estimation of any epistatic terms. When using a least squares solution, the relative magnitude of the standard errors for the components is determined by the design. In the tobacco combination design, for example, the standard error of σ^2_{AA} is much less than for σ^2_D, suggesting designs are available to estimate epistatic variances with standard errors comparable to those for other components.

It also appears unfortunate that in most experiments on the estimation of genetic parameters in the self-pollinated crops the data is merely used as an example. Few of the experiments are carried on into advanced generations to see if the estimates obtained are in agreement with the results of continued selection. As more efficient methods of estimation become available and alternative selection procedures compared the results will have far more relevance in increasing the efficiency of breeding procedures in self-fertilized crops.

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DISCUSSION

W. D. HANSON: To what extent do you feel that interplant competition affects your estimates of genetic variability since you have proposed the use of plot measures based on heterogeneous populations of plants?

D. F. MATZINGER: As illustrated in the paper and from much other evidence the presence of interplant competition is well established in certain material. However, the importance of competition effects will probably vary depending upon the species under test and the particular character measured. In space planted crops, such as tobacco, one might expect these effects to be much smaller than in densely planted species. Even if competition is present it need not necessarily affect the estimates of genetic variances from plot means of segregating material if a balanced situation of competition and compensation among genotypes occurs. Currently, studies are in progress to determine the bias of competition to plot means in tobacco.

R. W. TOUCHBERRY: Were the varieties of cotton, etc. used in this study widely used commercial varieties? If they were, it would seem that this would tend to minimize the interaction between heredity and environment. This is suspected to be true because commercial varieties are likely successful because they perform well over rather wide areas.

D. F. MATZINGER: Data were cited for two major types of genetic material, commercial varieties, and random selfed lines from crosses of commercial varieties. The varieties have been highly selected for performance in some designated area. Possibly random selfed lines from these varieties would also be expected to have similar adaptive values as their parents. However, in many of the studies the varieties evaluated in genotype × environment studies were grown in areas completely apart from where they were recommended. In Miller's cotton data, 13 of the 15 varieties evaluated in North Carolina were adapted to the area, one was from New Mexico and one was an experimental strain resulting from an interspecific cross. Deleting the two unadapted varieties from the analysis caused a large reduction in the variety variance component, but had very little effect on the interaction components. In much tobacco data the interaction of genotypes × environments is the same for relatively untested lines as for varieties released following superior performance over a wide environmental range.

J. A. NELDER: Would the speaker comment on σ^2_{vyl} being important while σ^2_{vy} and σ^2_{vl} are not. Does this mean that we have no idea what the determinants of yield are, and that this idea of a locality or a year is a needless one?

D. F. MATZINGER: The relative magnitude of σ^2_{vy}, σ^2_{vl}, and σ^2_{vyl} suggests to me that the environmental factors which are causing differential varietal

response are not those which occur at all locations in one year or all years at one location. However, this does not say that the factors responsible for σ^2_{vyl} are unknown. In some studies disease has occurred in only one location in one year, being absent in other years at that location and at other locations in that year. If the study involves both resistant and susceptible material, this will lead to a large estimate of σ^2_{vyl}. The environmental factor which leads to an occasional significant estimate of σ^2_{vyl} in many tobacco experiments is rainfall during the critical flowering period. Here the interaction results from a change in the range of flowering from the earliest to the latest variety. Since much of the rainfall during the flowering period occurs as scattered showers, again this is reflected mostly in σ^2_{vyl} and not in σ^2_{vy} and σ^2_{vl}.

Much work is needed in further identification of these environmental factors. When the relationship of genotypic response to a range of specific environmental conditions is known then one can attempt to evaluate varieties under field conditions. In many cases it will be difficult to regulate some of these factors under field conditions even after they are identified. Therefore, until these major factors are better known and can be controlled, the breeder evaluates his material in a sample of environments and hopes that a range of the important environmental factors will occur. As suggested in the paper, an analysis involving environments, rather than years and locations, will probably be as meaningful as the complete analysis.

H. F. ROBINSON: I would like to suggest that many results on genotypes (entries) tested over locations and years, showing low G × L and G × Y, interactions compared to high G × L × Y, appear to support "random" environment as far as locations and years with respect to genotype interactions are concerned. Environments do not appear to be repeatable in different years over a restricted range of locations.

JOHN GRAFIUS: It is not sufficient to discover a genotype × environment interaction. We must find out what it is due to. Testing may thus be carried out to determine the phenotypic response to a known variable such as temperature, water, etc., rather than to a random variable. Once these variables are known it may be possible to do something about it. For example, select for a universal type which is buffered or even use multilineal varieties rather than pure lines.

J. A. NELDER: There are two possible types of experiment for estimating genetic variances. In one, parents, F_1, F_2's, etc. are in separate plots, while in the other a completely randomized block for individual plants is used. The former type will exaggerate the genetic variance if the parents are uniform but not very vigorous compared to the F_1. On the other hand, the means of the populations are better estimated from this type. Then, is there a conflict between designs for measuring means and those for measuring variances?

D. F. MATZINGER: This question again seems to be related to the problem of competition as competition can exaggerate the variances in the manner described. I would include the solution to this problem within the framework of what I indicated in the paper to be a major limitation in this area, that of inadequate design estimates. The conflict between designs for estimating means and those for estimating variances is a general problem and different designs will probably be necessary depending upon which of the two types of information one desires greatest precision. For example, in the combination design described for tobacco, where primary emphasis is placed on estimating variances, the material is grown in small incomplete blocks so as to minimize the effects of soil heterogeneity. Such a design, however, necessitates block adjustments before comparing means of all families in the experiment.

The Partitioning Method of Genetic Analysis and Some Aspects of Its Application to Plant Breeding[1,2,3]

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The special problems and techniques to be discussed in this article pertain to the partitioning method of genetic analysis (6, 8, 9, 10, 14) and to some aspects of its application to plant breeding (11, 12, 13).

The partitioning method of genetic analysis is based on the facts that the frequency distribution of any segregating or heterogeneous population is composed of individuals having a number of genotypes, and that individuals possessing identical genotypes fluctuate about a common mean due to environmental variation. Consequently, any such population is composed of subgroup means, subgroup frequency distributions, and subgroup variances. The subgroup variances may or may not be of equal magnitude. Tests for the validity of the genetic model postulated are made by comparing obtained and theoretical means, obtained and theoretical frequency distributions, and obtained and theoretical variances.

Some of the more important types of application of the partitioning method of genetic analysis and some techniques used in testing the validity of the genetic model postulated are as follows: Type I, for some characters estimates of the frequency distributions of certain genotypes are available. These are partitioned out of the inclusive frequency distribution leaving the previously unknown frequency distribution of a certain genotype or certain genotypes (6, 9). Type II, for characters conditioned by "one effective factor pair" (for terminology see Mather 4) the data of the two parents and the F_1 are used to calculate theoretical means, theoretical frequency distributions, and theoretical genetic

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variances. These are compared with the obtained means, frequency distributions, and genetic variances to determine the validity of the genetic model postulated. Type III, for some characters for which, as in the two previous methods, no assumption is made regarding the type of frequency distribution, (normal or otherwise) an iterative procedure is used (10). The iterative procedure involves repeated adjustment of the postulated genetic model to some populations or parts of these populations until a satisfactory fit is obtained. Again, tests of the validity of the genetic model can be made by comparing theoretical means, frequency distributions, and genetic variances with those of populations not involved in the iterative procedure. Type IV, for characters whose variability due to environment follows the normal probability integral, the means and standard errors together with the normal probability integral can be used to calculate a theoretical frequency distribution (1, 8, 10). As before, theoretical means, frequency distributions, and genetic variances are compared with the obtained values to determine the validity of the genetic model postulated.

Also, this article will illustrate the application of the partitioning method of genetic analysis to a solution of some plant breeding problems. Specifically, population frequency distributions will be partitioned to determine the identifiable numbers and proportions of genetic deviates.

The data used for illustration are from wheat (*Triticum aestivum* L.), tomatoes (*Lycopersicon esculentum* Mill.) and sugar beets (*Beta vulgaris* L.).

EXPERIMENTAL DESIGN

The statistical design of the experiment from which the data are derived illustrating types II, III, and IV is a randomized complete block. The genetic design of the experiment is shown by listing the populations grown. They are the P_1, B_1 to P_1, F_1, F_2, B_1 to P_2, and P_2. P_1 designates one parent, P_2 the other parent and B_1 the first backcross generation. In some cases in addition to these six populations, progenies from a random sample of self-fertilized plants of the two B_1 populations are included. Numerous other modifications of the above genetic design are possible, such as including F_3 progenies, paired matings, etc. Also, in a number of the studies there is more than one entry of some populations. The ± values following the constants in many of the tables are standard errors.

TYPE I, PARTITIONING THE INCLUSIVE FREQUENCY DISTRIBUTION TO LEAVE THE FREQUENCY DISTRIBUTION OF PLANTS OF A CERTAIN GENOTYPE

For the details of this experiment and a description of the characters under investigation see (6).

The frequency distribution including plants of the genotypes *aaBBCC*, *aaBbCC*, and *aabbCC* is partitioned to leave the frequency distribution of plants of the *aaBbCC* genotype. The data are for weekly ripening periods of plants derived from crosses between varieties of wheat (*Triticum aestivum* L.) having spring habit of growth with those having winter habit of growth. In Table 1

TABLE 1.—THE INCLUSIVE FREQUENCY DISTRIBUTION EXPRESSED AS NUMBERS, THE PREDETERMINED FREQUENCY DISTRIBUTION OF CERTAIN GENOTYPES EXPRESSED AS PERCENTAGES AND NUMBERS, AND THE FREQUENCY DISTRIBUTION RESULTING FROM PARTITIONING EXPRESSED AS PERCENTAGES AND NUMBERS.[1]

Genotype		Plants in weekly ripening periods—						Total plants
		II	III				IV	
		4	5	6	7	8	9	10	
aaBBCC+ aaBbCC+ aabbCC	No.		17	28	84	34	153	86	402
−aabbCC	%						1.21	98.79	
	No.							−86	
aaBBCC+ aaBbCC	No.		17	28	84	34	153		316
−aaBBCC	%	7.45	17.39	18.32	11.49	10.25	35.10		
	No.		−18	−18	−12	−10	−35		101
aaBbCC	No.			10	72	24	118		224
	%			4.46	32.14	10.72	52.68		

[1]The organism is wheat (*Triticum aestivum* L.) and the character is number of days from July 21 to ripening.

are listed the inclusive frequency distribution expressed as numbers, the predetermined frequency distributions of certain genotypes expressed as percentages and numbers, and the frequency distribution resulting from partitioning expressed as percentages and numbers.

As shown in Table 1, the total number of plants in the progenies from F_2 plants of the *aaBBCC*, *aaBbCC*, and *aabbCC* genotypes is 402. The inclusive frequency distribution is shown opposite the row heading "No." under *aaBBCC+ aaBbCC+aabbCC*. All individuals fall into weekly ripening periods from 5 to 10 and within classes III and IV. An estimate of the number of plants of the *aabbCC* genotypes are the 86 in period 10 and may be subtracted to leave an estimate of those of the genotypes *aaBBCC* and *aaBbCC*. An additional individual of the *aabbCC* genotype would be expected to occur in class 9. Of the total number of plants, 402, one-fourth are expected to be of the genotype aaBBCC. This amounts to 100.5 plants. These would have the percentage frequency distribution given opposite "%" under *aaBBCC* of Table 1. Expressed as numbers they may be subtracted leaving the estimated frequency distribution

for plants of the *aaBbCC* genotype and one plant in class 9 of the *aabbCC* genotype.

There are two tests of the validity of the genetic model postulated (see 6). First, of the 402 plants, if the genetic model is valid, 301.5 should fall into class III and 100.5 into class IV. Adjusting for the one plant of the *aabbCC* genotype expected to fall in period 9, the obtained numbers are 315 and 87, respectively. Goodness of fit chi-square gives a *P* value lying between 0.20 and 0.10. Second, the number of such F_3 families expected from a total of 380 is 11.88 and the number obtained is 10. The value 11.88 equals 0.03125×380. Goodness of fit chi-square gives a *P* value lying between 0.70 and 0.50. The genetic model postulated is in accord with the data. It should be pointed out that the bimodal nature of the frequency distribution of the plants of the *aaBbCC* genotype indicates that effective factors other than those designated are also influencing date of ripening.

TYPE II, CHARACTERS DIFFERENTIATED BY ONE MAJOR EFFECTIVE FACTOR PAIR

Number of fruits per 10 centimeters of branch is used to illustrate the application of the partitioning method of genetic analysis to those characters differentiated by one major effective factor pair. The experimental organism is tomato (*Lycopersicon esculentum* Mill.) and the study extended over a 3-year period, 1938, 1939, and 1940. The number of replications grown per year is 20 for each entry and the design of the experiment is a randomized complete block. In 1938 two entries of each segregating population were grown. The populations, number of plants, means, and within plot variances for number of fruits per 10 centimeters of branch are listed in Table 2.

The theoretical values for the means and the theoretical values for the within plot variances are calculated from the data for the non-segregating populations. The calculations are based on the genetic model, assuming that one major effective factor pair differentiates the parents in respect to number of fruits per 10 centimeters of branch.

For example, the theoretical mean for the B_1 to Danmark population is the mean of the F_1 plus the mean of Danmark divided by two. Likewise, estimates of the environmental variances are calculated from the obtained variances of the non-segregating populations. For example, the obtained variance of the F_1 plus the obtained variance of Danmark divided by two give an estimate of the environmental variance of the B_1 to Danmark population. Making the calculations from the appropriate values in Table 2 gives $(0.5452 + 2.1252) \div 2$ equals 1.3352 ± 0.1136. This subtracted from 2.3892 ± 0.2337 gives the obtained genetic variance of the B_1 to Danmark (entry 11) which is 1.0540 ± 0.2598 (see Table 7). These data are for 1938. The theoretical genetic variance for the B_1 to Danmark is estimated from the means of the F_1 and the Danmark parent. In order to obtain an estimate of the standard error of the theoretical genetic variance, the calculations are made for each replication. It will be recalled that

TABLE 2.—POPULATIONS, NUMBER OF PLANTS, MEANS, AND WITHIN PLOT VARIANCES FOR NUMBER OF FRUITS PER 10 CENTIMETERS OF BRANCH, DANMARK X JOHANNISFEUER, YEARS 1938, 1939, and 1940.

Year and population	Number of plants	Mean	Within plot variance[1]
	No.	No.	
1938			
Johannisfeuer	452	2.16±0.063	0.5706±0.0457
B_1 to Johannisfeuer, 6	464	2.22±0.051	0.4487±0.0390
B_1 to Johannisfeuer, 7	464	2.27±0.062	0.6200±0.0533
F_1	469	2.44±0.066	0.5452±0.0522
F_2, 1	463	2.59±0.088	1.3770±0.1488
F_2, 2	469	2.64±0.064	1.3300±0.1248
B_1 to Danmark, 11	464	3.27±0.081	2.3892±0.2337
B_1 to Danmark, 12	459	3.13±0.064	2.0215±0.1642
Danmark	456	4.17±0.122	2.1252±0.2211
1939			
Johannisfeuer	224	2.22±0.088	0.4135±0.0653
B_1 to Johannisfeuer	230	1.99±0.083	0.3582±0.0344
F_1	209	2.13±0.072	0.3211±0.0388
F_2	215	2.43±0.106	0.9572±0.1554
B_1 to Danmark	231	2.76±0.124	1.0141±0.1292
Danmark	228	3.44±0.132	1.5993±0.2240
1940			
Johannisfeuer	220	2.02±0.057	0.3265±0.0288
B_1 to Johannisfeuer	224	1.94±0.061	0.3394±0.0581
F_1	224	1.97±0.057	0.3175±0.0452
F_2	223	2.42±0.078	1.8083±0.4058
B_1 to Danmark	219	2.68±0.121	1.8159±0.2564
Danmark	219	3.80±0.118	1.7240±0.2454

[1]The degrees of freedom for these variances are 20 less than the number of plants listed in column 2.

there are 20 replications per entry for each year. By so calculating the theoretical genetic variance, the environmental variability due to differences between plot means is included in the estimate.

The magnitude of the environmental variance due to differences between plot means for 1938 can be determined. For the B_1 to Johannisfeuer it was found to be 0.0012, for the F_2 0.0012, and for the B_1 to Danmark 0.0098. These values are so small as to have little bearing on the interpretation of the data. In this report the environmental variability due to differences between means of plots that is included with the estimate of the theoretical genetic variance will not be considered further. However, it is well to keep in mind that the theoretical genetic variance so calculated is slightly over-estimated.

The obtained frequency distributions expressed as percentages for populations and years together with the number of plants are listed in Table 3.

A study of the data in Table 3 reveals that all populations show con-

TABLE 3.—FREQUENCY DISTRIBUTIONS EXPRESSED IN PERCENTAGE FOR NUMBERS OF FRUIT PER 10 CENTIMETERS OF BRANCH, DANMARK x JOHANNISFEUER, YEARS 1938, 1939, AND 1940.

Year and population	Number of plants	Upper limit of class, number																					
		0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0
	No.	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
1938																							
Johannisfeuer	452	1.6	5.5	15.7	23.0	25.4	18.6	5.8	2.9	0.7	0.2	0.4		0.2									
B_1 to Johannisfeuer, 6	464		2.8	15.1	23.7	30.2	15.5	9.9	1.5	1.3													
B_1 to Johannisfeuer, 7	464	0.4	2.4	17.7	23.5	21.1	18.1	10.1	4.1	2.0	0.2		0.4										
F_1	469	0.2	2.2	8.7	21.3	26.9	22.6	9.8	5.1	1.5	1.1	0.2	0.4										
F_2, 1	463	0.2	3.7	12.7	19.0	24.8	13.4	10.2	3.9	3.5	2.6	2.6	1.3	1.3	0.4	0.4							
F_2, 2	469	0.2	2.6	10.9	20.5	24.1	15.1	10.2	5.3	3.0	4.3	1.1	1.3	0.2	0.8		0.2	0.2					
B_1 to Danmark, 11	464	0.2	0.9	6.7	14.2	17.7	14.2	11.4	8.0	7.1	6.3	5.0	2.8	1.9	1.3	0.9	0.2	0.4	0.4	0.2		0.2	
B_1 to Danmark, 12	459		1.5	7.6	13.5	19.2	18.3	9.2	6.5	7.2	7.4	3.7	2.0	1.3	0.9	0.9	0.2	0.2	0.4				
Danmark	456		0.7	2.0	2.4	6.4	11.8	15.6	10.5	14.7	10.8	8.3	6.1	4.0	2.4	1.8	0.7	0.2	0.7	0.7	0.2		
1939																							
Johannisfeuer	224		3.1	14.3	25.9	28.6	18.3	5.8	2.2	0.9	0.5	0.4											
B_1 to Johannisfeuer	230	0.4	6.5	19.6	27.9	27.4	12.2	4.8	0.4	0.4	0.4												
F_1	209		1.9	12.5	39.2	22.0	16.3	6.2	0.5	1.4													
F_2	215	0.9	2.8	15.4	22.3	20.9	16.7	7.4	4.7	4.6	1.9	0.5	0.9	0.5	0.5								
B_1 to Danmark	231		1.7	9.1	18.6	22.5	13.9	11.7	8.7	5.6	4.3	3.0	0.5			0.4							
Danmark	228		0.9	2.6	9.2	14.0	18.0	14.5	12.3	9.6	7.9	4.8	1.8	0.9	2.2	0.9				0.4			
1940																							
Johannisfeuer	220		2.7	23.7	26.8	26.8	12.7	7.3															
B_1 to Johannisfeuer	224		6.7	20.6	33.0	24.1	10.7	2.7	1.8	0.4													
F_1	224		4.0	19.2	39.3	23.2	7.6	5.8	0.9														
F_2	223		5.4	19.8	25.1	14.8	13.0	6.3	7.6	1.8	2.3	0.9	0.4	0.4	1.8								0.4
B_1 to Danmark	219		6.8	12.8	20.5	15.1	16.0	8.7	6.4	3.2	1.4	2.3	3.6	0.9	1.8	0.5							
Danmark	219			0.9	5.5	13.2	11.0	16.0	18.7	10.1	8.2	5.5	4.1	2.7	1.4	0.9	0.9	0.9					

tinuous variation for number of fruits per 10 centimeters of branch. The ranges are greater for the F_2, B_1 to Danmark, and Danmark populations. Such might be expected for the F_2 and B_1 to Danmark populations if the genes conditioning fewer fruits per 10 centimeters of branch are dominant or nearly so. None of the frequency distributions tend to be bimodal. As in previous tables those populations occurring more than once are followed by an entry number.

The theoretical frequency distributions are calculated from the obtained frequency distributions of Johannisfeuer, F_1, and Danmark given in Table 3. The calculations are based on the genetic model which assumes that the parents are differentiated by one major effective factor pair. For example, considering the B_1 to Danmark 1938 (Table 3) the theoretical frequency distribution expressed as a percentage for the class having an upper limit of 2.5 is $(0.50 \times 26.9) + (0.50 \times 6.4)$. Completing the calculations gives a value of 16.65 per cent. Then the theoretical number of individuals expected in this class for the B_1 to Danmark population (Table 5, entry 11), is (16.65% of 464) equals 77.

This completes the illustration of how the theoretical means, the theoretical variances and theoretical frequency distributions are calculated for characters conditioned by one major effective factor pair. Evidence as to the validity of the genetic model being tested is derived from comparisons involving the obtained and theoretical means, the obtained and theoretical frequency distributions, and the obtained and theoretical genetic variances.

Comparison between obtained and theoretical means.

The number of plants, and the obtained and theoretical means for Danmark × Johannisfeuer populations are listed in Table 4.

With the possible exception of the comparisons between the obtained and theoretical means for the F_2 populations in 1938 the differences between the obtained and theoretical means are readily accounted for by chance fluctuations. For the 3 years the greatest difference is between the mean of entry 1 (2.59) and the theoretical mean (2.80) in 1938. The difference is 0.21 ± 0.098. Considering that there are 12 comparisons and postulating independence, as great a difference as shown might be expected to occur due to chance. The other comparison for the F_2 in 1938 involves a difference of 0.16 ± 0.077. Again, the difference is about two times its standard error. Also, in all of the comparisons, the theoretical means are larger than the obtained means. This would hardly be expected to occur by chance if the comparisons are all independent. However, they are not all independent because within any one year in the calculation of the theoretical, the F_1 is used in all three estimates, and moreover, each of the parents is used in two of the three estimates. The overall means obtained by averaging the means for the 3 years are 2.53 ± 0.025 for the obtained and 2.57 ± 0.018 for the theoretical. The difference is slight and readily accounted for by chance. The data are in agreement with the genetic model which assumes that the parents are differentiated by one major effective factor pair. Effects, if any, of minor modifying genes must be slight.

TABLE 4.—NUMBER OF PLANTS, AND OBTAINED AND THEORETICAL MEANS FOR NUMBER OF FRUITS PER 10 CENTIMETERS OF BRANCH, DANMARK x JOHANNISFEUER, YEARS 1938, 1939, AND 1940.

Population	1938			1939			1940		
	Number plants	Mean		Number plants	Mean		Number plants	Mean	
		Obtained	Theoretical[1]		Obtained	Theoretical[1]		Obtained	Theoretical[1]
Johannisfeuer	452	2.16±0.063		224	2.22±0.088		220	2.02±0.057	
B_1 to Johannis., 6	464	2.22±0.051	2.30±0.046	230	1.99±0.083	2.18±0.057	224	1.94±0.061	2.00±0.040
B_1 to Johannis., 7	464	2.27±0.062	2.30±0.046						
F_1	469	2.44±0.066		209	2.13±0.072		224	1.97±0.057	
F_2, 1	463	2.59±0.088	2.80±0.042	215	2.43±0.106	2.48±0.047	223	2.42±0.078	2.44±0.038
F_2[1] 2	469	2.64±0.064	2.80±0.042						
B_1 to Danmark, 11	464	3.27±0.081	3.30±0.069	231	2.76±0.124	2.78±0.075	219	2.68±0.121	2.88±0.066
B_1 to Danmark, 12	459	3.13±0.064	3.30±0.069						
Danmark	456	4.17±0.122		228	3.44±0.132		219	3.80±0.118	

[1]Calculated from the obtained means of Johannisfeuer, F_1, and Danmark on the basis that the parents are differentiated by one major effective factor pair.

TABLE 5.—OBTAINED FREQUENCY DISTRIBUTIONS AND THEORETICAL FREQUENCY DISTRIBUTIONS FOR NUMBER OF FRUITS PER 10 CENTIMETERS OF BRANCH, DANMARK x JOHANNISFEUER, YEARS 1938, 1939, AND 1940.

Year, population, and frequency distribution	Upper limit of class, number																				Chi square	Degrees of freedom	P lies between
	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0 and over			
	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.			
1938																							
B_1 to Johannisfeuer, 6																							
Obtained, 464*		13	70	110	140	72	46	7	6														
Theoretical	4	18	57	103	121	95	36	19	5	3	1	1	1								16.366	6	0.02 & 0.01
Common		17.5	63.5	106.5	130.5	83.5	41.0	21.5															
Difference		−4.5	6.5	3.5	9.5	−11.5	5.0	−8.5															
B_1 to Johannisfeuer, 7																							
Obtained, 464*	2	11	82	109	98	84	47	19	9	1		2											
Theoretical	4	18	57	103	121	95	36	19	5	3	1	1	1								11.573	7	0.20 & 0.10
Common		17.5	69.5	106.0	109.5	89.5	41.5	19.0	11.5														
Difference		−4.5	12.5	3.0	−11.5	−5.5	5.5	0.0	0.5														
F_2, 1																							
Obtained, 463*	1	17	59	88	115	62	47	18	16	12	12	6	6	2	2								
Theoretical	2	12	41	79	99	88	47	27	21	15	11	8	5	3	2	1		1	1		13.155	10	0.30 & 0.20
Common		16.0	50.0	83.5	107.0	75.0	47.0	22.5	18.5	13.5	18.5		11.5										
Difference		2.0	9.0	4.5	8.0	−13.0	0.0	−4.5	−2.5	−1.5	−0.5		−1.5										

*Figures marked with an asterisk are total number in each obtained distribution.

F_2, 2																								
Obtained, 469*	1	12	51	96	113	71	48	25	14	20	5	6	1	4		1	1					11.992	10	0.30 & 0.20
Theoretical	2	12	41	80	100	89	48	28	22	15	11	8	5	3	2	1		1	1					
Common		13.5	46.0	88.0	106.5	80.0	48.0	26.5	18.0	17.5	15.0		10.0											
Difference		−0.5	5.0	8.0	6.5	−9.0	0.0	−1.5	−4.0	2.5	−4.0		−3.0											
B_1 to Danmark, 11																								
Obtained, 464*	1	4	31	66	82	66	53	37	33	29	23	13	9	6	4	1	2	2	1	1		3.874	11	0.98 & 0.95
Theoretical		7	25	55	77	80	59	36	38	28	20	15	9	5	4	2		2	2					
Common			34.0	60.5	79.5	73.0	56.0	36.5	35.5	28.5	21.5	14.0	14.5		10.5									
Difference			2.0	5.5	2.5	−7.0	−3.0	0.5	−2.5	0.5	1.5	−1.0	0.5		0.5									
B_1 to Danmark, 12																								
Obtained, 459*		7	35	62	88	84	42	30	33	34	17	9	6	4	4	1	1	2				9.963	10	0.50 & 0.30
Theoretical		7	25	54	76	79	58	36	37	27	20	15	9	6	4	2		2	2					
Common			37.0	58.0	82.0	81.5	50.0	33.0	35.0	30.5	18.5	19.5		14.0										
Difference			5.0	4.0	6.0	2.5	−8.0	−3.0	−2.0	3.5	−1.5	−4.5		−2.0										
1939																								
B_1 to Johannisfeuer																								
Obtained, 230*	1	15	45	64	63	28	11	1	1	1												11.378	5	0.05 & 0.02
Theoretical		6	31	75	58	40	14	3	2	1														
Common		11.0	38.0	69.5	60.5	34.0	17.0																	
Difference		5.0	7.0	−5.5	2.5	−6.0	−3.0																	
F_2																								
Obtained, 215*	2	6	33	48	45	36	16	10	10	4	1	2	1	1								5.997	6	0.50 & 0.30
Theoretical		4	22	61	47	37	18	8	7	5	3	1		2										
Common			33.5	54.5	46.0	36.5	17.0	17.5		10.0														
Difference			7.5	−6.5	−1.0	−0.5	−1.0	2.5		−1.0														

TABLE 5 (*Continued*).

Year, population, and frequency distribution	Upper limit of class, number																			Chi square	Degrees of freedom	P lies between
	0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0 and over				
	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.			
B_1 to Danmark																								
Obtained, 231*		4	21	43	52	32	27	20	13	10	7	1			1									
Theoretical		3	17	56	42	40	24	15	13	9	5	2	1	3	1						5.587	8	0.70 & 0.50	
Common			22.5	49.5	47.0	36.0	25.5	17.5	13.0	9.5	10.5													
Difference			2.5	−6.5	5.0	−4.0	1.5	2.5	0.0	0.5	−1.5													
1940																								
B_1 to Johannisfeuer																								
Obtained, 224*		15	46	74	54	24	6	4	1															
Theoretical		7	48	74	56	23	15	1													3.935	5	0.70 & 0.50	
Common		11.0	47.0	74.0	55.0	23.5	13.5																	
Difference		4.0	−1.0	0.0	−1.0	0.5	−2.5																	
F_2																								
Obtained, 223*		12	44	56	33	29	14	17	4	5	2	1	1	4					1					
Theoretical		6	35	62	48	22	19	11	6	4	3	2	1	1	1	1			1		7.542	6	0.30 & 0.20	
Common			48.5	59.0	40.5	25.5	16.5	19.0		14.0														
Difference			7.5	−3.0	−7.5	3.5	−2.5	2.0		0.0														
B_1 to Danmark																								
Obtained, 219*		15	28	45	33	35	19	14	7	3	5	8	2	4	1									
Theoretical		4	22	49	40	20	24	21	11	9	6	5	3	2	1	1			1		14.258	7	0.05 & 0.02	
Common			34.5	47.0	36.5	27.5	21.5	26.5		11.5		14.0												
Difference			8.5	−2.0	−3.5	7.5	−2.5	−5.5		−3.5		1.0												

Comparison between obtained and theoretical frequency distributions.

The obtained, theoretical, common frequency distributions, and differences together with the chi-square values, the degrees of freedom, and the *P* values are listed in Table 5. The data in Table 5 are used in comparing the obtained and theoretical frequency distributions.

A study of the data in Table 5, year 1938, reveals that for the B_1 to Johannisfeuer population, entry 6, the differences between the obtained and theoretical frequency distributions are somewhat greater than might be expected if the data for this entry were considered by themselves. The chi-square value is 16.366, the degrees of freedom are 6, and *P* lies between 0.02 and 0.01. For the second sample of B_1 to Johannisfeuer, entry 7, the deviations between the obtained and theoretical frequency distributions are no greater than might be expected due to chance fluctuations. The chi-square value is 11.573, the degrees of freedom are 7, and *P* lies between 0.2 and 0.1. For the F_2 populations and B_1 to Danmark, entry 12, the fits are good between the obtained and theoretical frequency distributions. The chi-square values are 13.155, 11.992, and 9.963. The degrees of freedom are 10 and the corresponding *P* values lie between 0.30 and 0.20, 0.30 and 0.20, and 0.50 and 0.30, respectively. For the B_1 to Danmark, entry 11, the agreement between the obtained and theoretical frequency distributions is somewhat closer than might be expected due to chance. Chi-square is 3.874, degrees of freedom are 11, and *P* lies between 0.98 and 0.95.

A study of the data in Table 5 for 1939 reveals that the agreement between the obtained and theoretical frequency distributions is not so close as might be expected for the B_1 to Johannisfeuer. The chi-square value is 11.378, the degrees of freedom are 5, and *P* lies between 0.05 and 0.02. For the F_2 and B_1 to Danmark populations the agreements between the obtained and theoretical frequency distributions are good. The *P* values corresponding to the chi-square values lie between 0.50 and 0.30, and 0.70 and 0.50, respectively.

Turning to a consideration of the data for 1940 the deviations between the obtained and theoretical frequency distributions are readily accounted for by chance for populations B_1 to Johannisfeuer and F_2. The chi-square values are 3.935 and 7.542, the degrees of freedom are 5 and 6, and the values of *P* lie between 0.70 and 0.50, and 0.30 and 0.20, respectively. For B_1 to Danmark the differences between the obtained and theoretical frequency distributions are not so readily explained as due to chance fluctuations when the data for this population are considered by themselves.

As was true of the theoretical means the theoretical frequency distributions for the different segregating generations are not all independent within years. However, they are independent between years within populations and entries. Hence, the chi-square values and their corresponding degrees of freedom may be totaled for years. Table 6 lists the homogeneity chi-square values for testing the fit between obtained frequency distributions and the theoretical frequency distributions totaled for years. The totals are within populations of the Danmark × Johannisfeuer hybrids. With the possible exception of the value for

the B_1 to Johannisfeuer entry 6, the chi-square values are those expected from chance deviation of frequency distributions. The high chi-square for B_1 to Johannisfeuer entry 6 is largely due to the high chi-square value for this population in 1938. The duplicate samples of B_1 to Johannisfeuer grown in 1938 furnish evidence whether the deviations are logically attributable to chance.

TABLE 6.—HOMOGENEITY CHI SQUARE VALUES FOR TESTING THE FIT BETWEEN THE OBTAINED FREQUENCY DISTRIBUTIONS AND THE THEORETICAL FREQUENCY DISTRIBUTIONS, TOTAL OF YEARS WITHIN POPULATIONS AND ENTRIES, DANMARK X JOHANNISFEUER.

Population and entry number	Chi square	Degrees of freedom	P lies between
B_1 to Johannisfeuer, 6	31.679	16	0.02 and 0.01
B_1 to Johannisfeuer, 7	26.886	17	0.10 and 0.05
F_2, 1	26.694	22	0.30 and 0.20
F_2, 2	25.531	22	0.30 and 0.20
B_1 to Danmark, 11	23.719	26	0.70 and 0.50
B_1 to Danmark, 12	29.808	25	0.30 and 0.20

There were duplicate samples of each of the following populations grown in that year; B_1 to Johannisfeuer, F_2, and B_1 to Danmark. Homogeneity chi-square was calculated for frequency distributions of duplicate samples within populations. The chi-square values obtained were 16.661, 3.983, and 8.444, respectively. The corresponding degrees of freedom are 6, 9, and 10. *P* lies between 0.02 and 0.01, 0.95 and 0.90, and 0.70 and 0.50, respectively. The differences between the two frequency distributions of the B_1 to Johannisfeuer are somewhat greater than might be expected due to chance fluctuations. However, since the two samples are genetically identical, having come from the same seed packet, the differences noted must be due to chance provided randomization of entries is adequate.

In evaluating whether randomization is adequate it is necessary to consider the number of plants per plot and the number of replications. In the 1938 study if the stand had been perfect each plot would have been composed of 24 plants, and the number of replications was 20. Hence, the frequency distributions are made up of 20 groups of potentially 24 plants each. Therefore, by chance, some of the comparisons between the obtained and theoretical frequency distributions have higher chi-square values than would be expected if the same number of plants were involved and if the size of plot were a single plant. Likewise some comparisons between the obtained and theoretical frequency distributions give lower chi-square values than would be expected if the same number of plants were involved and if the plot size were a single plant. This is clearly brought out by the individual and total chi-square values for the comparisons between duplicate samples previously analyzed and discussed in this

TABLE 7.—THE OBTAINED AND THEORETICAL GENETIC VARIANCES FOR NUMBER OF FRUITS PER 10 CENTIMETERS OF BRANCH, DANMARK X JOHANNISFEUER, YEARS 1938, 1939, AND 1940.

Population	1938		1939		1940	
	Obtained	Theoretical[1]	Obtained	Theoretical[1]	Obtained	Theoretical[1]
B_1 to Johannisfeuer, 6	−0.1713±0.0485	0.0190±0.0177	−0.0091±0.0446	0.0015±0.0045	0.0174±0.0626	0.0007±0.0040
B_1 to Johannisfeuer, 7	0.0621±0.0606	0.0190±0.0177				
F_2, 1	0.4280±0.1602	0.6292±0.0740	0.2934±0.1665	0.3040±0.0513	1.1369±0.4108	0.6092±0.0815
F_2, 2	0.3810±0.1382	0.6292±0.0740				
B_1 to Danmark, 11	1.0540±0.2598	0.7409±0.1054	0.0539±0.1720	0.4206±0.0776	0.7951±0.2852	0.8276±0.1094
B_1 to Danmark, 12	0.6863±0.1997	0.7409±0.1054				

[1]The theoretical genetic variances are calculated from the means of Johannisfeuer, F_1, and Danmark on the basis of the genetic model which assumes that the parents are differentiated by one major effective factor pair.

section. It follows that chi-square is a useful tool for analyzing such data if these facts are kept in mind and if both the individual chi-square values and their totals are studied. The writer has not encountered these extremes in chi-square values where the number of replications is 30 or more. Eighty replications with 6 plants per plot has proven very satisfactory. The total number of plants per entry is 480. Studies have involved a number of plant species and a considerable number of different characters and have been conducted over a considerable period of years.

For those cases in which the number of replications is not sufficient to provide adequate randomization it may be desirable to use within plot frequency distributions; that is, frequency distributions adjusted on the basis of the deviation of any given replication from its population mean. Hence, the adjustment is within populations.

Comparisons between obtained and theoretical genetic variances.

The obtained and theoretical genetic variances together with their standard errors are listed in Table 7.

A study of the data in Table 7 reveals that with the possible exception of the comparison between the obtained and theoretical genetic variances for the B_1 to Johannisfeuer for 1938 the differences between the two are not greater than might be expected due to chance fluctuations. The obtained variance for the B_1 to Johannisfeuer 1938, as estimated, is negative and hence, must be a chance deviation from some positive value.

Means of the obtained genetic variances and means of the theoretical genetic variances for number of fruits per 10 centimeters of branch are listed in Table 8. These are the averages of the 3 years (1938 to 1940, inclusive) within populations and entries for the Danmark × Johannisfeuer segregating populations. The data for the two entries of each of the three populations are given. A study of the data reveals that for all populations and entries the differences between the obtained and theoretical variances are readily accounted for by chance fluctuations. The comparisons between the obtained and theoretical variances support the genetic model assuming that the parents are differentiated by one major effective factor pair as regards number of fruits per 10 centimeters of branch.

TABLE 8.—MEANS OF THE OBTAINED GENETIC VARIANCES AND MEANS OF THE THEORETICAL GENETIC VARIANCES FOR NUMBER OF FRUITS PER 10 CENTIMETERS OF BRANCH, MEANS OF VARIANCES OF YEARS WITHIN POPULATIONS AND ENTRIES, DANMARK X JOHANNISFEUER.

Variance and entry	B_1 to Johannisfeuer	F_2	B_1 to Danmark
Obtained, 1	−0.0543±0.0371	0.6194±0.1924	0.6343±0.1724
Theoretical	0.0071±0.0076	0.5141±0.0496	0.6630±0.0697
Obtained, 2	0.0235±0.0400	0.6038±0.1896	0.5118±0.1585

Linkage as determined by the Sp, sp marker genes.

The *SpSp* gene pair conditioning the non-self-pruning phenotype and the *spsp* gene pair conditioning the self-pruning phenotype were used as markers. Two different crosses were involved in this study, namely Danmark *(spsp)* × Johannisfeuer *(SpSp)* and Danmark *(spsp)* × Red Currant *(SpSp)*.

The phenotypic classification for number of plants having the non-self-pruning and number of plants having the self-pruning habit of growth are given in Table 9. It is evident from a study of the data of Table 9 that for the F_2 and B_1 to Danmark generations the number of plants in the two phenotypic classes are those expected on the basis that the parents of each cross are differentiated by one gene pair. The fact that the recessive phenotype in all cases is somewhat fewer than expected indicates that those plants of the *spsp* genotype have a lower survival value than plants of the *SpSp* genotype. This would in part explain the lower values of the obtained means of Table 4 compared with the theoretical means of the same table.

TABLE 9.—NUMBER OF PLANTS CLASSIFIED AS NON-SELF-PRUNING AND NUMBER OF PLANTS CLASSIFIED AS SELF-PRUNING FOR THE CROSSES DANMARK (*spsp*) X JOHANNISFEUER (*SpSp*) AND DANMARK (*spsp*) X RED CURRANT (*SpSp*), 1938.

Cross and population	Non-self-pruning	Self-pruning	Chi square	P lies between
Danmark × Johannisfeuer				
F_2	714	218	1.288	0.30 & 0.20
B_1 to Danmark	472	451	0.478	0.50 & 0.30
Danmark × Red Currant				
F_2	717	215	1.854	0.20 & 0.10
B_1 to Danmark	486	448	1.546	0.30 & 0.20

The number of plants, means and standard errors for number of fruits per 10 centimeters of branch for the Danmark × Red Currant cross grown in 1938 are given in Table 10. These data are comparable with the corresponding data given in Table 2 for the Danmark × Johannisfeuer cross as they were grown in the same randomized complete block experiment. There were 20 replications. The following comparisons are pertinent to the linkage studies reported in this section. In Table 2 the greatest difference in number of fruits per 10 centimeters of branch is between the Johannisfeuer and Danmark parents. Whereas, comparatively speaking, the difference between the Red Currant parent and the Danmark parent is slight and both parents are rather prolific as regards number of fruits per 10 centimeters of branch. Also, in this cross the F_1 shows heterosis for fewer fruits whereas in the Danmark × Johannisfeuer cross the F_1 shows a high degree of partial phenotypic dominance, approaching complete dominance rather closely.

TABLE 10.—NUMBER OF PLANTS, MEANS AND STANDARD ERRORS FOR NUMBER OF FRUITS PER 10 CENTIMETERS OF BRANCH, DANMARK (*spsp*) X RED CURRANT (*SpSp*), 1938.

Population and entry number	Number of plants	Mean
Red Currant, 10	420	4.43±0.168
B_1 to Red Currant, 8	463	4.30±0.166
B_1 to Red Currant, 9	469	4.17±0.148
F_1, 13	475	3.59±0.092
F_2, 3	465	4.20±0.179
F_2, 4	467	4.39±0.143
B_1 to Danmark, 14	466	4.01±0.165
B_1 to Danmark, 15	468	4.08±0.116
Danmark, 17	457	4.11±0.118

The obtained and estimated within plot variances for number of fruits per 10 centimeters of branch for the first and second entries of the F_2 and B_1 to Danmark populations are listed in Table 11. The obtained variances of this table were calculated within the non-self-pruning and within the self-pruning phenotypes and then combined by pooling the sums of squares and their corresponding degrees of freedom. Since the calculations were within replications and since there were 20 replications, the degrees of freedom for each of the 2 phenotypes are 20 less than for number of plants for each phenotype (see Table 2).

TABLE 11.—THE OBTAINED AND ESTIMATED WITHIN PLOT VARIANCES FOR NUMBER OF FRUITS PER 10 CENTIMETERS OF BRANCH, JOHANNISFEUER (*SpSp*), X DANMARK (*spsp*), 1938.

Population and variance	Entry	
	1st	2nd
F_2		
Obtained[1]	0.7732±0.0756	0.8913±0.0756
Estimated[2]	0.8061±0.0549	0.8472±0.0549
Difference	−0.0329±0.0934	0.0441±0.0934
B_1 to Danmark		
Obtained[1]	1.4918±0.1445	1.2288±0.1445
Estimated[2]	1.3656±0.0579	1.2504±0.0579
Difference	0.1262±0.1557	−0.0216±0.1557

[1]Calculated within non-self-pruning and within self-pruning types of segregates.
[2]Estimated from Johannisfeuer, F_1, and Danmark by regression of variances on the means. Hence these are estimated environmental variances.

The obtained variances listed in Table 11 were calculated by dividing the sums of squares by their corresponding degrees of freedom (see Table 10 for number of plants). The estimated environmental variances were calculated from the data of Johannisfeuer, F_1, and Danmark using regression of the variances on the means. For details of the methods employed see (12).

If only one effective factor pair differentiates the Johannisfeuer and Danmark parents and this effective factor pair is closely linked with the gene pair differentiating non-self-pruning and self-pruning habit of growth, then the obtained variances as calculated would be attributable to environmental differences. Hence, any differences between the obtained and estimated variances because of the linkage relations postulated for the genetic model would be attributable to chance fluctuations. The same would be true of the genetic model postulating pleiotropy rather than close linkage.

In none of the four comparisons involving the two entries and the two populations are the differences between obtained variances and estimated environmental variances greater than expected on the basis of chance fluctuations. In fact, in two of the four comparisons the obtained is larger than the estimated, and in two, smaller than the estimated. These findings confirm the previous conclusions showing that Johannisfeuer and Danmark are differentiated by one major effective pair regarding number of fruits per 10 centimeters of branch. It will be remembered that these conclusions were drawn from a study of the means, frequency distributions, and variances.

Since the F_1 of the Danmark $\times$ Red Currant cross showed heterosis and since the Danmark and Johannisfeuer parents were shown to be differentiated by one major effective factor pair and the F_1 did not show heterosis, the Danmark and Red Currant cross would be expected to differ by more than one gene pair. The Red Currant parent has non-self-pruning habit of growth whereas the Danmark parent has self-pruning habit of growth.

The obtained and estimated within plot variances and the differences (other genes) between the two are listed in Table 12. The obtained and estimated variances were calculated in the same manner as the corresponding values for the Danmark $\times$ Johannisfeuer cross. Hence, the estimated variances are due to environmental differences. Then the differences obtained by subtracting the estimated variances from their corresponding obtained variances are attributable to genes not closely linked with the *Spsp* gene pair or to non-pleiotropic gene effects.

Each of the four values listed opposite "other genes" in Table 12 are significantly different from zero, proving that genes other than those closely linked with the *Spsp* marker genes are segregating in these hybrid populations of the Danmark $\times$ Red Currant cross. The question whether there is a major effective factor pair linked with the *Spsp* marker gene pair segregating in the F_2 and backcross to Danmark populations can be answered by the data given in Table 13.

This table gives the total genetic variances and the genetic variances

TABLE 12.—THE OBTAINED AND ESTIMATED WITHIN PLOT VARIANCES FOR NUMBER OF FRUITS PER 10 CENTIMETERS OF BRANCH, DANMARK (*spsp*) X RED CURRANT (*SpSp*), 1938.

Population and variance	Entry	
	1st	2nd
F_2		
Obtained[1]	3.7704±0.6147	4.1839±0.6147
Estimated[2]	2.3835±0.2326	2.7943±0.2326
Other genes	1.3869±0.6572	1.3896±0.6572
B_1 to Danmark		
Obtained[1]	3.4358±0.3401	3.0152±0.3401
Estimated[2]	1.9727±0.1477	2.1240±0.1477
Other genes	1.4631±0.3708	0.8912±0.3708

[1]Calculated within non-self-pruning and within self-pruning types of segregates.
[2]Estimated from Johannisfeuer, F_1, and Danmark by regression of the variances on the means. Hence these are estimated environmental variances.

TABLE 13.—THE TOTAL GENETIC VARIANCES AND THE GENETIC VARIANCE ACCOUNTED FOR BY SEGREGATION OF OTHER GENES AND BY SEGREGATION OF THE GENES DIFFERENTIATING NON-SELF-PRUNING (*Sp*) AND SELF-PRUNING (*sp*) TYPES OF GROWTH.

Population and variance	Entry	
	1st	2nd
F_2		
Total	3.2836±0.6897	3.9552±0.6897
Other genes	1.3869±0.6572	1.3896±0.6572
Spsp genes	1.8957±0.9527	2.5656±0.9527
B_1 to Danmark		
Total	3.1554±0.4141	2.6821±0.4141
Other genes	1.4631±0.3708	0.8912±0.3708
Spsp genes	1.6923±0.5559	1.7909±0.5559

accounted for by segregation of genes other than those linked with the *Spsp* marker gene pair. By subtracting those attributable to other genes from the total genetic variances, the genetic variance due to a major effective factor pair or effective factor pairs linked with the *Spsp* marker genes is obtained. Again pleiotropy could be involved. The differences are given opposite the row heading *Spsp* genes. It is apparent that the greater proportion of the genetic variance

is attributable to an effective factor pair closely linked with the *Spsp* marker genes, to pleiotropy, or to a combination of the two.

It seems probable that the same major effective factor pair found to be segregating in the F_2 and B_1 to Danmark populations of the Danmark × Johannisfeuer cross is also segregating in the corresponding populations of the Danmark × Red Currant cross.

The data for both crosses are rather conclusive in confirming that one major effective factor pair differentiates Danmark and Johannisfeuer. This same gene pair seems to be segregating in the F_2 and B_1 to Danmark populations of the Danmark × Red Currant cross. The effectiveness of using marker genes to study linkage relations when employing the partitioning method of genetic analysis is demonstrated. The applications to studying gene interactions are apparent.

TYPE III, AN ITERATIVE PROCEDURE

For some characters for which, as in the previous two methods, no assumption is made regarding the type of frequency distribution (normal or otherwise) an iterative procedure may be used. Iterative procedure involves repeated adjustment of the postulated genetic model to some populations or parts of these populations until a satisfactory fit is obtained. The data for illustrating the procedure are taken from the parents and hybrid populations of crosses involving tomato (*Lycopersicon esculentum* Mill.) varieties Ponderosa and Porter. The character is number of locules per tomato fruit. The populations studied are Porter, B_1 to Porter, F_1, F_2, B_1 to Ponderosa, and Ponderosa. For further details concerning the experiment see (10).

In this illustration of the use of iterative procedure the frequency distributions of the B_1 to Porter and the B_1 to Ponderosa populations are used to estimate the theoretical frequency distributions. A comparison of the obtained frequency distribution of the F_2 and this theoretical frequency distribution so calculated is used to test the validity of the genetic model. The method of determining the theoretical means and theoretical genetic variances is similar to that given in the immediately following section (characters whose variability due to environment follow the normal probability integral) of this paper and need not be repeated here. Since the F_2 population, if of sufficient size, encompasses all genotypes, it may be more appropriate to use that population in the iterative process and then test the validity of the genetic model by comparing the obtained values of the two backcross populations with the theoretical values. The use of iterative procedure to estimate the theoretical frequency distributions follows. For details of how the tentative theoretical means and the tentative theoretical frequency distributions of Table 14 are calculated see (10).

A study of the obtained means and the end classes of the obtained frequency distributions indicates that three major effective factor pairs are differentiating the parents. For details of the method employed to set up a tentative genetic model see (8, 9, 10). The three major effective factor pairs

TABLE 14.—TENTATIVE THEORETICAL MEANS, GRAND-TOTAL VARIANCES AND STANDARD DEVIATIONS, AND TENTATIVE FREQUENCY DISTRIBUTIONS OF THE B_1 TO PORTER POPULATION FOR NUMBER OF LOCULES.

Population and genotype	Mean	Grand-total variance	Grand-total standard deviation	Frequency distribution by average number of locules per fruit							Proportion
				2	3	4	5	6	7	8	
	No.	No.	No.	%	%	%	%	%	%	%	%
B_1 to Porter:											
AABBcc	2.1	0.033775	0.184	98.5	1.5						12.5
AABbcc	2.7	0.274181	0.524	35.2	58.5	6.3					12.5
AaBBcc	2.7	0.274181	0.524	35.2	58.5	6.3					12.5
AaBbcc	3.2	0.474519	0.689	15.4	51.6	30.1	2.9				12.5
AABBCc	3.4	0.554655	0.745	11.3	43.9	37.9	6.7	0.2			12.5
AABbCc	3.9	0.754993	0.869	5.4	26.9	43.2	21.2	3.2	0.1		12.5
AaBBCc	3.9	0.754993	0.869	5.4	26.9	43.2	21.2	3.2	0.1		12.5
AaBbCc	4.5	0.995400	0.998	2.3	13.6	34.1	34.1	13.6	2.2	0.1	12.5
Total	3.3			26.1	35.2	25.1	10.8	2.5	0.3		100.0
Balance[1]				18.0	44.4	27.8	8.7	1.1			100.0

[1]Total less plants of the F_1 and parental genotypes. The theoretical proportion of each genotype in balance of population is 16.6667 percent.

are designated as *AaBbCc*. The iterative procedure will be illustrated by using the data for B_1 to Porter. Frequency distributions for Porter, F_1, and Ponderosa are accepted as the best estimates of those for the genotypes *AABBcc*, *AaBbCc*, and *aabbCC*, respectively. Hence the frequency distribution given (Table 14) for the balance of the backcross population does not include plants of these three genotypes. The frequency distribution of the balance of the B_1 to Porter (Table 14) was obtained by multiplying each class percentage of each genotype from *AABbcc* to *AaBBCc*, inclusive, by 0.166667 and summing the results. The value 0.166667 is 1/6, expressed as a decimal fraction, and its use follows from the fact that the six genotypes in the balance of the B_1 to Porter occur with equal frequency. In order to estimate the theoretical frequency distributions, it was necessary to obtain frequency distributions for the balance of the B_1 to Porter. These were calculated by deducting the frequency distributions of Porter and F_1 genotypes from the obtained distributions of the B_1 to Porter population. The method of procedure and results are given in Table 15.

The theoretical proportions of the *AABBcc* (P_1) and *AaBbCc* (F_1) genotypes of the B_1 to Porter population were taken for each class of the frequency distributions (last two lines of Table 15). The sums of the values thus obtained were entered as the second line of Table 15, opposite the entry "*AABBcc* + *AaBbCc*". These values were subtracted from the values of line 1, and the remainders (with the minus value for the "8 locules" class eliminated by combination with a plus value), on the basis of 100 per cent, were entered as line 4.

To determine the proportions that the obtained frequency-distribution values are of the theoretical ones, each value in line 4 of Table 15 was divided

TABLE 15.—DEDUCTION OF THE FREQUENCY DISTRIBUTIONS OF THE P_1 AND F_1 GENOTYPES FROM THE B_1 TO PORTER FREQUENCY DISTRIBUTION FOR NUMBER OF LOCULES.

Genotype or genotypes of B_1 to Porter population	Frequency distribution by average number of locules per fruit								Theoretical proportion[1]
	2	3	4	5	6	7	8	9	
	%	%	%	%	%	%	%	%	%
All genotypes	36.6	32.2	18.1	10.0	2.2	0.5	0.0	0.4	100.0
AABBcc + AaBbCc	12.2	2.4	4.4	4.5	1.1	0.3	0.1	0.0	25.0
Balance[2]									
As a part of B_1 to Porter	24.4	29.8	13.7	5.5	1.1	0.2	0.0	0.3	75.0
As a unit	32.5	39.7	18.3	7.3	1.5	0.3	0.0	0.4	100.0
AABBcc (P_1)	96.5	3.5	0.0	0.0	0.0	0.0	0.0	0.0	12.5
AaBbCc (F_1)	0.9	15.9	35.6	36.0	8.6	2.6	0.4	0.0	12.5

[1]Base is B_1 to Porter except in line 4, in which it is balance of B_1 to Porter.
[2]Line 3 was obtained by subtracting line 2 from line 1 and adjusting the resulting values in the "8 locules" and "9 locules" columns to eliminate a minus quality. Line 4 is values of line 3 expressed on basis of 100 per cent.

by the corresponding value of the theoretical frequency distribution of the balance of B_1 to Porter (Table 14). For example, 32.5 ÷ 18.0 = 1.805556, the value for class 2. Then the corresponding figures of the theoretical frequency distributions of the genotypes from *AABbcc* to *AaBBCc* of the B_1 to Porter (Table 14) were multiplied by the appropriate class proportions to obtain the frequency distributions listed in Table 16 opposite the portion of the stub headed "First operation." For example, (35.2) (1.805556) = 63.6.

The second operation involved placing the figures for each frequency distribution given under the first operation on the basis of 100 per cent. This was done by dividing each figure by the appropriate total percentage given in the last column of Table 16 and multiplying by 100. For example, (63.6 ÷ 120.0)100 = 53.0, the figure listed under the second operation for genotype *AABbcc* and class 2. The new theoretical frequency distribution for the balance of the B_1 to Porter population, given in the next-to-last line of Table 16, was obtained by multiplying the class values by 0.166667 and summing for each class. The ratio of the percentage value for each of the classes 2 to 6 of the obtained frequency distribution (line 4, Table 15) to that (balance of population) in this new theoretical frequency distribution was calculated and appears in the last line of Table 16. For example, 32.5 ÷ 30.0 = 1.083333, the first figure in the last line of Table 16.

The two operations given in Table 16 were repeated twice. Usually, two repetitions are sufficient to give a very good fit between the obtained and the theoretical frequency distributions. The theoretical frequency distributions for the genotypes of the balance of the B_1 to Porter are given in Table 17 together with those for the balance of the B_1 to Ponderosa and the parental and F_1 genotypes. That a good fit was obtained by two repetitions can be seen by

TABLE 16.—CALCULATION OF THEORETICAL FREQUENCY DISTRIBUTIONS OF THE GENOTYPES OF THE BALANCE OF THE B_1 TO PORTER FOR NUMBER OF LOCULES.

Item	Frequency distribution by average number of locules per fruit					Total
	2	3	4	5	6	
	%	%	%	%	%	%
First operation:						
AABbcc	63.6	52.3	4.1	0.0	0.0	120.0
AaBBcc	63.6	52.3	4.1	0.0	0.0	120.0
AaBbcc	27.8	46.1	19.8	2.4	0.0	96.1
AABBCc	20.4	39.3	24.9	5.6	0.4	90.6
AABbCc	9.8	24.1	28.4	17.8	6.6	86.7
AaBBCc	9.8	24.1	28.4	17.8	6.6	86.7
Second operation						
AABbcc	53.0	43.6	3.4	0.0	0.0	100.0
AaBBcc	53.0	43.6	3.4	0.0	0.0	100.0
AaBbcc	28.9	48.0	20.6	2.5	0.0	100.0
AABBCc	22.5	43.4	27.5	6.2	0.4	100.0
AABbCc	11.3	27.8	32.8	20.5	7.6	100.0
AaBBCc	11.3	27.8	32.8	20.5	7.6	100.0
Balance of population	30.0	39.0	20.1	8.3	2.6	100.0
Ratio of obtained to theoretical[1]	1.083333	1.017949	0.910448	0.879518	0.846154	———

[1]Ratio of value given in line 4 of table 8 to value given for same class of frequency distribution of balance of B_1 to Porter in table 9.

comparing the obtained and theoretical frequency distributions of these two backcross populations (Table 18). Any degree of accuracy desired can be had by varying the number of repetitions when partitioning the backcrosses into their component genotypes by using iterative procedure.

The means of the genotypes of Table 17 other than *AAbbCc* and the parental and F_1 genotypes were estimated from the frequency distributions by the standard methods. According to the genetic model postulated, the 27 genotypes of the F_2 population have only 12 different means and in this respect are represented by the 12 genotypes given in Table 17. The eight genotypes of the B_1 to Porter have six different means, and the same is true of the eight genotypes of the B_1 to Ponderosa. The two backcross populations have only one mean in common, that of the F_1 genotype. For further details as to determining what genotypes, according to the genetic model postulated, have the same means see (10).

The only genotypes whose theoretical frequency distributions were not determined by partitioning the frequency distributions of the B_1 into those of the component genotypes are *AAbbCc* and *AABBCc*. For the method of estimating these frequency distributions see (10).

TABLE 17.—ESTIMATED THEORETICAL MEANS AND FREQUENCY DISTRIBUTIONS OF THE GENOTYPES OF THE BALANCE OF B_1 TO PORTER, THE F_2, AND THE BALANCE OF B_1 TO PONDEROSA FOR NUMBER OF LOCULES AND PROPORTIONS OF B_1 AND F_2 POPULATIONS THAT ARE OF INDIVIDUAL GENOTYPES.

Genotype or population	Mean	Frequency distribution by average number of locules per fruit														Proportion of	
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	B_1	F_2
	No.	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	%
AABBcc[1]	2.10	96.5	3.5													12.5	1.5625
AABbcc[1]	2.48	55.2	51.9	2.9												25.0	6.2500
AaBbcc[1]	2.91	31.5	48.4	18.0	2.1											12.5	6.2500
AABBCc[1]	3.11	25.1	44.8	24.5	5.3	0.3										12.5	3.1250
AABbCc[1]	3.74	13.4	30.5	31.1	18.5	6.5										25.0	17.1875
AaBbCc[1,2]	4.50	0.9	15.9	35.6	36.0	8.6	2.6	0.4								12.5	25.0000
AAbbCc[2]	5.46	1.7	6.2	16.6	26.7	26.1	15.5	5.7	1.3	0.2						—	6.2500
AaBbCC[2]	5.69	0.2	0.3	5.9	43.6	30.1	14.6	4.2	0.9	0.2						12.5	6.2500
AabbCc[2]	6.67	0.1	0.1	2.7	24.3	24.6	21.4	13.1	6.9	4.9	1.7	0.2				25.0	17.1875
AabbCC[2]	7.56	0.1	0.1	1.6	14.8	17.8	18.5	15.6	11.2	12.3	6.8	0.8	0.3	0.1		25.0	6.2500
aabbCc[2]	8.55	0.0	0.0	0.8	8.5	11.1	13.8	13.9	12.8	19.0	15.1	2.6	1.4	0.7	0.3	12.5	3.1250
aabbCC[2]	10.00	0.0	0.0	1.1	2.8	7.8	5.0	10.5	10.0	20.5	12.2	15.6	6.7	2.2	5.6	12.5	1.5625
B_1 to Porter	3.13	36.4	32.2	18.3	10.0	2.7	0.3	0.1								—	———
F_2	4.97	10.4	16.7	18.3	22.3	12.6	7.9	4.5	2.6	2.5	1.4	0.4	0.2	0.1	0.1	—	———
B_1 to Ponderosa	7.15	0.2	2.1	6.5	21.1	17.8	14.5	10.8	7.5	9.3	5.5	2.5	1.1	0.4	0.7	—	———

[1]Present in B_1 to Porter population.
[2]Present in B_1 to Ponderosa population.
[3]The theoretical frequency distribution for this genotype was calculated by use of the normal probability integral. The standard deviation for this genotype is 1.393.

A study of the obtained and theoretical frequency distributions and the *P* value for the F_2 population (Table 18) reveals that the obtained frequency distributions are in close agreement with the theoretical frequency distribution based on the genetic model assuming that Porter and Ponderosa are differentiated by three major effective factor pairs. Two of these effective factor pairs are partially dominant for fewer locules and one is partially dominant for more locules per fruit. The comparison between (see 10) the obtained and theoretical means of the F_2 also supports these conclusions.

TYPE IV, CHARACTERS WHOSE VARIABILITY DUE TO ENVIRONMENT FOLLOW THE NORMAL PROBABILITY INTEGRAL

Theoretical frequency distributions may be calculated from the means and standard errors of the genotypes in accordance with the genetic model postulated. The genetic model postulated assumes that Danmark *(AAbb)* and Johannisfeuer *(aaBB)* are differentiated by two major effective factor pairs. For the methods of setting up a plausible genetic model see (8, 9). Also for the methods of determining the means of the genotypes and their corresponding variances see (8). In order to conserve space these methods are not given here.

The means, standard errors of a single determination, and theoretical percentage frequency distributions for genotypes of F_2 and backcross populations of the Danmark × Johannisfeuer cross grown in 1939 are given in Table 19. The character is number of locules per fruit transformed to logarithms. The organism is tomato (*Lycopersicon esculentum* Mill.).

The method of calculating the theoretical means of the segregating populations from the theoretical means of the genotypes is illustrated for the F_2. The means listed in the second column of Table 19 together with the percentages listed in the last column of Table 19 are used in the calculations. In making the calculations the percentages listed in the last column of Table 19 are expressed as decimal fractions. For example, the calculation $(0.0625 \times 0.598320) + (0.1250 \times 0.652458) + (0.1250 \times 0.657900) + (0.0625 \times 0.786440) + (0.2500 \times 0.776403) + (0.1250 \times 0.831417) + (0.0625 \times 0.952126) + (0.1250 \times 0.997198) + (0.0625 \times 1.035071) = 0.797220$ and is the theoretical mean of the F_2. The theoretical means for the B_1 to Danmark and B_1 to Johannisfeuer populations are calculated in an identical manner. The obtained and theoretical means for the segregating populations are listed in Table 20.

An examination of the means in Table 20 reveals that the obtained and theoretical means are in close agreement for both years. Furthermore there are no consistent trends. That is, the obtained means are neither consistently lower nor consistently higher than the theoretical means. Hence, as would be expected, the *F* value derived from an analysis of variance within years is not larger than would be expected due to chance. The resulting *F* was less than one. The data for the obtained and theoretical means support the genetic model

TABLE 18.—THEORETICAL AND OBTAINED FREQUENCY DISTRIBUTIONS, CHI-SQUARE VALUES FOR TESTING GOODNESS OF FIT, DEGREES OF FREEDOM, AND VALUES OF *P* FOR NUMBER OF LOCULES.

Population	Frequency distribution by average number of locules per fruit										Chi-square	Degrees of freedom	P lies between
	2	3	4	5	6	7	8	9	10	11			
	%	%	%	%	%	%	%	%	%	%			
Balance of B_1 to Porter[1]													
Obtained	32.5	39.7	18.3	7.3	2.2								
Theoretical	32.3	39.7	18.4	7.4	2.2						—	—	———
F_2													
Obtained	12.4	20.5	19.6	20.8	8.8	8.4	4.0	2.9	2.6				
Theoretical	10.4	16.7	18.3	22.3	12.6	7.9	4.5	2.6	4.7		8.888	8	0.50 and 0.30
Balance of B_1 to Ponderosa[2]													
Obtained	0.0	0.0	2.8	21.9	21.1	18.0	12.5	8.3	8.8	6.6			
Theoretical	0.0	0.0	2.8	21.7	21.0	18.0	12.6	8.3	8.9	6.7	—	—	———

[1]Total population less plants of the P_1 and F_1 genotypes.
[2]Total population less plants of the P_2 and F_1 genotypes.
[3]Homogeneity chi-square was calculated from the numbers; 448 for B_1 to Porter, 455 for F_2, and 450 for B_1 to ponderosa.

TABLE 19.—MEANS, STANDARD ERRORS OF A SINGLE DETERMINATION, AND THEORETICAL PERCENTAGE FREQUENCY DISTRIBUTIONS FOR NUMBER OF LOCULES PER FRUIT (TRANSFORMED TO LOGARITHMS) FOR GENOTYPES OF F_2 AND BACKCROSS POPULATIONS, DANMARK X JOHANNISFEUER CROSS GROWN IN 1939.

Genotype and population	Mean	Standard error	Upper limit of class in logarithms														Percentage of F_2 population
			0.397940	0.544068	0.653212	0.740363	0.812913	0.875061	0.929419	0.977724	1.021189	1.060698	1.096910	1.130334	1.161368	1.190332	1.217484	
			%	%	%	%	%	%	%	%	%	%	%	%	%	%	%	
AABB	0.598320	0.066978	0.1	20.8	58.5	18.9	1.0	0.1										6.25
AaBB[1]	0.652458	0.075386		7.5	42.9	37.5	10.4	1,5	0.2									12.50
AABb[2]	0.657900	0.066978		4.5	42.7	41.9	9.9	0.9	0.1									12.50
AAbb[2]	0.786440	0.066978			2.3	22.2	41.0	25.2	7.6	1.5	0.2							6.25
AaBb[3]	0.776403	0.075386		0.1	5.1	26.4	36.8	22.1	7.4	1.7	0.3	0.1						25.00
Aabb[2]	0.831417	0.075386			0.9	10.4	28.8	31.8	18.4	7.1	2.0	0.5	0.1					12.50
aaBB[1]	0.952126	0.054525					0.5	7.4	25.8	34.4	21.7	7.9	1.9	0.3	0.1			6.25
aaBb[1]	0.997198	0.054525						1.3	9.4	25.2	31.1	20.7	8.9	2.7	0.6	0.1		12.50
aabb	1.035071	0.054525						0.2	2.4	12.1	25.4	28.0	19.0	8.9	3.0	0.8	0.2	6.25
B_1 to Danmark	0.763040	———		1.1	12.8	25.2	29.1	20.0	8.4	2.6	0.6	0.2						
F_2	0.797220	———		2.8	15.9	20.4	18.0	12.0	7.6	7.5	7.2	4.9	2.4	0.9	0.3	0.1		
B_1 to Johannisfeuer	0.844546	———		1.9	12.0	16.0	11.9	8.1	10.7	15.3	13.3	7.2	2.7	0.7	0.2			

[1]Genotypes occurring in the backcross to Johannisfeuer population.
[2]Genotypes occurring in the backcross to Danmark population.
[3]Genotypes occurring in both backcross populations.

TABLE 20.—OBTAINED AND THEORETICAL MEANS FOR NUMBER OF LOCULES PER FRUIT (TRANSFORMED TO LOGARITHMS) FOR SEGREGATING POPULATIONS.

Year and population	Obtained	Theoretical
1939		
B_1 to Danmark	0.759480	0.763040
F_2	0.811669	0.797220
B_1 to Johannisfeuer	0.840356	0.844546
1940		
B_1 to Danmark	0.748490	0.751010
F_2	0.811895	0.784651
B_1 to Johannisfeuer	0.828537	0.831231

postulating that the parents are differentiated by two major effective factor pairs and that there are interactions between the major factor pairs.

The method of calculating the theoretical frequency distribution is illustrated using the *AaBB* genotype of Table 19. The mean is 0.652458 and the standard error is 0.075386. The method is illustrated for the classes having upper limits of 0.544068 and 0.653212. First consider the class having an upper limit of 0.544068. The difference between it and the mean is 0.544068—0.652458 = —0.108390 and this divided by the standard error (0.075386) gives a value of —1.44. The value 1.44 is x of Pearson's (5) tables of the normal probability integral. From his tables the value of $1/2(1 + a)$ is 0.925. This is subtracted from 1 and multiplied by 100 to give 7.5 the figure listed under the class heading 0.544068 and opposite the row heading *AaBB*. Turning to the calculations for the class having an upper limit of 0.653212 the difference between it and 0.652458 is 0.000754. Hence, 0.000754 ÷ 0.075386 = 0.01. From Pearson's probability tables an x of 0.01 gives 0.504 for $1/2(1 + a)$. This multiplied by 100 gives 50.4 which includes the 7.5 per cent in class 0.544068. The value 50.4 per cent minus 7.5 per cent gives 42.9 per cent the value listed under class 0.653212 and opposite row heading *AaBB*. The values for the other classes and row headings are obtained in an identical manner.

These values listed under the classes and opposite the genotypes in Table 19 are used to calculate the theoretical frequency distributions for the B_1 to Danmark, F_2, and B_1 to Johannisfeuer populations. The procedures will be illustrated for the F_2 population and class 0.740363 of Table 19. The percentage values expressed as decimal fractions are multiplied by their corresponding values listed under class 0.740363. The calculations are as follows: (18.9 × 0.0625) + (37.5 × 0.1250) + (41.9 × 0.1250) + (22.2 × 0.0625) + (26.4 × 0.2500) + (10.4 × 0.1250) = 20.4 per cent. This is the value listed under 0.740363 and opposite row heading F_2 of Table 19. All the other values for the F_2 and all the values for the B_1 to Danmark and B_1 to Johannisfeuer were obtained by identical procedure. These values multiplied by the total number of plants in the population give the theoretical frequency distribu-

TABLE 21.—OBTAINED AND THEORETICAL FREQUENCY DISTRIBUTIONS (NUMERICAL BASIS) FOR NUMBER OF LOCULES PER FRUIT (TRANSFORMED TO LOGARITHMS), AND DEGREES OF FREEDOM, CHI-SQUARES, AND *P* VALUES FOR TESTING THE FIT BETWEEN OBTAINED AND THEORETICAL DATA FROM DANMARK X JOHANNISFEUER CROSS.

Year and population	Upper limit of class in logarithms												Degrees of freedom	Chi square[1]	P lies between
	0.544068	0.653212	0.740363	0.812913	0.875061	0.929419	0.977724	1.021189	1.060698	1.096910	1.130334	1.161368			
	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.		
1939:															
B_1 to P_1[2]	2	30	69	60	44	18	5	2	1				2	1.416	0.50 and 0.30
Theoretical	3	30	58	67	46	19	6	2							
F_2	4	27	36	53	26	18	16	13	14	5	3		5	4.550	0.50 and 0.30
Theoretical	6	34	44	39	26	16	16	15	11	5	2	1			
B_1 to P_2[2]		32	45	29	12	19	35	33	19	3	3		5	3.332	0.70 and 0.50
Theoretical	4	28	37	27	19	25	35	31	16	6	2				
1940:															
B_1 to P_1[2]	13	53	45	42	18	22	10	3	4	5	3	1	7	7.990	0.50 and 0.30
Theoretical	15	38	50	44	32	19	10	5	3	1	1	1			
F_2	17	27	39	28	34	16	17	9	11	14	5	6	9	10.216	0.50 and 0.30
Theoretical	19	36	38	31	25	21	18	14	10	6	3	2			
B_1 to P_2[2]	19	21	29	34	26	20	19	20	19	7	4	6	9	7.340	0.70 and 0.50
Theoretical	15	26	27	24	25	29	28	22	14	7	4	3			

[1]Totals for the segregating populations for 1939: degrees of freedom, 12; chi square, 9.298; and P lies between 0.70 and 0.50. For 1940: degrees of freedom, 25; chi square, 25.546; and P lies between 0.50 and 0.30. And for the 2 years, the $\sqrt{2\chi^2} - \sqrt{2n-1}$ is −0.196 and P is 0.84.

[2]P_1 is Danmark and P_2 is Johannisfeuer.

tions listed in Table 21. For example, 231 × 25.2, the value for B_1 to Danmark for class 0.740363 (Table 19), gives 58 the value listed under class 0.740363 and opposite B_1 to P_1 theoretical of Table 21.

Homogeneity chi-squares are calculated to test whether the differences between the obtained frequency distributions and theoretical frequency distributions are greater than would be expected by chance fluctuation. The degrees of freedom, chi-squares, and *P* values are listed in the last three columns of Table 21. The *P* values are those expected on the basis that the differences between the obtained and theoretical values are due to chance fluctuations.

The obtained and theoretical genetic variances, together with their standard errors, are listed in Table 22. The obtained genetic variances were estimated by subtracting the environmental variance from the total obtained variance. For more details of the methods employed in estimating the obtained genetic variances see (8). The theoretical genetic variances were calculated from the theoretical means listed in Table 19. For the F_2 the calculation

$$[(0.598320)^2 0.0625] + [(0.652458)^2 0.1250] + [(0.657900)^2 0.1250] + [(0.786440)^2 0.0625] + [(0.776403)^2 0.2500] + [(0.831417)^2 0.1250] + [(0.952126)^2 0.0625] + [(0.997198)^2 0.1250] + [(1.035071)^2 0.0625] - 0.635560$$

$= 0.017814$. The correction factor (0.635560) is calculated as follows:

$$[(0.598320 \times 0.0625) + (0.652458 \times 0.1250) + (0.657900 \times 0.1250) + (0.786440 \times 0.0625) + (0.776403 \times 0.2500) + (0.831417 \times 0.1250) + (0.952126 \times 0.0625) + (0.997198 \times 0.1250) + (1.035071 \times 0.0625)]^2$$

For the method of estimating the standard errors of the theoretical genetic variances see (8). These standard errors are approximations.

TABLE 22.—OBTAINED GENETIC VARIANCES AND THEIR STANDARD ERRORS AND THEORETICAL GENETIC VARIANCES AND THEIR STANDARD ERRORS FOR NUMBER OF LOCULES PER FRUIT (TRANSFORMED TO LOGARITHMS) FOR SEGREGATING POPULATIONS OF DANMARK X JOHANNISFEUER.

Population	Genetic variance		
	1939 obtained	Theoretical	1940 obtained
B_1 to Danmark	0.004313±0.000807	0.004115±0.000506	0.007865±0.002177
F_2	0.015554±0.002302	0.017814±0.000464	0.020778±0.002870
B_2 to Johannisfeuer	0.018517±0.001376	0.019105±0.000490	0.022003±0.003071

From an examination of the data given in Table 22 it can be determined that in no case are the theoretical genetic variances significantly different from those obtained for either 1939 or 1940, if odds of 19:1 are accepted as a criterion of significance. The obtained variances for 2 years can be averaged and an analysis of variance calculated involving the three obtained genetic variances and the three theoretical genetic variances. The value of *F* for testing

the significance of the difference between the grand obtained mean variance and the grand theoretical mean variance is 6.12 and that for the 5 per cent point is 18.51. Both tests give the same results as would be expected if the approximations of the standard errors for the theoretical genetic variances given in Table 22 are reasonably close to the legitimate standard errors. The comparisons between the obtained genetic variances and the theoretical genetic variances support the genetic model postulating that two major effective factor pairs differentiate the parents and that there are interactions between the major effective factor pairs.

PARTITIONING POPULATION FREQUENCY DISTRIBUTIONS TO DETERMINE THE IDENTIFIABLE NUMBERS AND PROPORTIONS OF GENETIC DEVIATES

In breeding any crop plant it is desirable to have an estimate of the identifiable numbers and identifiable proportions of genetic deviates in certain classes of the frequency distribution. This is accomplished by partitioning the obtained frequency distribution into three sets. These sets are lower classes for which the proportions of genetic deviates are estimated, a middle class for which the proportions of genetic deviates are not estimated, and higher classes for which the proportions of genetic deviates are estimated. In this paper, the term genetic deviates is used to designate those individuals among the identifiable numbers and identifiable proportions and hence, does not include all of the genetic deviates in the frequency distribution. Further, such individuals, due to environmental variability, are fluctuating about a mean different from that of the mean of the population in which they occur.

The means, obtained and calculated frequency distributions, and identifiable numbers and proportions of genetic deviates for percentage sucrose and weight per root of sugar beets are listed in Tables 23 and 24, respectively. The methods of procedure are outlined in detail in (11, 12). Before discussing the data in Tables 23 and 24 it should be pointed out that the calculated frequency distribution is attributable to environmental variability. It is calculated from the mean, environmental standard error, and tables of the normal probability integral. As is shown by the solid vertical lines the classes of the frequency distributions are divided into three sets as follows. For Table 23 the differences are positive up to and including class 15.75, negative in classes 16.50 to 18.75, inclusive, and positive in classes 19.50 and higher. For Table 24 the frequency distribution is again composed of three sets, the lower and higher classes having positive values. In this and other earlier publications the first set of classes is designated as lower classes of the frequency distribution, the second set as middle classes of the frequency distribution and the last set as higher classes of the frequency distribution. The identifiable numbers and proportions of genetic deviates are shown in the last two columns of Tables 23 and 24. The characters studied are percentage sucrose and weight per root in sugar beets (*Beta vulgaris* L.).

The bivariate frequency distribution for percentage sucrose and weight

TABLE 23.—MEAN, OBTAINED AND CALCULATED FREQUENCY DISTRIBUTIONS, AND IDENTIFIABLE NUMBERS AND PROPORTIONS OF GENETIC DEVIATES FOR PERCENTAGE SUCROSE, A54–1, NON-FERTILIZED, POPULATION GENETIC STUDIES, 1956.

Distribution, difference and proportion	Mean	Upper limit of class, per cent															Identifiable numbers and proportions of genetic deviates	
		0 to 11.25	12.00	12.75	13.50	14.25	15.00	15.75	16.50	17.25	18.00	18.75	19.50	20.25	21.00	21.75 and over	Lower classes	Higher classes
	%	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.
Obtained	17.9	3	1	0	1	4	12	11	25	36	62	66	58	26	11	4	32	99
Calculated		0	0	0	0	0	3	10	28	56	74	71	47	22	7	2	13	78
Difference		3	1	0	1	4	9	1	− 3	−20	−12	− 5	11	4	4	2	19	21
Proportion		1.00	1.00	0.00	1.00	1.00	0.75	0.09					0.19	0.15	0.36	0.50	0.59	0.21

TABLE 24.—MEAN, OBTAINED AND CALCULATED FREQUENCY DISTRIBUTIONS, AND IDENTIFIABLE NUMBERS AND PROPORTIONS OF GENETIC DEVIATES FOR WEIGHT PER ROOT, A54–1, NON-FERTILIZED, POPULATION GENETIC STUDIES, 1956.

Distribution difference and proportion	Mean	Upper limit of class, pounds										Identifiable numbers and proportions of genetic deviates	
		0 to 0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5 and over	Lower classes / Higher classes
	Lbs.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No. / No.
Obtained	1.93	8	35	56	80	72	38	19	9	2	0	1	43 / 31
Calculated		3	17	57	99	90	42	10	2	0	0	0	20 / 12
Difference		5	18	−1	−19	−18	−4	9	7	2	0	1	23 / 19
Proportion		0.62	0.51					0.47	0.78	1.00	0.00	1.00	0.53 / 0.61

per root is given in Table 25. For details of the earlier approach to this method of analysis see (2, 7). The vertical and horizontal lines within the bivariate frequency distribution are based on limits set by the vertical lines in Tables 23 and 24. They are the limits for the three sets designated as lower classes, middle classes, and higher classes. This divides the bivariate frequency distribution into nine sets shown by the Roman numerals. The sugar beet breeder working with percentage sucrose and weight per root is primarily interested in sets IV, V, and VI. If attempting to increase both percentage sucrose and weight per root, interest lies in the number and proportion of individuals in set V. The number of individuals of average sucrose percentage but having increased weight per root are shown in set IV. Finally the number of individuals having average weight per root but increased percentage sucrose are shown in set VI. It is not necessary to calculate homogeneity chi-squares to show that the expected and obtained numbers in sets IV, V, and VI are not materially different. The obtained number of seven in set V indicates that by the use of appropriate breeding methods and procedures it should be possible by breeding within variety A54–1 to improve both percentage sucrose and weight per root. Further, by conducting research on different methods of breeding within A54–1 for increased sucrose and weight per root simultaneously, information of fundamental importance to the breeding of sugar beets should be obtained. Hence, it was decided to work intensively with variety A54–1.

The data in set V for years 1955, 1956, 1958, and 1959 were used to calculate the data tabulated in Table 26. Table 26 lists the estimation by years of the numbers and proportions of genetic deviates among 10,000 individuals superior for both percentage sucrose and weight per root in classes having identifiable proportions of genetic deviates. Homogeneity chi-square tests applied to the numbers in column 5 and the numbers from which the proportions were

TABLE 25.—BIVARIATE FREQUENCY DISTRIBUTION EXPRESSED IN NUMBERS FOR PERCENTAGE SUCROSE AND WEIGHT PER ROOT SHOWING NUMBER OF INDIVIDUALS IN CLASSES HAVING IDENTIFIABLE PROPORTIONS OF GENETIC DEVIATES, A54–1, NON-FERTILIZED, POPULATION GENETIC STUDIES, 1956.

Percentage sucrose, upper limit of class, percent	Weight per root, upper limit of class, pounds											Total	
	0 to 0.5	1.0	1.5	2.0	2.5	3.0	3.5	4.0	4.5	5.0	5.5		
%	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	No.	
	I Expected 4 Obtained 7		II Expected 25 Obtained 18				III Expected 3 Obtained 7						
0 to 9.75				1								1	
10.50												0	
11.25					1	1						2	
12.00					1							1	10.0000%
12.75												0	
13.50			1									1	
14.25				1	1		1				1	4	
15.00	1	3	1	3	2	1			1			12	
15.75	1	2	1	1		2	2	2				11	
16.50		3	3	11	3	3	1	1				25	
17.25	VIII Expected 25 Obtained 21 1	3	8	8	6	6	2	2		IV Expected 18 Obtained 17		36	59.0625%
18.00	3	5	7	17	IX 16	7	5	1	1			62	
18.75	1	5	7	18	21	10	2	2				66	
19.50	1	10	18	9	11	5	3	1				58	
20.25		4	4	6	9	1	2					26	30.9375%
21.00			5	2	1	2	1					11	
21.75			1	1								2	
22.50				2								2	
	VII Expected 13 Obtained 15		VI Expected 76 Obtained 77				V Expected 10 Obtained 7						
Total	8	35	56	80	72	38	19	9	2	0	1	320	
	13.4375%		76.8750%				9.6875%						

calculated under sucrose and weight in column 6 provide evidence as to whether the numbers of genetic deviates in 10,000 differ between years, and between the two fertilizer treatments in 1956. Significant differences in the numbers obtained (column 5) or the proportions listed under sucrose and weight (column 6), barring compensating differences, indicate significant differences between years and between treatments within 1956 as regards the numbers of genetic deviates in 10,000. The estimated numbers of genetic deviates in 10,000 are listed in the last column of Table 26.

Homogeneity chi-square calculated from the data of column 5 for years is 7.205 and P lies between 0.20 and 0.10. The two chi-square values calculated from the numbers giving the proportions listed under sucrose and weight in column 6 for years are 50.1388 and 10.0513, respectively, and the corresponding P values lie between 0.01 and 0 and between 0.02 and 0.01. For fertilizer treatments within the year 1956 the two chi-square values are 7.2895 and 4.3494, and the corresponding P values lie between 0.01 and 0 and 0.05 and 0.02. For testing the differences between years the two fertilizer treatments were combined to make a population composed of 640 individuals

Also a t test using the binomial can be employed. (This method of testing the significance of differences between proportions in column 6 was suggested by Dr. W. T. Federer of Cornell University. He points out that it is an approximation). The formula and its application follow:

$$t = \frac{P_1 - P_2}{\sqrt{\frac{P_1(1-P_1)}{n_1} + \frac{P_2(1-P_2)}{n_2}}}$$

It will be used to test whether the proportions are different for the fertilized and non-fertilized populations grown in 1956. P_1 equals 0.1281, P_2 equals 0.0342, n_1 equals 320, and n_2 equals 320 (see Table 26). By substitution and solution of the formula

$$t = \frac{0.1281 - 0.0342}{\sqrt{\frac{0.1281(1-0.1281)}{320} + \frac{0.0342(1-0.0342)}{320}}} = \frac{0.0939}{0.0212} = 4.43.$$

As expected, the t test leads to the same conclusion drawn from applying the chi-square test, namely, that the differences between treatments are not attributable to chance.

Since an examination of the data in Table 19 does not reveal compensating differences, the data are fairly conclusive in showing that the number of genetic deviates in 10,000 calculated from the identifiable proportions of genetic deviates is not the same for all years or for fertilizer treatments in the same year. This may be taken as indicating that breeding for both high percentage sucrose and weight per root would be more effective for some years than for

TABLE 26.—ESTIMATION BY YEARS OF IDENTIFIABLE NUMBERS AND PROPORTIONS OF GENETIC DEVIATES AMONG 10,000 SUPERIOR FOR BOTH PERCENTAGE SUCROSE AND WEIGHT PER ROOT IN HIGHER CLASSES HAVING IDENTIFIABLE PROPORTIONS OF GENETIC DEVIATES, POPULATION A54–1.

Year and treatment	Number of plants in population (n)	Root over[1]		Number obtained (x)	Identifiable proportion of genetic deviates in x (y)	Number of genetic deviates in population (xy)	Proportion of genetic deviates in population (xy/n)	Number of genetic deviates in 10,000
		Sucrose	Weight					
	No.	%	Lbs.	No.	Suc. Wt. Pro.	No.	Pro.	No.
1955	520	13.50	8.0	8	$(0.36 \times 0.46) = 0.1656$	1.3248	0.002548	25
1956								
Fertilized	320	17.25	3.5	9	$(0.09 \times 0.38) = 0.0342$	0.3078	0.000962	10
Non-fertilized	320	18.75	3.0	7	$(0.21 \times 0.61) = 0.1281$	0.8967	0.002802	28
1958	320	17.25	4.5	4	$(0.26 \times 0.59) = 0.1534$	0.6136	0.001918	19
1959	320	14.25	4.0	1	$(0.59 \times 0.68) = 0.4012$	0.4012	0.001254	13

[1]Classes having values greater than those listed in these two columns have some identifiable numbers and proportions of genetic deviates.

others. The same is true for fertilizer treatments. However, as for fertilizer treatments, other considerations make it seem desirable to do the breeding work at the level of soil fertility at which it is anticipated the crop will be grown (13). Probably one of the most important conclusions to be drawn from the data of Table 26 is that some genetic deviates occur in the desirable classes every year and in both fertilizer treatments. The range was from 10 to 28 genetic deviates in 10,000. It would be interesting to know if the genetic deviates from the fertilized and non-fertilized areas are similar genetically or if there is a fertility × genotype interaction. This information should be valuable to the sugar beet breeder. Application of the partitioning method of genetic analysis provides a method of evaluating populations as breeding material and provides estimates of the size of the populations that should be carried. It also provides information on the feasibility of accomplishing the goals of the breeding program and provides a means of evaluating the breeding material as the program progresses.

SUMMARY

1. The special problems and techniques discussed in this article pertain to the partitioning method of genetic analysis.

2. In a frequency distribution composed of plants of the genotypes *aaBBCC*, *aaBbCC*, and *aabbCC* the frequency distribution for plants of the *aaBbCC* genotype was partitioned out. The character was weekly periods of ripening and the material studied was parents and hybrids of common wheat.

3. Theoretical means, frequency distributions, and genetic variances are compared with the obtained values to determine the validity of the genetic models postulated.

4. Number of fruits per 10 centimeters of branch was found to be conditioned by one major effective factor pair and was used to illustrate the application of the partitioning method of genetic analysis to such simply inherited characters. Marker genes are used to study linkage relations.

5. The use of an iterative procedure was illustrated for a case in which no assumption is made regarding the type of distribution, nor is any necessary in the estimation of the theoretical frequency distributions.

6. The use of the means, standard errors and tables of the normal probability integral to estimate the theoretical means, frequency distributions, and genetic variances of the segregating populations was illustrated. The basic assumption is that the environmental variances of the genotypes follow the normal curve.

7. The application of the partitioning method of genetic analysis to estimate the identifiable numbers and proportions of genetic deviates for the lower classes and the higher classes of the frequency distribution is illustrated.

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DISCUSSION

R. E. COMSTOCK: Do you think there is much risk of accepting the wrong hypothesis? Do you know what chance there is of two quite different hypotheses being equally acceptable in terms of your "goodness of fit" test?

LEROY POWERS: I do not believe that there is much risk in arriving at an incorrect genetic hypothesis in those studies in which the parents are differentiated by three or fewer effective factor pairs. As the number of effective factor pairs differentiating the parents increases the reliability of the partitioning method of genetic analysis decreases.

The probability of two different hypotheses giving acceptable fits (when

goodness of fit tests of the frequency distributions are used as a criterion of reliability) occurs quite frequently when more than five effective factor pairs are involved. However, as is emphasized in the article, the reliability of the genetic analysis is tested by comparing obtained and theoretical means, obtained and theoretical frequency distributions, and obtained and theoretical genetic variances. Also marker genes may be used in the studies.

W. D. HANSON: In dealing with individual plant distributions, would not the abnormal distributions associated with environmental patterns create a serious problem in the use of your partitioning method?

LEROY POWERS: I do not believe that as regards the partitioning method of genetic analysis abnormal distributions associated with environmental patterns will lead to misinterpretation of the data if an adequate genetic design and an adequate statistical design are used in the genetic study. These abnormal patterns should show up in the frequency distributions of the non-segregating generations and hence misinterpretations can be avoided. If the interactions between the genotypes and the abnormal environment are such that the environment causing abnormal patterns does not influence the frequency distributions of the non-segregating generations, the data of the F_2, backcross, F_3 families, etc. would not be expected to fit the same genetic hypothesis since the genotypes of the parents and F_1's would occur in some, if not all, of the segregating generations and in different frequencies. It cannot be overemphasized that the genetic design and the statistical design must be adequate. This fact is discussed in more detail in the article.

Also, I would like to point out that the reliability of the genetic hypothesis advanced by use of the partitioning method of genetic analysis is tested by comparing obtained and theoretical means and obtained and theoretical genetic variances as well as by comparing obtained and theoretical frequency distributions. Also, other tests such as the use of marker genes are available.

Discussion: Some Considerations in Variance Component and Partitioning Methods of Genetic Analysis[1]

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ALTHOUGH differing in detail, experimental techniques for estimating genetic parameters in cross fertilizing and self-fertilizing plants are in many respects similar. For example, Experiment III results reported by Gardner as well as the diallel experiments reported by Matzinger utilize variance components. Recognizing that estimation of all genetic parameters is not from variance components, the general approach represented by these two papers will be termed the "variance component" approach. On the other hand, the partitioning method advocated by Powers may seem on superficial examination to be quite dissimilar to the techniques presented in either of the other papers. Of necessity, however, there must be many similarities. Some of these similarities and dissimilarities will be examined, anticipating general limitations of the various methods will then become more evident.

Consider first certain quantitative aspects of the partitioning method. Suppose that two homozygous lines, following the customary notation, are symbolized as P_1 and P_2. Let us suppose the F_1 of these two inbred lines is heterozygous at s loci. The three possible genotypes at the *ith* locus in segregating populations can be symbolized as B_iB_i, B_ib_i, and b_ib_i, respectively. The values of the genotypes for a particular character will be taken to be $2u_i + z_i$, $u_i + a_iu_i + z_i$, and z_i, respectively, where z_i is the value of the homozygote b_ib_i, u_i is a measure of the effect of adding gene B_i, a_i is a measure of dominance at the *ith* locus. The capital letter, B_i, does not necessarily refer to either dominance or favorableness, but merely parental origin. Therefore both a_i and u_i may take either negative or positive values. These genotypic values are frequently coded by subtraction of $u_i + z_i$. The symbols used correspond to those of Comstock and Robinson (1) and have the following relationship to others currently used in the literature:

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	BB	*Bb*	*bb*
Comstock and Robinson (1).....	u	au	−u
Mather (5).....	d	h	−d
Kempthorne (4).....	y	(y−x)/2	0

The (coded) genetic means of variance populations follow from these definitions and are given in the first part of Table 1. The figures in the table show genotypic means with respect to one segregating locus. Given the values for the various populations and their respective frequencies, derived from elementary considerations, it is then possible to derive the genetic variances presented in the right-hand side of Table 1.

TABLE 1.—TABLE OF GENETIC MEANS AND VARIANCES OF INBRED POPULATIONS.

Population	Coded Mean		Variance		
	u_i	a_iu_i	u_i^2	$a_iu_i^2$	$a_i^2u_i^2$
P_1.....	1	0	0	0	0
P_2.....	−1	0	0	0	0
F_1.....	0	1	0	0	0
F_2.....	0	1/2	1/2	0	1/4
$BC_1(P_1 \times F_1)$.....	1/2	1/2	1/4	−1/2	1/4
$BC_2(P_1 \times F_1)$.....	−1/2	1/2	1/4	1/2	1/4
$S_{11}(BC_1$ selfed).....	1/2	1/4	1/2	−1/4	3/16
$S_{21}(BC_2$ selfed).....	−1/2	1/4	1/2	1/4	3/16

Various relationships required by the partitioning method can be easily derived from Table 1. For example, the expected genetic value of backcross to P_1 is taken as the means of the F_1 and P_1 populations,

$$\bar{B}_1 = \frac{\bar{F}_1 + \bar{P}_1}{2} = \frac{1}{2}(u + au).$$

The genetic variances of the back cross generation can be shown to be identical to a variance derived from the means of two of the non-segregating generations, P_1 and F_1, as required in the type II partitioning method. i.e.,

$$\frac{1}{4}(\bar{P}_1 - \bar{F}_1)^2 = \frac{1}{4}(u - au)^2 = \frac{1}{4}u^2 - \frac{1}{2}au^2 + \frac{1}{4}a^2u^2.$$

Hence for a single locus, the basis for theoretical means and variances required by the type II partitioning method are in accord with quantitative values employed in the variance component method.

Consider now the influence of all s heterozygous loci on a particular character. The net effect with regard to the means listed in Table 1 is that the column headings u_i and a_iu_i, are replaced by Σu^2, Σau^2, and Σa^2u^2, respectively. These quantities are the D and H of Mather (5) and the C of Kempthorne (4),

respectively. Relationships of means identical to those used for a single factor pair hold for an arbitrary number of segregating loci. This is not true with respect to the variances since now

$$\frac{1}{4}(\bar{P}_1 - \bar{F}_1)^2 = \frac{1}{4}(\Sigma u - \Sigma au)^2 = \frac{1}{4}(\Sigma u)^2 - \frac{1}{2}(\Sigma u)(\Sigma au) + \frac{1}{4}(\Sigma au)^2$$

$$\neq \frac{1}{4}\Sigma u^2 - \frac{1}{2}\Sigma au^2 + \frac{1}{4}\Sigma a^2u^2, \text{ unless } \sum_{i \neq j}\sum_{j} u_i u_j = 0, \text{ etc.}$$

Hence in contrast to the means, a generalization of this relationship to an arbitrary number of loci is not possible.

The variance component approach also utilized relationships similar to those described. What then are the underlying genetic assumptions in either instance? It appears that the basic assumptions required for these relationships are essentially the same as listed explicitly by Gardner in the first paper of this session and given implicitly by Matzinger. Assumption 1, random choice of individuals mated for production of experimental progenies, is not required for the non-segregating generations, although it would be for the segregating generations. The assumption concerning no epistasis is relaxed to some extent in partitioning methods I, III, and IV. The eighth assumption, concerning gene frequencies of one-half, is not of serious concern with genetic material selfed only as far as the F_2 or F_3 generation. However, for preciseness, another assumption should be added to both approaches, that of no mutation, even though mutations at the rate generally believed to occur will not seriously affect the utility of the expectations premised on the absence of mutation.

If the underlying genetical assumptions concerned with quantitative relationships among means, and particularly among variances, are so similar, then in what manner do the two approaches differ? The discussion of some dissimilarities, chiefly of statistical nature, will of necessity be limited to that experimental material which is adapted to the two approaches, namely those organisms capable of self-fertilization.

1. Time required. The most obvious difference between the two approaches is that the partitioning method gives information in earlier generations. The papers referred to by Powers generally contained the following genetic populations: P_1, P_2, B_1, B_2, F_1, and F_2. Contrast this with the variance component approach which generally requires genetic material to be advanced at least to the F_4 generation for estimating linkage and epistatic effects. The variance component approach makes relatively little use of the non-segregating generations, except for estimating environmental variance. In addition to this usage, the partitioning approach employs the non-segregating generations for tentative hypotheses concerning postulated genotypes.

2. Frequency distributions. The partitioning method utilizes frequency distributions while the variance component approach is not concerned with frequency distributions, except to ascertain second degree statistics, i.e., variances

and covariances. In dealing with frequency distributions, it is well to keep in mind that a certain amount of arbitrariness is implied in their usage. Choice of the *width* of the class interval, to say nothing of *positioning* of the class intervals, can alter modes with respect to both their height and location. On the one hand, too few classes may disguise a bimodal distribution. On the other hand, too many classes may give spurious modes, due merely to random choice.

3. Differences in inferences. The variance component approach is generally concerned with estimation of genetic parameters which are considered to be representative of some hypothetical or real population of much greater extent than the material contained in the experiment. For example, a diallel cross of randomly selected homozygous lines leads to estimates of additive genetic and dominance variance of the entire population. Here the concern is to make inferences to a wider population than those relatively few homozygous lines sampled; the inferences seemingly are representative of Eisenhart's (2) random model.

On the other hand, the chief concern of the partitioning method appears to be in the selection of postulated genotypes that fit the observed facts as closely as possible. The procedure is not amenable to broadening the scope of the inferences beyond the specific genetic material in hand; the inferences seem more representative of Eisenhart's (2) fixed model.

4. *A posteriori* statistics. The phrase is taken to be indicative of the situation where a formal method of procedure used to analyze a set of data is determined by that particular set of data. The basic difficulty in letting a set of data prescribe its own analysis, without verification by subsequent experimentation, is that in any set of data there exists certain perturbations of the data, due solely to random chance. In the words of Sir Ronald Fisher (3):

> "...no isolated experiment, however significant in itself, can suffice for the experimental demonstration of a natural phenomenon; for the 'one chance in a million' will undoubtedly occur, with no less and no more than its appropriate frequency, however surprised we may be that it should occur to *us*. In order to assert that a natural phenomenon is experimentally demonstrable, we need not an isolated record, but a reliable method of procedure."

This type of approach is in distinct contrast to the variance component approach wherein the analysis is determined prior to observation of the data and where any competently trained person will arrive at identical estimates of genetic parameters. These identical estimates may well be open to different interpretation even by competent observers, but at least the starting point is the same. The partitioning method does not enjoy this advantage.

Finally, a comment concerning Matzinger's paper. As has been pointed out by Matzinger, scaling tests are applied to data to detect the presence of epistasis or genotype-environmental interaction. Since both approaches use similar experimental material under similar assumptions, it is obvious that both procedures should be equally concerned with scaling tests and transformations.

Although there are exceptions, several of which were pointed out by Matzinger, users of the variance component approach traditionally ignore scaling tests. Conversely, advocates of the partitioning approach traditionally employ scaling tests and transformations, if deemed suitable. One reason the variance component procedure ignores scaling tests and transformations is because convenient scaling tests are not available in the ordinary diallel designs with only F_1's and/or their reciprocals, for example. However, the basic reason may be deeper than that. The variance component approach assumes the genetic model to be the same in all generations and environments. The partitioning method is not so restricted, and as reported by Powers (6), has led to different scales postulated for identical genetic populations grown under different environments. This result does not seem reasonable and probably is due to genotypic-environmental interactions. Consider a simple mathematical model similar to that given by Matzinger.

$$y_{ijk} = \mu + g_i + e_j + (ge)_{ij} + \epsilon_{ijk} \tag{1}$$

where y_{ijk} is the *kth* observed measurement on the *ith* genotype in the *jth* environment, μ is the common mean, g_i the additive genetic and dominance effects of the *ith* genotype, e_j the effect of the *jth* environment and $(ge)_{ij}$ the interaction effect of the *ith* genotype in the *jth* environment and ϵ_{ijk} the residual. To eliminate genotypic-environmental interaction, we hope to find a transformation on y_{ijk} so that

$$y_{ijk}' = \mu' + g_i' + e_j' + (ge)_{ij}' + \epsilon_{ijk}' \tag{2}$$

where $(ge)_{ij}'$ is negligible (y_{ijk}' is the transformed value of y_{ijk} and the other symbols in the model are effects analogous to the first model defined in terms of the transformed values). In other words, a transformation is desired so that genotypes are independent of environment. To eliminate epistatic effects, one begins with the model (for the value of the *ith* genotype with only two loci):

$$y_{ijk} = \mu + g_i + e_j + \epsilon_{ijk} \tag{3}$$

where

$$\begin{aligned} g_i = {} & \alpha_{1i} + \alpha_{2i} + \delta_{1i} + \delta_{2i} \\ & + (\alpha_1\alpha_2)_i + (\delta_1\delta_2)_i \\ & + (\alpha_1\delta_2)_i + (\alpha_2\delta_1)_i, \end{aligned} \tag{3a}$$

and the α's are additive effects, the δ's dominance effects and the remainder various non-allelic interactions, so that

$$y_{ijk}' = \mu' + g_i' + e_j' + \epsilon_{ijk}'. \tag{4}$$

In model (4), all of the non-allelic interaction components in g_i' are hopefully negligible. There is some question of the meaning of genetic parameters derived from an equation similar to (4). That is, of what utility is additive genetic variance defined in terms of the transformed values, such as logarithms? Can it be used to predict a meaningful measure of genetic progress from selection for yield, as an example?

The most general model is one combining genotypic-environmental and non-allelic interaction effects from models (1) and (3). The same questions asked

with regard to model (4) may be asked also with regard to this most general model. However, this model involves the interaction of environmental and epistatic effects and is even more difficult of interpretation.

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DISCUSSION

D. D. RUBIS: Are scaling tests or transformations necessary only for Power's or Mather's method? Certainly they are important in the variance component methods too, especially in cases when data are taken on the rank scale of 1 to 5 or 1 to 9 where the means and variances are often correlated. When do you use transformations and what kind of transformations are used?

C. E. GATES: I agree with Dr. Rubis' response to his own first question. The answer to his second question deserves further comment. The problem of transformations with respect to purely statistical problems, such as heterogeneous variances and various types of non-normality is considered in some detail in the March 1947 issue of Biometrics. The question when to transform with respect to statistical genetic considerations such as genotypic-environmental interactions, non-allelic interactions and combinations of both is considerably more difficult to answer. While there are in general a few specific tests for epistatic effects and for genotypic-environmental interactions, such as those proposed by Mather (1949) and Horner (1955), there is, to my knowledge, no general solution. The area appears to be ripe for a considerable amount of research.

SEWALL WRIGHT: It seems to me that the main difference between the type of analysis made by Dr. Powers and the analysis of variance components is that he has attempted to determine the effects of actual genes. The use

of transformation of scale seems desirable if the effects of the genes can be made additive in all combinations by so doing. However, it would seem that consistent use of a transformation is also desirable in estimating variance components if it makes possible virtual elimination of an interaction component. A simple example is given by a study of white spotting in guinea pigs that I made a good many years ago (1920). Twenty-three strains derived from single matings after several generations of brother-sister mating all showed extensive variability, ranging from almost 0 per cent white to 100 per cent white in those with medians near 50 per cent. Comparison of quartile deviations (upper and lower) showed that small percentage increments in the neighborhood of 5 per cent or of 95 per cent would have to be considered equivalent to large ones in the neighborhood of 50 per cent, and that the distributions could best be interpreted on the hypothesis of normal distributions of elementary areas of the skin with respect to tendency to be white. This implied an inverse probability transformation of the scale of percentages as suitable. On making this transformation systematically, the correlation between parent and offspring did not differ significantly from zero within inbred strains but was about .20 in a random bred control stock. The latter figure indicates about 50 per cent determination by heredity, assuming no dominance or interaction (in harmony with other results) ($r_{op} = \frac{1}{2}h^2$). The variance of the inbred strain was actually 40 per cent less than that of the random bred stock on the transformed scale, giving a direct wholly independent verification of this estimate of heritability which should have been impossible on the original scale on which there would have appeared to be much interaction and on which variance of inbred strains differed enormously in relation to the position of the median.

Selection Programs

E. J. WELLHAUSEN, *Chairman*

Realized Yield Improvement From Twelve Generations of Progeny Selection in a Variety of Upland Cotton

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Empire Cotton Growing Corporation, Kampala, Uganda

THE BP52 variety of Upland cotton can be traced to a single plant selection made in 1933 by officers of the Uganda Department of Agriculture. During the period 1933 to 1945 further selection was exercised, mainly in respect to lint quality, but attention was also drawn to the variety's apparent tolerance to the bacterial blight disease *Xanthomonas malvacearum* (5). Two projects were considered by the officers of the Empire Cotton Growing Corporation when they took over the breeding work in 1946. The first was to pursue intensive line selection to exploit any residual genetic variability for yield. The second was based on a program of hybridization with exotic varieties resistant to bacterial blight. This latter project has not so far provided material which is competitive within the three way classification of quality, yield, and disease resistance, and this paper is concerned solely with the realized yield advance from intensive line selection within high quality BP52 which has been inbred since 1947.

Expectation of relatively large yield improvement following intensive selection in inbred lines of the variety was discussed in a previous paper (4). In any one season the breeding system tests progenies, strains derived from the previous season, and lines derived in turn from strains. With 12 generations of progeny selection there will therefore be data for 11 seasons of strain tests and 10 seasons of line tests. The range of environmental conditions under which the line tests are made gives a very widespread representation of the commercial crop. Furthermore, the early selections have now been grown over the whole area growing BP52 so that it is appropriate to consider the extent to which this breeding system, based upon a yield selection index technique, has been effective in increasing yield.

During the early stages of the breeding project, selection was effected only at the environment of the Namulonge Cotton Research Station. When later tests were conducted at other localities, it became apparent that certain environmental factors dominated the expression of yield. Not the least of these were sowing date and the time of onset of water strain, which were important because of the indeterminate fruiting habit of cotton. In consequence, any assessment

of yield advance, either as a total in yield units, or expressed as a percentage to reduce the effects of fertility differences, must be considered in the light of these environmental effects.

At the time of the initiation of the new breeding scheme, some 150,000 bales of 400 pounds lint were grown entirely by small land holders. Both standards of cultivation and yield levels are poor by comparison with those of the United States. In spite of this, the area now covered by the new seed issues has been largely extended and produces a crop of the order of 225,000 bales. With this extension of area it is hardly surprising that the precision of acreage estimates is not high. However, since seed for planting is completely controlled by the Department of Agriculture, there is an excellent opportunity for measuring the actual improvement in production effected on the commercial crop.

This paper covers the period 1948–49 to 1959–60 and proposes to show how the project has led to a material increase in production.

EXPERIMENTAL DATA

Genetic variability, of a magnitude worth exploiting by a selection index technique, has persisted at least up to the 13th generation of inbreeding in BP52 cotton, so it is worth describing the actual breeding procedure. Yield data are obtained from replicated progeny rows of open pollinated material and inter-progeny selection is made on the basis of total score of index. Seed for the following season's progenies is obtained from self-fertilized single plants taken from non-replicated rows grown from sister seed. One part provides the non-replicated progeny rows of the succeeding season; the other part is used to sow the replicated progeny rows, usually in the form of a lattice square arrangement. Successful progenies are bulked as strains individually, for large scale field tests in the second season, using open pollinated seed from the replicated rows. A further test is made of a reduced number of lines in the third season. Consequently, by the time selections are ready for commercial multiplication, they have been grown and tested for three seasons. The schematic arrangement of the system is shown in Figure 1.

A second breeding system involving a form of mass selection in open pollinated material has been run in parallel throughout the period. This has also been described (4) as the "modal bulk" series and, since it has been used as a reference standard, is worthy of a brief description. Each season about 300 plants are chosen in the field. The produce is then analyzed for the three traits: (a) Lint per seed, (b) seed weight, and (c) lint length, in that order. Plants with traits that occur one standard deviation of the mean are retained in the successive analyses, and the remaining nucleus forms the modal bulk for the following season. Over the 12 seasons the successive modal bulks have shown a steady yield increase which will be discussed at the relevant stage.

Progeny rows.

Since quality was already satisfactory, the major effort was directed towards yield improvement. Yield traits actually chosen were three components

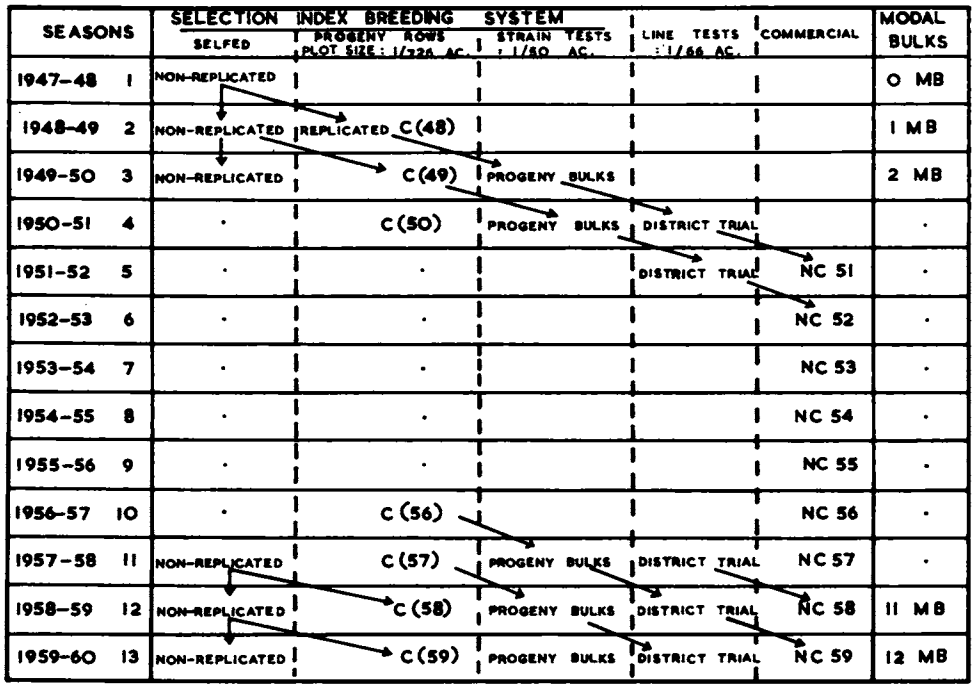


FIGURE 1. *Diagrammatic arrangement of BP52 breeding systems.*

of yield, namely, bolls per plant, seeds per boll, and lint per seed. It can be shown theoretically that an index based on a combination of these is more efficient than selection for yield alone. During the early seasons the trait bolls per plant were estimated by a count of all green bolls immediately before the first picking. Lint per seed was estimated from the entire produce and seeds per boll from a 15 boll sample. The product of the three traits so determined did not agree closely with the actual yield of lint per plant mainly because only a portion of the green bolls was actually reaped. Later a bolling index, derived directly from lint per plant divided by the product of seeds per boll and lint per seed, was used. Expected advance from selection for the three traits and for lint yield alone was recalculated and those data are summarized in Table 1.

Table 1 shows the wide range of variation for yield characters, particularly for bolling index and lint per plant. Moreover, in seasons of low yield and low bolling index, environmental variances are relatively high and tend to reduce the estimate of genotypic variances. The table is also of interest in showing that selection for yield alone might have been more efficient on two occasions. The first, when the primary selection was made and when genetic variability due both to different biotypes and additive variance might be expected to be large, was hardly surprising, but no satisfactory explanation exists for the advances made in the 1951–52 season, by which time differences due to homozygous biotypes should have been eliminated.

TABLE 1.—YIELD COMPONENT DATA AND EXPECTED GENETIC ADVANCE FOR 11 GENERATIONS OF PROGENY SELECTION IN BP52.

Season	Yield Components				Expected Genetic Advance				
	Bolling Index	Seeds per Boll	Lint per Seed	Lint per Plant. dgm.	Proportion Retained	Yield Alone Annual	Yield Alone Cum.	All Traits Annual	All Traits Cum.
1948–49	17.8	26.6	0.487	231.3	12/38	13.4		9.6	
1949–50	17.9	31.1	0.459	255.6	6/44	2.6	16.0	3.8	13.4
1950–51	14.7	24.3	0.499	178.9	6/30	2.9	18.9	3.8	17.2
1951–52	17.9	18.5	0.526	268.7	10/48	6.8	25.7	5.9	23.1
1952–53	10.3	29.8	0.550	169.1	8/43	0	25.7	0.5	23.6
1953–54	17.0	28.5	0.464	224.5	9/65	1.8	27.5	2.7	26.3
1954–55	7.1	28.7	0.567	115.9	14/58	6.0	33.5	6.3	32.6
1955–56	15.5	29.6	0.493	226.8	12/47	3.9	37.4	4.0	36.6
1956–57	10.6	30.3	0.554	178.6	8/73	0	37.4	1.3	37.9
1957–58	5.3	27.7	0.597	87.0	8/43	0	37.4	2.1	40.0
1958–59	21.5	29.7	0.580	336.8	10/44	5.0	42.4	6.5	46.5
1959–60	15.7	28.0	0.533	234.7	10/75	1.8	44.2	4.0	50.5

An attempt has been made to assess the realized advance for comparison with the cumulative expected genetic advance shown in Table 1. Seasonal variation in bolling index is too large to be able to demonstrate any trend, but the two other component traits, being somewhat less subject to environmental variation, are more useful. For this purpose, the product of seeds per boll and lint per seed, as lint per boll, may be examined. An analysis of the change in lint per boll over the period shows that the major effect of this selection procedure has been to increase boll size. These data are presented diagrammatically in Figure 2.

A linear regression analysis of lint per boll on generation of selection indicated that there has been a real increase from 1.34 grams in generation 1 to 1.67 grams in generation 13. It seemed more reasonable, however, that a symptotic level might be anticipated and the data were therefore tested for curvilinearity. The resulting regression suggests a decreased rate of improvement in the later seasons but the improvement in goodness of fit was not statistically significant. An overall improvement of about 30 per cent from the first to the 13*th* generation is indicated. The discrepancy between the cumulative predicted advance of 50 per cent for the comparable generation of selection by the index, will be considered later.

Strain tests.

In the second stage of the breeding system, selected progenies from the previous season are tested against a reference modal bulk standard. The yield

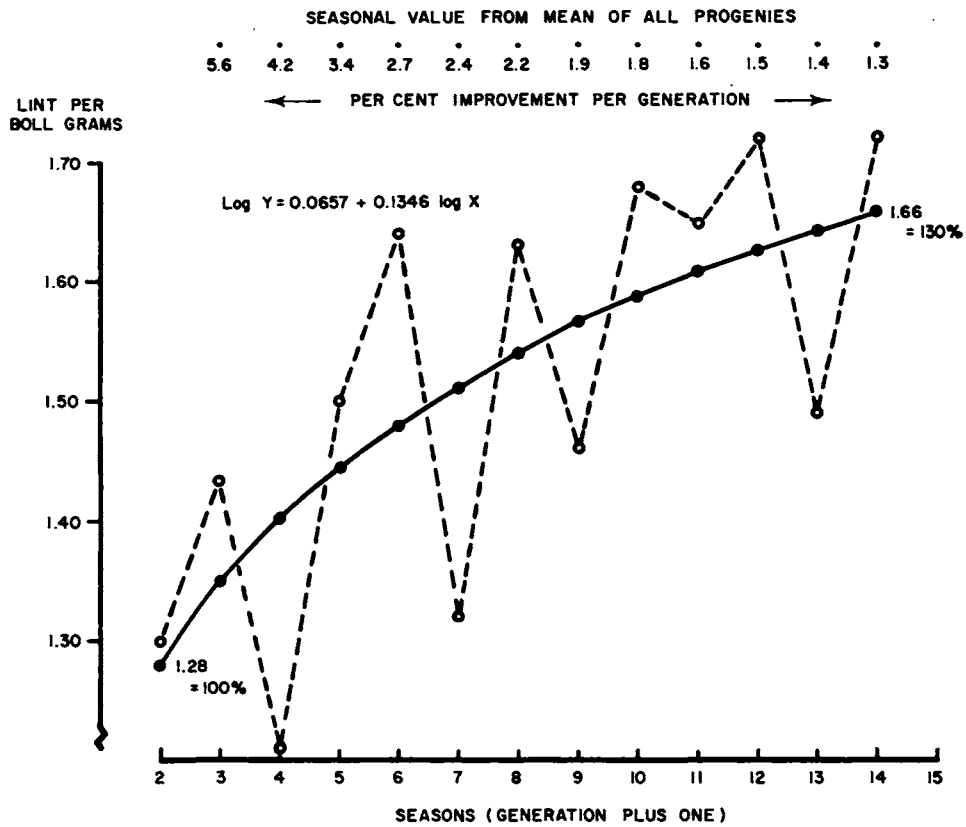


FIGURE 2. *Lint per boll increase over 13 generations of selection.*

advance of the modal bulk has been shown in field trials to be described by the regression equation:

2.60 (GENERATION) + 101.80 expressed as a percentage of original bulk and with $r^2 = 0.91$.

Selected progenies, now as strains, can be considered relative to the changing reference modal bulk and then equated to the estimated original bulk. At first sight this procedure may appear to be highly irregular since yield of the modal bulk itself has been estimated, but it can be justified on the grounds that the estimated original bulk yield level has shown no significant change over the seasons, both for this series of tests and in the later line tests.

During the early seasons the strain tests were restricted to the Research Station area, but more recently, four other centers have been added. This has had the effect on the one hand of broadening the basis of the tests, but on the other, of lowering the mean yield of the control variety. Yield data for the seasonal means of the "original" bulks, together with increments due to the reference modal bulks, and those for all strains, are summarized in Table 2 for the 11 seasons during which the strain tests have been conducted.

TABLE 2.—LINT PER ACRE INCREASE OF ALL STRAINS AND MODAL BULKS COMPARED WITH ORIGINAL BULK.

Season	Modal Bulk Data				All Strain Data			
	Bulk	Original	Increase	Per cent	Localities	Generation	Increase	Per cent
1949–50	1 MB	276.8	12.2	4.4	1	1	35.7	12.9
1950–51	2 MB	217.8	15.2	7.0	1	2	27.2	12.5
1951–52	3 MB	364.0	35.0		3	3	84.5	23.2
		349.3	33.5	9.6			42.5	12.2
		299.9	28.8				94.3	31.4
1952–53	4 MB	239.5	29.2	12.2	2	4	50.0	20.9
		236.6	28.9				22.0	9.3
1953–54	5 MB	204.0	30.3		3	5	64.4	31.6
		191.6	28.4	14.8			29.9	15.6
		241.0	35.7				71.5	29.7
1954–55	6 MB	67.7	11.8		5	6	50.6	74.7
		83.9	14.6				25.2	30.0
		72.1	12.6	17.4			36.0	49.9
		170.1	29.6				52.8	31.0
		146.7	25.5				66.2	45.1
1955–56	7 MB	126.4	25.3		5	7	40.9	32.4
		119.3	23.9				27.8	23.3
		153.5	30.8	20.0			59.5	38.8
		139.1	27.9				38.7	27.8
		214.2	42.8				65.2	30.4
1956–57	7 MB	228.8	45.8		5	8	46.5	20.3
		280.3	56.1				84.5	30.1
		86.8	17.4	20.0			11.5	13.2
		289.7	57.9				113.2	39.1
		355.0	71.0				147.3	41.4
1957–58	9 MB	107.8	27.2		5	9	21.9	20.3
		73.5	18.5				23.5	32.0
		165.6	42.5	25.2			41.2	24.4
		221.2	55.7				64.3	29.1
		152.7	38.5				44.5	29.1
1958–59	10 MB	109.7	30.5		4	10	61.6	56.2
		189.5	52.7	27.8			66.9	35.3
		182.5	50.7				60.5	33.2
		161.8	45.0				64.8	40.1
1959–60	11 MB	306.6	93.2		5	11	102.7	33.5
		325.3	98.9				52.8	16.2
		160.3	48.7	30.4			49.1	30.6
		289.3	87.9				122.8	42.4
		128.1	38.9				14.0	10.9

Table 2 shows the size of the increment of the selected progenies varied considerably with the yield level of the control. This indicates that a simple relationship between generation of selection and per cent improvement would not be entirely satisfactory. By employing a multiple regression analysis with the dependent variables generation of selection and yield of the original bulk, it was possible to estimate the change in increment over the period with a fair degree of precision ($r^2 = 0.51$). The regression equation as pounds lint per acre was estimated to be

$$y = 3.594 \text{ (Generation)} + 0.256 \text{ (Yield of original)} = 20.591.$$

A substitution of 100 pounds lint per acre for original indicates that the increment would vary from 8.6 pounds for generation 1 to about 40.9 pounds in generation 10. At the higher yield level of 300 pounds lint per acre, the comparable figures vary from 60.0 to 95.6 pounds lint per acre representing per cent advance from 20.0 for generation 1 to 31.8 for the 10*th*. Since the line tests now to be described, averaged some 270 pounds lint per acre for the control variety, it is reasonable to accept the higher original yield level for the regression estimate. The large primary yield advance from the early selection is thus confirmed as well as the steady improvement up to the 11*th* generation of selection.

Line tests.

Attention has been drawn to the expansion of the areas now growing the BP52 variety. Advantage was taken of this to increase the number of centers testing the new selections. During the early seasons only 10 to 12 centers were available but now 30 are included in this important stage of the breeding project. With this expansion, over quite wide areas, it was difficult to obtain the necessary trained staff and the type of experiment which could be grown was somewhat restricted, a 5 × 5 latin square design being used. While the precision of these line tests may not be regarded as high by standards of comparison with other countries, of 116 trials grown between 1949–1950 and 1957–58, 74 had coefficients of variation of less than 15 per cent. This precision can be regarded as satisfactory for Uganda.

Trials are divided into four areas differing in rainfall distribution, which has been shown to account for a very large proportion of the yield variation between seasons and sites (2). Straight line distances between the extremes of Group I and Group III are as much as 220 miles. Even where distances are considerably less, such as between Group I and II, the climatic patterns can differ widely. It is therefore hardly surprising that differences in growing conditions and, consequently, per cent improvement vary widely. A first estimate of this yield improvement, over the 10 generations available, can be obtained by examining the Group means summarized in Table 3.

Data for the separate 199 trials require an unusually large table which is, however, available for reference. It has been necessary here to summarize these data by Groups containing a varying number of centers. Means by zones are given for coded sowing date, the yield level of the standard variety, and the

TABLE 3.—INCREMENT OF BEST LINES OVER ORIGINAL BP52 OR ITS EQUIVALENT OVER TEN GENERATIONS OF SELECTION YIELD IN LB. LINT PER ACRE.

Group	Trait	Generations of Selection						
		1	3	5	6	8	9	10
I	Tests	16	12	10	5	5	6	16
6 Centers	Sowing date	13.0	21.8	12.1	13.8	13.0	17.5	10.7
	Yield of local	333.2	303.9	307.2	379.4	298.6	261.7	331.5
	Increment	41.3	46.4	69.2	88.2	50.0	55.5	51.3
	% Advance	12.4	15.3	22.5	23.2	16.7	21.2	15.5
II	Tests	15	12	10	6	5	7	21
10 Centers	Sowing date	22.3	30.8	18.9	16.5	19.6	12.6	14.2
	Yield of local	311.9	234.6	214.8	337.3	260.6	248.9	253.7
	Increment	11.9	11.5	22.6	99.3	34.6	36.0	72.0
	% Advance	3.8	4.9	10.5	29.4	16.7	14.5	28.4
III	Tests	6	4	4	3	4	5	17
8 Centers	Sowing date	16.3	9.8	11.0	8.0	9.5	24.6	14.4
	Yield of local	217.5	282.3	269.5	274.5	329.8	220.6	234.3
	Increment	10.5	59.5	52.5	89.5	79.3	57.6	60.3
	% Advance	4.8	21.1	19.5	32.6	24.0	26.1	25.7
IV	Tests			1	1	1	2	6
3 Centers	Sowing date			41.0	5.0	5.0	16.5	16.8
	Yield of local			89.0	198.0	84.0	192.5	220.8
	Increment			15.0	04.0	39.0	34.0	67.8
	% Advance			16.8	27.3	46.4	17.7	30.7
All	Tests	37	28	25	14	15	20	60
Trials	Sowing date	17.3	24.0	15.8	13.5	13.7	17.5	13.6
	Yield of local	305.8	271.1	255.5	333.4	279.9	240.0	265.7
	Increment	24.4	33.3	45.7	90.7	54.9	47.1	62.7
	% Advance	8.0	12.3	17.9	27.2	19.6	19.6	23.6

increment of the best single line for each season. In addition, the improvement of this increment is shown as a per cent over the equivalent original bulk. Coding of the sowing dates is carried out as days deviation from the optima derived from a yield/sowing date relationship, ignoring sign. This criterion is based on the assumption that sowing too late, or too early, will have an equal effect in terms of shortage of rainfall.

Table 3 shows that both the absolute increment and its alternative expression as a percentage, are much affected by the conditions affecting the control yield. Figure 3 summarizes the gain for all zones over 10 seasons with the increment expressed as a percentage of the control.

After 10 generations of selection the yield advance of about 24 per cent, on overall yield of standard, appears to be satisfactory. However, it raises two questions; the most important of these is the use of the local BP52 as a standard, the other being the extent to which the seasonal mean truly reflects the per-

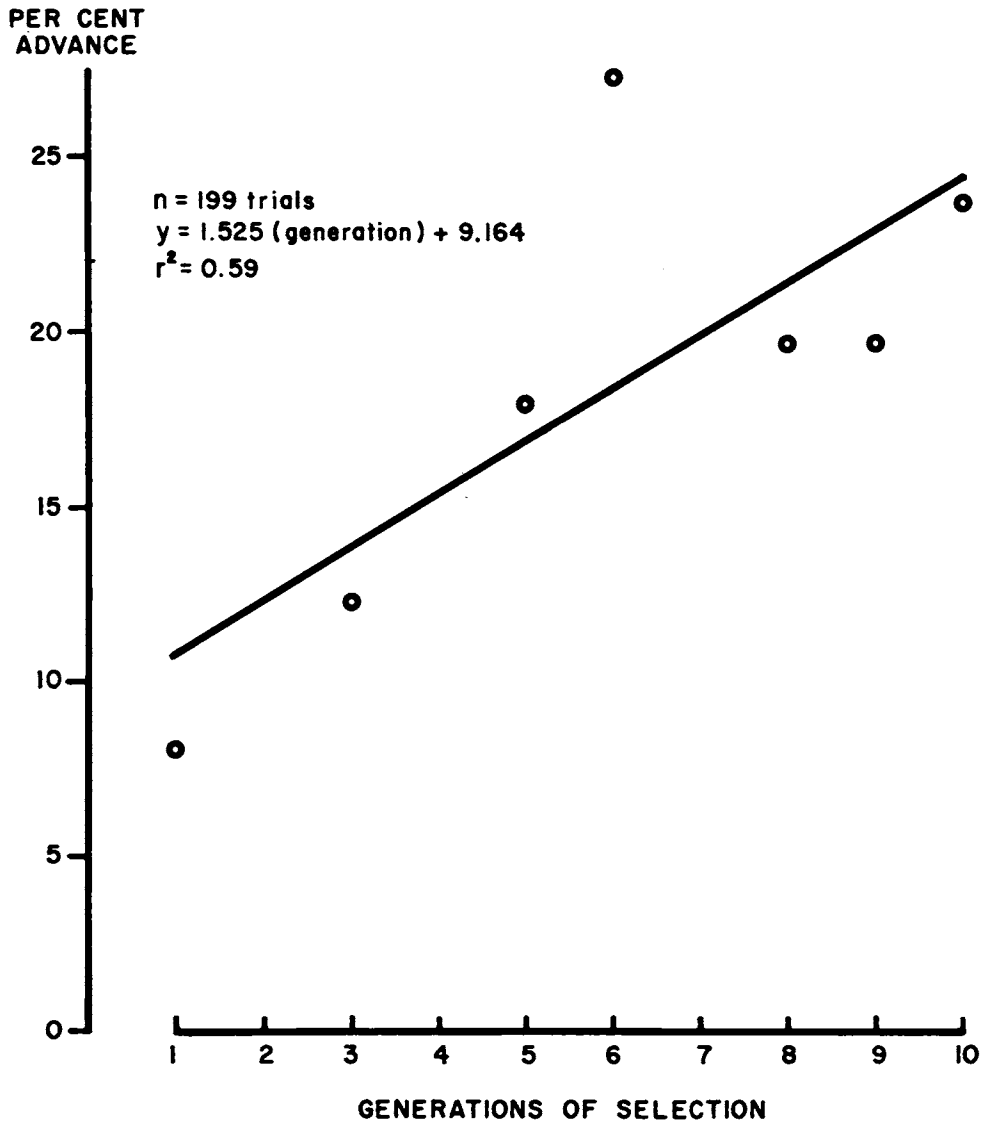


FIGURE 3. *Lint yield advance of best single lines over original bulk from all trials over 10 generations.*

formance over the area as a whole. Consideration may first be given to the performance of the local BP52 yield during the twelve seasons in which it has been used as a standard of comparison.

Standard of comparison.

Data relating to yield of local given in Table 3 might indicate a possible yield decline during the period. It has, however, already been pointed out that during that time the number of centers increased from 10 to 30. It may therefore

be inferred that such an expansion might include sites of less favourable growing conditions. This might be expected for areas only recently brought into cultivation of a crop which has been grown in Uganda for some 50 years. A more satisfactory test is to examine the yield of local for a constant number of sites over the 12 seasons. Five centers in Group I were chosen as being representative of reasonably uniform growing conditions. In fact, there was a small positive trend shown by the regression of yield on season, but this was not statistically significant.

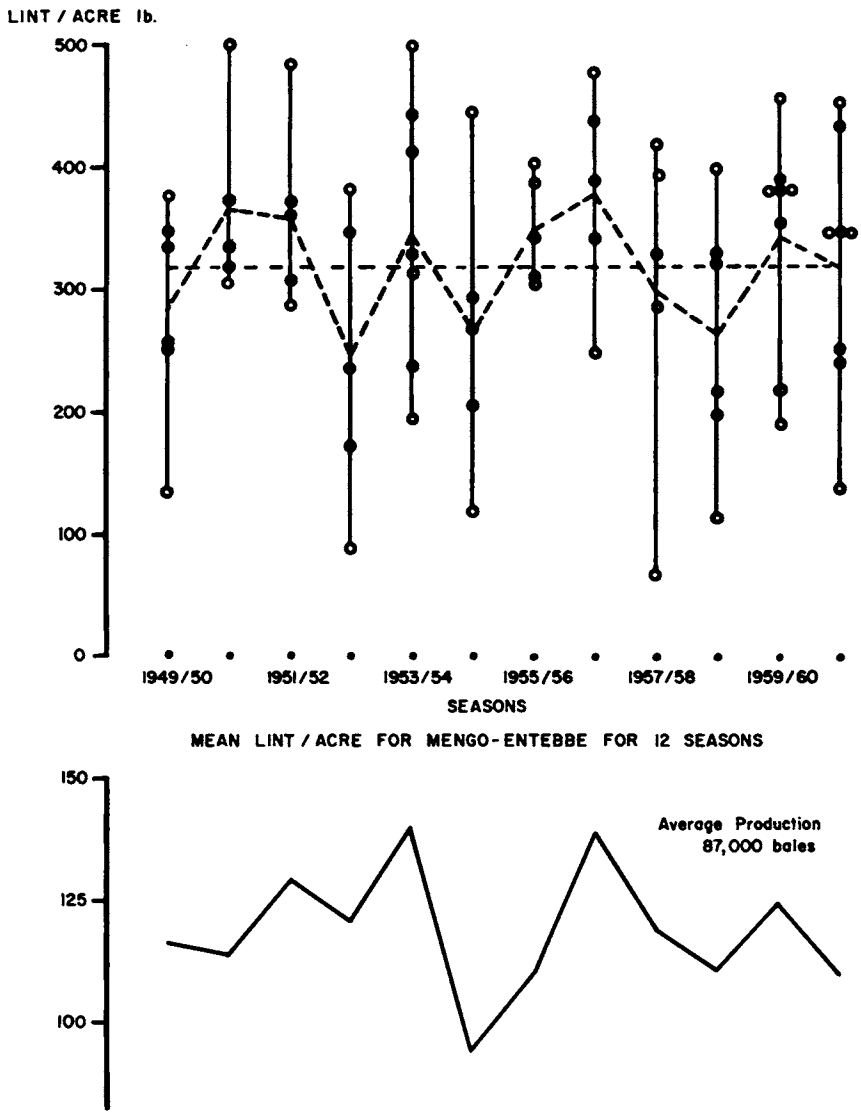


FIGURE 4. *Lint yield of local BP52 in group II. Trials over 12 seasons.*

Since the area represented by these centers grows the greater proportion of the crop in the BP52 area, it seemed worthwhile at the same time to ascertain whether a relationship existed between seasonal mean yield from the trials and mean lint per acre from the district. These data together are shown in Figure 4 where it will be seen that the local BP52 has varied between about 250 and 350 pound lint per acre. There is some indication that the major differences between the seasons are also reflected in the lint yield differences for the district, but the correlation coefficient 0.55 just fails to attain statistical significance with only 11 degrees of freedom available.

Environmental factors.

Data have been presented in the previous sections to indicate that an appreciable yield advance, confirmed on a very wide scale, has been affected by this breeding system. No standard measure of the absolute improvement realized has, however, been so far made, but attention has been drawn to the profound effect of the environment on the size of the increment. There is now much evidence to suggest that two important effects, themselves a composite of climatic factors, can account for a large part of the yield variation. The first of these has been described as a sowing date effect. The precise mechanism of this effect is not fully understood, but it has been shown that there exists a well marked optimum sowing date. Planting either before or after this date leads to a marked yield decline (3). The most recent analyses of Namulonge yield data indicate that yield expectation, for sowings around June 30, would be about 350 pounds lint per acre, sowing before mid-May or after mid-August having yield expectations of 200 pounds or less. Attention has already been drawn to the importance of the rainfall during the critical growth period which occurs between the twelfth and sixteenth weeks after sowing (2). Where yield/sowing date relationships are available, over an adequate run of seasons, it can be shown that sowing dates derived from the trials themselves, considered together with the pattern of crop water use, are explained by the opportunity for making the best use of the rainfall expectation. This concept is perhaps best illustrated diagrammatically in Figure 5.

Rainfall for crop establishment is shown in Figure 5 to be adequate in all zones if cotton were planted about standard week 23 (June 9th). At the same time it will also be seen that cotton planted during such a period might also experience inadequate rainfall, resulting in a soil moisture deficit during the important period of leaf area expansion and flower production. The most satisfactory sowing date must, therefore, be a compromise weighted more heavily in favor of the more important water requirement during the major period of growth. This offers at least one explanation for the success associated with the sowing dates given in Figure 5. At Kyanamukaka in Group III, it would appear that while sowings about week 25 might be best within the limits of the prescribed sowing period May to August, a new range of sowing dates is worthy of consideration. However, even more important is the observation that examina-

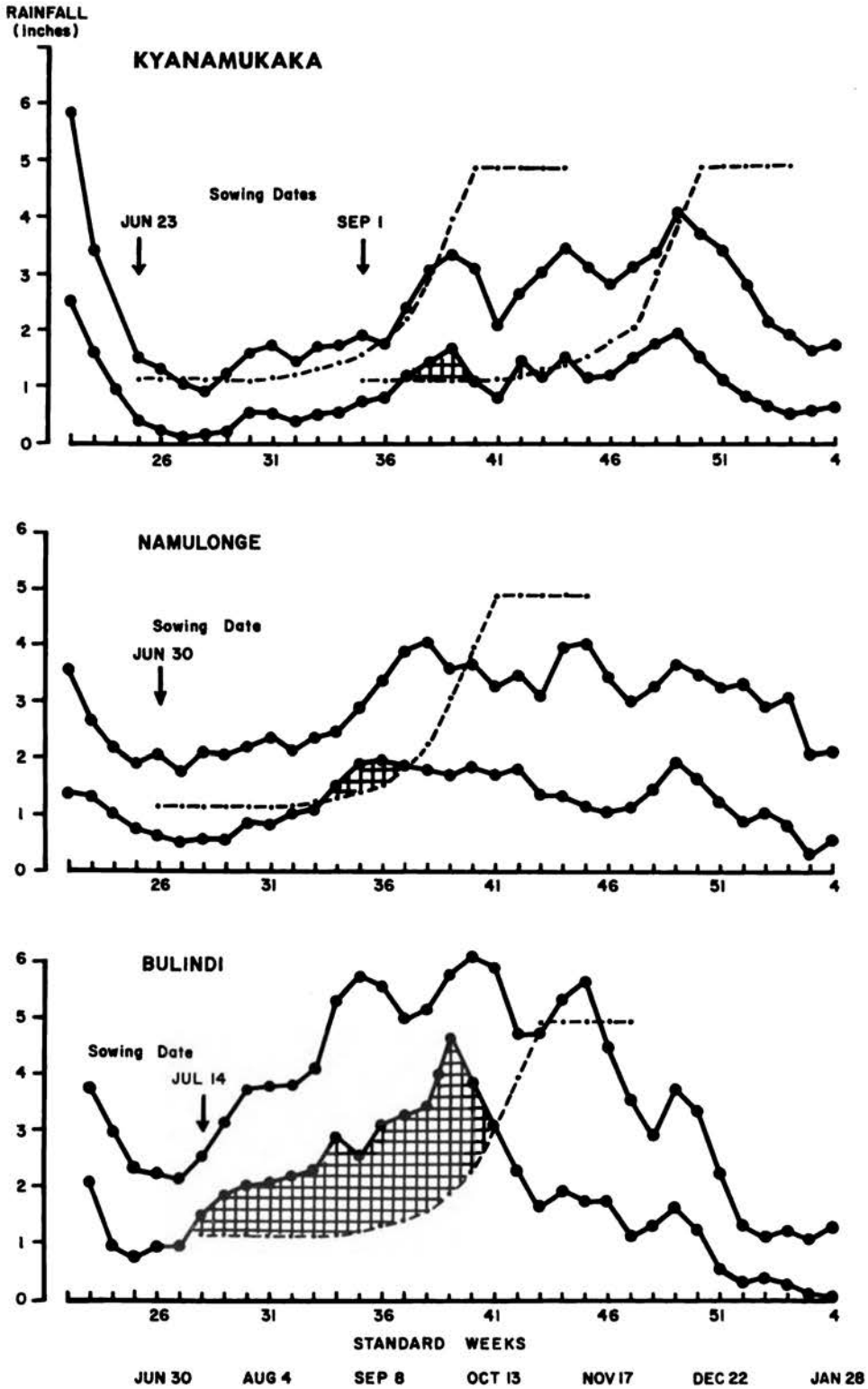


FIGURE 5. *Moisture requirement for cotton at specific sowing dates at three centres with 1:1 confidence limits of three week rainfall.*

tion of these rainfall patterns presents a method for determining sowing dates where no adequate run of yield data are available. That this method of assessing optimum sowing dates is of value is demonstrated with the analysis of the line trial data now to be considered.

ANALYSIS OF LINE TRIAL DATA

Yield improvement at various stages of the breeding program has been demonstrated for the general case by means. Moreover, this advance has been shown to be much influenced by climatic factors. Therefore, the question may well be asked as to the response under adverse conditions. The relative frequency of successes and failures will influence the growers of new seed, and a favourable mean could obscure a number of relative failures.

Taking the related variables, generation of selection, sowing date, and yield of local standard, an analysis of yield improvement was made using the separate 199 trials grown over eleven seasons. The analysis of variance of the multiple regression shows that each of these variables accounted for a statistically significant proportion of the variation of the yield increment. Consequently, it seems reasonable to estimate the actual lint increment per generation for these trials, at an average sowing date and for the general mean level of yield of the local. This latter can be justified on the grounds that there has been no significant increase or decline of local yield during the period. These data are summarized in Figure 6.

The mean lint yield per acre of local BP52 over the period was 275.9 lb. per acre. The sowing date value was 16.4, indicating that trials were generally sown within about 16 days either side of the specific optimum. Substituting these values in the multiple regression equation, the realized lint increment per generation would be expected to be

$$3.961 \times \text{Gen.} + 24.740.$$

The change from generation 1 with an expectation of 28.4 pounds to 64.1 pounds for generation 10, represents a percentage yield advance from 10.3 to 23.2 per cent. The spread of the individual trials around this regression is also of interest as one in three of the early selections, while showing a mean improvement of about 10 per cent, was no better than the control. This relatively poor performance of the selections caused some concern, particularly in Group II. Complete data in Table 3 indicate that in the later seasons the proportion of low yielding lines was much reduced, and for generation 10, only 1 in 12 tests was no better than the control. The justification for the overall regression analysis is perhaps best demonstrated by Groups in Table 4 where appropriate values for generation, sowing date and mean yield of local, are substituted. Actual and expected advances are given for generations of selection together with the number of trials from which these expectations were derived.

PROVINCIAL PRODUCTION

While the demonstration of yield improvement on the widest possible scale is, of course, the main test of the breeding system, there are a number of

TABLE 4.—COMPARISON OF ACTUAL AND EXPECTED LINT YIELD ADVANCE FROM 10 GENERATIONS OF SELECTION ADVANCES EXPRESSED AS PERCENTAGES OF APPROPRIATE GROUP MEAN OF LOCAL.

Gen[N]	Group I					Group II					Group III					Group IV					All trials				
	n	Local	Inc.	Actual	Exp.	n	Local	Inc.	Actual	Exp.	n	Local	Inc.	Actual	Exp.	n	Local	Inc.	Actual	Exp.	n	Local	Inc.	Actual	Exp.
1	16	333.1	41.3	12.4	10.7	15	311.9	11.9	3.8	9.8	6	217.5	10.5	4.8	10.8	.	.	.	.	.	37	305.8	24.4	8.0	10.3
2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
3	12	303.9	46.4	15.3	13.2	12	234.7	11.5	4.9	12.8	4	282.3	59.5	21.1	14.0	.	.	.	.	.	28	271.1	33.3	12.3	13.2
4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
5	10	307.2	69.2	22.5	15.7	10	214.8	22.6	10.5	15.8	4	269.5	52.5	19.5	17.2	1	89.0	15.0	16.8	18.7	25	255.5	45.7	17.9	16.1
6	5	379.4	88.2	23.2	17.0	6	337.3	99.3	29.4	17.3	2	274.5	89.5	32.6	18.8	1	198.0	54.0	27.3	20.7	14	333.4	90.7	27.2	17.5
7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
8	5	298.6	50.0	16.7	19.4	5	250.6	43.6	16.7	20.3	4	329.7	79.2	24.0	22.0	1	84.0	39.0	46.4	24.9	15	279.9	54.9	19.6	20.4
9	6	261.7	55.5	21.2	20.7	7	248.9	36.0	14.5	21.8	5	220.6	57.6	26.1	23.6	2	192.5	34.0	17.7	27.0	20	240.0	47.1	19.6	21.8
10	16	331.5	51.2	15.4	21.9	21	253.7	72.0	28.4	23.3	17	234.3	60.3	25.7	25.1	6	220.8	67.8	30.7	29.1	60	265.7	62.7	23.6	23.2
Weighted	n=70					n=76					n=42					n=11					n=199				
Means		318.8	53.6	16.8	16.3		263.7	41.1	15.6	17.2		249.2	55.3	22.2	20.5		189.2	53.0	28.0	26.6		275.9	49.1	17.8	17.7

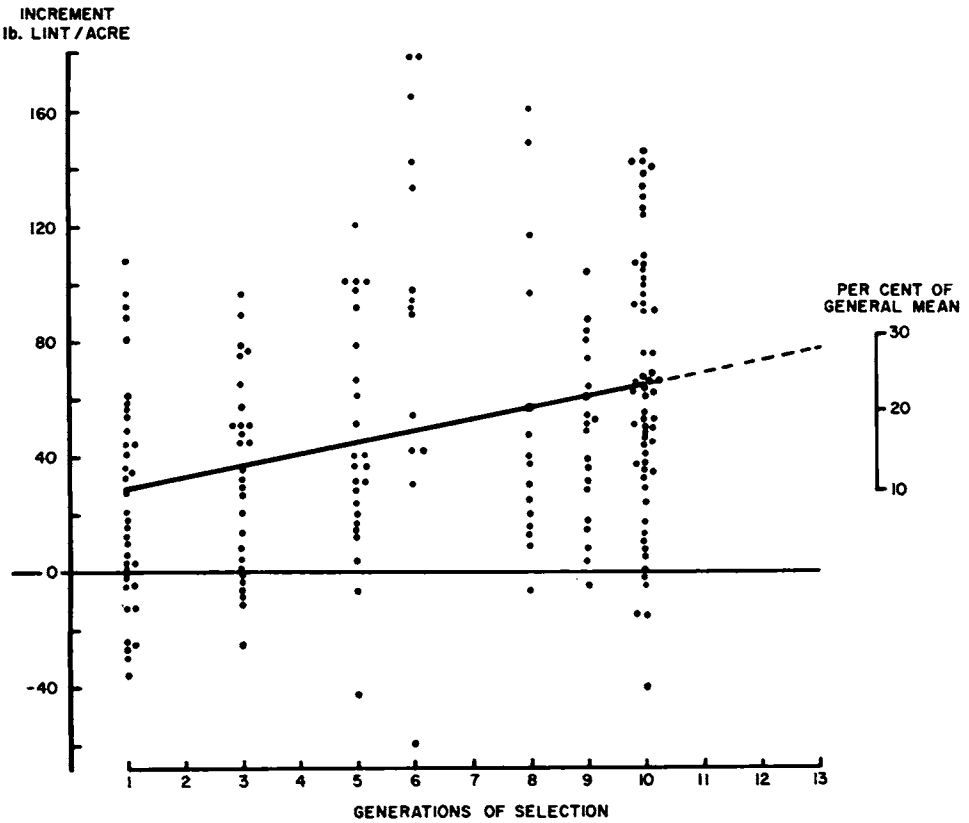


FIGURE 6. *Lint yield increment of selected strains over control from 10 generations of selection in BP52—data from 5 plot means in 199 trials.*
$y = 3.961$ (gen.) + 0.105 (local yield) − 0.523 (sowing date) + 4.466*

factors which prevent this at the present stage. The first of these is that with an excessively large number of ginneries operating, there is severe competition for seed cotton purchases. This makes it difficult to obtain accurate records of production in the separate administrative zones growing successive annual waves of the new multiline mixtures. Furthermore, with the large number of small holders receiving free planting seed, considerable allowance must be made for waste with the result that rate of increase is low. Fortunately, a number of the areas are relatively isolated and have now been growing the multilines long enough to obtain some indication of yield improvement. These data are summarized in Table 5.

The year of introduction of the improved lines is shown by underlining and it is apparent that for Toro, with only one ginnery, current production is about double that before these introductions. Moreover, mean production of the past 4 seasons for the four areas in Table 5, and where only part of the area grew the new seeds, is about 23 per cent greater than for the previous 6 seasons. That this production increase was only partly due to extension of acre-

TABLE 5.—COTTON PRODUCTION OF FOUR AREAS NOW GROWING NEW BP52 STRAINS. UNDERLINING INDICATES YEAR OF INTRODUCTION OF NEW STRAINS.

Season	Production by Districts. Thousands of Bales				
	Bunyoro	West Nile	Mubende	Toro	Totals
1950/51	7.8	6.0	20.7	4.2	38.7
1951/52	7.7	11.8	18.6	4.0	42.1
1952/53	7.2	8.1	13.5	4.0	32.8
1953/54	9.5	14.5	19.5	5.6	49.1
1954/55	7.3	9.0	13.7	4.0	34.0
1955/56	9.1	15.8	17.7	5.1	47.7
1956/57	7.9	11.8	15.9	8.2	43.8
1957/58	8.1	13.0	20.0	8.1	49.1
1958/59	11.3	17.9	20.8	9.7	59.7
1959/60	8.1	16.0	16.4	7.9	48.4

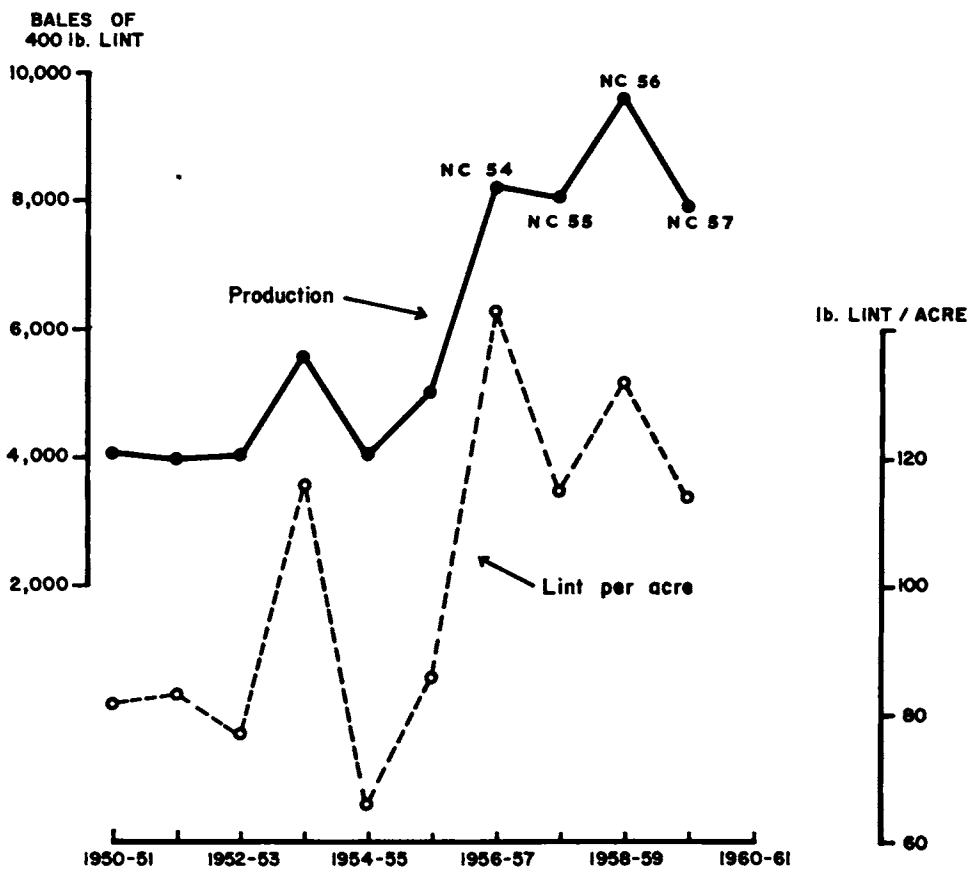


FIGURE 7. *Toro district production and yield data for 10 seasons. Namulonge multiline mixtures introduced 1956–57.*

age is demonstrated by the yield per acre estimates for Toro shown in Figure 7.

A striking yield increase was obtained in the year of the introduction of NC/54. The mean lint per acre for the 6 year period prior to the introduction of these lines, was 65.2 pounds. By contrast, the 4 year period during which NC/54, NC/55, NC/56, and NC/57 were grown successively, averaged 105.0 pounds lint per acre. It is therefore claimed that this breeding system has successfully produced improved lines.

DISCUSSION

Much of the success of the breeding work here described has depended on the efficient exploitation of genetic variability which has persisted through 12 generations of in-breeding. This self-fertilization, and the later analyses of variance of the replicated progeny row trials, provides the justification for partitioning phenotypic variance and inferring that, for certain traits, the genotypic portion is mainly additive.

Were the cultivated allopolyploid cottons to behave as functional diploids, it might be supposed that heterozygosity would, after 13 generations of inbreeding, have been so reduced as to make further line selection of little value. However, it was shown in a previous paper (4) that genetic variability of appreciable magnitude does persist. Moreover, with precise field experiments, the project has led to appreciable yield advance. The extent to which expected improvement has in fact been realized may now be considered.

Yield advance from experiments.

Cumulative expected genetic advance by progeny selection for the three component traits—bolling index, seeds per boll, and lint per seed—has increased from about 10 per cent from the first generation to about 40 per cent at the end of the tenth. This advance is based on the single environment of the Research Station where cultural conditions may be expected to be above the average for the commercial area.

Of the yield traits considered in the selection index, bolls per plant (bolling index) and lint yield itself are greatly influenced by environmental factors. There is also evidence to suggest that estimates of genetic variance for these two traits are biased by non-additive contributions. By contrast, the estimates of heritability for the traits, seeds per boll, and lint per seed appear to be due mainly to additive genetic variance. This is borne out by the analysis of the realized yield improvement due to lint per boll. The improvement for the means of all progenies over 12 seasons was of the order of 27 per cent, mainly attributable to boll size.

No simple expression of yield improvement from the second stage was worthy of consideration. This was because of the close relationship between the size of the increment and the yield level of the control, so that under poor growing conditions this improvement tended to be over-estimated. When the mean yield of the control obtained from the representative line tests was substi-

tuted in the multiple regression equation found to be necessary, a more reasonable estimate was obtained. Advance was expected to increase from 53 pounds of lint per acre from the first generation to 85 pounds from the tenth. This improvement, now expressed as a percentage, represents a yield advance from 19.4 to 31.1 per cent.

A similar multiple regression technique was found to be necessary for the line test stage. An additional variable based on sowing date was included. This factor had a profound effect on both yield of the standard and, consequently, the size of the increment. Where an adequate run of data was available planting dates were determined from yield/sowing data relationships. But for new areas the sowing dates were estimated from climatic patterns. The validity of this assessment is established by the statistical significance of sowing date/increment relationship. Advance in this third stage of test may then be expressed as a percentage, being 10 per cent from the first to about 23 per cent at the end of the tenth generation.

Crop improvement due to selection.

Because of the demonstrably wide climatic differences it was thought that a mechanical mixture of seed of different inbred lines, each chosen on the results from district trials, would be likely to give a higher average performance than any single selection grown over a wide area. This would obviate the necessity for separate multiplication of the distinct lines and accelerate the early stages of multiplication. The first of these mixtures released for commercial test was designated NC/54 indicating that it was bulked from tested lines at the end of the 1953–54 season. Later mixtures have been released in the annual seed renewal system and production data from Toro are now available for 4 seasons. The production increase from about 4,500 to 7,900 bales has provided valuable confirmatory evidence of the success of this line breeding, but of the later mixtures particularly NC/57 does not appear to reflect the same order of increase. Data now available from a series of diallel trials have thrown some light on this. It now appears that NC/54 and NC/55 contained a large proportion of a line which has now been shown to exhibit good general combining ability (6). Indeed there is evidence that NC/54 grown in successive seasons up to the fourth re-growth has shown a continuous yield improvement. The success of the later multiline mixtures will depend on the release of heterotic variance and therefore upon the amount of out-crossing which takes place. There is some evidence in Uganda that this is at a fairly high level (7). It is clear that in an area of appreciable out-crossing a breeding program based on progenies, strains, and lines is incomplete without parallel studies on the combining ability of the high yielding lines.

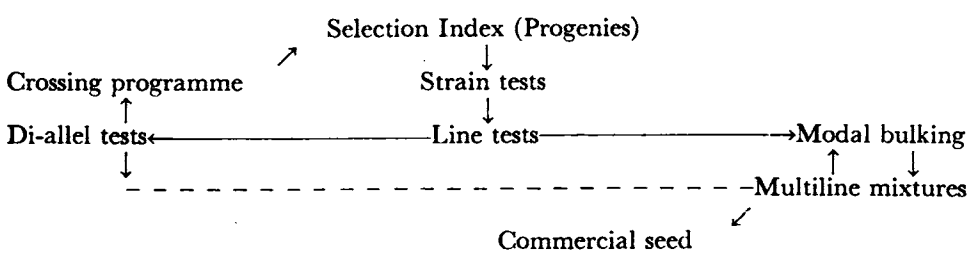
The certainty of yield advance over the entire BP52 area is not yet proved. The evidence from the Toro district (Figure 7) and the areas of relative isolation (Table 5) is quite impressive. Furthermore, record crops have been obtained from two districts growing the new seed, one of which has produced over 110,000

bales. To offset these advances, the equally important district of Mengo has produced one of the smallest crops so far recorded. This is almost certainly due to the greater reward from coffee growing which has increased as the cotton production has decreased over the last 10 years. In fact this trend of declining cotton production in Mengo has been evident before the introduction of the new lines, but it is confidently anticipated that, as more production data become available, the improvement demonstrated on the smaller scale will be confirmed.

Future program.

The question may well be asked as to the lessons learned from 13 seasons of this method of selection. In fact, were a new project to be launched, what changes would be made? It is unreasonable to expect a linear increase in yield traits to continue over an extended period of time and, indeed, there is some evidence that lint per boll, for example, is now increasing at a much reduced rate at the end of the twelfth generation. This decline was anticipated when the selection index work was first described, and it was then proposed to set up a panmictic population, derived from inter-crosses of selection lines, "to provide a higher base to build through future selection." Again, it has been found that an index based on seeds per boll, lint per seed, and lint yield itself is more efficient than the combination here reported. Although the estimates of genotypic variance for lint yield, like those of bolling index, probably include a large non-additive contribution, it is reasonable to assume that estimates of expected genetic superiority from an index based on the three alternative traits will be more efficient than one based merely on the two traits controlling lint per boll. Certainly the improvement in this latter has been shown to be consistent with the demonstrable overall improvement in the three stages of test, as well as over the widest possible commercial scale.

Following the strain and line tests, it is proposed that two parallel projects be considered. One would concern the modal bulking of a number of desirable lines. The second would be concerned with assessment of combining ability from di-allel trials. Combinations of the best lines would then be fed back into the selection index work as straight hybrids and, for multiline mixtures, as mechanical seed mixtures. Advantage could thus be taken of the improvements accruing from both methods of selection. In the case of the multiline mixture it is proposed to test for at least one season against the proven standards. The program could be summarized as follows:



Other breeding systems.

Many field breeders assert that computational requirements for the selection index breeding method are often beyond the capacity of small field stations. Furthermore, in the initial stages of programs involving hybridization, less precise breeding methods are all that is required, and there is a need for a simpler breeding method even if it is less efficient. In this respect the modal bulk technique has certain merits in that a number of plants can be chosen in the field and picked for later laboratory analysis when time permits. It has been shown that by employing the traits lint per seed, seed weight, and lint length, a moderate annual yield advance has been secured over 12 generations. But the precise mechanism by which this advance has been achieved is not fully understood.

Another equally simple method has been proposed by Harland (1). Only those plants above the average for a number of traits, are chosen to be parents for the following season. Thus, assuming normal frequency arrays, he supposed that in order to retain a nucleus of 8 plants satisfying these selection criteria for 7 traits, an initial choice of 1,024 plants should be made. However, in both of these systems, it does not appear to the writer that sufficient attention is paid to the phenotypic correlations between traits. The magnitude of these may, if negative, seriously affect the proportion retained in the succeeding trait. This in turn may require a rearrangement of the rank order of the traits in which the successive selection is made.

There would appear to be, therefore, scope for investigation by biometricians into the mechanism by which selection advance is achieved in these and other successful breeding systems. This is not to say that more complex systems are to be replaced, but merely to emphasize that their proper place is at the stage when the rate of advance of the simpler system is reduced to a level when the more refined techniques become essential.

SUMMARY

The BP52 variety of Upland cotton can be traced to a single plant in 1933. During the next 12 seasons, selection was exercised in respect of quality although disease resistance and yield were also considered. More recently, a selection index technique for yield has been used in self-fertilized material for 13 generations. The magnitude of the genetic variability which has persisted, has been sufficient to lead to appreciable yield improvement. At the end of the tenth generation the realized advances for the three stages of testing, progenies, strains and lines, were respectively 27, 32, and 24 per cent better than the composite yield standard representing the commercial crop in 1946. Comparable improvement in yield has also been shown over that part of the commercial area which has grown the new seed more than one season.

Suggested modifications to the breeding system are discussed briefly in the light of information on combining ability from a series of di-allel trials. A delay of one season in release of commercial seed issue is more than offset by the advantages likely to result from these changes.

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ACKNOWLEDGEMENTS

The organization involved in running the large number of line tests now employed reflects great credit on the Department of Agriculture, to whose Director and Staff acknowledgement is now made. My colleagues J. T. Walker and J. E. Dale are now engaged in important developments which have arisen from the first di-allel trial laid down by the former, and I am indebted to them for helpful discussion during the later stages of this work.

DISCUSSION

F. H. W. MORLEY: Why not simplify the selection procedure by simply selecting for yield per unit area—or at least include yield in the index?

H. L. MANNING: The question of including yield in the index has already been taken into consideration and, indeed, we now use the component seeds per boll, lint per seed, and yield itself. The only reason for continuing to estimate bolling index is to employ it for indirect estimates of genetic net worth to check the direct $g\ i\ w$ values.

Selection for yield per unit area is automatic, on the per plant basis, so long as the optimum spacing in relation to the normal environment has been previously ascertained.

R. J. MIRAVALLE: I would like to add a piece of supporting evidence from the cotton breeding program at the Shafter Station. The selection advance for pounds of lint per acre over the last 10 years has been estimated to be 33⅓ per cent or an average of 3.3 per cent per year. The selection procedure used was not based on a discriminant function or selection index nor was the Modal Bulk System used. A selfing system, individual plant to row procedure was used. Selection was based on superiority in agronomic, fiber and seed quality factors. Selection pressure for each of the traits involved varied from generation to generation.

H. L. MANNING: I am very pleased to hear of the similar annual advance to which Dr. Miravalle has referred. Although the system he describes is not comparable with the Modal bulk technique it would appear that the agronomic characters must have had specific advantages for the different seasons since the selection pressure differed for the generations.

JOHN GRAFIUS: I am delighted with your example of improvement in yield through selection of optimum in the components. I do not find this hard to believe and I feel that this has large implications.

H. L. MANNING: The importance of some of these environmental effects is apparent when estimating true advance at different yield levels and has previously been discussed by Dr. Grafius. Certainly the improvement in yield through selection of optima appears to have been very satisfactory when considering the various modal bulks.

SEWALL WRIGHT: The progress in yield that occurred following cyclic bulk selections from the middle halves of the distributions of lint per seed, average seed weight, and lint length is surprising. Only the first of those characters, however, is a direct component of yield. The result suggests that extreme values of one or more of these characters are incompatible with a harmonious combination of genes with respect to yield but that intermediate values are favorable, or in other words, that the optimum model applies in relation to yield.

H. L. MANNING: When the Modal bulk technique was first considered in 1947–48, it was hoped, as it now clearly transpires in error, that the selection for optima of these three traits would tend to stabilize the variety. Although lint per seed is, in fact, one of the yield components in the distinctive selection index method, it was not considered on these grounds in the modal bulk system. I agree with Dr. Wright that extremes of one or more of these characters are likely to be incompatible with harmonious gene combinations, particularly if there are known negative correlations. Perhaps this would explain why the "upper half mean" technique, suggested by Dr. Harland, is unlikely to prove a satisfactory selection method. I would like to go further and ask why mathematical geneticists don't devote some of their efforts to investigate the means by which some of these simple proven selection methods do in fact work.

Recurrent Selection[1]

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MANY of the attributes under selection in plant breeding programs are conditioned by many genes. The genotypic values of individual members within a population are the result of the cumulative effects of the individual genes and their interactions. Phenotypic expression of an attribute is a function of these genotypic values, the effects of environment, and genotype × environmental interactions. The efficiency of standard selection and inbreeding procedures, when applied to such quantitative characters, is limited by the types of gene action and interaction operative, genetic linkage, sampling limitations, and the masking effects of the environment.

In a breeding system embodying continuous self-pollination following selection of individual plants from a heterozygous population, the frequency of superior individuals in the population is of utmost importance. A ceiling upon possible progress from selection is established by the genotypes of the original S_0 plants. Subsequent opportunities for selection within inbred lines are restricted to recombinations of genes present in the parental plants. With continuous selfing the opportunities for selection rapidly dissipate due to the rapid approach to homozygosity. A substantial increase in the frequency of superior S_0 plants in the population used as source material for initiating a selection and self-pollination program would enhance greatly the chances of success in such a program.

From a comparison of top-cross yields of a group of lines in successive generations of inbreeding, Jenkins (3) concluded that inbred lines became rather stable for yield prepotency early in the inbreeding process. He explained this conclusion on the basis that yield was controlled by a large number of dominant genes with nearly equal effects. Although segregation occurred for particular dominant genes, little variation for total numbers of such genes would occur among plants within a line. Selection within a line through successive generations of inbreeding would preserve or fix essentially equal numbers of dominant genes in each of the individual plants selected. In discussing further studies of

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segregation for yield prepotency, Jenkins (4) emphasized the greater chances of obtaining high combining lines by selecting among lines rather than within progenies during inbreeding.

As a natural outgrowth of his conclusions relative to early testing, Jenkins (4) outlined a breeding procedure for the development of superior synthetic varieties of corn. The steps in the procedure were:

1. The isolation of one-generation selfed lines.
2. Testing these lines in top crosses for yield and other important attributes.
3. Intercrossing of a group of the selfed lines deemed superior on the basis of the top-cross evaluation.
4. Repetition of the process.

In this plan, Jenkins contemplated using the bulk population from which the selfed lines were derived as the tester parent of the top crosses. This would be a test for general combining ability.

Hull (2) later outlined a similar procedure and designated it as recurrent selection for specific combining ability. This was the first usage of the term "recurrent selection." He assumed that hybrid vigor for yield was due to the over-dominant expression of genes at numerous loci. Thus, the heterozygous condition at a locus would be more favorable than the homozygous condition of any of the possible alleles at that locus. For greatest efficiency in selection, a homozygous inbred line was suggested as the tester to which individual S_0 plants from a heterozygous population would be crossed. The ultimate objective of the plan was the production and commercial use of the first generation cross of the tester line with the improved population under selection.

Comstock, *et al.* (1) presented a third plan which they called "recurrent reciprocal selection," now usually called "reciprocal recurrent selection." This plan involved the use of two heterozygous populations, each serving as the source material for selection and also serving as the tester for the other population. Thus, individual S_0 plants from source A would be self-pollinated and also outcrossed to several plants of the tester, source B. Likewise, individual plants from source B would be self-pollinated and outcrossed to several plants of the tester, source A. After the two sets of test crosses were grown and evaluated in yield trials, two new populations would be produced by intercrossing selected superior S_1 lines within each source. The process was to be repeated through successive cycles. The ultimate goal was the production of commercial hybrids by crosses between the two sources. This could be done at any degree of inbreeding, ranging from crosses between the non-selfed bulk populations to crosses between homozygous lines developed from the two sources.

Comstock, *et al.* (1) presented the reciprocal recurrent selection plan in the belief that hybrid vigor in corn probably was due to a combination of the additive effects of favorable dominant genes at some loci and over-dominance at others. The relative efficiency and effectiveness of recurrent selection for specific combining ability, recurrent selection for general combining ability, and recipro-

cal recurrent selection were discussed for several genetic situations. They concluded that reciprocal recurrent selection was superior to selection for general combining ability for loci exhibiting over-dominance, superior to selection for specific combining ability for loci at which there was partial dominance of the more favorable allele, and therefore superior to either if a combination of loci exhibiting over-dominance and others exhibiting partial dominance existed.

The recurrent selection plans of Jenkins (4), Hull (2), and Comstock, *et al.* (1) differed in the basic concept of the cause of hybrid vigor, the type of tester to be used, and the ultimate goal for the use of the material developed. In spite of these differences, the three plans were very similar in procedure, and all incorporated the two basic principles of successive cycles of selection and recombination of a selected portion of the population.

Recurrent selection is a breeding system having some theoretical superiority over the standard system of continuous self-pollination. It has considerable promise as a method of effecting stepwise changes in gene frequency within a population without the rapid approach to homozygosity which limits selection under the selfing system. It is a method for improving populations. As such, it may have value if the ultimate goal is the development of a superior population to be used for commercial production *per se*. It also may have value when coupled with the standard inbreeding procedure if the ultimate goal is the utilization of inbred lines for the production of commercial hybrids. In this case, the usefulness of recurrent selection rests in its effectiveness in increasing the gene frequency for desired alleles, thus providing a population for inbreeding having a high frequency of elite or superior plants.

It appears appropriate at this time to review the results available from recurrent selection programs up to the present time. The following discussion will be based upon a review of published data and upon some previously unpublished data obtained in the corn improvement program being conducted in the Iowa Agricultural Experiment Station. In any reference to the number of years required per cycle or progress per year, it is assumed that one crop is grown per year. In corn the possible utilization of Florida plantings to obtain two crops in one year might speed-up progress on a per year basis. In the following discussion the designation C_0 will be used to indicate the original population from which the first selections are made; C_1 will indicate the first cycle population or the population formed by intercrossing selected individuals from the C_0 population, etc.

The best method to be used in evaluating the progress made with recurrent selection poses some problems. One method is to use a constant hybrid or group of hybrids as a check for comparison in the test-cross trials in each cycle. The difference between the mean of the checks and the mean of the test crosses in each cycle forms the basis for judging progress. In view of the large genotype-environmental interaction frequently reported from yield trials, it is doubtful that much confidence can be placed in such yield comparisons if only one check hybrid was used. Using the mean of several checks as the basis for comparison

would be much more meaningful. Another method for judging progress is to compare the tester × population crosses for successive cycles of selection, such crosses being grown all together in the same experiment. Unless progress has been of considerable magnitude relative to the standard error of such an experiment, a large number of replications may be necessary for conclusive results. A consistent trend in the means of these tester × population crosses from cycle to cycle could indicate that some progress had been made even though no significant differences were found from an analysis of variance of the data.

For convenience of discussion, recurrent selection will be divided into two types, phenotypic recurrent selection and genotypic recurrent selection. Phenotypic recurrent selection will include those cases in which the phenotype of the S_0 plant was the basis of selection. Genotypic recurrent selection will include all types of recurrent selection in which the basis of selection was the genetic worth of the S_0 plant as evaluated in some type of progeny test. This evaluation may have been on the basis of selfed-progeny performance or test-cross progeny performance. The test-cross progeny evaluation may be further subdivided on the basis of the degree of heterozygosity or heterogeneity of the tester.

PHENOTYPIC RECURRENT SELECTION

Phenotypic recurrent selection was defined as recurrent selection in which the phenotype of the individual S_0 plant serves as the basis of selection. This type of selection would be most useful for characters little affected by environment, thus having a high degree of heritability. Only one year is required per cycle if evaluations can be made before silking. Two years are required if evaluation is not possible that early.

Sprague and Brimhall (11) reported results of a program of selection for higher oil content in corn. Three sources of material were under selection using the recurrent selection method. In all three sources the full selective advantage of the selected sample from the original population was retained in the first cycle population. One of the sources was continued to the C_2 generation, retaining in the C_2 generation approximately $\frac{2}{3}$ of the selective advantage of the selected sample from the C_1 population. Mean oil content was shifted from 7.8 per cent to 10.5 per cent by the two cycles of selection. In a companion program beginning with the same plants from the original population and employing the approach of continuous selfing with selection within lines, the mean oil content was shifted from 7.0 per cent to 7.5 per cent through five generations of selection. Approximately equal numbers of pollinations and oil analyses and the same amount of time were employed in both programs. Compared on the basis of net increase in oil percentage, the recurrent selection series was more efficient than the selfing with selection series by a factor of 5.4. Later Sprague, *et al.* (13) reported on a second source of material which underwent selection by both systems. Two cycles of recurrent selection increased the mean oil content from 4.9 per cent to 7.0 per cent or an average of .4 per cent increase per year. In the series employing selfing with selection, the oil content increased from 5.0 per cent to 5.6

per cent or an average increase of .1 per cent per year. Considerable genetic variability remained in the recurrent selection material at the end of the study, whereas the lines in the selfing series were approaching homozygosity.

Jenkins, *et al.* (5) reported on the use of phenotypic recurrent selection in conjunction with a backcrossing program in an effort to accumulate genes for resistance in corn to *Helminthosporium turcicum*. Selections were made at pollinating time, thus allowing for one cycle per year. Their data indicated that two generations of intercrossing resistant plants was sufficiently effective to be warranted in all families with which they were working. A third cycle of selection was effective in some families but not in others. The effectiveness of the third cycle was inversely proportional to the amount of improvement obtained in the first two cycles, thus indicating a rapid decline in the genetic variance within some families. This would be expected with an attribute conditioned by relatively few genes and having high heritability.

A program similar to the one described by Jenkins, *et al.* (5) is being conducted in Iowa in an attempt to develop strains of corn resistant to the European corn borer (*Pyrausta nubilalis* (Hbn.)) Borer resistance in corn is thought to be conditioned by relatively few gene pairs, ranging from one to perhaps four or five in any one cross. However, the heritability or reliability of individual plant ratings varies considerably from season to season due to unexplained differences in the general level and uniformity of borer survival. Several agronomically desirable but borer susceptible inbred lines of corn were crossed to a source of resistance, backcrossed to the susceptible lines for two generations, and self-pollinated one generation. Following this first selfing, two cycles of intercrossing of plants on which no borers survived were used in an attempt to increase the frequency of resistant plants and perhaps intensify the resistance. Data are presented in Tables 1 and 2 to show the results from the selection programs

TABLE 1.—A SUMMARY OF EUROPEAN CORN BORER RATINGS OF INDIVIDUAL PLANTS OF 38–11 BACKCROSS MATERIAL IN SUCCESSIVE STAGES OF SELECTION COMPARED AT AMES, IOWA IN 1957.

Generation	Total plants	Mean rating[1]	Per cent plants rated		
			Resistant	Intermediate	Susceptible
38–11	212	4.9	16	69	15
S_1	231	4.7	26	52	22
S_1–I_1	239	3.5	52	41	7
S_1–I_2	262	3.8	42	49	9

[1]1—Most resistant; 9—Most susceptible.

involving the inbred lines 38–11 and WF9.The generation designations S_1, S_1–I_1, and S_1–I_2 refer to the selfing generation and the two intercrossing generations which followed the backcross phase of the program. The data presented are a condensation of individual plant ratings on a nine class scale of leaf feeding severity. In the 38–11 program, reported in Table 1, one cycle of recurrent selec-

TABLE 2.—A SUMMARY OF EUROPEAN CORN BORER RATINGS OF INDIVIDUAL PLANTS OF WF9 BACKCROSS MATERIAL IN SUCCESSIVE STAGES OF SELECTION, COMPARED AT AMES, IOWA IN 1957.

Generation	Total plants	Mean rating[1]	Per cent plants rated		
			Resistant	Intermediate	Susceptible
WF9	210	8.5	0	4	96
S_1	210	7.0	10	18	72
S_1–I_1	198	6.5	12	27	61
S_1–I_2	206	4.8	30	41	29

[1]1—Most resistant; 9—Most susceptible.

tion increased the frequency of resistant plants, but the second cycle was ineffective. In the WF9 program reported in Table 2, the first cycle of recurrent selection resulted in a minor shift in the number of plants from the susceptible to intermediate classification. A much greater improvement accompanied the second cycle of selection. An important factor to be considered in judging the value of recurrent selection would be the relative degree of resistance or possible intensification of resistance. A progeny test of the individual plants might have demonstrated different genotypes among the plants in the resistant classification. Unfortunately, the individual plant ratings provided no information on this point.

Both the Iowa data on corn borer resistance and Jenkins' data on *Helminthosporium turcicum* resistance demonstrated that recurrent selection could be used effectively to increase the frequency of desirable plants in a heterozygous population. However, neither of these studies provided any direct comparison of the efficiency of this method relative to that of selfing and selection within segregating lines. The oil data of Sprague and co-workers did provide this contrast and demonstrated considerable superiority of the recurrent selection method.

RECURRENT SELECTION BASED UPON S_1 PROGENY PERFORMANCE

In Iowa, three recurrent selection programs are being conducted with corn using S_1 progeny performance as the basis for selection. One population is undergoing selection for resistance to stalk rot, using artificial inoculation with *Diplodia zeae;* five populations are undergoing selection for resistance to the European corn borer; and one population is undergoing selection for yield. Only one cycle of selection has been completed in each program. No data are available from either the stalk rot or borer resistance programs with which to make a valid comparison of the C_0 and C_1 populations. However, the frequency of resistant progenies obtained from selfing in the C_1 populations was sufficiently high in both programs to indicate that the first cycle of selection was fairly effective in increasing the frequency of desired genes. The program of selection for yield involved a strain of the Krug variety obtained from Dr. J. H. Lonnquist of Nebraska. In a comparison involving two yield trials in each of 2 years, the

C_1 population yielded 105.4 bushels per acre as compared to 98.1 bushels per acre for the C_0 population. Thus, one cycle of selection based on S_1 progeny performance resulted in a population yield gain of 7.3 bushels per acre.

RECURRENT SELECTION FOR GENERAL COMBINING ABILITY

Jenkins (4) outlined the procedure of recurrent selection for general combining ability as a method for developing high yielding synthetic varieties. He suggested that random plants from the population under selection be used as the tester to which selected plants would be crossed. For the purposes of this discussion, recurrent selection for general combining ability will include any cases in which the tester was other than a homozygous line.

Johnson (6) reported results from a recurrent selection program for forage yield in Madrid sweet clover. Open-pollination or top-cross progeny performance of individual plant selections from the C_0 and C_1 populations was obtained. Yield data were presented as per cent of the parental Madrid populations used as a check. Although the top crosses representing the two populations were grown in different years, performance relative to the Madrid check was considered a valid base for comparison. The mean top-cross performance of the original selections was 91.9 per cent of Madrid and that of the first cycle selections was 121.1 per cent of Madrid. The mean of the first cycle selections exceeded the mean of the selected sample from the original population, thus retaining the full selective advantage of the selected sample. The variances among top crosses of the two populations were very similar with no indication of a reduction in genetic variance from one cycle of recurrent selection.

Lonnquist (7, 8), McGill and Lonnquist (10), and Lonnquist and McGill (9) described in detail the methods used and some of the results obtained from a program of recurrent selection for general combining ability being conducted with corn in Nebraska. One of the objectives of the Nebraska program has been to develop high yielding synthetic varieties for possible commercial use. Lonnquist and McGill (9) presented yield results obtained with the synthetics after one and two cycles of selection. Yields of the first cycle synthetics of three varieties exceeded those of the parental varieties by an average of 13 per cent. In another comparison, yields of the first and second cycle synthetics from four sources of material were compared with the yield of the double-cross hybrid US 13. The first cycle synthetics averaged 82 per cent and the second cycle synthetics averaged 96 per cent of US 13. The authors concluded that recurrent selection resulted in a rapid improvement in the yield of the corn varieties.

McGill and Lonnquist (10) presented some interesting comparisons from one of their selection programs involving the variety Krug. The parental variety Krug was used as the tester parent in the original sampling of the C_0 population. Eight S_1 lines having the highest top cross yields were intercrossed forming a high-yield synthetic. Seven S_1 lines having the lowest top-cross yields were intercrossed to form a low-yield synthetic. Both the high and low yield C_1 synthetics were sampled for the next cycle of selection. However, the single-cross hybrid

WF9 × M14 was used as the tester parent in the test crosses of the C_1 material. A C_2 low-yield synthetic, designated KL_{II} was produced from intercrosses of the 11 lines from the C_1 low-yield synthetic having the lowest test-cross yields. Two C_2 high-yield synthetics were produced. One, designated KH_{II} (31), was produced from intercrosses among the 31 lines from the C_1 high-yield synthetic whose test-cross yields exceeded the mean yield of all test crosses by one or more standard deviation units. The other designated KH_{II} (10) was produced from intercrosses among the 10 lines from the C_1 high-yield synthetic whose test-cross yields exceeded the mean of all test crosses by 2 or more standard deviation units. A concurrent program of selfing within lines accompanied by test-cross yield evaluation in each generation from S_1 to S_5 was carried out beginning with the same lines as were used for producing the C_1 high-yield and low-yield synthetics. Test crosses of individual plants from the three C_2 synthetics and the parental Krug variety and of S_5 lines from the high and low yield selfing series were compared in a yield trial. Some of the data are presented in Table 3. There appeared to

TABLE 3.—YIELDS AND GENETIC VARIANCE ESTIMATES OBTAINED WITH TEST CROSSES OF KRUG LINES PRODUCED UNDER DIFFERENT BREEDING SYSTEMS. (MCGILL AND LONNQUIST, 10).

Source of test crosses	Number of crosses	Mean yield (Bu/A)	$s^2_p/1$
KH_{II} (31)	76	97.5	0.392
KH_{II} (10)	75	97.9	0.374
"High" lines	22	97.1	——
Krug (original)	76	92.4	0.815
KL_{II}	75	90.1	0.245
"Low" lines	8	90.5	——

[1]Estimated genetic variance among test crosses.

be no difference in mean test-cross yield between the plants of the two high-yield synthetics and the lines developed by selfing with selection for high yield in each selfing generation. Both of the high-yield recurrent selection synthetics and the S_5 high-yield lines were superior to the original Krug. Selection for low yield appeared equally successful under the two selection systems. Estimated genetic variances among test crosses indicated a considerable reduction in genetic variability in the populations after two cycles of recurrent selection. However, some genetic variability did remain in these populations whereas little if any would be expected to remain within the lines developed under the continuous selfing system. Thus, further progress might be possible from selection in the recurrent selection populations, but none would be expected from further selection within the S_5 lines.

Sprague and Brimhall (11) presented data obtained from one cycle of recurrent selection for general combining ability. The population under selection was a synthetic variety called Stiff Stalk Synthetic. The tester was the double-cross hybrid Ia. 13. Test-cross yields of selections from the C_0 and C_1 populations

were obtained in different years. The Ia. 13 tester was included in the test-cross trials each year and was used as a basis of comparison for judging the effectiveness of the one cycle of selection. When compared through this common check hybrid, the yields of the test crosses of C_1 selections exceeded those of the test crosses of the C_0 selections by approximately 7 bushels per acre. The authors concluded, "It is apparent that one cycle of recurrent selection has resulted in a marked shift in the mean."

The Stiff Stalk Synthetic recurrent selection program with Ia. 13 as tester now has been carried through four cycles of selection in Iowa. Data bearing on the effectiveness of this program are presented in Table 4. The population × Ia. 13 data are a summary of results from 1958 and 1959 yield trials, two test locations each year. All other data were obtained in different years for each generation. Only one test-cross trial each was grown for the C_0 and C_1 generations. The

TABLE 4.—YIELD DATA OBTAINED IN IOWA FROM RECURRENT SELECTION IN STIFF STALK SYNTHETIC, IA.13 BEING USED AS TESTER.

Generation	Test-cross yield trials			1958–59 yield trials	
	Ia.13 (Bu./A)	Mean of test crosses (Bu./A)	Calculated genetic advance (%)	Population × Ia.13 (Bu./A)	Observed genetic advance (%)
C_0	88.9	82.3	10.1	104.8	—
C_1	86.1	85.9	5.9	102.3	−1.4
C_2	104.3	104.2	6.5	108.0	5.6
C_3	74.3	72.1	0.0	108.0	0.0
C_4	103.6	111.3	3.1	110.0	1.9

C_2 and C_3 data were obtained in two yield trials in 1 year for each generation. The C_4 data are a summary of results from two trials in each of 2 years. The expected genetic advance was calculated as follows:

$$\text{Genetic advance} = (\bar{x}_s - \bar{x})\, s_g^2 / \left(s_g^2 + \frac{s_{gt}^2}{t} + \frac{s^2}{rt}\right)$$

Where: $\bar{x}_s$ and $\bar{x}$ are the mean yields of the selected sample and all test crosses, respectively.

s_g^2, s_{gt}^2, and s^2 are the estimated variance components for test-cross differences, interaction of test crosses with environments, and experimental error, respectively.

t and r are the number of trials and the number of replications per trial, respectively.

In the above formula for expected genetic advance, the variance component s_{gt}^2 could not be estimated for those generations in which only one test-cross trial was conducted and therefore was assumed to be zero. This assumption is known

to bias upward the estimate of expected genetic advance. For those generations in which the test crosses were grown at more than one location or in more than one year, the trials were assumed to represent a random sample of trial environments. Thus, the estimated variance component s_{gt}^2 was not sub-divided into location, year, or location × year components. Observed genetic advance values in Table 4 from the 1958–59 yield trials for each generation should be compared to the calculated genetic advance estimates from the test-cross yield trials of the preceding generation.

The mean test-cross yield in comparison with the yield of Ia. 13 was lowest for the C_0 generation and highest for the C_4 generation. Considerable genetic variance among test crosses was present for each cycle of selection except for the C_3 generation as indicated by the calculated genetic advance values. The relative yields of the test crosses in the two C_3 test-cross yield trials differed widely giving a high test cross × environment interaction in the analysis of the combined data. Since the two trial locations were considered to represent random environments, the high test cross × environment interaction led to a zero estimate of the variance due to test-cross differences. Although there were no statistically significant differences among the population × Ia. 13 crosses grown in 1958 and 1959, an increasing yield trend was indicated. If the population × Ia. 13 yields are assumed to represent accurately the true yield values of those crosses, four cycles of recurrent selection resulted in a yield increase of 5.2 bushels per acre. This amounts to a disappointing 1.2 per cent increase per cycle over the original population.

RECURRENT SELECTION FOR SPECIFIC COMBINING ABILITY

Hull (2) first suggested the procedure for recurrent selection for specific combining ability. He pointed out that a homozygous line would be the most efficient tester, althought he did not limit the method to this type of tester. Sprague and Miller (12) suggested using recurrent selection for specific combining ability for obtaining information on the relative importance of overdominance and partial or complete dominance of favorable alleles as the cause of heterosis in corn. Their plan involved concurrent selection within two heterozygous sources using a common inbred line as tester for both sources. Two such selection programs were begun in Iowa. It is not the purpose of this presentation to discuss the relative importance of dominance and overdominance. However, results from these two selection programs provide some information on the effectiveness of recurrent selection for specific combining ability.

Available data from one of the Iowa programs were reported by Sprague, *et al.* (14). The two sources of material under selection were strains of open-pollinated varieties called Lancaster and Kolkmeier. The first cycle of selection was carried out in Indiana with the single-cross hybrid WF9 × Hy as tester. Yield data obtained on crosses involving the populations derived after successive cycles of selection are presented in Table 5. These data are a summary of yields obtained in comparative trials for the 3-year period, 1955–1957. Significant yield

TABLE 5.—AVERAGE YIELDS AND OBSERVED AND CALCULATED GENETIC ADVANCE FOR SUCCESSIVE CYCLES OF RECURRENT SELECTION FOR SPECIFIC COMBINING ABILITY (SPRAGUE, *et al.* 14).

Cross	Yield (Bu./A)	Genetic Advance	
		Calculated (Bu./A)	Observed (Bu./A)
Lancaster C_0 × Hy	76.4	—	—
Lancaster C_1 × Hy	80.3	2.6	3.9
Lancaster C_2 × Hy	82.9	14.9	6.5
Kolkmeier C_0 × Hy	69.1	—	—
Kolkmeier C_1 × Hy	76.1	3.5	7.0
Kolkmeier C_2 × Hy	89.1	9.0	20.0

improvement was obtained from selection within both sources of material. Expected genetic advance values were calculated from the test-cross yield data for the successive cycles of selection. In three of four possible comparisons of the calculated and observed gains, the observed gains actually exceeded the expected gains.

The other Iowa program of recurrent selection for specific combining ability involved the use of the inbred line B14 as tester. The two sources of material for selection were an open-pollinated variety called Alph and the F_2 generation of the cross WF9 × B7. Data obtained after two cycles of selection in this program are presented in Table 6. The calculated genetic advance values were obtained from the test-cross trials for each cycle of selection. For ease in comparison they are presented in the table for the generation in which the advance should be realized rather than the generation from which the values were calculated. The acre yields in bushels per acre and the observed genetic advance values in per cent of the previous generation are a summary of data from 7 com-

TABLE 6.—MEAN YIELDS AND OBSERVED AND CALCULATED GENETIC ADVANCE FOR SUCCESSIVE CYCLES OF RECURRENT SELECTION FOR SPECIFIC COMBINING ABILITY.

Cross	Yield (Bu./A)	Genetic Advance	
		Calculated (%)	Observed (%)
Alph C_0 × B14	111.3	—	—
Alph C_1 × B14	117.4	16.7	5.5
Alph C_2 × B14	127.3	8.5	8.4
(WF9 × B7) C_0 × B14	119.8	—	—
(WF9 × B7) C_1 × B14	123.4	7.1	3.0
(WF9 × B7) C_2 × B14	123.6	7.2	0.2

parative trials over a 3-year period, 27 replications in all. Significant yield improvement, approximately 7 per cent per cycle, was obtained in the Alph material. Yield improvement was much less in the WF9 × B7 material, averaging approximately 1.5 per cent per cycle. The difference in calculated genetic advance between the two selection sources could hardly explain the excellent results of the selection in Alph but very mediocre results in WF9 × B7.

RECIPROCAL RECURRENT SELECTION

Iowa data are available for evaluating two cycles of selection in one reciprocal recurrent selection program. The two populations under selection were synthetic varieties designated Stiff Stalk Synthetic and Corn Borer Synthetic. A summary of data obtained in eight yield trials conducted over a 2-year period are presented in Table 7. Four of the yield trials contained 103 test crosses of individual plants from the C_2 generation of Stiff Stalk Synthetic crossed to the tester, Corn Borer Synthetic C_2. The other 4 trials contained 103 test crosses of individual plants from Corn Borer Synthetic C_2 crossed to Stiff Stalk Synthetic C_2. Four adapted double-cross hybrids and the bulk $C_0 \times C_0$ and $C_1 \times C_1$ crosses of the recurrent selection populations were included in all eight yield trials. Thus, in Table 7 the yields of the checks and the $C_0 \times C_0$ cross and the yield and observed genetic advance of the $C_1 \times C_1$ cross were obtained from a summary of all 8 trials or 24 replications in all. The yield and observed genetic advance for the $C_2 \times C_2$ cross were obtained from a summary of mean yields of 206 test crosses, each cross being grown in 4 yield trials. The calculated genetic advance values were obtained from the previous test-cross evaluation trials for each cycle of selection and are the sum of the individual values obtained from the Stiff Stalk Synthetic selections crossed to Corn Borer Synthetic as tester and the Corn Borer Synthetic selections crossed to Stiff Stalk Synthetic as tester.

The low calculated genetic advance value obtained from the first cycle of selection was the result of very low genetic variance estimates obtained in the C_0 test-cross trials. In the analysis of variance of the data from the test-cross trial of selections from the Stiff Stalk Synthetic C_0 population, the mean square for test crosses was actually numerically less than that for experimental error. This

TABLE 7.—MEAN YIELDS AND CALCULATED AND OBSERVED GENETIC ADVANCE FOR SUCCESSIVE CYCLES OF RECIPROCAL RECURRENT SELECTION.

Cross	Yield (Bu./A)	Genetic Advance	
		Calculated (%)	Observed (%)
SSS C_0 × CBS C_0	76.3	—	—
SSS C_1 × CBS C_1	81.1	3.0	6.3
SSS C_2 × CBS C_2	84.1	12.8	3.7
Mean of checks	84.9		

appeared to be the result of low variance among test crosses rather than an unusually high experimental error. In spite of the low genetic variance estimates in the C_0 generation, considerable progress in yield improvement was made from selection in this generation. Additional improvement was obtained from the second cycle of selection. On the basis of these data, approximately 5 per cent improvement per cycle or 2½ per cent per source per cycle was obtained from reciprocal recurrent selection. As previously noted, approximately 1.2 per cent improvement per cycle was obtained from four cycles of recurrent selection in Stiff Stalk Synthetic with the double cross Ia. 13 as tester.

One cycle of selection in another reciprocal recurrent selection program in Iowa has been completed. This program utilized the F_2 generation from two single crosses as the source populations for selection. Only meager data are available for judging the success of this program. However, if judged on the basis of available data, little if any progress was made in the one cycle of selection.

GENETIC VARIANCE ESTIMATES

Theoretically, recurrent selection is a method for making stepwise changes in gene frequency within a population while maintaining sufficient genetic variability for continued selection. The data of McGill and Lonnquist (10) presented in Table 3 indicated that two cycles of recurrent selection reduced considerably the genetic variance in the two high-yield Krug synthetics. Genetic variance estimates were obtained from the test-cross trials of each cycle of selection in the various recurrent selection programs underway in Iowa. These trials were grown in different years and at different locations and involved different selection populations and testers. No consistent pattern of these estimated genetic variances was apparent from the individual trials. The variance estimates were then summarized by generation and source of material under selection. This summary is presented in Table 8. The individual genetic variances were calculated as a per cent of the mean yield of all test crosses included in the particular yield trial involved. This basis was considered to be satisfactory for summarizing over several trials in which the actual yield levels differed widely. The data in Table 8 would indicate that greater genetic variability was present in the open-pollinated varieties than in the other two types of populations, but sufficient variability was present in all types of populations for effective selection. The data were not sufficiently consistent to estimate any rate of decline of genetic variability with each cycle of selection. The level of genetic variability maintained is of such importance in judging the value of recurrent selection that experiments adequate to assess this characteristic of populations undergoing selection should receive high priority in future experimentation.

DISCUSSION

As mentioned previously, evaluating the progress made with recurrent selection poses some problems. The coefficients of variation in corn yield trials in Iowa usually average approximately 8 per cent, frequently are as high as 12

TABLE 8.—SUMMARY OF TEST-CROSS VARIANCE ESTIMATES OBTAINED FROM RECURRENT SELECTION TEST-CROSS YIELD TRIALS IN IOWA.[1]

Generation	Types of population		
	Open-pollinated variety	Synthetic variety	F_2 of single cross
C_0	73.6 (1)	16.2 (3)	30.4 (5)
C_1	127.6 (6)	38.9 (5)	32.7 (10)
C_2	45.2 (5)	21.3 (10)	22.3 (2)
C_3		41.4 (2)	
C_4		21.5 (4)	

[1]Estimate of variance among test crosses in per cent of mean yield of test crosses. Number in parenthesis indicates the number of trials from which estimates were obtained.

per cent, and almost never are below 5 per cent. Yield differences of the magnitude found in some of the recurrent selection studies would necessitate the use of many replications for statistical significance. Assuming a coefficient of variation of 8 per cent, approximately 21 replications would be required for a yield difference of 5 per cent to be considered significant at the 5 per cent probability level. Furthermore, sizeable genotype × environmental interactions are known to occur. Relative yields obtained from trials grown in one year or period of years could differ considerably from those obtained from trials grown in other years. A third problem arises from the possible bias of published reports of research. Positive results would be much more likely to be published than would negative results.

Subject to the foregoing considerations, certain comparisons of the results appear worth mentioning. Phenotypic recurrent selection has been very successful. This may be due in part to the fact that this type of selection has been practiced primarily for attributes having relatively high heritability under most normal environmental conditions. Results of selection for combining ability as judged by grain yield have been more erratic. Of four populations undergoing selection for specific combining ability in Iowa, the three derived from open-pollinated strains of corn have had observed yield gains averaging approximately 7.5 per cent per cycle through two cycles. The other, derived from the F_2 generation of a cross between two inbred lines, had a yield improvement approximating 1.5 per cent per cycle. Recurrent selection with a single cross as tester in Nebraska was considered successful in improving the yield of synthetic varieties as well as in providing improved populations from which to obtain high combining inbred lines by self-pollination. Selection in Iowa with a synthetic variety as the source material and a double-cross hybrid as tester gave yield increases of only slightly over 1 per cent per cycle through four cycles. Reciprocal recurrent selection with two synthetic varieties gave observed yield increases of approximately 5 per cent per cycle or 2.5 per cent per source per cycle through two cycles. The first cycle of reciprocal recurrent selection with two F_2 popula-

tions from single crosses gave essentially no yield increase. Many of the yield increases have been too small to be adjudged statistically significant. However, the increasing yield trends in nearly all cases would indicate that real progress has been made.

Regardless of the type of recurrent selection practiced, the observed gains from F_2 populations have been consistently lowest, those from open-pollinated varieties highest, and those from synthetics somewhat intermediate. Differences in the amount of genetic variability probably are responsible for some of these differences in gains from recurrent selection. However, the genetic variance estimates presented in Table 8 indicated that considerable genetic variability was present in the populations derived from the crosses of two inbred lines. Genetic linkage might provide a possible explanation of the poor results of selection in these populations. The open-pollinated varieties would be in approximate linkage equilibrium whereas linkage effects would be at their maximum in F_2 populations. If genetic linkage does provide a serious barrier to effective selection, this effect could be minimized by a few generations of random mating in these populations before selection is started.

An important consideration in evaluating the effectiveness of selection in an open-pollinated variety is the relationship of improvement of mean combining ability of the population to the combining ability of the extreme deviates. An improvement in mean performance could occur merely through an elimination of the extremely poor material from the population. This improvement in mean performance might or might not be accompanied by a higher level of performance of the upper extreme deviates of the population. Little if any information bearing on this possible result of selection is available at present.

The contribution of the tester parent to the test-cross variance in yield trials deserves some consideration. If an inbred line, single cross, or group of single crosses is used as tester, each of the selected plants from the selection population are compared in the same tester background. Thus, the differences in yield among test crosses, aside from differences due to experimental error, are a true reflection of genic differences among the selected plants. However, in reciprocal recurrent selection and recurrent selection for general combining ability with a heterogeneous tester, the test-cross differences arise not only from genetic differences among the selected plants being tested, but also from the differences in the sample of plants from the tester parent. The magnitude of the contribution of this latter source of variability would decrease with an increase in the number of tester plants for each plant being tested. Whether the sampling of the tester parent is a serious source of error is not known. However, research on this question would seem desirable.

Many important questions concerning recurrent selection remain unanswered. In fact consideration of the data presently available seems to raise many questions and answer few.

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DISCUSSION

WILLIAM L. BROWN: When comparing genetic variability between recurrent and selfing schemes, is it not more realistic to compare genetic variability of the intercrosses of the selfed lines with the C_3, C_4, etc. generations?

L. H. PENNY: The high oil selection experiments were designed to provide a comparison of the efficiency and effectiveness of recurrent selection and continuous self-pollination with selection. The two systems were designed to require approximately equal numbers of pollinations and oil analyses and to take approximately equal time. Comparisons of mean oil percentages and genetic variances in the material from the two selection systems after a specified period of time would appear realistic and justified. Comparisons of mean oil percentages and genetic variances in the intercrosses of the self-pollinated lines also would appear realistic if the material were available. Which comparison would be most realistic would depend upon the use to be made of the material at the end of this specified period of time.

Phenotypic Stability of Growth in the Self-Fertilized Species. *Arabidopsis thaliana*

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CONSIDERABLE evidence has accumulated which demonstrates that, in cross-fertilized species, heterozygotes exhibit greater phenotypic stability ("developmental homeostasis") than homozygotes when exposed to a spectrum of environmental conditions. The experimental evidence comes from many species of plants and animals but the most elegant and conclusive data come from *Drosophila* experiments.

In contrast to the consistency of evidence for heterozygote superiority of phenotypic stability in outbreeding species, the evidence for inbreeding species is conflicting. Among others, see Lerner (9) for review of early work, Jinks and Mather (6), Lewis (10, 11) and Williams (16). For example, Lerner (9) concluded that: "On the grounds which form the basis of the postulate for cross-fertilized organisms (i.e., that departure from the breeding system normal for the species leads to loss of buffering powers), the expectation for autogamous populations is that the variance of the F_1 will be higher than that of the parents." More recent experimental evidence not only fails to support this conclusion, but suggests that the phenotypic stability of heterozygotes of inbreeding species may be equal to, and in some cases greater than, that of the homozygotes (11).

The major difficulty in an experimental examination of Lerner's (9) hypothesis has been the lack of an inbreeding species with at least some of the desirable properties of Drosophila, which include, (i) short life cycle, (ii) small organisms, and (iii) availability of diverse genetic material. However, the development of techniques (7) in which Arabidopsis plants are grown aseptically in test tubes, and the design of suitable growth cabinets, provide material and facilities comparable to Drosophila and its culture.

Arabidopsis plants will flower and set seed within a test tube (Figure 1). Some races have an extremely short life cycle when grown in continuous light, flowering within 10 to 12 days after germination. Since a plant requires only the space of a single test tube, large numbers of plants can be grown in a relatively small space, which facilitates exact control of environmental conditions. For example, a growth cabinet having a tray space of 12.5 square feet has a capacity of 840 plants.

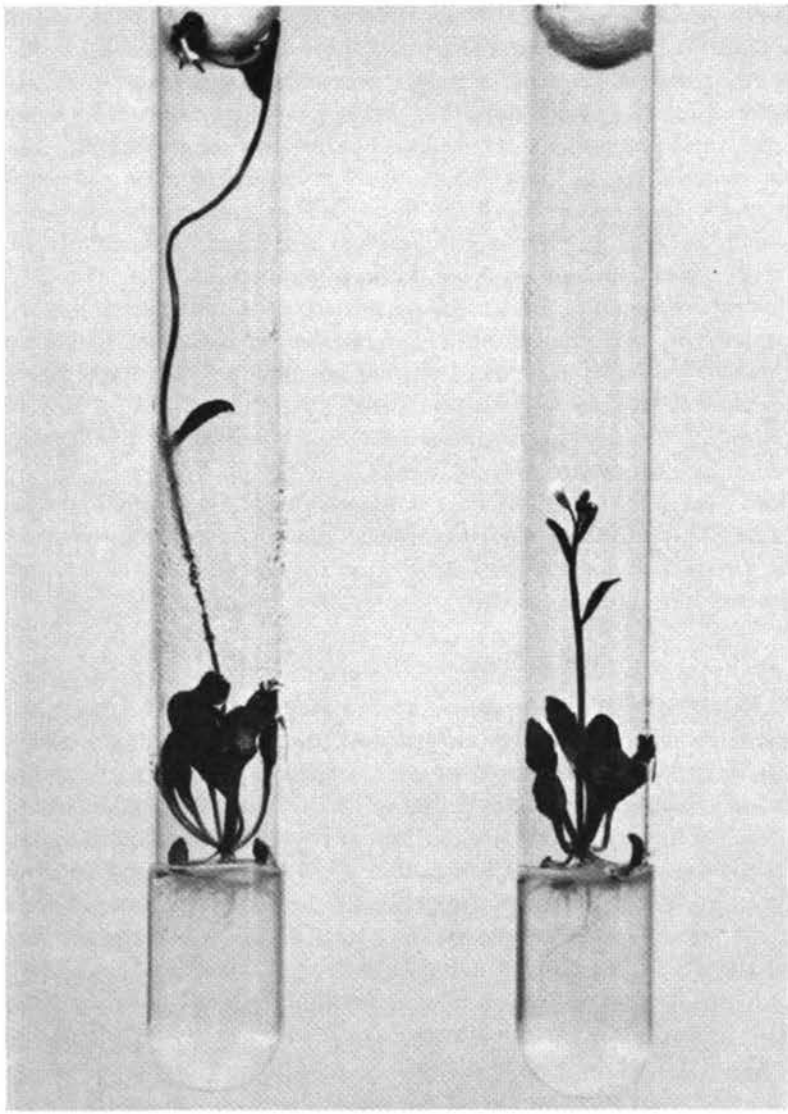


FIGURE 1. *Growth and flowering of Arabidopsis plants in test tubes.*

Arabidopsis thaliana is a widespread species, plants from different geographical areas being locally adapted and homozygous. As with Drosophila, collections from natural environments provide adequate sources of genetic diversity. Like Drosophila it has a small number of chromosome pairs, namely five.

Thus, it is clear that Arabidopsis under laboratory conditions and culture has many of the advantages of Drosophila. In fact it is frequently known as the Drosophila of the plant kingdom.

The object of this study is to examine phenotypic stability in an inbreeding species and to compare the results with those from similar studies in Drosophila. For this purpose, an array of genotypes was exposed to each of a series of temperatures, equally spaced, so as to obtain response curves which could be analysed by various methods, especially by the orthogonal fitting of fourth degree polynomials to the data. The use of equal increments of temperature also facilitates an understanding of the nature of the greater phenotypic stability in the hybrids by enabling an examination of the mean performance of heterozygous versus homozygous genotypes at each temperature.

This experimental approach has permitted, (i) the formulation of a genetic hypothesis for the basis of heterosis for phenotypic stability with respect to temperature, (ii) a reasonable explanation of some of the inconsistencies of past experimental studies with self-fertilized species, and (iii) a physiological interpretation of at least part of the heterosis observed in field-grown crops which are subject to environmental stresses.

The importance of this subject is obvious from the plant breeding point of view. The plant breeder's choice between homozygous or heterozygous plants as the end product of his selection may often depend on information as to the relative phenotypic stability of the two sorts of material.

MATERIALS AND METHODS

Thirty-eight races (ecotypes) of *Arabidopsis thaliana* (L.) Heynh. formed the experimental material. The races represent part of a collection from Professor F. Laibach, Frankfurt-am-Main. They were originally obtained in the geographical area extending from Holland (Hiversum) to Japan (Tsu Islands) and from Sweden (Stockholm) to North Africa (Martuba). All plants of each race used in the experiments were grown from seeds of a single plant. Because they are obligately self-fertilized, individual plants may be regarded as homozygous.

Plants were grown aseptically in standard test tubes containing an inorganic nutrient salt solution solidified with agar (7). Plants of each experiment were grown for 14 days in continuous fluorescent light of approximately 1,200 foot-candles intensity and in an atmosphere of 70 per cent relative humidity. The growth chambers in which the plants were grown were especially manufactured for the study of temperature effects on plant growth by the Engineering Section, C.S.I.R.O., Melbourne, Australia.

Fresh weight was taken as the measure of growth. Plants were pulled from the agar without loss of root tissue, moisture was removed from the roots by blotting, and the plants were weighed immediately. Because the plants were grown on an agar substrate which was 99 per cent water and in an atmosphere of high and constant relative humidity, it is unlikely that growth responses were obscured by variations in moisture content.

Each genetic type was grown at six constant temperatures (16°, 19°, 22°, 25°, 28°, and 31°C). A number of plants (10–20 for non-segregating generations and 25–40 for segregating generations) were grown for each genetic-temperature

combination. The basic data, then, for any given genetic type consist of a number of observations for growth at each of six temperatures. Since the plants, when harvested, were in the exponential growth phase, all data were transformed to logarithms for analysis. Table 1 gives the basic analysis of variance for data of this sort. This analysis permits estimates of

$$\sigma_t^2 = \frac{1}{5}\sum_i t_i^2 = \text{macro-environmental mean square generated by the different temperatures,}$$

$$\sigma_e^2 = \text{pooled micro-environmental variance.}$$

TABLE 1.—ANALYSIS OF VARIANCE TABLE FOR THE ESTIMATION OF MICRO- AND MACRO-ENVIRONMENTAL VARIANCE COMPONENTS FOR ANY GIVEN GENETIC TYPE.

Source	D.F.	Mean Square	Expectation of Mean Square
Temperatures	5	M_t	$\sigma_e^2 + n\,\sigma_t^2$
Micro-environments	6 (n − 1)	M_e	σ_e^2

Estimate Components as: $\hat{\sigma}_e^2 = M_e$, $\hat{\sigma}_t^2 = \frac{1}{n}(M_t - M_e)$.

The parameter σ_t^2 is a measure of the phenotypic stability of the genetic type with regard to the set of macro-environments. The sources of variation contributing to σ_e^2 include, among others, all micro-environmental effects which occur during the growth of the plant, maternal influences varying from seed to seed causing slight differences in germination time (which could be important when the total experimental growth period is only 14 days), and the "noise" component which, as defined by Waddington (14), is due to variation in a completely constant environment, i.e., variation which results from developmental accidents.

Besides the above preliminary analysis, a polynomial of the fourth degree was fitted to each set of data. Such a polynomial represents a continuous growth response curve for the entire temperature range. By setting the differential coefficient of the polynomial equal to zero, it is possible to estimate the temperature at which maximum growth occurs and the value for maximum growth.

In summary, the analyses provide the following temperature response parameters for any given genetic type:

(i) mean over-all temperatures,
(ii) the optimum temperature for maximum growth,
(iii) growth at the optimum temperature,
(iv) σ_t^2 = measure of the phenotypic stability for the range of temperatures, and
(v) σ_e^2 = pooled error due to micro-environmental differences as well as developmental noise.

The experimental procedure consisted of two main parts. Firstly, the parameters of 38 races, for which 10 observations were obtained at each temperature, were tested for differences among races. Secondly, a genetic analysis was made of some of the F_1's and all the possible F_2's from a set of five races. The data from these experiments not only provide genetic analyses of the temperature response parameters, but also permit a comparison of the performances of the homozygous races with their heterozygous crosses.

Error variances were estimated for variables (ii), (iii), (iv), and (v) by dividing the F_2 observations into two equal parts by use of random numbers and estimating the parameters for each set of data. A simple analysis of variance then gave an estimate of error, admittedly somewhat inflated by a genetic component. However, numbers in the other populations were insufficient to estimate the error term with sufficient accuracy.

GROWTH OF HOMOZYGOUS GENOTYPES AT DIFFERENT TEMPERATURES

Table 2 presents the analysis of variance of the mean log plant weights which result from the growth of all races at each temperature. In deriving the expectations of mean squares, it is assumed that the races represent a random sample of homozygous forms of the species, and the temperatures represent a fixed set of environmental conditions. The tests of significance indicate that the different temperature regimes induce highly significant variation, and that the races are not only significantly different in their over-all responses to the temperatures, but that they do not behave similarly at different temperatures.

TABLE 2.—ANALYSIS OF VARIANCE OF MEANS FOR 38 RACES GROWN AT ALL TEMPERATURES.

Source	D.F.	Mean Squares	Expectations of Mean Squares
Races (R)	37	0.4915***	$\sigma_e^2 + 6\,\sigma_r^2$
Temperatures (T)	5	36.6784***	$\sigma_e^2 + \sigma_{rt}^2 + 38\,\sigma_t^2$
R × T	185	0.0956***	$\sigma_e^2 + \sigma_{rt}^2$
Micro-environment	2280	0.0110	σ_e^2

*** = P $<$.005

The performances of races at different temperatures may also be examined through pairwise genetic correlations for different temperatures (Table 3). In general, growth at one temperature is more closely correlated with that at an adjacent temperature than with one far removed.

The results from these analyses suggest that (i) races differ significantly in their over-all performance to the range of temperature regimes and (ii) the promotion of growth at one temperature may have quite a different genetic basis from that at another temperature.

A micro-environmental variance can be estimated for each race-temperature

TABLE 3.—ALL POSSIBLE CORRELATIONS* FOR THE GROWTH OF 38 RACES AT PAIRS OF DIFFERENT TEMPERATURES.

	16°	19°	22°	25°	28°	31°	Correlation with over-all mean
16°		.75	.51	42	.32	.17	.69
19°			.77	.58	.38	.41	.84
22°				.79	.66	.43	.88
25°					.59	.13	.73
28°						.36	.72
31°							.63

*A correlation coefficient greater than 0.33 is significant at the 5 per cent level.

combination since each such combination contains 10 observations. Following Scheffé (12), the logarithms of the estimated variances were used for the analysis of variance presented in Table 4. The error mean square was obtained from the divided F_2 data.

TABLE 4.—ANALYSIS OF VARIANCE OF LOG (MICRO-ENVIRONMENTAL VARIANCE) FOR THE GROWTH OF 38 RACES AT ALL 6 TEMPERATURES.

Source	D.F.	Mean Squares	Expectations of Mean Squares
Races (R)	37	0.2420***	$\sigma_e^2 + 6\,\sigma_r^2$
Temperatures (T)	5	3.0041***	$\sigma_e^2 + \sigma_{rt}^2 + 38\,\sigma_t^2$
R × T	185	0.1024**	$\sigma_e^2 + \sigma_{rt}^2$
Error ϕ	10	0.0225	σ_e^2

**= $.005 < P < .010$
***= $P < .005$
ϕ= error mean square based on divided F_2 data.

Again the mean squares for races, temperatures, and interactions are all highly significant. As with the mean values, these analyses indicate that the average stabilities [as measured by log $(\hat{\sigma}_e^2)$] of the races not only differ, but that the races do not behave similarly in different temperatures. Since the $\hat{\sigma}_e^2$ differ, the tests of significance of means, using a pooled sums of squares, are only approximate.

It must be remembered that the composition of σ_e^2 is varied, and that it represents a parameter completely different from σ_t^2.

Table 5 represents the analyses for the remaining three temperature response parameters: optimum temperature, growth at the optimum temperature, and log $(\hat{\sigma}_t^2)$. Using the error variance estimated from the divided F_2 data, the races are found to be significantly different for each parameter.

These preliminary analyses show that the races of Arabidopsis exhibit significant genetic differences in all of the temperature response parameters which have been examined. Therefore, it is legitimate to consider a genetic analysis of these differences.

TABLE 5.—ANALYSIS OF VARIANCE OF OPTIMUM TEMPERATURE, GROWTH AT OPTIMUM TEMPERATURE AND PHENOTYPIC STABILITY [LOG (ϑ_t^2)] FOR ALL 38 RACES.

Source	D.F.	Optimum Temperature M.S.	Growth at Optimum Temperature M.S.	Log (ϑ_t^2) M.S.
Races	37	0.6204*	0.0110***	0.0287**
Error$^\phi$	10	0.2199	0.0010	0.0059

* = .010 < P < .050
** = .005 < P < .010
*** = P < .005
ϕ = error mean square based on divided F_2 data.

GROWTH OF HETEROZYGOUS GENOTYPES AT DIFFERENT TEMPERATURES

Comparison of heterozygous and homozygous material

The experimental material for genetic analysis consisted of the following five races, some of the F_1's, and all of the F_2's (not including reciprocals):

B = race from Blanes, Spain,
C = race from Catania, Sicily,
D = race from Dijon, France,
M = race from Martuba, North Africa, and
R = race from Rschew, Russia.

All F_1's including reciprocals, were planted, but germination difficulties prevented the inclusion of data from most of them. However, a set of F_1's with race B (i.e., B × C, B × D, B × M and B × R) germinated sufficiently well to provide some F_1 data.

For each genetic type (parent race, F_1, and F_2), the number of plants at each of the six temperatures was the same. This number, however, varied from one genetic type to another. For the parents, the average number of plants for each temperature was 14.8; for the four F_1's, 13.5; and for the F_2's, 32.3.

Typical response curves for a pair of parents, B and D, their F_1 and F_2 are drawn in Figure 2. This figure shows that:

(i) The heterozygous generations are only slightly superior at the low to medium temperatures but are considerably superior at the high temperatures as compared with the parent races.
(ii) The F_1 generation is best at all temperatures and the F_2 is intermediate between the F_1 and the midparent.

These trends may be examined more closely in Table 6 where the data are considered in two parts. The first set of data compares the midparental values with the set of F_1's having race B as common parent and with the corresponding F_2's. This permits simultaneous comparisons of the three generations. The average F_1 value for these lines is significantly greater than the average midparental value at each temperature, the superiority of the F_1's being greatest at the highest temperature. The four F_2's from race B show clear superiority over the midparental averages only at the higher temperatures.

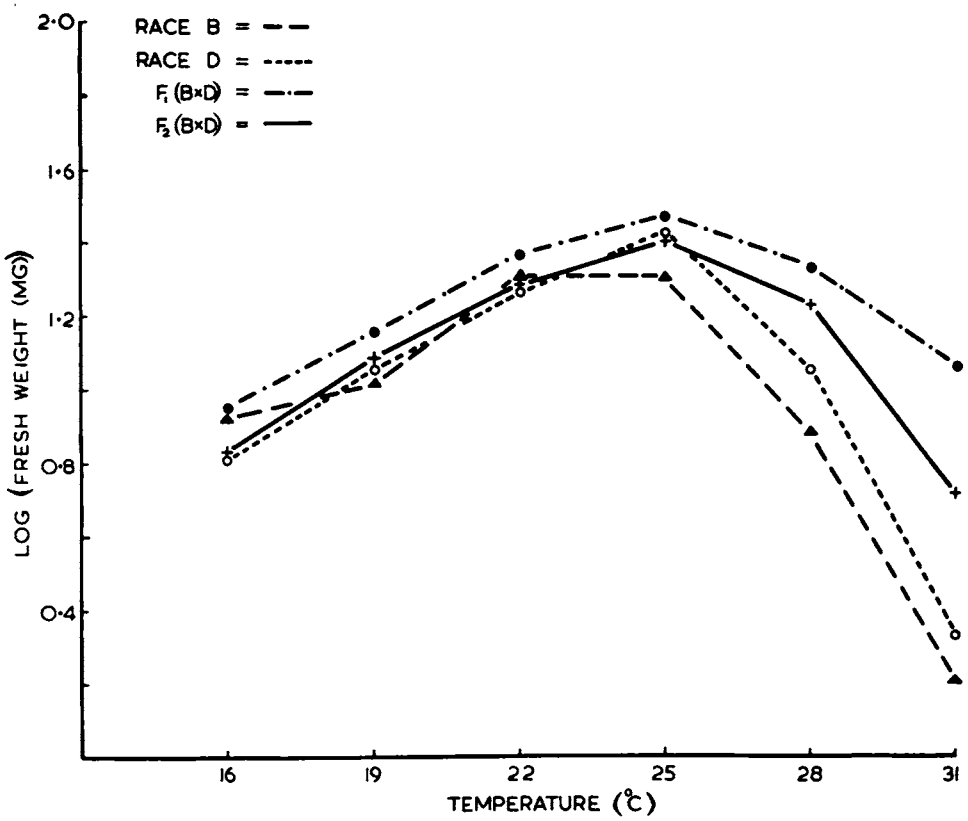


FIGURE 2. *Temperature response curves for Races B and D, their F_1 and F_2.*

In the second part of the data, which contrasts the performance of all 10 F_2's with their parents, the average F_2's are superior to the average parents at all temperatures. The differences between F_2's and parents are least at the middle temperatures (22° and 25°), moderately large at lower temperatures (16° and 19°), and greatest at the higher temperatures (28° and 31°).

Temperature response parameters have been estimated for each parent, F_1, and F_2. These are given in Table 7.

There is a considerable range among the parents for the over-all mean and for log ($\hat{\sigma}^2_t$); for example, race R is a superior homozygote; race C is a very inferior one. The former has a value for log ($\hat{\sigma}^2_t$) that is lower than that of any other parent or F_2, and its over-all mean is greater than three out of four of its F_2's. On the other hand, all other parents have greater values for log ($\hat{\sigma}^2_t$) and lower over-all means than any of their F_2's.

In Table 8 exact comparisons may be made between the averages for each of the five parameters for the midparents and the heterozygous generations. These may be summarized as follows: for the crosses having race B as a common parent, the F_1's are superior to the midparent in all parameters except log ($\hat{\sigma}^2_e$); three of

TABLE 6.—AVERAGE VALUES FOR LOG (FRESH WEIGHT) OF MIDPARENTS, F_1'S AND F_2'S WITH RACE B AS COMMON PARENT, AND AVERAGE VALUES OF MIDPARENTS AND F_2'S FOR ALL CROSSES, AT EACH TEMPERATURE.

	16°	19°	22°	25°	28°	31°
A. Crosses with race B.						
$\overline{MP}$	0.869 ± .017	1.038 ± 0.14	1.312 ± .014	1.371 ± .011	1.006 ± .021	0.327 ± .026
$\overline{F}_1$	0.959 ± .024	1.168 ± .018	1.363 ± .013	1.476 ± .015	1.300 ± .026	0.998 ± .029
$\overline{F}_2$	0.872 ± .009	1.120 ± .008	1.307 ± .008	1.396 ± .007	1.216 ± .011	0.718 ± .020
$(\overline{F}_1 - \overline{MP})$	0.090 ± .029	0.130 ± .023	0.051 ± .019	0.105 ± .019	0.294 ± .033	0.671 ± .038
$(\overline{F}_2 - \overline{MP})$	0.003 ± .019	0.082 ± .016	−0.005 ± .016	0.025 ± .013	0.210 ± .023	0.391 ± .033
B. All parents and F_2's						
$\overline{MP}$	0.830 ± .013	1.045 ± .011	1.311 ± .011	1.403 ± .009	1.072 ± .016	.0399 ± .020
$\overline{F}_2$	0.905 ± .006	1.129 ± .005	1.336 ± .005	1.425 ± .005	1.216 ± .007	0.768 ± .014
$(\overline{F}_2 - \overline{MP})$	0.075 ± .014	0.084 ± .012	0.025 ± .012	0.022 ± .010	0.144 ± .018	0.369 ± .024

TABLE 7.—TEMPERATURE RESPONSE PARAMETERS FOR EACH PARENT, F_1 AND F_2.

Race		B	C		D		M		R	
			F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
	A	.949	1.121	1.066	1.226	1.098	1.314	1.142	1.182	1.113
	B	23.6	24.1	24.0	24.7	24.9	25.0	24.9	24.6	24.9
B	C	1.368	1.451	1.388	1.466	1.395	1.516	1.427	1.405	1.351
	D	2.215	1.881	1.947	1.584	1.855	1.543	1.815	1.453	1.744
	E	1.328	1.493	1.196	1.405	1.367	1.061	1.384	1.469	1.170
	A			.748		1.082		1.152		1.115
	B			23.8		24.5		25.7		24.2
C	C			1.387		1.393		1.478		1.421
	D			2.369		1.937		1.950		1.871
	E			1.373		1.303		1.114		1.204
	A					.992		1.211		1.164
	B					24.2		24.6		24.9
D	C					1.387		1.521		1.452
	D					2.157		1.829		1.820
	E					1.143		1.238		1.236
	A							1.173		1.236
	B							25.7		26.1
M	C							1.519		1.446
	D							2.217		1.558
	E							.935		1.220
	A									1.188
	B									24.3
R	C									1.376
	D									1.532
	E									.940

A = Mean over-all temperatures; B = Optimum temperature (°C); C = Growth at Optimum temperature;
D = log (Temperature variance component) coded by adding 3.000 to logarithms;
E = log (Pooled error) coded by adding 3.000 to logarithms.

these differences are highly significant. The F_2's of both the restricted and all-inclusive sets also are superior to the midparents, but less so than are the F_1's.

An expressive presentation of the relative performances of homozygous races, F_1's and F_2's for the joint distribution of the over-all mean and log ($\hat{\sigma}^2_t$) is given in Figure 3. It shows how the desirable performances [high over-all mean, low log ($\hat{\sigma}^2_t$)] of the F_1's regress to the F_2 mean values which are generally superior to the average parental values.

Another notable feature of the heterozygous populations is the relatively uniform expression of the F_2 values for both over-all mean and log ($\hat{\sigma}^2_t$) as compared with the scattered parental values (Figures 3 and 4).

Finally, the question can be asked: If the set of parental races is regarded as a sample from a population of races, then what is the variance of the average differ-

TABLE 8.—AVERAGE VALUES OF MIDPARENTS, F_1's AND F_2's WITH RACE B AS COMMON PARENT, AND AVERAGE MIDPARENTS AND F_2's OF ALL CROSSES FOR EACH OF THE FIVE TEMPERATURE RESPONSE PARAMETERS.

	Mean over-all temperatures	Optimum temperature (°C)	Growth at Optimal temperature	log (δ_t^2)*	log (δ_e^2)*
A. Crosses with race B					
$\overline{MP}$	0.987 ± .007	24.05 ± .22	1.393 ± .015	1.142 ± .036	0.213 ± .071
$\overline{F}_1$	1.211 ± .009	24.61 ± .21	1.459 ± .014	.615 ± .034	0.357 ± .067
$\overline{F}_2$	1.105 ± .005	24.66 ± .13	1.390 ± .009	.840 ± .021	0.279 ± .040
$(\overline{F}_1 - \overline{MP})$	0.224 ± .011	0.56 ± .30	.066 ± .021	−0.527 ± .050	0.144 ± .097
$(\overline{F}_2 - \overline{MP})$	0.118 ± .009	0.61 ± .25	− .003 ± .017	−0.302 ± .042	0.066 ± .081
B. All parents and F_2's					
$\overline{MP}$	1.010 ± .006	24.32 ± .18	1.408 ± .012	1.098 ± .029	0.144 ± .056
$\overline{F}_2$	1.138 ± .003	24.86 ± .08	1.427 ± .006	.833 ± .014	0.243 ± .026
$(\overline{F}_2 - \overline{MP})$	0.128 ± .007	0.54 ± .19	+.019 ± .013	−0.265 ± .032	0.099 ± .062
S.E. based on experimental lines representing a random sample (for $\overline{F}_2 - \overline{MP}$)	0.049				

*Variances coded by adding 2.000 to logarithms.

ence, $(\overline{F}_2 - \overline{MP})$, derived from the sample, as an estimate of the mean of the population of such differences? It can be shown that this variance is estimated by

$$\frac{4}{p}\hat{\sigma}^2_{g.c.a.} + \frac{2}{p(p-1)}\hat{\sigma}^2_{s.c.a.} + \left[\frac{2}{p(p-1)}\right]^2 \sum_{i<j} \frac{1}{n_{ij}} (_{F_2}\hat{\sigma}^2_e) + \left[\frac{1}{p}\right]^2 \sum_i \frac{1}{n_{ii}} (_P\hat{\sigma}^2_e),$$

where,

p = number of parent races in the sample,

$\hat{\sigma}^2_{g.c.a.}$ = general combining ability from the modified diallel analysis of differences, $(F_2 - MP)$,

$\hat{\sigma}^2_{s.c.a.}$ = specific combining ability from the modified diallel analysis of differences, $(F_2 - MP)$,

$_{F_2}\hat{\sigma}^2_e$ = micro-environmental variance for F_2's,

$_P\hat{\sigma}^2_e$ = micro-environmental variance for parental races,

n_{ij} = number of observations of the F_2 $(P_i \times P_j)$, and

n_{ii} = number of observations for the *ith* parent race.

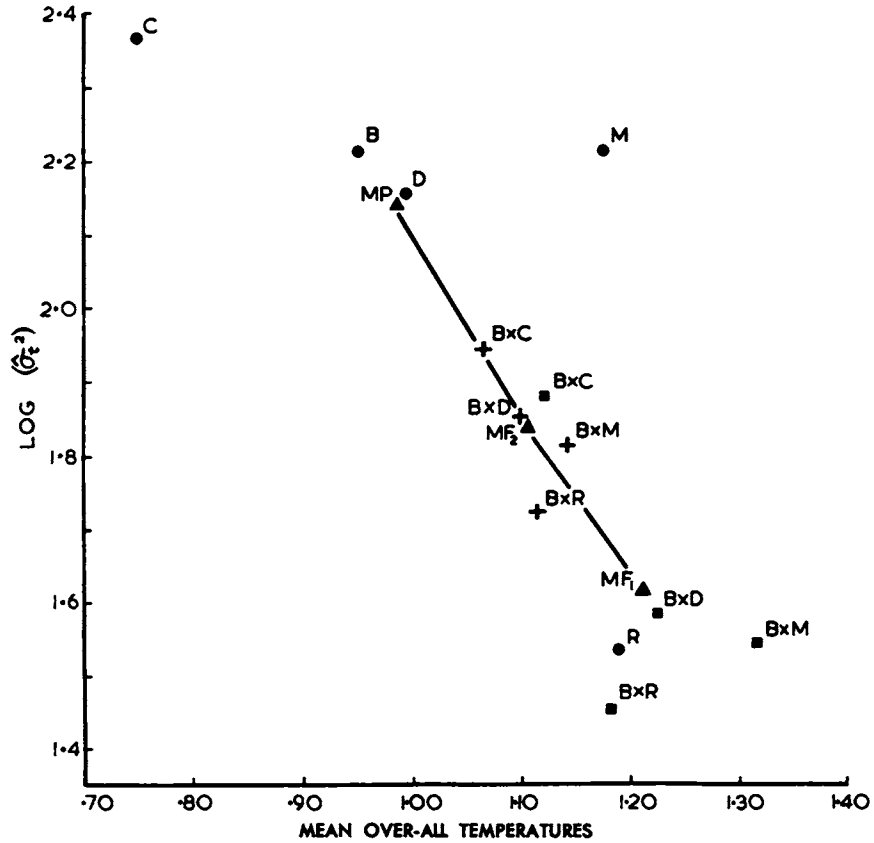


FIGURE 3. *Joint distribution of phenotypic stabilities, [log ($\hat{\sigma}_i^2$)], and over-all means, [log (fresh weight)], for parent races (•), F_1's (■), and F_2's (+) with race B. The mean values for parents and the F_1 and F_2 generations are shown as* ▲.

The statistic "mean over-all temperatures" is the only one for which all variances can be estimated accurately. The estimated standard error for the average difference, $(\bar{F}_2 - \overline{MP}) = 0.128$, was computed from the above expression to be 0.049 (Table 8). Thus, even with the above assumptions the estimated difference appears to be significant.

In summary, the heterozygous material exhibits a greater mean over-all temperatures, an increased temperature optimum, an increased growth at the optimum temperature, and a greater stability of phenotypic expression over the entire temperature range, than does the parental material. These differences are due partly to the superiority of the hybrids over the parents in the lower and medium temperature range, but more importantly to the considerable heterotic expression of the hybrids at the higher temperature.

Selection involving temperature response parameters

A theory of selection in which the individual members of the breeding population are tested by their selfed progeny, has been considered by Griffing

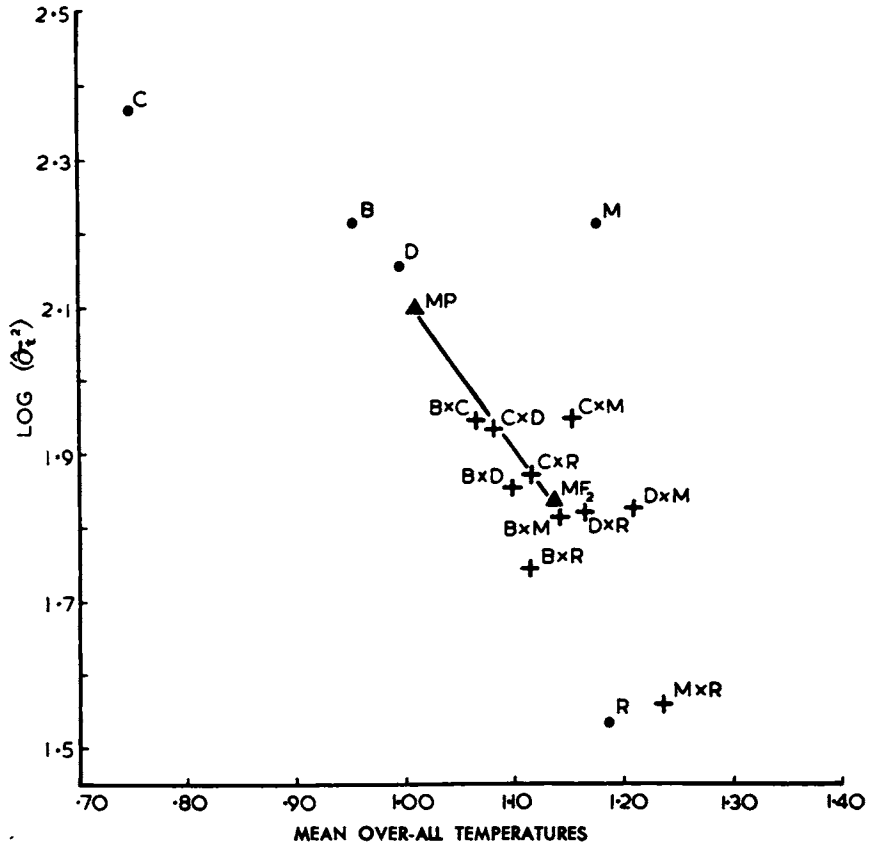


FIGURE 4. *Joint distribution of phenotypic stabilities,* [*log* ($\hat{\sigma}^2_t$)], *and over-all means,* [*log* (*fresh weight*)], *for parent races* (●) *and* F_2*'s* (+). *The mean values for the parents and the* F_2 *generations are shown as* ▲.

(unpublished). It was shown that the increment advance as measured in the population of selfed progenies is a function of the parent-offspring covariance involving elements which are selfed one generation. It was also found that, if chromosome configuration effects are ignored, an estimate of this covariance can be obtained from the general combining ability variance component from a modified diallel analysis involving F_2's from a random set of homozygous forms. Hence, it is of considerable interest to perform combining ability analyses on the diallel set of F_2 progenies in order to estimate the parent-offspring covariance and to partition the total heritable variance into general combining ability, specific combining ability, and error components.

This partitioning of the heritable genetic variance may be set out more exactly as follows:

$$\sigma_G^2 = 2\,\sigma^2_{g.c.a.} + \sigma^2_{s.c.a.} + \sigma_\epsilon^2$$

where,

σ_G^2 = total heritable genetic variance in a population whose elements have been derived from a random mating population by one generation of selfing,

$\sigma^2_{g.c.a.}$ = general combining ability component,

$\sigma^2_{s.c.a.}$ = specific combining ability component, and

σ_e^2 = pooled variance within selfed progenies.

Table 9 provides the results of combining ability analyses of the diallel F_2 material for each temperature. The most striking aspect of these data is the fact that the general combining ability effects are apparently not detectable in and around the optimum, whereas they are significant at the extreme temperatures.

TABLE 9.—COMBINING ABILITY ANALYSES OF THE DIALLEL F_2 MEANS AT EACH TEMPERATURE.

	16°	19°	22°	25°	28°	31°
A. Tests of significance						
General combining ability	***	N.S.	N.S.	N.S.	**	*
Specific combining ability	N.S.	N.S.	***	***	***	**
B. Estimates of variance components						
$2\hat{\sigma}^2_{g.c.a.}$	0.0030	0.0004	0.0016	0.0010	0.0113	0.0338
$\hat{\sigma}^2_{s.c.a.}$	−0.0001	0.0000	0.0011	0.0006	0.0022	0.0031
$\hat{\sigma}_e^2$	0.0108	0.0081	0.0083	0.0073	0.0155	0.0582
$\hat{\sigma}_P^2$	0.0137	0.0085	0.0110	0.0089	0.0290	0.0951
$\frac{2\hat{\sigma}^2_{g.c.a.}}{\hat{\sigma}_P^2}$ (%)	21.9	4.7	14.5	11.2	39.0	35.5

N.S. = $.05 < P$, * = $.01 < P < .05$, ** = $.005 < P < .010$, and *** = $P < .005$

It is possible that in the natural habitat, selection has been primarily for growth at intermediate temperatures, with the result that strong selection pressure has exhausted the additive genetic variance. Selection for growth at extreme temperatures has been weak, thus allowing a residual additive genetic variance for growth to remain.

It is also significant that specific combining ability effects, which are due to dominance and epistasis, are not detectable at the low temperatures, are apparent at the moderate temperatures, and are greatest at the extreme high temperatures. This will be discussed later in terms of gene action responsible for heterosis.

The data in Table 9 also provide information on the relative progress of selection possible at the various temperatures. This information is reflected in the magnitude of the ratio $\frac{2\hat{\sigma}^2_{g.c.a.}}{\hat{\sigma}_P^2}$. If selection were to be practiced on the population from which it is assumed that the F_1's are a random sample, greatest progress would be effected at the high temperatures. This is because the increase of $\hat{\sigma}^2_{g.c.a.}$ in this temperature range is sufficiently great to offset the corresponding increase in the non-additive genetic and error variances.

Table 10 presents combining ability analyses for each of the five temperature response parameters. It shows that additive and perhaps non-additive genetic variability exist for the three important parameters; over-all mean, growth at the optimum, and phenotypic stability. Therefore, if selection were to be carried out in a population of which these F_1's are representative, improvement could be expected in any one or all three characteristics.

TABLE 10.—COMBINING ABILITY ANALYSES OF THE DIALLEL F_2 TEMPERATURE RESPONSE PARAMETERS.

	Over-all Mean	Optimum Temperature	Growth at opt. temp.	Log (δ_t^2)	Log (δ_e^2)
A. Tests of significance					
General combining ability	$P < .005$	$P > .05$	$.01 < P < .05$	$.01 < P < .05$	$P > .05$
Specific combining ability	$.05 < P < .10$	$.05 < P < .10$	$P = .10$	$.10 < P < .20$	$P > .05$
B. Estimates of variance components					
$2\,\delta^2_{g.c.a.}$	0.0042	0.0816	0.0025	0.0135	—
$\delta^2_{s.c.a.}$	0.0001	0.2673	0.0005	0.0028	—
δ_e^2	0.0180	2.1991	0.0100	0.0595	—
δ_P^2	0.0223	2.5480	0.0130	0.0758	—
$\frac{2\,\delta^2_{g.c.a.}}{\delta_P^2}$ (%)	18.8	3.2	19.2	17.8	—

DISCUSSION

Comparison of Arabidopsis and Drosophila data and an explanation of the inconsistencies of past data with inbreeding species

Since Drosophila experiments form the major basis on which the inference of heterozygote superiority in outbreeding species is made, it is desirable to make a detailed comparison of results obtained with Drosophila and with Arabidopsis. The Drosophila studies of Dobzhansky *et al.* (2, 3) are particularly suited for comparison with experiments using inbreeding species, because one set of the homozygous genotypes was selected from a wild *Drosophila pseudoobscura* population on the basis of equivalence with the heterozygote in the standard cultural environment. Thus, the Drosophila material represented a highly selected class of homozygotes. This puts them on a par with the Arabidopsis races which have had an evolutionary history of natural selection.

In the experiments reported by Dobzhansky *et al.* (2, 3), 19 second chromosomes were isolated from a natural population of *Drosophila pseudoobscura.* Ten of these, denoted by H, produced normally viable or supervital homozygotes in cultures reared at 25°C and fed Fleischmann's yeast. Nine chromosomes, denoted by L, produced subvital homozygotes under the same conditions. The

viabilities of the 19 homozygotes and 27 heterozygotes involving H × H, H × L, and L × L were tested in 9 different environments. These included combinations of four different temperatures and three different foods (yeasts).

In Drosophila the behaviour of the homozygotes in one environmental regime was found to be quite different from that in another regime. Arabidopsis responds similarly as shown by pairwise correlations of the races at different temperatures, where the magnitude of the correlations decreased progressively as the growth temperature diverged. Hence, the behaviour of Drosophila and Arabidopsis is similar on this point.

The important Drosophila findings with respect to the micro- and macro-environmental variance analyses were that both variances were significantly greater in homozygotes than in heterozygotes. This constitutes strong evidence for superior phenotypic stability in heterozygotes. The macro-environmental variance analysis for Arabidopsis similarly indicated heterozygote superiority. However, because most comparisons were between F_2's and parents, it was not possible to examine critically the micro-environmental variance relationships. As pointed out before, this is because the F_2 micro-environmental variance contains a genetic component due to segregation.

Although the Drosophila homozygotes (H) were chosen to be equivalent to the heterozygotes at one regime, in most environments the mean viability of the H homozygotes was significantly lower than that of the heterozygotes in the same environment. This is true, of course, for the Arabidopsis races, in which heterozygote superiority is especially manifest at the high temperatures (see especially Figure 5). In this connection a re-examination of the Drosophila data as illustrated in Figure 6 shows a similar accentuation of heterosis at the highest temperature. The average superiority of the F_1 over the midparent at 16°C is 0.34 per cent, at 25°C it is 1.86 per cent, and at 27°C it rises sharply to 6.35 per cent. Possibly the same genetic mechanisms are responsible for the differential heterotic response in both Drosophila and Arabidopsis.

In summarizing the Drosophila experiments Dobshansky *et al.* (3) conclude that:

> "...the homozygotes for some of the chromosomes found in natural populations of Drosophila are 'narrow specialists.' Such homozygotes do quite well in a restricted range of environments, but they lack the resilience necessary to maintain their fitness in other environments. By contrast, the heterozygotes are more often many-sided and versatile in their adaptedness, hence able to live successfully in a broader range of environments."

It appears that the Arabidopsis results could be framed in very much the same terms, except perhaps that Arabidopsis homozygotes represent a more select class and hence the superiority of the heterozygotes is not so marked.

It is evident that the responses of the inbreeding species, Arabidopsis, closely parallel those of the outbreeding species, Drosophila. The differences which exist are only ones of degree.

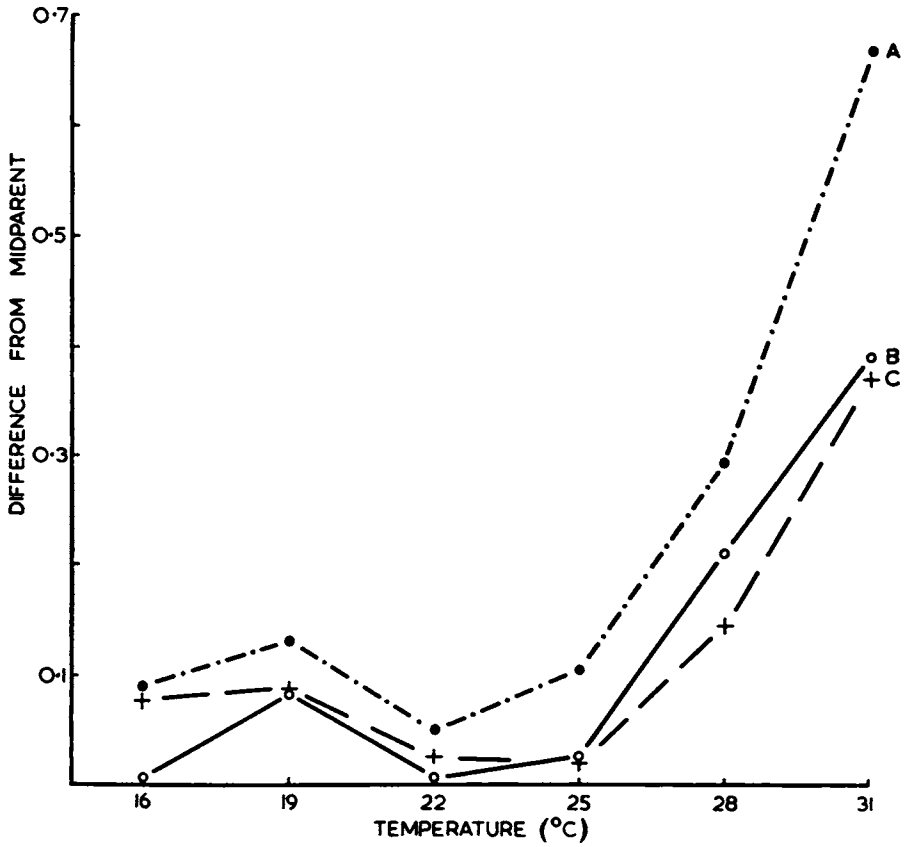


FIGURE 5. *Superiority in growth, measured as log (fresh weight), of heterozygous populations over homozygous populations.*

(i) Crosses with race B: $A = (\bar{F}_1 - \overline{MP})$ *and* $B = (\bar{F}_2 - \overline{MP})$.

(ii) All inclusive sets of F_2*'s:* $C = (\bar{F}_2 - \overline{MP})$.

Turning now to the inconsistencies of past data with regard to the measurement of the relative phenotypic stability of homozygotes and heterozygotes of inbreeding species, it appears that these inconsistencies are due to one or more of the following: (i) the range of environmental conditions in which the material is grown; in this case high temperatures seem to be important: (ii) the plant characteristic which is measured; that is, whether the magnitude of the variable is a direct function of the magnitude of plant growth: (iii) the genetic relationship among the parents which are used; the degrees of genetic diversity generated by crossing depends on the genetic divergence of the parental material, and (iv) the use of different stability parameters; that is, the use of micro- or macro-environmental variances.

As an example of how past inconsistent data may be explained, consider the environmental circumstances of a tomato experiment which led Williams (16) to state:

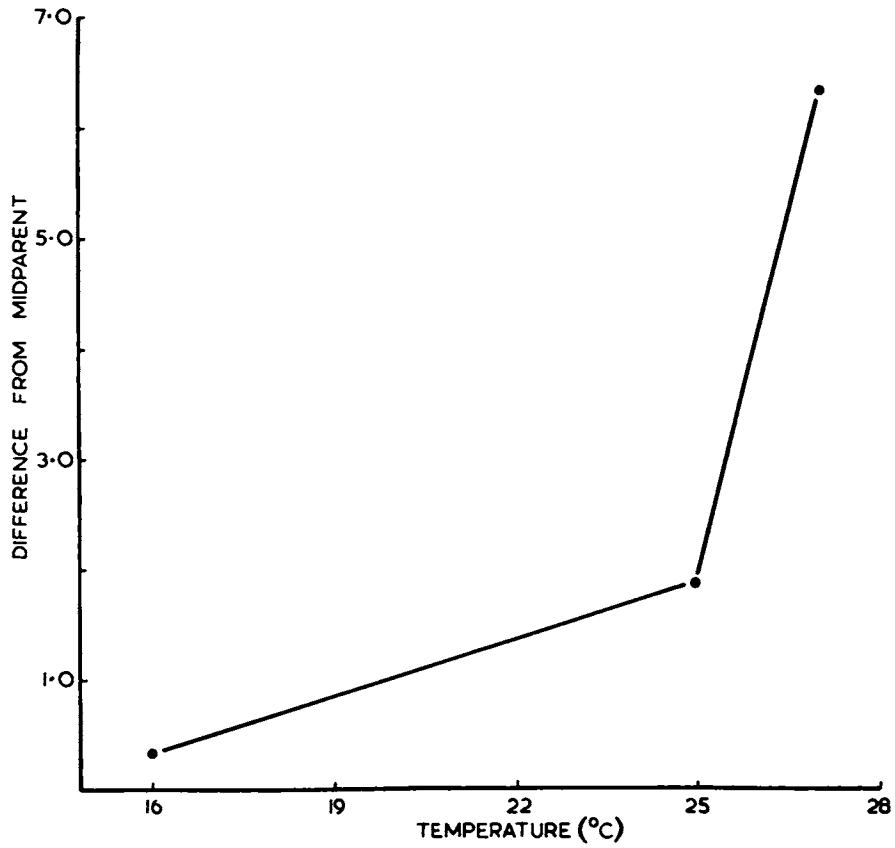


FIGURE 6. *Differences in relative viability of F_1's ($H \times H$) and Parents (H), i.e., ($\bar{F}_1 - \overline{MP}$), averaged over three genera of yeast. Data are for Drosophila pseudoobscura reported by Dobzhansky et al. (2).*

> "None of the data suggests any intrinsic difference between inbred lines and hybrids in respect of their ability to buffer or to eliminate the variability that is induced by the environment."

Williams' experiments were conducted in the glasshouses of the John Innes Institute, Bayfordbury, England (during 1959). Although he did not give the growth temperatures for his material, both air and soil temperatures for two of these glasshouses in the years 1954–55 have been published by Whittle and Lawrence (15). During the period of the year in which Williams' plants were grown, the average air temperature did not rise above 78° to 80°F, while the soil temperature averages ranged from 59.9° to 63.0°F.

It is probable that Williams did not find stability differences between his heterozygous and homozygous plants because the experimental temperature range was about the optimum. Extrapolating from the Arabidopsis results, only slight differences in phenotypic stability would be expected in such a temperature range.

The evolution and physiology of temperature stability

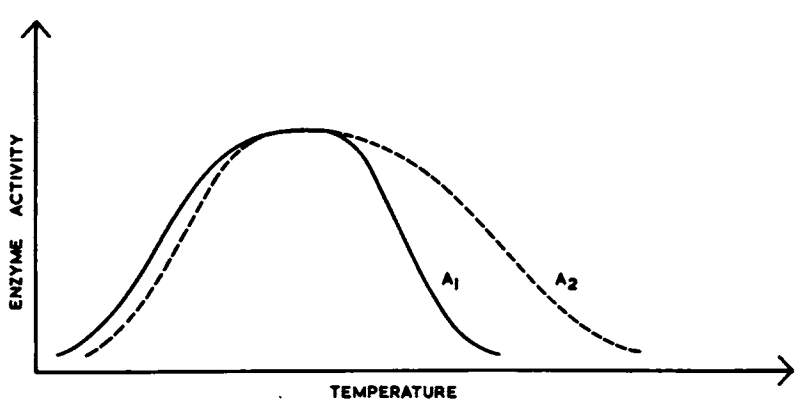
The pattern of response to temperature disclosed by these experiments emphasizes the immediate objectives of natural selection. As plants are exposed to temperatures about the optimum during most of their life cycle, there exists a strong selection pressure to maximize growth in this temperature range. They are exposed to the non-lethal extreme temperatures less frequently and so at these temperatures selection pressures for growth are weaker. This supposition is supported by the combining ability analyses reported earlier which showed that in the region of the optimum temperature, additive genetic variance was not detectable, whereas, in the high and low temperature regions significant additive genetic variance was found. Also the survey of 38 races showed little correlation of gene expression between optimum and extreme temperatures. Hence, strong selection for growth at the optimum need not exert any direct pressure at the extreme temperatures.

The conclusion is that strong selection pressure has produced very efficient homozygous genotypes capable of growth comparable with that of heterozygotes over the optimum part of the temperature range. However, at extreme temperatures selection pressure has been weaker and, therefore, it is possible that different, slightly deficient constellations of genes have been fixed in different races. When these diverse, slightly defective systems are brought together, greater genetic diversity results, deficiencies are repaired and heterosis is manifest.

The problem now, is to explain how the genetic diversity of hybrids causes a *differential* heterosis with respect to the range of growth temperatures. More specifically, it is necessary to set up a genetic hypothesis which will explain the following facts: (i) little or no heterosis at low and optimum temperatures, (ii) considerable heterosis at high temperatures, and (iii) the possibility of obtaining homozygous genotypes (such as race R) which exhibit phenotypic stability comparable to heterozygotes.

Haldane (5) gave biochemical reasons why the phenotypic manifestation of different alleles at a single locus may be superior to that of identical alleles at the locus. Let us now incorporate this suggestion to fit our specific case of temperature dependent heterosis.

Suppose, as illustrated below, that the alleles, A_1 and A_2, have different



temperature ranges for activity. The alleles are also assumed to be equally effective at the optimum temperature and the A_2 allele can, by itself, produce sufficient enzyme at the high temperature to yield the normal phenotype, i.e., dominance of high enzyme activity.

This model for a single locus is not sufficient to explain all the facts. However, with two or more temperature differentiated loci, it is possible to do so. For simplicity, consider two such loci, A and B. For both loci, the two alleles would have the same activity about the optimum, so that both alleles would have equal potence as far as major selection pressure is concerned. However, homozygous genotypes $A_1A_1B_2B_2$ and $A_2A_2B_1B_1$ could obviously occur. The diversity generated by crossing these races would not yield heterosis at the optimum, i.e., $A_1A_2B_1B_2 = A_1A_1B_1B_1 = A_1A_1B_2B_2 = A_2A_2B_1B_1 = A_2A_2B_2B_2$. At the high temperature, however, $A_1A_2B_1B_2$ would exhibit the high activity of A_2 and B_2 and heterosis would be expressed. Also, it would be possible to fix the desirable alleles at both loci to yield a homozygote which has high phenotypic stability, as is the case with race R. With a large number of environmentally sensitive loci, however, this would be a rare event.

Finally, with this model one would expect little genetic variability for parents and crosses in the lower and optimum temperature ranges. However, in the higher range, temperature sensitivity would generate genetic variability which when partitioned would yield both general and specific combining ability variance components. Such expectations agree with the actual data as given in Table 9.

Thus, the genetic model as outlined above, when applied to several loci, is capable of explaining all of the facts of this temperature dependent heterosis phenomenon.

Lewis (11) suggests that the genetic differences which lead to heterosis are not strongly contrasting ones like fully-efficient versus lethal or sub-lethal genes, but are of the type he calls "environmental alleles." These are alleles which control the same enzyme but possess different optima of temperature, pH or substrate affinity. The hypothesis assumes that change in the external environment can so alter cellular conditions as to favor the products of one or the other allele.

This assumption may not be true for changes in hydrogen ion concentration. The cell fluids of most organisms are fairly strongly buffered with respect to pH and are thus quite resistant to this type of environmental change. No mutant enzyme has yet been described with an altered pH optimum, the pH effect in sensitive mutants being on the composition of the medium rather than the activity of an enzyme (13). As far as the alteration in the substrate specificity of a given enzyme is concerned, mutational events of this sort seem to be exceedingly rare. No convincing evidence for mutational alteration in enzyme specificity has so far appeared. This leaves temperature optima of enzymes as the most likely differences to exist between the products of alleles.

Experiments with biochemical mutants of Neurospora, Escherichia, and Arabidopsis have shown that mutation to temperature sensitivity occurs very frequently. Specific enzymes need not always be more thermolabile in such high temperature sensitive mutants, but those that have been examined (pantothentic

acid synthetase, tyrosinase, pyrroline-5-carboxylate reductase, glutamic acid dehydrogenase, and adenylosuccinase) have been found to be so (4).

Therefore, the experiments of Langridge and Griffing (8) which showed that several wild races of Arabidopsis cease growth at high temperatures because of deficiencies in particular organic substances, indicate that thermolabile alleles commonly differentiate homozygous ecotypes.

These findings, with mutants of micro-organisms and races of Arabidopsis, confirm the theoretical considerations above and suggest that heterosis at high temperatures is a consequence of the combination in the hybrid of the more thermostable alleles of different genes.

Heterosis in the breeding of self-fertilized crops

These experiments with Arabidopsis suggest that self- and cross-fertilized plants are essentially similar in their heterotic responses. Therefore, the use of heterosis should be carefully considered in all crop plants, irrespective of their type of breeding system.

So far, the commercial use of heterosis in self-fertilized crops has been infrequent for at least two reasons: (i) homozygous varieties because of their long history of self-fertilization have proved to yield satisfactory uniform crops which, once developed, are easily maintained and (ii) the cost of production of hybrid seed may be so high as to nullify some of the hybrid advantage. However, the use of male-sterility genes, cytoplasmic sterility factors, and gametocides will undoubtedly solve some of the cost problems of seed production. Modifications of the ingenious methods used by Burton (1) in the application of heterosis to specialized pasture breeding problems may also be applicable.

Moreover, appropriate heterotic combinations of an inbreeding crop would provide solutions to several selection barriers which would be more difficult to overcome in breeding pure lines. Some of the advantages of heterosis breeding are: (i) It provides maximum performance in optimal growing conditions and at the same time confers phenotypic stability in times of environmental stress, (ii) it allows the simultaneous improvement of yield components which may be negatively associated because of pleiotropy or, more usually, because of linkage, and (iii) it facilitates the inclusion in individuals of genetic diversity from very different parents without destroying the complex interrelationships conferring agronomic value.

Finally, if the results of this study are found to hold generally for self-fertilized crops, the relative magnitude of heterosis, for those plant characteristics which are a direct function of growth, can be expected to increase if the hybrid crop is exposed to high temperatures. With field grown crops in continental climates, plants may be exposed to heat wave conditions at times of critical growth. The data from Arabidopsis suggest that under such conditions, the growth of homozygous plants may be retarded at temperatures much lower than those which cause retardation of growth in hybrids. This fact could be a major physiological explanation of heterosis as observed under field conditions.

SUMMARY

The aseptic culture of Arabidopsis permitted the investigation of phenotypic stability of growth by methods experimentally comparable with those used with Drosophila. This allowed a direct comparison of phenotypic stability between an inbreeding and an outbreeding species.

Arabidopsis races, together with their F_1's and F_2's were grown in controlled environment cabinets for the study of response to a graded set of temperatures. In a survey of 38 races, it was found that the races differed significantly for each of 5 temperature response parameters. Correlations between growth responses at different temperatures showed that genes behaved differently according to the temperature.

Comparisons of heterozygous (F_1 and F_2) populations with the homozygous parents showed that the heterozygous material exhibited a greater mean growth over all temperatures, an increased temperature optimum, an increased growth at the optimum temperature, and a greater stability of phenotypic expression over the entire temperature range, than did the parental material. These differences were due partly to the superiority of the hybrids over the parents in the lower and medium temperature range, but more importantly to the considerable heterotic expression of the hybrids at the higher temperatures.

The responses of the inbreeding species, *Arabidopsis thaliana,* were shown to closely parallel those of the outbreeding species, *Drosophila pseudoobscura,* the differences which exist being only in degree. A reanalysis of certain Drosophila data disclosed the same accentuated heterosis at high temperatures as is manifest by Arabidopsis.

The Arabidopsis results permit: (i) a genetic hypothesis based on temperature-sensitive alleles to explain differential heterosis over a range of temperatures, (ii) a plausible explanation of some of the inconsistencies of past experimental studies with self-fertilized species, and (iii) a physiological interpretation of at least part of the heterosis observed in field grown crops which are subject to high temperature stresses.

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DISCUSSION

ADAMS: Breeders are concerned with fitness over a variable environment, not a constant one. Thus, for example, it is important that a genotype be optimumly functional over a range of temperatures. Even the environment of the Central Valley of California—uniform though it might appear to be—is variable in ways sufficiently important that significant shifts in frequency of certain genes in lima beans grown over several generations resulted. Possibly related to the temperature sensitivity of certain lines is the idea of Bonner on climatic lesions, repairable by addition of essential substances to the nutrient medium.

GRIFFING: The objective of our first temperature study, using *Arabidopsis,* was to test the composite Bonner temperature lesion hypothesis which asserts that (i) at certain temperature extremes, plant growth is depressed by the inactivation of one or a few especially sensitive reactions and (ii) such growth depression may be prevented by providing the plant with the normal products of the inhibited reactions.

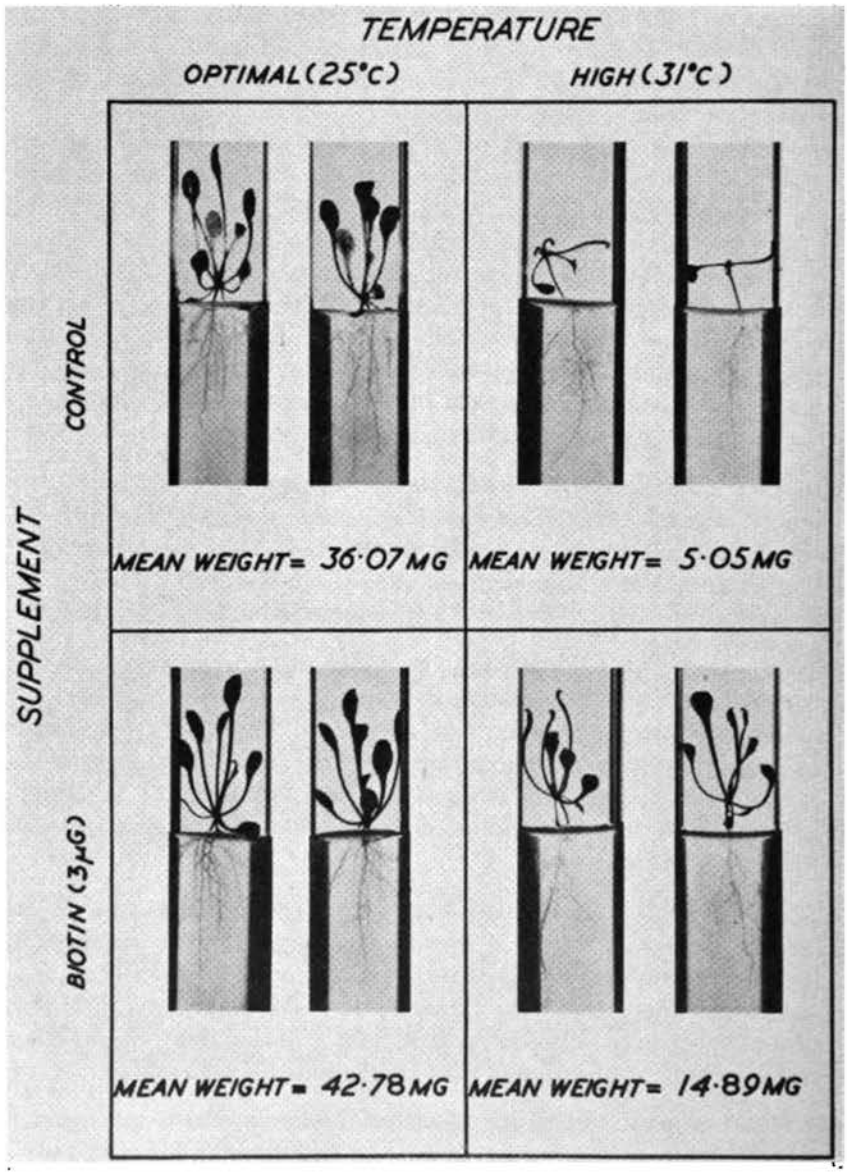
In a survey, 8 out of 43 *Arabidopsis* races showed a disproportionately large decrease in growth at high temperature when compared with growth at optimum temperature. Five of the eight possessed pronounced morphological symptoms of high temperature damage. Three of these five races gave significantly increased growth at high temperatures when vitamins, yeast extracts or nucleic acids were added. Therefore we concluded that the first part of the Bonner hypothesis is true for an appreciable fraction of *Arabidopsis* races. With regard to the second part of the hypothesis, although it is possible to chemically cure some of the high temperature lesions, we suggested that it would be more satisfactory to use a genetic cure, i.e., either replace (in a homozygous condition) the temperature sensitive allele with a temperature resistant one, or, in more complex cases, make use of hybrids as suggested in the present study. The following figure presents a high temperature lesion and its chemical cure:—

HATHEWAY: Temperatures did not vary between night and day, and day length was 24 hours. Consequently, I am surprised to learn that no significant variance in general combining ability was found at "optimum" temperature. Were these genes already fixed in nature? That is, were the plants preadapted for growing under these unvarying conditions?

GRIFFING: Arabidopsis, fortunately, is a plant that grows successfully under constant light and temperature conditions. In interpreting the combining ability analyses we presume that growth at constant 25°C is comparable to growth at somewhat fluctuating temperatures with a mean at 25°C. It is of interest to find with *Drosophila* that the differential heterosis which is found with constant temperatures is not markedly changed with fluctuating temperatures.

BARNES: Light intensity and quality in natural environments may or may not be closely approximated in growth chambers. Do you think that these factors are one explanation for differences in the results of your experiments and the greenhouse experiments of Williams? Do you think the possible disparity between natural and artificial light conditions would seriously limit application of your results to field conditions, i.e., using F_1's?

GRIFFING: The main difference between William's results and ours is that under his regimes the homozygotes and heterozygotes were equally stable, whereas in our temperature regimes the heterozygotes were, generally, more stable than the homozygotes. In the experiments of Williams the light factors may have varied slightly from one regime to another but in our experiment the light factors were nearly constant from one temperature regime to another. In order to explain the divergent results in terms of light factors, it would be necessary to assume a very specific and complicated light-temperature interaction which appears to us completely unwarranted. Also, in our cultural conditions we have found that the



differential intensity of light over the surface of the growing area did not produce significant growth differences. Hence light intensity is not a limiting factor in our experimental methods. Therefore, it seems that the simplest and most logical hypothesis to explain the difference in the results of Williams and those of ours, is that given in the text, which involves different ranges of temperatures in the two experiments.

PFEIFER: Were differences in seedling growth rate noted among lines grown in temperature extremes?

GRIFFING: Except for preliminary tests of the duration of the logarithmic growth phase, we have not measured growth rate changes during ontogeny. High temperature does not seem to differentiate races as far as germination is concerned.

SCOSSIROLI: I am interested in estimates of the amount of genetic variability which arise in self-fertilizing species through spontaneous mutations. I wonder if you had the opportunity to observe differentiation of lines within the same race?

GRIFFING: The structure of the *Arabidopsis* flower ensures self-fertilization, and consequently there seems to be little variation between individuals of the same race. Occasional variants do appear, but whenever they have been tested, they turn out to be single gene mutations.

HANSON: Would you expand on the problems of hybridization in *Arabidopsis?* Also, what are the characteristics of your "races" discussed in paper?

GRIFFING: The various races of Arabidopsis readily set seed on crossing, and we have not observed any hybrid sterility.

Most of the races are very alike morphologically, but they may differ markedly from one another in physiological characteristics. Thus, we have found pronounced differences in high temperature sensitivity, sulfanilamide resistance, phosphate requirement, etc. The characteristics with respect to temperature for many of our races are set out in an earlier paper on temperature lesions (see Langridge and Griffing, (1959), *A.J.B.S. 12:* 117–35).

ROBINSON: I question the interpretation given to 31° performance of F_1, F_2, and parents as a situation relevant to the optimum performance level (25°). In self-fertilizing species (economic crops) performance at the optimum conditions seemed much more appropriate as a source of information to consider in selection as well as in heterosis phenomena. Superiority of F_1 at 31° may have little consequence if this is largely outside the range of conditions of importance to production of the species.

GRIFFING: The emphasis given to the differential heterosis phenomenon in the paper was that it afforded a partial physiological explanation of heterosis as found with field grown crops in continental climates where the plants may be exposed to heat-wave conditions.

With regard to selection problems, the point was made in the talk that it would be extremely unwise to select on performance at, say, 31°C if, in fact, the material is to be grown at 25°C. This is so, since the genetic correlation of growth responses for these two regimes is $r = 0.13$ (Table 3). Likewise, it would not be profitable to select at 25°C for performance at 31°C. Under natural conditions, of course, the temperature fluctuates, and clearly selection for an economic crop should be carried out in the environment in which the crop must be grown eventually. In this way correct

weightings would be given to the various temperature conditions.

However, under natural conditions, there is still another complication in that the pattern of fluctuating temperatures is not constant from one season to another. That is to say, high temperatures may occur in different intensities, and at different periods of growth in different seasons. This may lead to genotypic × environmental interactions which reduce the effectiveness of selection.

It need not necessarily follow that greater phenotypic stability to environmental stresses automatically leads to less genotypic × environmental interaction. However, with temperature studies involving *Drosophila* and *Arabidopsis*, such seems to be the case. Parsons (2) found that with *Drosophila* reared in different temperatures regimes, the inbred lines exhibited a greater genotypic × environmental interaction than the hybrids. With our diallel data, we find that the interaction component for inbreds is 0.0215 whereas for the F_2's (involving the same inbreds) this component is 0.0048. Thus, if our results hold generally for self-fertilized crops, it would appear that the greater phenotypic stability of hybrids implies (i) less genotypic-temperature interaction and therefore more effective selection and (ii) wide adaptability for a single end product of selection.

With maize, Jones (1) argues that double crosses are phenotypically more stable than single crosses in a range of diverse environments. He suggests that use of hybrid mixtures in self-fertilized crops may result in the same phenomenon. Our data, involving F_2's substantiate this suggestion. Hence, this brings up the entire question as to whether the plant breeder's end product should be a single homozygous genotype, mixture of homozygotes, single cross, double cross, synthetic or advanced generation mixture. Of course, such decisions largely rest on the cost of seed production and the agronomic feasibility of the utilization of the various types of populations. As far as phenotypic stability in a variable environment is concerned, we should suppose that reliance on a single homozygous genotype would be the least desirable, if other types of populations are economically and agronomically possible.

It may be argued that eventually a homozygous variety may be produced which is as phenotypically stable as most other sorts of populations. Although we doubt that this is possible, surely the above general argument holds for most situations until such a super-homozygous genotype is found.

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Selection Studies of Quantitative Traits With Laboratory Animals[1]

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THE first experiment that uncovered the basic principles of genetics was conducted with a particular set of "all or none" characters of a particular species, garden peas. It was not, however, too long before biologists recognized that the genetic principles discovered in this pea experiment were not restricted to only pea species or to species in the plant kingdom, but they were universal for all higher plants and animals. Such experiences by geneticists widened the scope of genetical research by giving opportunities to investigate an experimentally suited organism for genetic questions without losing implication of the results general to other organisms. Today, most biologists believe that a discovery made from a study of a particular organism can be applied to other organisms under similar circumstances.

Drosophila and mice have often been used for the exploration of knowledge of quantitative genetics. Several expedient characteristics of these organisms for such a purpose are high reproductivity, fast turn over of life cycle, small body size, and high versatility in adaptation to laboratory conditions. Moreover, the biology of these organisms, including genetics of qualitative traits, is extensively known. Thus, information necessary for breeding experimental materials and knowledge for supplementing interpretation of analyses of quantitative traits are more accessible with these organisms than with others. These considerations on the nature of experimental organisms become extremely important when one attempts to investigate slow genetic changes caused by continuous selection on the performance of quantitative characters over a number of generations.

The purpose of this paper is to present some information, available from experiments with Drosophila and mice, which is considered to be relevant to the planning of selection programs and the understanding of genetic changes in populations under continuous selection programs. First, general information will be given for the bases of choosing a selection criterion, of determining base populations, and of deciding the types of control material to be included in each test

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of improved populations. Next, an examination will be made of the types and magnitudes of response to selection, the predictability of changes in mean performance and problems of selection limits. Finally, a few special problems, such as repeatability of response in separate runs of a selection experiment from one initial population, effects of linkage on response to selection and differential response in different environments, will be discussed.

CHOICE OF SELECTION CRITERIA

The selection criterion is the standard of judgement, upon which the fate of the members of the population is decided. This standard includes the trait or traits to be measured, the relationship of individuals to be evaluated as units, and the form in which test information is to be used in selecting actual parents of the following generation. The choice of selection criterion is intimately associated with the genetic structure of base populations and with the final form of populations which the investigator wishes to achieve through the selection program.

One of the important factors in choosing selection criteria is the magnitude of hereditary variation relative to the non-hereditary or to the total phenotypic variation. The magnitude of hereditary variation depends primarily upon the genetic make-up of populations; *i.e.*, the number of segregating loci, the gene frequencies at such loci, and the effects of intra- and inter-locus gene actions. The extent of non-hereditary variation, on the other hand, is affected by various levels of heterogeneity and relative frequencies of such levels occurring in an environment encountered by a genetic population and by random fluctuations within and between the heterogeneity levels in the environment. A general and intuitive consideration is that the effects of selection become more distinct as the ratio of hereditary to total phenotypic variation increases. A high ratio can be obtained either by choosing a trait with large hereditary variation or by reducing non-hereditary variation through management of environmental conditions.

The work by pioneers of population genetics, notably Wright, Fisher, and Haldane, however, revealed that the progress expected from selection is not fully understood by the consideration of only the ratio of the total hereditary to the non-hereditary variations. They found that the changes in gene frequencies are the most basic quantities which characterize various changes in a population as the result of selection among individuals or among groups of individuals. Gene frequency changes are directly proportional to the additive genetic effects at each locus, which effects contribute only a part of the total hereditary variance. Such a part is usually called additive genetic variance. These and other theoretical developments, such as the genetic evaluation of parent-offspring regression, lead one to accept the ratio of total additive genetic variance to total phenotypic variance (heritability when the selection criterion is individual performance) as a basic quantity to represent the effectiveness of mass selection. In Table 1 heritabilities of various characters in Drosophila and mice, reported by several workers, are given.

TABLE 1.—ESTIMATES OF HERITABILITY FOR VARIOUS TRAITS IN DROSOPHILA AND MICE (FROM FALCONER, 1960)

Organism and Trait	Heritability estimates	Source
Mice		
Tail length at 6 weeks	.6	Falconer, 1954
Body weight at 6 weeks	.35	Falconer, 1953
Litter size (1st litters)	.15	Falconer, 1955
D. melanogaster		
Abdominal bristle number	.5	Clayton, Morris, and Robertson, 1957
Body size (thorax length)	.4	F. W. Robertson, 1957b
Ovary size	.3	F. W. Robertson, 1957a
Egg production	.2	F. W. Robertson, 1957b

The values of heritability in Table 1 should not be considered as absolute ones, since the additive genetic variance as well as the total phenotypic variance is subject to experimental techniques and environments. On the whole, the traits with low heritabilities are those closely related to selective advantage of organisms, and a high heritability is found with a trait the expression of which is rather irrelevant to the survival of bearers. For example, a genotype with high egg production has a selective advantage over genotypes with low and medium egg productions in a relatively stable environment such as that in a cage population. As a consequence, a large proportion of the genetic variance has been eliminated, and this results in a low heritability.

Approximate knowledge of heritabilities of various traits will help to choose selection criteria on which selection programs may be carried out efficiently. With a high heritability trait such as bristle numbers of Drosophila, mass selection on bristle counts of individual flies is expected to be efficient. With a low heritability trait such as litter size in mice, attempts should be made to reduce the proportion of non-hereditary variance in the total variance of selection criteria. This can be achieved by reducing the heterogeneity in testing conditions or by choosing average values of genotypically similar groups such as full-sib or half-sib families for the selection criteria. A selection criterion which consists of more individual measurements will have smaller components of environmental variation. In consequence, there will be an increase in the ratio of hereditary variance to the total variance on such selection criteria.

In the present paper the general term heritability will be used for the ratio of additive genetic variance present among selection criteria to the phenotypic variance found among the criteria. Let H_i and H_f be the heritability of a certain trait when the selection criterion is measurements of individual members of a population, and that when the selection criterion is means of groups of genetically related individuals, respectively. Then,

$$H_i = \sigma_A^2/\sigma_T^2 \text{ and } H_f = C\sigma_A^2/\sigma_f^2$$

where σ_A^2, σ_T^2, and σ_f^2 stand for the total additive genetic variance, the total phenotypic variance and the variance among the means of groups, respectively. C represents the fraction of the total additive genetic variance contained among the means of groups. The relative value of two heritabilities, H_f/H_i, is equal to $C\sigma_T^2/\sigma_f^2$. For example, C is $\frac{1}{2}$ when the full-sib means are used as selection criterion and the following generation is made by random mating among the selected full-sib groups. Thus, a more efficient selection is possible by full-sib family selection than by mass selection, when σ_T^2 is larger than $2\sigma_f^2$.

STUDIES OF BASE POPULATIONS

Usually there are not many alternatives in choosing the base population when farm animals and crops are to be improved. The two major concerns in deciding a base population for such practical selection programs are the level of yield of the base population and the rate of improvement expected from the first several cycles of selection. The ideal base is one which has a high yield level at the initial stage and is expected to show a fast rate of improvement from selection. When such ideals are not available, the base is chosen to optimize these two factors within the scope of the proposed programs.

In laboratory experiments the basis of choosing a base population is not necessarily the same as the case of practical selection programs. This is particularly true when laboratory organisms are used for purposes of exploration of genetic mechanisms in quantitative traits. The base population used for such purposes is usually preferred to approximate, as closely as possible, a stable random mating population with an appropriate amount of genetic variability. Such a population will possess desirable characteristics for selection experiments; stability with respect to natural selection, linkage equilibrium among loci, and reproducibility of similar samples from the base population.

Some types of genetic populations often used as base populations in laboratory selection experiments are considered in relation to these ideal characteristics in the following part of this section. Characterization studies to obtain preliminary information on the base population can be made through such techniques as parent-offspring regression, half-sib and full-sib analysis of variance, and the analysis of variance of diallel crosses. Description of actual designs for these analyses can be found in text books of quantitative genetics (11, 15, 17).

Cage populations of Drosophila, in which a few thousand adults, pupae, and larvae are bred continuously, can be used as base populations. These populations, which resemble an open-pollinated variety of such plants as corn, will be stable random mating populations. Kojima and Kelleher (unpublished) analyzed two similar cage populations of *D. pseudoobscura* with respect to two characters, abdominal bristle counts, and egg production. The results are summarized in Table 2. It is clear that the types of selection employed for the two

TABLE 2.—HIGH AND LOW HERITABILITY TRAITS IN TWO CAGE POPULATIONS OF *D. pseudoobscura*.

	Mean	σ_A^2	H_i
Mather			
egg production	41.7	6.40	.032
bristle count	31.5	1.81	.405
Mono			
egg production	39.2	7.62	.039
bristle count	30.1	1.85	.433

characters must be different for both cage populations. According to the discussion given in the previous section, the use of bristle counts of individuals as selection criterion would be effective, while selection criteria for egg production should be some kind of family means in order to improve the trait significantly.

Although cage populations can certainly serve as good base populations for the short term experiment, the structure of the population may change over a long run, causing deterioration in many directions in the selected lines. This happens quite often when cage populations are started from wild stocks. It is known that there are numerous lethal and sub-lethal genes in wild populations of Drosophila which are not noticed in large random mating populations. When such populations are subjected to a particular pattern of mating and pressured by selection, the effects of lethal and sub-lethal genes are exposed and they may cause deteriorations of lines.

This drawback is not usually present if the base population is an intermixed population from crosses of two or more inbred lines. The majority of selection studies with laboratory animals are initiated from base populations of this type. This is often a logical consequence, because laboratory stocks are usually maintained in rather small sizes, resulting in considerable degrees of inbreeding in each stock. In most Drosophila laboratories, for example, stocks are kept in small containers such as one-half pint milk bottles, and approximately 20 to 25 adults of each sex, on the average, are transferred into fresh media each generation. The effective breeding size in this procedure is considerably smaller than the actual numbers transferred. Crow and Morton (7) estimated adjustment factors for the effective size to be about 0.7 and 0.4 for females and males of laboratory Drosophila. With this information and Wright's formula for approximate proportions of unfixed loci (31), it is easy to visualize that most Drosophila stocks kept in bottles have lost considerable amounts of genetic variation over time. In a stock with 20 generations a year, the proportions of unfixed loci after 1, 2, and 3 years would be, at most, 0.69, 0.48 and 0.32, respectively. These figures represent probable maxima, because bottle necks of population size are usually inevitable once in a while in maintenance of stocks. These considerations suggest that most Drosophila stocks kept in bottles should be taken as partial inbreds.

Intermixed populations from crosses of only two or three inbred lines will not be in linkage equilibria in the early generations following the initial

cross. This is particularly true when the lines are deliberately chosen to be extremely divergent. With linkage disequilibria estimates of genetic variances are biased from what would be in the population with linkage equilibria (6). Furthermore, all of the potentially possible genetic variations, which come out as a result of recombinations among genes on progenitor chromosomes, may not be in such a population. If the intermix is advanced through random mating for several generations, extreme linkage disequilibria break down and the advanced population tends to linkage equilibria. Disequilibria with tight linkage may not be reduced much, but these do not exert serious effects on the rate of change in the population mean due to selection (Kojima and Kelleher, 16).

As the number of lines brought into the intermix increases, and as the number of loci affecting the trait increases, the effects of linkage disequilibria decrease and the rate of change in the population mean from selection tends to become equal to the rate expected in a population at linkage equilibrium. The possible effects from linkage disequilibrium on response to selection will be discussed later in connection with the results from simulated selection studies on high speed computers.

The base population made of the advanced generations of crosses among inbred lines is reproducible as it is needed. As to the stability with respect to natural selection, it will be a safe guide to carry the base population along with the selected lines and test it at one of the later generations. By this procedure the changes in the base population which may have taken place through natural selection can be detected, at least in part.

Random mating populations are sometimes crossed to obtain a base population with more genetic variability than that present in each of the original populations. In order to achieve this aim, one may wish to intermix populations which are quite divergent and unrelated in origins. Before such a newly arisen population is used for a selection program, it must be studied in some detail with respect to the stability of mean performance over the first few generations beyond the cross.

Vetukhiv conducted a series of such tests among several geographic populations of *D. pseudoobscura* with respect to several traits (e.g., viability, 26; fecundity, 27; longevity, 28). One of the typical results is given in Figure 1a. The parental populations for individual localities are obtained by crossing 10 or more strains collected from each location. The reciprocal F_1's are made by crossing virgins and males from all possible pairs of locations, and the F_2's are obtained by random mating of the F_1 flies within each F_1 progeny group. General results obtained from a series of tests are that the F_1's show heterosis for the traits studied in most locality combinations, and that not only do such expressions of heterosis disappear in the F_2 hybrids, but also the F_2 generation means are often lower than those of the low parental populations. Such phenomena were called "F_1-heterosis and F_2-breakdown." Vetukhiv considered that the F_1-heterosis in his study was probably due to the superiority of heterozygosis *per se,* and that the F_2-breakdown was caused by the disintegration of previously co-adapted genomes

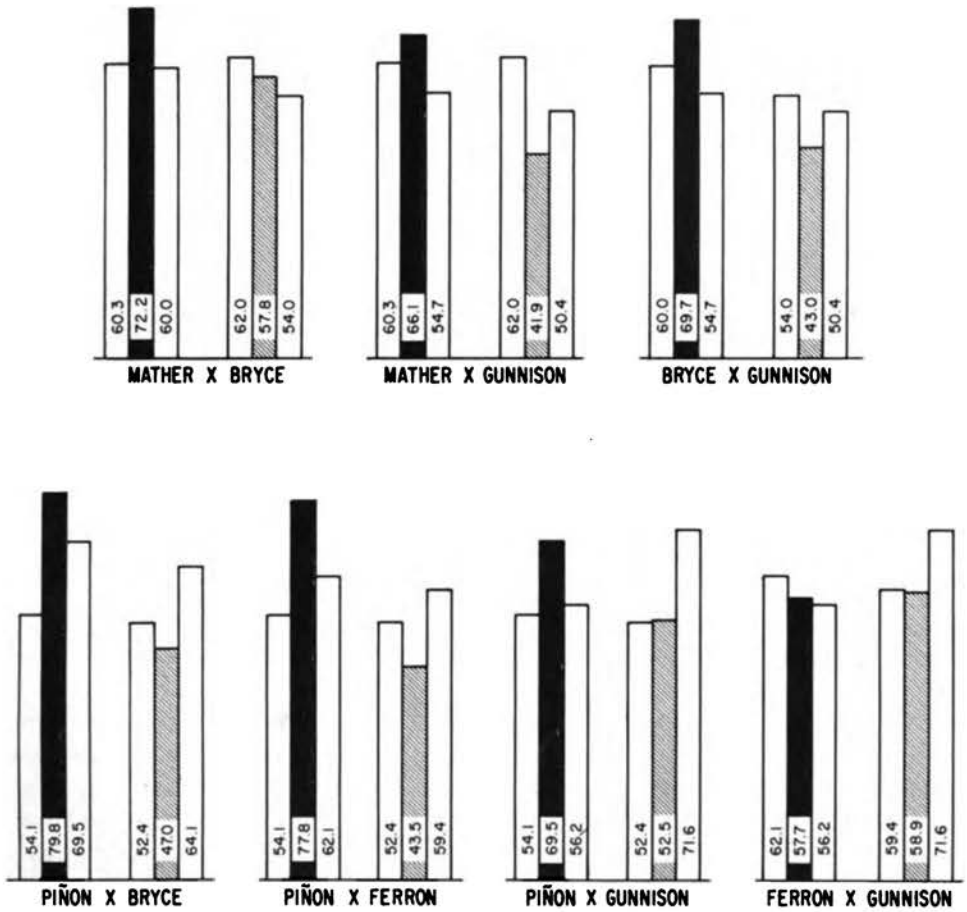

FIGURE 1a. *Viability of geographic populations of D. pseudoobscura and their intercrosses. White = parents; black = F_1; cross hatched = F_2. (Taken from Vetukhiv, Evol. 7, 1954).*

through gene recombination (28). Wallace and Vetukhiv (30) found also that recombinations within and between chromosomes produce inferior genotypes with respect to fitness component characters in *D. melanogaster*. It should be pointed out that breakdown of this type is only possible when epistasis and linkage disequilibria are present in hybrid populations. A more recent study by Vetukhiv and Beardomore (29) shows that the F_1-heterosis and F_2-breakdown are also conditioned by testing environments (Figure 1b). This indicates the existence of genotype by environment interactions and points out the importance of such interactions in determining heterosis mechanisms.

Although marked effects of heterosis and breakdown have been observed mainly on the characters closely associated with selective fitness, the same phenomena may occur with characters less related to fitness when genetically divergent populations are brought together into one gene pool. It is preferable, there-

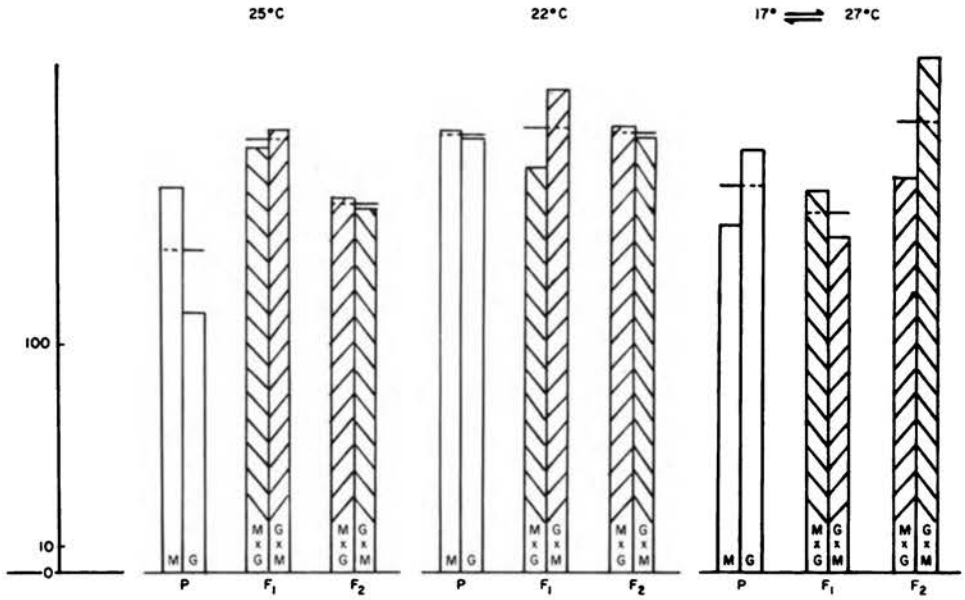

FIGURE 1b. *Viability of geographic population of D. pseudoobscura and their intercrosses tested under different environments. (Taken from Vetukhiv and Beardomore, Gen. 44, 1959).*

fore, to advance hybrid populations by random mating for several generations prior to selection studies in order to reduce drastic effects of linkage-epistasis complexes, and to choose hybrids which do not show pronounced instability with respect to environments.

CONTROL OF EXPERIMENTS

The primary role of control in experimentation is to establish the point of reference for an entire system of measurements obtained in various parts of an experiment. The system of measurements in a continuous selection study covers a wide range of time and space. Thus, considerable fluctuations are expected in actual test environments at the successive cycles of selection even under laboratory conditions. The performance of proper control material becomes, therefore, an important indicator of accidental, temporary, and random fluctuations in the test environments. Genetic changes due to selection can be shown only after a proper adjustment of raw data is made for the environmental fluctuations represented by the performance of control included in each test.

Qualifications for an ideal control are dependent upon kinds of organisms, nature of traits selected, and types of adjustments to be made. In the following a set of basic requirements for controls in continuous selection experiments is listed:

1. *Reproducibility:* A group of genotypes used as control can be reproduced with constant relative frequencies of individual genotypes as they are needed.

2. *Genotypic variation:* The range of genotypic variability in control material should be the same as or close to that of lines under selection.

3. *Average response:* The pattern and magnitude of average response of control to environmental fluctuations are, as a whole, similar to those of selection lines.

4. *Degree of homeostasis:* Various degrees of homeostasis are desirable for different genotypes included in control material.

5. *Practicality:* The preparation of a set of controls from basic stocks should be so practical that an experimenter can produce it whenever needed.

How strictly these requirements must be met in a particular selection study depends upon behaviors of selection criterion and the objectives and design of each experiment. Generally speaking, the importance of control becomes less as the sensitivity of the trait to environmental fluctuations decreases and as its heritability increases. In selection studies of abdominal bristle counts in Drosophila, for example, it is not really necessary to use any particular control material for each generation (20). On the other hand, in selection studies for egg production in Drosophila, a well qualified control is usually necessary to detect the genetic changes due to selection.

As shown by the list, the qualifications for a good control are in many respects similar to those of the base populations. Hence, the same genetic materials may be used for control as were considered for base populations. In considering the use of a random mating population as control, however, it must be remembered that such a population should be maintained in rather large numbers, and that large samples have to be taken from it and included with each test. Only through such procedures can one be reasonably sure of having small genetic sampling fluctuation in controls.

At somewhat the other extreme, inbred stocks have occasionally been used as controls. These stocks would be reproducible and relatively easy to maintain. However, many laboratory animals have high degrees of inbreeding depression for various characters. Such depressions result in a large difference between the mean of control and that of selected lines. Also, inbred stocks are usually less homeostatic than non-inbred lines.

Single crosses and double crosses from a number of inbreds can overcome some of the drawbacks of either of the two types already discussed. They are reproducible, possess varying degrees of homeostasis, and are relatively practical to prepare. Their genotypic variation and average response are expected to be similar to those of the population under selection, when the parental inbreds of the single crosses are randomly derived from the same source materials as those for the population under selection. Thus, such a group of single crosses or double crosses should serve satisfactorily as controls of experiments.

An illustration of the use of controls for checking shifts in mean performance is given in Figure 2a for a reciprocal recurrent selection program on egg production in *D. pseudoobscura*. Details of this program will be given later. The

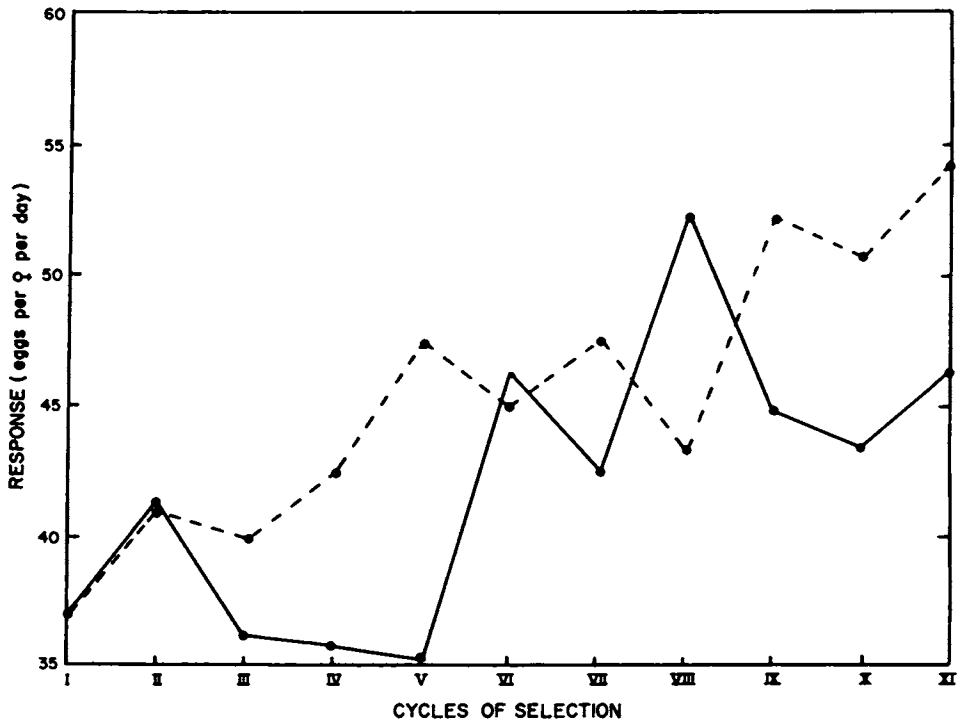

FIGURE 2a. *Response to selection in a reciprocal recurrent selection study on egg production of D. pseudoobscura for eleven cycles. The solid line represents unadjusted mean performance. The broken line is the mean performance adjusted for control performance. The method of the adjustment is given in text.*

present figure shows the effects of control adjustment on the changes in mean response to selection. In this program single crosses among four inbred lines were used in Cycle I–VI and single crosses among nine lines in Cycles VI–XI. For each cycle the change in the mean of the selected populations, ($\Delta\bar{Y}$), was calculated as:

$$\Delta\bar{Y} = (\bar{Y}_i - \bar{C}_i) - (\bar{Y}_{i-1} - \bar{C}_{i-1})$$

where $\bar{Y}_i$ = mean of selected population for *ith* cycle and

$\bar{C}_i$ = mean of control crosses for *ith* cycle.

It is quite clear in Figure 2a that the adjusted and unadjusted responses to selection reveal important differences. The average slope of response is much higher with the adjusted points than with the unadjusted points. Secondly, the adjusted points line up more closely along the adjusted average slope than the unadjusted points along the unadjusted average slope.

Changes in genetic and environmental components of variance due to various fluctuations of test environments can also be checked with control performance as shown in Figure 2b. The use of controls for this purpose often arises when investigators want to know changes of genetic variance in selected

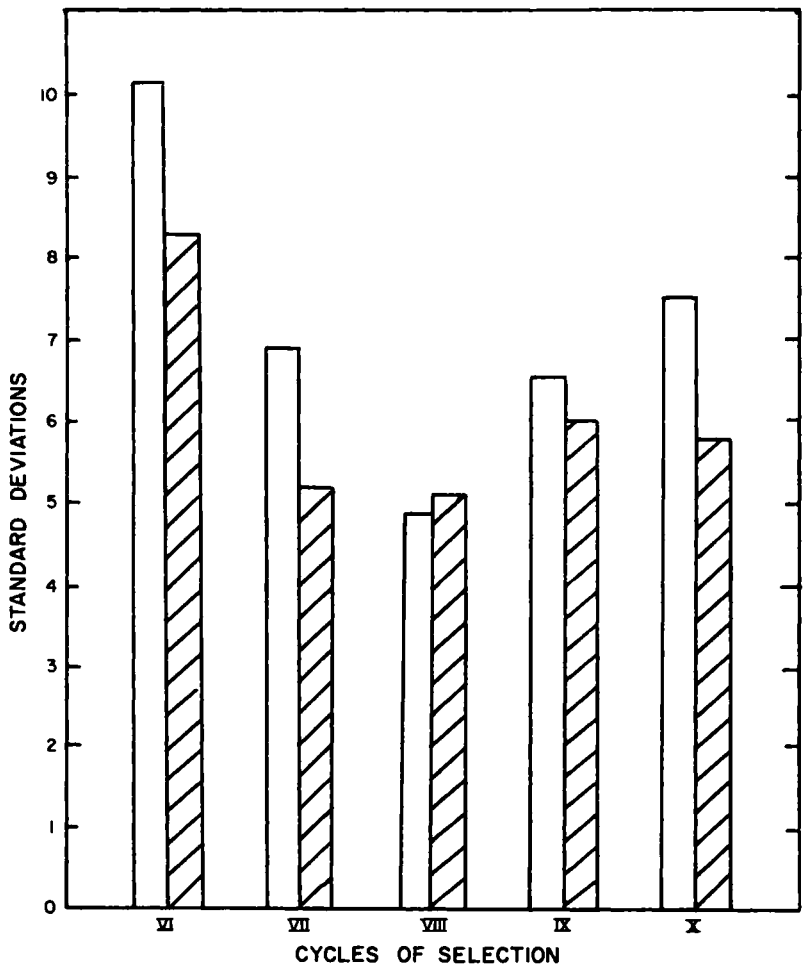

FIGURE 2b. *Comparisons of variations in test progenies and control materials (18 single crosses) at each cycle of selection. Data are taken from a reciprocal recurrent selection study on egg production of D. pseudoobscura. Only a part of the continuous selection cycles are shown (cycles, VI–X). White: Standard deviation of family means in tests. Shaded: Standard deviation of single cross means in controls.*

populations. While heritability estimates at two different stages of selection can be used for the same purpose, a well-qualified group of controls serves the role of independent check on the magnitude of variance. Thus, in Figure 2b, it is seen that, in general, the fluctuations in standard deviation of control material and those of test material from cycle to cycle in the same direction and usually are of the same order of magnitude.

A final example of control is taken from experiments which are directed to find the effects of selection by two-way high- and low-line selection conducted

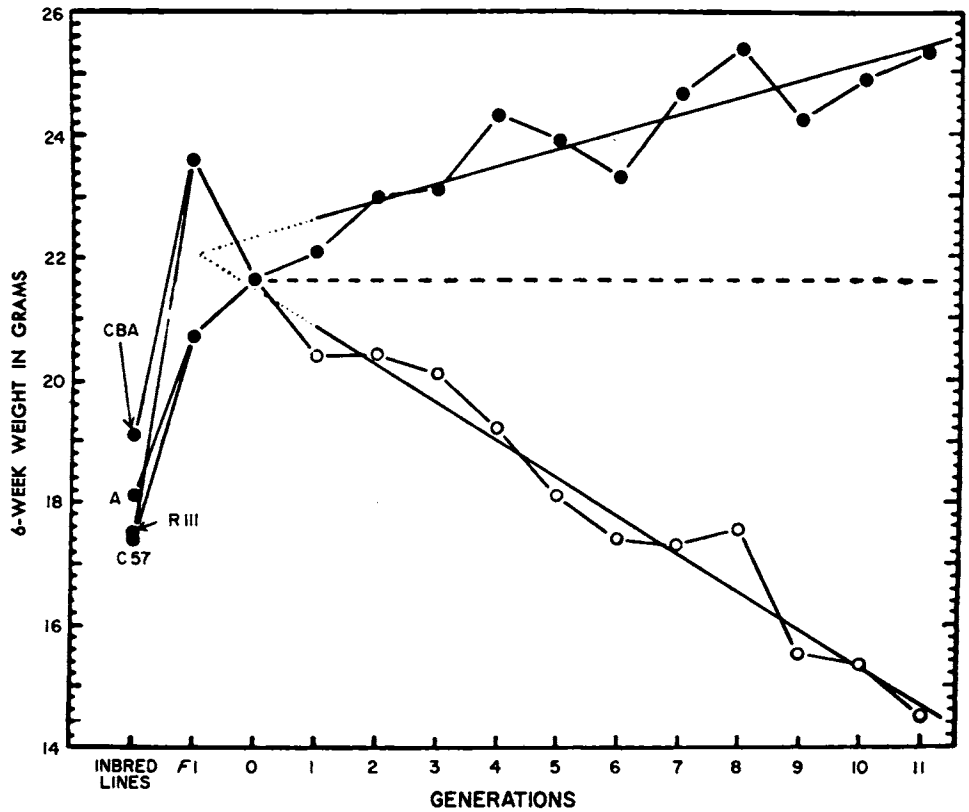

FIGURE 3a. *Response to two-way selection on 6-week weight of mice. Full circle = upward line; open circle = downward line. (Taken from Falconer, J. of Gen., 51, 1953).*

in a common environment for both lines, starting from one base population. Falconer (8) reported the results of a two-way selection study on 6-week weight in mice. Selection was made among mice from the same litter in order to avoid differential maternal influences. In Figure 3a the result for the high and low lines are drawn separately. The upper is the result of high selection, while the lower is that of low selection. In this figure it is obvious that on several occasions the changes in performance from one generation to the next were opposite in sign from what were expected from the directions of selection (4–5, 5–6, and 8–9 cycles in the high line and 7–8 in the low line). The divergence between the two lines given in Figure 3b, however, shows a never-decreasing pattern over a number of generations. This means that, when the high line performance decreased because of an environmental deviation, the low line performance was decreased by the same deviation, yielding a further divergence, and *vice versa*. In this experiment the performance of one line can be considered to provide a control for the other line, reciprocally.

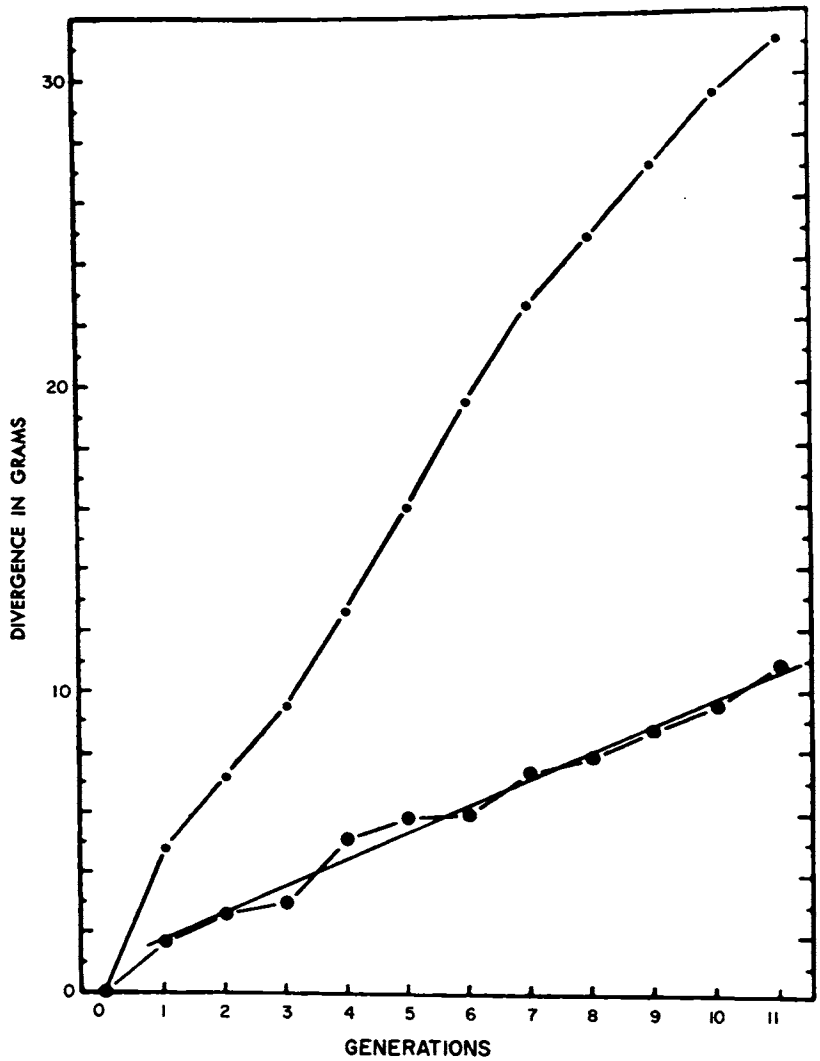

FIGURE 3b. *Divergence between the upward and downward lines in Figure 3a. The upper graph = accumulated selection differential; the lower graph = divergence. (Taken from Falconer, J. of Gen., 51, 1953.)*

RESPONSES TO SELECTION[2]

The basic effect of selection is to change the array of frequencies of gametic types which form the population of genotypes after mating. In a random mating population with linkage equilibrium, the gametic array is simply generated from

[2]The details of the reciprocal recurrent selection study presented in this section will appear in January or February issue of *Genetics*, Vol. 48 under the title of "A Comparison of Purebred and Crossbred Selection Schemes with two Populations of *D. pseudoobscura*" by K. Kojima and T. M. Kelleher.

the arrays of gene frequencies at individual loci by the factorial law of multiplication. Thus, the basic effect of selection is, under normal breeding programs, described by the changes in the gene frequency of each locus. The changes of gene frequency themselves, however, are not observable, because the effects of individual loci are inseparable on phenotypic measurements of quantitative traits. Quantities observable on these measurements are the *statistical averages* of various degrees such as means, variances and covariances, etc.; the changes which reflect the basic effects of selection.

When a population is selected with respect to a certain selection criterion, the changes take place not only on the statistical averages of the criterion, but also on those of many other traits. This is expected because the distributions of genes for various traits are often correlated by linkages, and some genes are known to exhibit pleiotropy. Changes in traits other than the selection criterion are called correlated response to selection but will not be discussed in detail in this paper.

The change of the population mean due to selection, *mean response,* was formulated by pioneers in the fields of population genetics and animal breeding. Let $\Delta\bar{Y}$, S, and H be the mean response (i.e., the difference between the means of parental and offspring populations), the selection differential (i.e., the difference between the mean of the entire parental population and that of the selected parents), and the heritability of selection criterion. Then the simple relation,

$$\Delta\bar{Y} = SH \tag{1}$$

is derived for one cycle of truncated selection in a large random mating population. Falconer (9) proposed a pictorial representation of mean response by plotting accumulated response, $\Sigma\Delta\bar{Y}_i$, against the accumulated selection differential, ΣS_i, over the successive cycles of selection, where i represents each cycle.

Results for a reciprocal recurrent selection experiment being conducted by the authors on egg production of *D. pseudoobscura* will be presented as an illustration. The base populations for this selection study were two cage populations kept under a constant stock room condition for a period of more than 2 years. They came from two different localities in the western United States. Each of 60 males taken at random from 1 population was mated to 2 females taken at random from the other population (See Figure 4). Reciprocal crosses of the same size were made simultaneously. The female offspring from the reciprocal crosses were used to evaluate their male parents. The test for 1 cycle consisted of the 2 crosses, 60 half-sib families for each cross, 2 full-sib families for each half-sib family, duplicate test bottles for each full-sib family, and 3 daughters per bottle. Thus, both sides of reciprocal tests in each cycle had the design structure of nested analysis of variance. Immediately after the mating for the test crosses, each male was remated to three random females from his own population in order to provide the two populations for the next cycle.

In Figure 5 the accumulated mean responses (adjusted for control) plus the base value (= 37.20) take positions quite linearly against the accumulated selection differentials for the entire period of 11 cycles. Therefore, a linear regres-

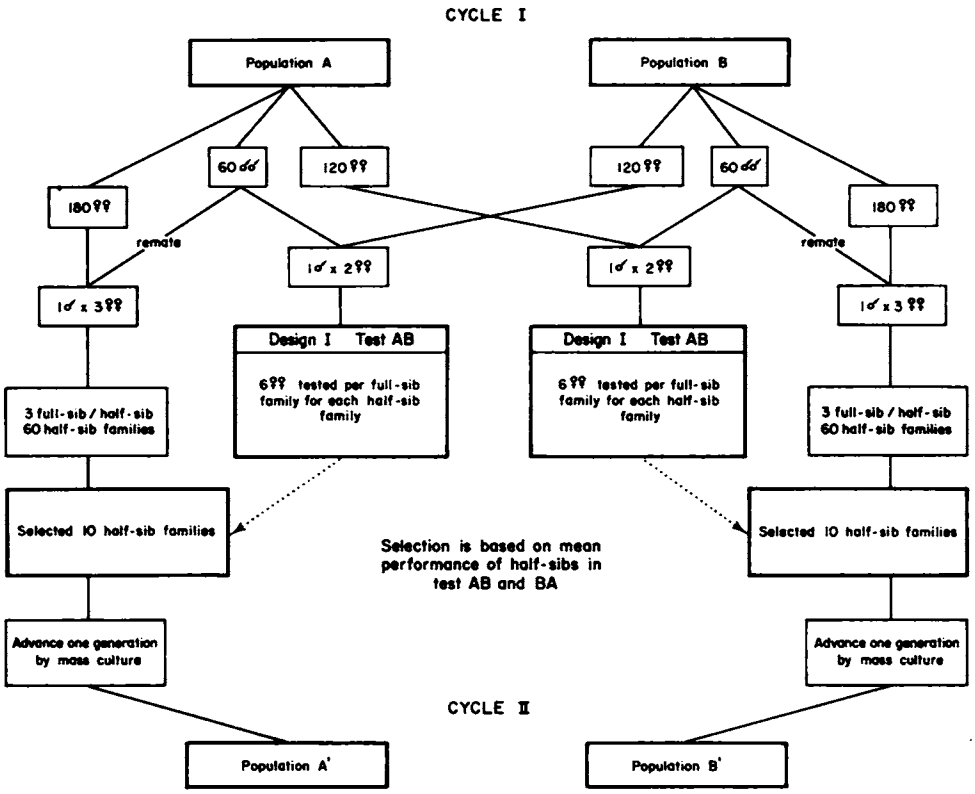

FIGURE 4. *Schematic representation of reciprocal recurrent selection procedure.*

sion line is fitted to the points. The regression coefficient of this kind is an estimate of H in formula (1) for the present scheme of selection. This estimate, 0.148 ± 0.032, is the "realized heritability" of this selection program for the first through eleventh cycle.

Since the response to selection is linear and the selection differentials for individual cycles have not changed, there is no indication of substantial changes either in heritability or in genetic variance through all cycles of selection. Thus, the average genetic variance among half-sib means and average total variance among half-sib means were computed from the estimates of genetic variances and of variances among half-sib means, obtained from the analysis of variance in individual cycles. This was done separately for reciprocal tests. Let σ_{m1}^2, σ_{m2}^2, σ_{f1}^2, and σ_{f2}^2 be the average estimates of the genetic variances among half-sib means in one cross (1) and its reciprocal cross (2), and the total variances among half-sib means in cross (1) and cross (2), respectively. Now the contribution of genetic variance to the rate of change in egg production (an average slope in Figure 5) is obtained as

$$H_f = \frac{1}{2}\frac{\sigma_{m1}^2}{\sigma_{f1}^2} + \frac{1}{2}\frac{\sigma_{m2}^2}{\sigma_{f2}^2}$$

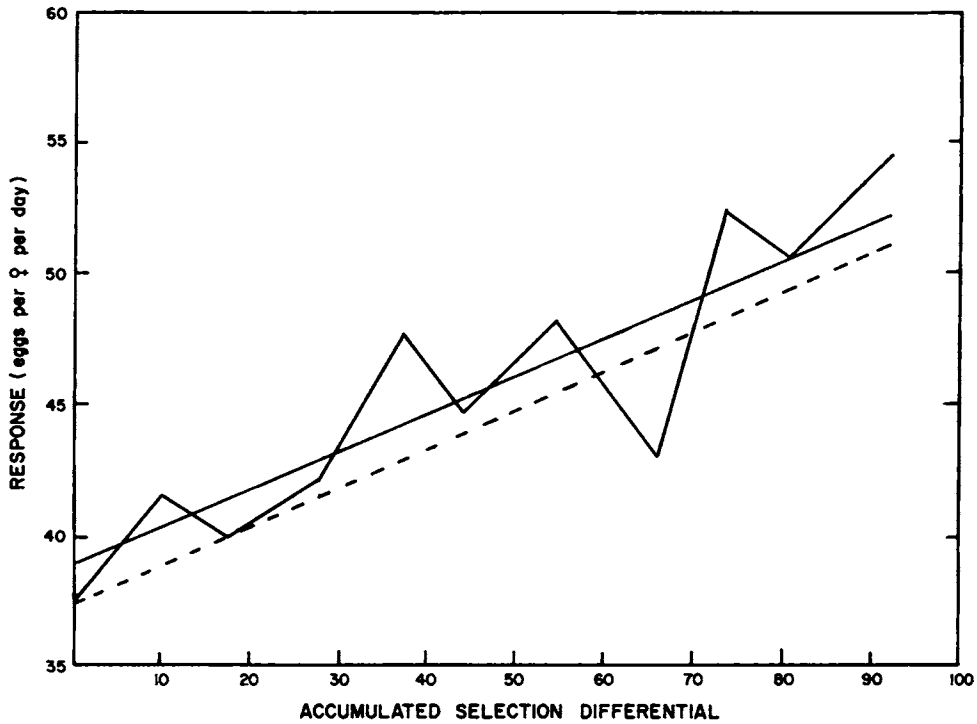

FIGURE 5. *Response to reciprocal recurrent selection on egg production of D. pseudoobscura. The accumulated response is plotted against accumulated selection differential. The solid linear line = a linear regression line of the points of which slope is the estimate of "realized heritability." The broken linear line = a linear prediction line which passes through the point of the base population with the slope equal to the average heritability estimate obtained from full- and half-sib family analysis at each cycle.*

which turns out to be 0.156 in this experiment. In Figure 5 a line is drawn with this slope, passing through the base point (37.20). It is clear that the two linear lines in Figure 5 are essentially parallel to each other. This indicates that the realized heritability agrees well with the estimate of heritability from the analysis of genetic components of variance.

The total response for the 11 cycles was 15.3 eggs per day per female. This corresponds to 41.1 per cent of the average cross performance of the base populations (4.11 per cent per cycle of selection). The total response also corresponds to $2.2\sigma_f$ where σ_f^2 is the total variance among the selection criteria (i.e., half-sib family means in the reciprocal tests). The accumulated response in egg production may be compared with the performance of single cross hybrids. From each of the base populations, a number of inbred lines were derived by brother-sister mating, avoiding selection. A series of random single crosses were made between inbreds from one population and those from the other population. Mean daily egg production of these single crosses was distributed approximately in normal shape with mean = 40 and genotypic standard deviation = 10. The mean

performance of the reciprocal tests at the eleventh cycle of this selection experiment deviates about 15 eggs from the mean of single cross hybrids. This deviation corresponds to 1.5 times the standard deviation of the distribution of single cross hybrids. It may be said, therefore, that the reciprocal recurrent selection experiment has improved egg production to the level equivalent to the top 7 per cent of single cross hybrids between random inbreds from the base populations. As seen in Figure 5, the mean performance of the reciprocal tests is still responding linearly to selection at the eleventh cycle. Thus, it is not difficult to imagine that the mean of reciprocal tests can excell the performance of the best single cross hybrid available from a moderate number of inbreds.

In computing the average slope of mean response in Figure 5, it was assumed that the change did not occur in the magnitude of heritability in any appreciable amount. This supposition is supported by the analysis of heritability estimates from the full-sib and half-sib data in each cycle. Table 3 presents various estimates for the first five cycles and the last six cycles, separately.

TABLE 3.—CHANGE IN ESTIMATES OF ADDITIVE GENETIC VARIANCE AND HERITABILITIES THROUGH 11 CYCLES OF RECIPROCAL RECURRENT SELECTION FOR EGG PRODUCTION IN *D. pseudoobscura*. (1) = ONE CROSS; (2) = RECIPROCAL CROSS. FORMULA FOR H_f GIVEN IN TEXT.

Cycles	σ_m^2		σ_f^2		H_f	$H_f(1-XI)$
	(1)	(2)	(1)	(2)		
I–V	8.0	2.2	43.7	34.2	0.124	
VI–XI	10.1	7.9	51.1	52.1	0.173	0.156

The estimates of σ_m^2 seem to have increased from the I–V cycles to VI–XI cycles, particularly in cross (2). The increase in the heritability, however, is only 0.05, since the estimates of σ_f^2 have also increased. The analysis of individual cycles reveals that the fluctuations in the estimates of σ_m^2 and σ_f^2 are rather large from one cycle to another. Furthermore, a parallel pattern of fluctuations has been observed in the magnitudes of genotypic and environmental components of variance in the control material of each cycle. These findings suggest that an increase of 0.05 in heritability estimate does not indicate any intrinsic change in the genetic variance.

The mode of mean response to selection is generally the same in many other experiments as that of the reciprocal recurrent selection experiment just described, when the first period of selection (10 to 15 cycles) is considered. Some examples of such experiments are: individual mass selection, full-sib selection and half-sib selection carried out on abdominal bristle counts of Drosophila (3), full-sib (within litter) selection on 6-week weight of mice (8, 10), and mass selection on body size of Drosophila (22, 25). The estimates of heritability for these experiments range widely from a low value for egg production in Drosophila

to a high value for bristle counts. From these findings it may be concluded that the total response in the mean of the population continues to change, on the average, *linearly* in the direction of selection during the early period of selection, regardless of the kinds of organisms and traits and of the methods of selection.

LIMITS OF SELECTION RESPONSE

When selection is practiced further, the response in the mean and genetic variance of the population is expected to cease eventually. Populations which have arrived at the limit of selection may be called "plateaued" populations. In such populations, all loci are fixed with only one allele through the processes of selection and random fixation. Some exceptions are; loci with marked overdominance on the expression of the selection criterion, and loci of which alleles, unfavorable in the direction of selection, are favored to remain in the population, because of tight linkages with fitness genes or in virtue of pleiotropy on fitness values.

The analysis of the process of changes toward a plateaued population is extremely difficult. A proper analysis of the process involves specification of a number of variables and evaluation of deterministic and stochastic effects on these variables over many generations. There exists virtually no theoretical investigation on this problem, except a recent work by A. Robertson (21). In the following a few long term selection experiments are presented in order to indicate possible outcomes of such experiments.

Falconer (10) presented the results from a long term selection study of six-week weight of mice diagrammatically (Figure 6). The upward selection was

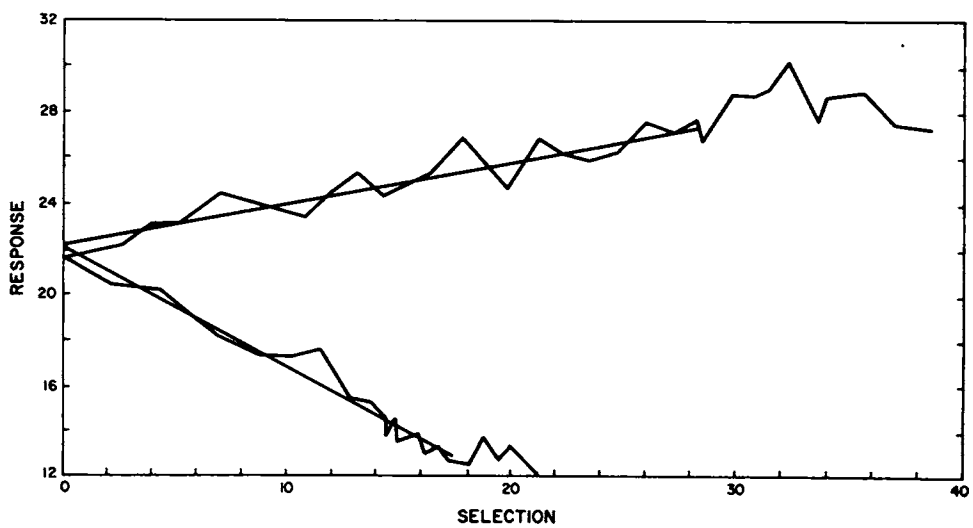

FIGURE 6. *Long term response to two-way selection for 6-week weight of mice. Mean weights of generations plotted against accumulated selection differential. (Taken from Falconer, Cold Spring Harbor Symposium, Vol. 20, 1955).*

kept for 30 generations and the downward selection for 24 generations. In this study he concluded that the upward selection reached a plateau at about generation 22 and the downward selection at approximately generation 17. Since the original data were not available to the present authors, approximate computations were made from Figure 6 as shown in Table 4. From Table 4 one can easily observe that the selection differential and the response per generation both decline as the cycle of selection advances. The average realized heritability,

TABLE 4.—RESPONSE TO TWO WAY SELECTION FOR 6-WEEK WEIGHT OF MICE. COMPUTATIONS MADE FROM FIGURE 6.

	Selection differential per generation (grams) S	Response per generation (grams) ΔY	Realized heritability $\Delta Y/S$
Up-ward selection generation			
0–11	1.50	0.35	0.23
11–22	1.20	0.28	0.23
22–30	1.02	−0.16	(0)
Down-ward selection generation			
0– 9	1.40	0.67	0.48
9–18	0.51	0.29	0.57
18–24	0.64	0.16	0.25

$\Delta\bar{Y}/S$, decreases from 23 per cent to essentially zero per cent in the upward selection and from 50 per cent to 25 per cent in the downward selection. The magnitudes of selection differential became significantly small after the 12–13th and 20–22nd generations in the downward and upward selection lines, respectively. The information thus obtained indicates that plateaus have been established, or nearly so, in Falconer's populations of mice with respect to the upward and downward selection of body weight, although the genetic variance has probably not been completely exhausted.

Clayton and A. Robertson (4) carried a series of two-way mass selections on abdominal bristle counts for a period of 20 to 35 generations. Mean response slowed down considerably in many lines after 20 generations, although in some lines it continued until the thirtieth generation. The plateauing appeared rather abruptly in most lines. The authors concluded that the genetic variance was not exhausted in these plateaued lines. A more extreme case was reported by F. Robertson and Reeve (25) in that selection for wing length in Drosophila increased heritability appreciably in a long term of selection (50 generations). In this study and some others, the authors explained the non-exhaustive genetic variance in long term selection experiments by the existence of linkages of subvital and lethal genes with genes for the trait under selection. Such systems can lead to genetic equilibrium (plateau), though they may be unstable, forced by artificial and natural selection. Bell *et al.* (1) reported a long term experiment on fecundity of

D. melanogaster in which the plateaued population was analysed with respect to lethal and sublethal genes on each chromosome. They did not find such genes that could be responsible for the plateau. From this and other evidences they concluded that the additive genetic variance was exhausted.

The total response and the duration of the response depend upon many factors such as the genetic variability and other characteristics in the base populations and the number of parents selected at each cycle of selection. Falconer (11) tabulated the results of four different two-way selection studies carried till apparent plateauing as in Table 5. The duration of response is about 20 to 30 generations. The total response is approximately 15 to 30 folds of the square

TABLE 5.—FOUR EXAMPLES OF LONG TERM SELECTION, SHOWING DURATION OF RESPONSE AND AMOUNT OF RESPONSE IN RELATION TO BASE POPULATIONS.

Organism and trait	Duration of response (generations)	Total Range T/σ_p*	T/σ_A**	Source
Drosophila				
Abdominal bristles.....	30	20	28	Clayton, Morris, & Robertson, 1957
Thorax length.....	20	12	22	F. W. Robertson, 1955
Mice				
6-week weight.....	25	8	12	Falconer, 1955
60-day weight.....	20	10	21	MacArthur, 1959 Butler, 1952

σ_p* phenotypic standard deviation of selection criterion, measured in base population.
σ_A** square root of additive genetic variance, measured in base population.

root of the additive genetic variance, or about 10 to 20 times the phenotypic standard deviation observed in the base populations. These figures are fairly consistent, despite the biological and methodological differences in these selection experiments. Although all four experiments were carried out with fairly large populations, there must have been fixation of unfavorable alleles at some loci. As it will be discussed in the following section, the fixation of such alleles can amount to quite a large reduction in selection limit when repulsion linkages among favorable and unfavorable alleles are predominant in the base populations. In view of these considerations, the selection limits and durations of selection given in Table 5 should be looked at as underestimates of the respective values potential in the original base population.

The two base populations, Mather and Mono, for the reciprocal recurrent selection experiment discussed in the previous section had very small additive genetic variances on egg production as given in Table 2. The estimates of herit-

ability on individual basis were 0.032 and 0.039 for Mather and Mono, respectively. They suggest that selection within populations such as mass selection and family selection would be ineffective. In other words, the populations, Mather and Mono, are essentially in a plateauing stage with respect to egg production. Two full-sib family selection experiments, one from each of the two, were conducted for eight cycles. The estimates of realized heritability were 0.001 and 0.056 for Mather and Mono selected lines, confirming that the two populations are, in fact, plateauing with respect to egg production.

The findings from the reciprocal recurrent selection and family selection studies point out an important problem in improvement of quantitative traits. While selection may be ineffective within each population, performance can be improved further by applying a selection procedure which enables one to utilize genetic variations and divergences between separate populations. Such variations and divergences must be of the types that cannot be used by intra-population selection and that are not fixed in each population. It is too early to decide whether the results found in the present Drosophila study can be used for making a general recommendation when intra-population selection has become ineffective. In addition to experimental evidences on this matter, theoretical examinations of possible genetic models for such cases are needed for critical evaluation of the recommendation.

SAMPLING VARIATIONS IN SELECTION EXPERIMENTS

The responses in individual runs of selection experiments are subjected to various kinds of genetic sampling variations in each cycle of selection, although the behavior of the population may give, on the average, a relatively consistent picture. These sampling variations include those associated with (i) the intensity of selection, (ii) the number of parents selected, (iii) the recombination among genes, (iv) the initial gene frequencies, and (v) the mating systems. The accumulated effects of such variations over generations will influence the repeatability of the response to selection. Only a limited amount of information is available mainly from experimental and empirical studies.

In the reciprocal recurrent selection study described in the previous section, prediction was made for the mean response in egg production for each cycle from the genetic component of variance obtained in the analysis of the immediately preceding cycle. The results are given in Figure 7. The theoretical deductions about the response (mean gain) to truncated selection are, strictly speaking, limited to the change in only one cycle of selection. In this sense Figure 7 represents a true picture of agreement and disagreement between the predicted and observed results. From Cycle I to Cycle VII, the agreement is fairly good, between Cycles VII and X the predicted and observed results show apparent discrepancy, and from the X*th* to the XI*th* cycle the agreement becomes better.

A possible factor in the apparent discrepancy between the predicted and observed results during the VII*th* to the X*th* cycle, is the fact that during this

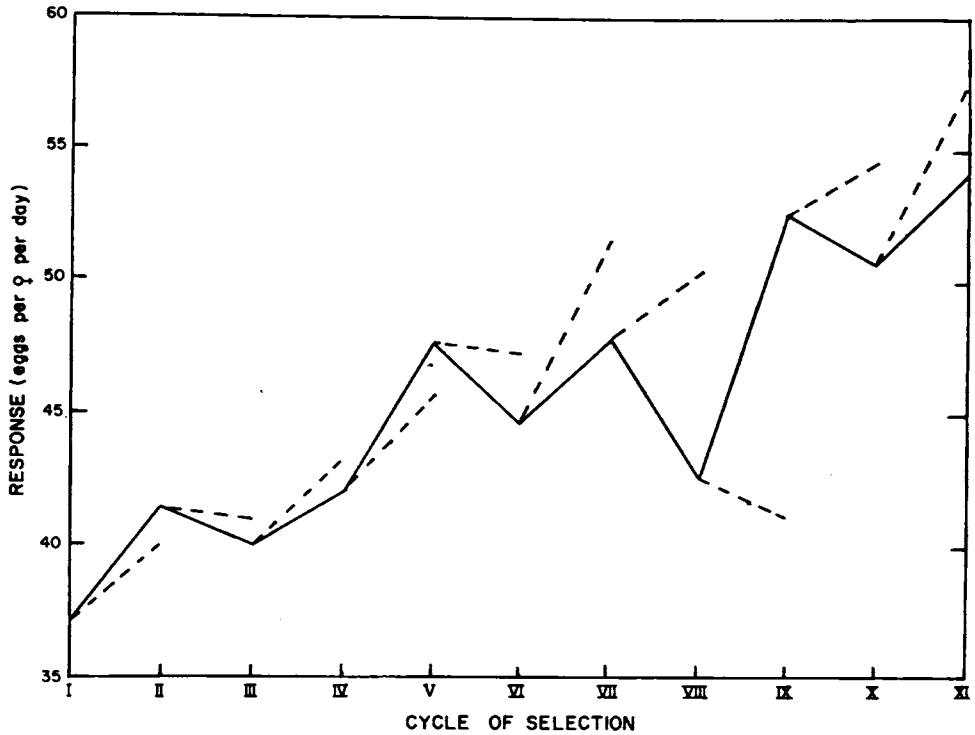

FIGURE 7. *Predicted and realized responses to selection for each cycle of reciprocal recurrent selection on egg production of D. pseudoobscura. Solid line = realized response; broken line = predicted response for each cycle.*

period eggs were counted for a 3-day period rather than 4, and this procedure led to more misclassification of genotypically superior families. Since this aspect of the program is still under study and is not directly related to the sampling errors of this section, detailed discussion is not appropriate at this time.

The corresponding predicted and realized values from each cycle of selection are both subjected to sampling errors. The genetic variance in each generation was estimated from about 60 half-sib families for one side of the reciprocal tests and about the same number of half-sib families for the other side. Missing full-sib families in each half-sib and missing bottles (plots) in each full-sib must have influenced the deviations not only in the estimates of genetic variances but also in the realized gains in egg production from the true values. Ten males, whose half-sib offspring in test crosses were the highest 10 among the 60 half-sib families, were used as parents for the next cycle in each of the reciprocal tests. There was no inbreeding in the tests (because the test crosses were made between the two populations), but there must have been misclassifications of genotypic superiority of these ten male parents.

Each of the 10 selected male parents were crossed with 3 females taken at random from his own population on each of the reciprocal lines. Recombina-

tions must have taken place between chromosomes in the male progenies and between and within chromosomes in the female progenies. Accidents of sampling must have accompanied such recombinations.

The realized gain adjusted for control could not have been completely free from environmental shifts from one cycle to the next, although the control in each test was composed of fairly satisfactory single crosses. Some of the accidents of sampling from various sources and the effects of environmental fluctuations are expected to cancel each other in determining the mean of each cycle and the corresponding prediction. Such effects of cancellation were quite remarkable when the averages were taken over all 11 cycles of selection as already seen in the preceding section. For individual cycles, however, the discrepancy between the predicted and observed results was not so small as the present investigators hoped to see.

Clayton, Morris, and A. Robertson (3) analysed a series of runs of mass selection on abdominal bristle counts with five replicates for high- and low-selection, starting from one base population of *Drosophila melanogaster*. The results are given in Figure 8, where H_1, H_2—and L_1, L_2,—represent five high and five low lines respectively. One hundred flies of each sex were examined, and 20 pairs of parents were selected in each line. Only the upward lines are considered in the following. At the fifth cycle the variance among the replicate runs is about 5.4, and the ratio of the square root of this variance to the total response (coefficient or variation of response) is approximately 18.3 percent. This experiment was continued till the twentieth to thirtieth generation (4). The divergence among the replicates must have increased through accidents of sampling during additional selection cycles. At the twentieth generation the highest and lowest replicates had 70.2 and 53.7 bristles in males, respectively (31.4 in the base population). In females the highest and lowest were 83.6 and 69.5, respectively (the base was 39.2). Such divergences in bristle counts among the replicates may be compared with the divergence observed among control lines taken from the base population. Five control lines (20 ♀ ♀ and 20 ♂ ♂ /line) were kept without selection for 20 generations. The bristle counts (sex combined) were about 38.0 and 32.5 for the highest and lowest lines, respectively. The divergence among replicates due to chance is $38.0 - 32.5 = 5.5$ as compared to about 15 bristles in selected lines. Since different replicate lines under selection possessed quite a divergent genetic make-up with respect to, say, lethal gene complexes, the mechanism for the divergence of bristle counts in different replicates appears to be rather complex. It may be suggested that the greater degree of divergence under selection than in control replicates has been brought out by accidents of selecting unfavorable genes and by chance recombinations not only among bristle genes, but also between bristle and fitness genes.

A series of simulated mass selection studies on high speed computers were carried by several authors (14, 19). The basic idea of such studies is to simulate stochastic processes of selection, which are affected by the joint actions of many

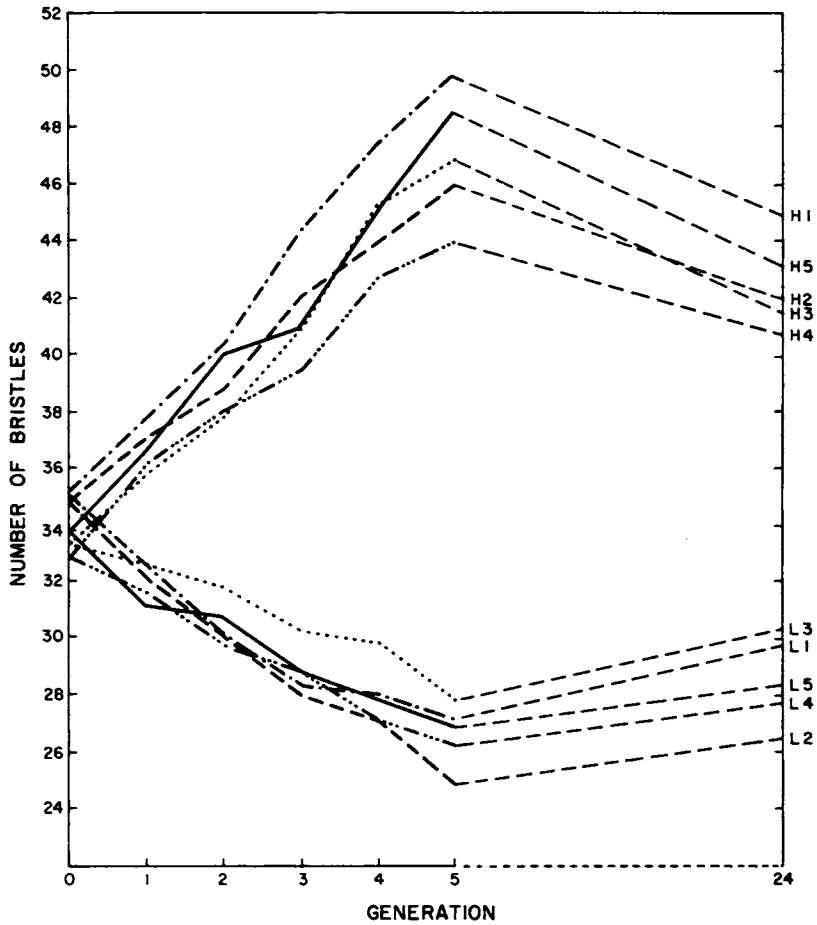

FIGURE 8. *Replicated results of response in two-way individual selection on abdominal bristle number of D. melanogaster. H1, H2,—L1, L2,—represent five upward lines and five downward lines, respectively. Selection is relaxed at generation five for nineteen generations. (Taken from Clayton, Morris and Robertson, J. of Gen., vol. 55, 1957).*

factors, in a short period of time, and to repeat the processes many times in order to obtain average behaviors and distributions of selected lines from a single base population (i.e., from a set of the same values for various parameters). Only one example of this type of approach is illustrated here. In order to evaluate the effects of linkage disequilibrium in the base population, one pair of diagrams by Martin and Cockerham (19) are reproduced in Figure 9. With tight linkages the progress not only slows down but also becomes limited severely when the repulsion phases are predominant in the base population. Appropriate uses of such an approach should lead one to a position where sampling errors associated with various parameters of population can be empirically evaluated to a more satisfactory degree than is possible today.

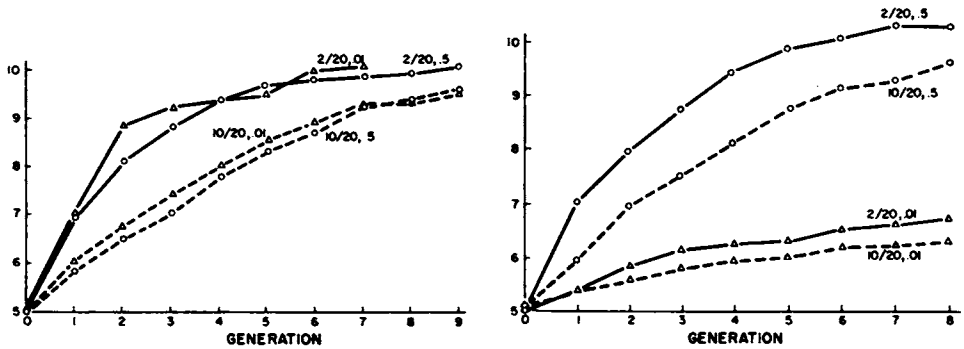

FIGURE 9. *Simulated mass selection studies. (Taken from Martin and Cockerham, Biometrical Genetics, 1960). The intensity of selection and recombination fraction between adjacent loci are given for each graph in that order.*

Left: Additive gene action with 5 loci. Heritability is ½ in the base population. Linkage equilibrium. Each point in the graphs is average of five replicated runs.

Right: Additive gene action with 5 loci. Heritability is ½ in the base population. Linkage disequilibrium (loaded repulsion). Each point in the graphs is average of four replicated runs.

SELECTION IN DIVERGENT ENVIRONMENTS AND CONCLUDING REMARKS

So far the changes in different genetic populations caused by different methods of selection have been discussed on the supposition that the populations are kept under uniform and constant environments throughout all cycles of selection. Various genetic parameters of populations; means, variances, and heritabilities, were defined for a theoretically uniform environment, and their estimates were obtained from experiments conducted in a single environment controlled by laboratory technique. Under these circumstances all fluctuations in environmental conditions are considered to be a source of random errors which would blur the results but not distort them.

Generally speaking, the findings from laboratory experiments of this type were, as have been seen in the preceding sections, in fairly good agreement with the theoretical expectations which were mathematically deduced from the knowledge of genetics. Although knowledge and theory of quantitative inheritance are still imperfect, it may be concluded that the prediction of average behavior of populations under selection can be made fairly accurately as long as the environmental condition of a given selection experiment is restricted to a narrow range of all potential environments.

Phenotypes in general, however, are jointly determined by genotypes and environments. The phenotypic expression of a genotype is generally different in different environments, just as one environment produces different phenotypes with different genotypes. This point is well illustrated by Vetukhiv's experiment described in one of the previous sections (Figure 1b). There, the "F_1-heterosis and F_2-breakdown" phenomenon was influenced by the temperature conditioning.

The different conditionings not only affect the general level of average performance of all genotypes from one condition to another, but also the order of performance of each genotype in different conditions. In terms of selection studies, it is the latter type of environmental influences that need further consideration.

The quantification of the differential actions of environments on different genotypes can be approached by various methods, two of which are widely used. One is factorial analysis of variance in which the genotype by environment interactions are separated from the main effects of genotypes. The variance due to interactions are, often, further subdivided factorially according to the classification of genotypes and environments. A review of this approach was given by Comstock (5). The primary use of this approach for selection studies is to remove possible biases due to the interactions in estimates of genetic components of variance. When selection is carried out in a set of varying environments, unbiased estimates thus obtained are the ones that should be used for the predictions of average changes in the offspring population grown over the heterogeneous environments.

The other approach is correlation analysis of genotypic expressions in different environments. Genetic correlation studies can be made with genotypic expressions of individual families grown in a pair (or more than two) of different environments, just as in the case of two correlated characters measured in one environment.

Unfortunately, there are not many experimental evidences from studies with laboratory animals which help a general understanding of differential effects of environments on the response to selection. Falconer and Latyszewski (13) and Falconer (12) reported the results of two-way selection on body weight of mice in two nutritional levels (full diet and restricted diet). Two strains derived from a single base population were selected (within-litter selection) by exactly the same method for high and low weights. One strain was subjected to the full diet condition and the other to the restricted condition. After several cycles of selection, both full and restricted strains were reared on the full diet and on the restricted diet. On the full diet, the strain selected in the full diet was superior to the strain selected in the restricted diet, but the difference was very small. On the restricted diet, the strain selected in this condition was superior, and the strain selected in the full diet condition did not show any improvement over the base population. One of the critical questions here is whether the same set of alleles at the same loci were selected favorably in both nutritional levels. Falconer (12) postulated three classes of genes: one, genes that affect the character under one condition; two, genes that affect the character under the other condition; three, genes that affect the character under both conditions.

According to such a postulate, he analysed the data from this experiment by considering the performance of one strain on the full diet as a character and that on the restricted diet as another character. Thus, the performance of the strain selected on the full diet but tested on the restricted diet becomes a correlated response of the selection made on the full diet condition, and *vice versa*. Over

the first few cycles of selection, the results were adequately explained by the theory of selection for correlated response, but in the later cycles the results did not agree too well with the theory. The solution to this problem seems still unlikely to come until more experimental evidences accumulate on correlated responses to selection and interactions among classes of genes in different environments.

It is very important to note, nevertheless, that studies of this type may lead one to find the "best environment" in which selection can be carried out most efficiently in order to provide a strain with high positive correlated responses, on the average, over a variety of environments. That is to say, the breeder may be able to find one environment under which his selection should be made in order to obtain a strain with a high performance general for a wider range of environments. It is too early to lay down a general rule on the choice of the "best environment" for various selection programs. The present indications from selection studies on growth rates of mice and some farm animals point out, however, that slightly restricted nutritional levels are better than fully sufficient levels, though the exact genetic mechanisms are not known.

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Discussion: Selection Problems in Plant Breeding

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THE March 6, 1961, issue of NEWSWEEK contained under the heading "Mechanical Answer-Man" the following statement:

"Here we have a fine group of Shell Oil Co. engineers, laboring away with their slide rules for a full year, and finally coming up with three possible solutions for a chemical plant the company plans to build. Over there is another smaller group of engineers and mathematicians working on the same program, aided and abetted by a ringer—an IBM 7090 computer. They spend four months feeding a flock of formulas and 16,000 possible designs into the machine, which bleeps and bloops for a half an hour before it comes up with the solution.

"Who's right? The computer, of course. So Shell announced last week. Its design will save about $600,000 in construction costs on a $10 million plant, said Thomas Baron, the Hungarian-born, University of Illinois-trained scientist who ran the computer program. More important, the computer's plant will save up to 10 per cent in production costs because of the more efficient use of electricity, water, and raw materials. 'But the real gain here,' said Baron, 'is that highly trained engineers will be freed for more creative work. The computer takes the drudgery out of the job.' "

This has been an excellent conference, but I must admit I'm a bit disappointed. Having read the quote above, I had hoped to go home "freed for creative work" with a computer to "take the drudgery" out of plant breeding. Unless I missed something, I'm not going to be able to do this. But really I had no reason to expect so much, for further on in this article, there is a sentence that reads, "The computer has its limitations...it doesn't know that steel will melt above a certain temperature—unless we tell it so."

If the mathematicians have failed to tell us geneticists and plant breeders how to build a better plant or population more efficiently, it is due to our failure to give them enough information about the building materials and their organization. When the biochemical geneticists learn more about the basic breeding materials, RNA and DNA, when physiologists and physiological geneticists understand the complex enzyme systems that determine the development and growth of the plant under the direction of the complex entity that we call the

"gene," when we know more about the interaction of the genotype with the environment, then and only then can we expect mathematicians to do for us as much as they can now do for those who construct buildings and factories. We need not wait this long, however. A continuing, close liaison between all groups involved can result in a step-wise advance that will give us the benefit of each major break-through in this broad inter-related field.

I suppose a discussant should criticize, eulogize, emphasize, and summarize.

I could begin with H. L. Manning's unusual success story and express surprise that straight progeny selection could continue to give substantial advances in yield through 12 generations of inbreeding. Such advances would have been unexpected, even if cotton were an autotetraploid instead of an allotetraploid. I suppose none of us would have expected his "modal bulking" to do more than maintain the yield level and yet, he reports a lint yield advance of some 20 per cent for this method. I could join H. L. Manning in wishing he had had a better base or control from which to measure the actual genetic progress realized in these breeding programs. I would also acknowledge the very real problems associated with providing such a control over a long period of years.

I think I would prefer, however, to commend H. L. Manning for his unexpected success and suggest that we should not let theories, usually extrapolated, keep us from trying new ideas. Most of the significant improvements in the world were made in the face of a strong opposition based on extrapolated information that simply said, "It won't work."

The real merits of a breeding system cannot be judged with a very few tests with a single crop. Therefore, I was delighted that Drs. L. H. Penny, W. A. Russel, G. F. Sprague, and A. R. Hallauer considered 14 publications and some unpublished data in their excellent review of recurrent selection. Even so, it was necessary for them to complete their appraisal as follows: "Many important questions concerning recurrent selection remain unanswered. In fact, consideration of the data presently available seems to raise many questions and answer few."

Drs. K. Kojima and T. M. Kelleher have drawn upon 30 books and papers, most of which deal with mice and Drosophila, to clarify the basic relationships and processes involved in selection within a population that exhibits continuous variation. As I reviewed their excellent paper, I was particularly impressed with their section on control of experiments. In this discussion, they point out that an ideal control will have a range of genotypic variability and a degree of homeostasis comparable to the selection lines. It will exhibit a pattern and magnitude of average response to environmental fluctuations similar to those of lines under selection. And, finally, it can be easily reproduced with constant relative frequencies of individual genotypes from basic stocks whenever needed. Plant breeders and population geneticists should never forget that their measures of genetic change due to selection can be no better than the controls provided throughout the test period.

Drs. B. Griffing and J. Langridge have used the self-fertilized *Arabidopsis*

thaliana, the Drosophila of the plant world, to demonstrate the superior phenotypic stability or homeostasis of heterozygous material compared with the homozygous parents. They obtained a striking genotype × temperature interaction, which gave them significant additive genetic variance in the high- and low-temperature regions, but no detectable additive genetic variance in the region of optimum temperature. I hope you who know my interest in heterosis will forgive me for quoting the following sentences from their paper: "These experiments with *Arabidopsis* suggest that self- and cross-fertilizing plants are essentially similar in their heterotic responses. Therefore, the use of heterosis should be carefully considered in all crop plants irrespective of their type of breeding system."

I sometimes tell my lay friends that plant breeding is really quite simple. All one must do is create a desired individual or population, usually by hybridizing two or more individuals or populations that separately embody the traits desired. If my friends have time to listen, I point out that while it may often be very difficult to make the hybrids, the big problem really stems from the fact that we usually have to produce hundreds of hybrids to find our ideal. The biggest job very often is adequately screening this huge population to find the individual or population desired. This screening is, of course, the selection process with which we have been concerned in this session of the Conference.

First, the breeder must find or create genetic variability and the greater the variability the easier the selection becomes. I learned very early in my career, as I tried to improve dallisgrass and common bahiagrass, that selection applied to obligate apomicts is of no avail because they exhibit no genetic variability. Dr. L. H. Penny has reminded us that some selection programs, such as recurrent and reciprocal recurrent selection, can help to bring together the genes required to realize our objective. All our plant-breeding efforts will be futile, however, unless we succeed in selecting that which we set out to create. That selection is extremely important, no one can deny.

Many questions have been asked at this Conference. This is good. Certainly, our research can be no better than our questions. In closing, I should like to add three more that have received little, if any, emphasis during this Conference. The first of these is "What should I select for?" and "Is my ideal compatible with maximum performance?".

We now know that the 1920 wheat breeders' ideal of awnlessness is not compatible with maximum grain yield but we had to learn it the hard way. We need many studies like Dr. I. M. Atkins' isogenic line investigations with wheat before we can answer this question.

How should I manage my population during the selection period in order to simulate farm management? This is not much of a problem with corn. It's a very real problem, however, with grass that ultimately will be grown in a sward often with legumes and grazed by animals. Many times, there is a genotype × management interaction that cannot be ignored.

What can be done to increase the precision of our selection or research effort? Dr. Penny stated that the average corn-yield trial conducted in Iowa has had a coefficient of variation of 8 per cent. "Assuming a coefficient of variation of 8 per cent, approximately 21 replications would be required for a yield difference of 5 per cent to be considered significant at the 5 per cent probability." I realize there is nothing sacred about the 5 per cent probability, but when faced with such a situation, I wonder if we ought to test at all unless we are willing to use 21 replications or improve the precision of our techniques so that we can lower the coefficient of variation and the number of replications required.

I believe devoting time and energy to sharpening our research techniques and developing better assembly-line methods to increase our research capacity so that we can handle 21 replications, if need be, is just as important as anything we have talked about in this Conference and to do one without the other falls in the realm of unfinished business.

Résumé

Résumé: Statistical Genetics and Plant Breeding

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SUMMARIZING the developments of the week of this symposium should begin with a repeat of the objectives set forth by the committee of the Agricultural Board, NAS–NRC, on Plant Breeding and Genetics in arranging for these meetings; namely, (1) a review of the statistical genetics theory and the philosophy on which it is based, (2) the integration of the statistical genetic developments with plant breeding problems and the practices being followed, and (3) the development and fostering of an appreciation of mutual advantages to be derived from joint attacks upon problems of major importance. The stage for our discussion was very adequately set by Dr. G. F. Sprague in his tracing of the developments in plant breeding from the early work in genetics. He selected a very appropriate example in corn breeding to demonstrate the need of the integrated approach from both theory and experimentation.

The problem which he posed of where do we go from conventional hybrid corn in our breeding of this crop is, within itself, an excellent justification for our efforts in statistical genetics during the past 15 years, if even a small contribution has been made toward a solution to this problem. This question in corn and similar ones for self-fertilizing crops will probably provide the incentive for a great deal of our work during the next decade or more. It is such questions posed by the breeder that lead to considerations in theory. The results from well-designed and conducted experiments must be available for the adjustment and re-evaluation of the theory, and it is from interpretation of these experimental findings that improved breeding procedures will evolve. While it is true that many of the developments of the past have not resulted from such an organized approach, it is my opinion that we can expect the more systematic attack to be the process in our work that will lead to new and more important future developments in genetics and breeding. The plant breeder must accept the substantial improvement realized in crops that have been studied intensively as evidence for increasing difficulty in achieving additional increments of progress. He must meet this problem with new ideas and a continuing increase in the competence of the scientist.

In evaluating the accomplishments of the symposium, I think it is important to consider statistical and quantitative genetics from the standpoint of what has been contributed in the basic aspects of genetics and what its role

is in resolving problems of the plant breeding. I take issue with any who question the contribution of statistical and population genetics, or any other areas of basic genetics, to plant breeding. I have many times been faced with the argument that we cannot hope to resolve the mysteries in the science of heredity through the use of mathematics and statistics, since we are not working at the most basic levels of the science. It is true that we are not studying the nature of the gene from the standpoint of its basic chemical and physical structure and we do not propose to develop the biochemical theories that are so important in these aspects of the science. Neither are we concerned with the chromosomes in terms of their individual pairing and affinity relationships that provide the foundation of our work in speciation, cytogenetics, and cytotaxonomy. But, the very nature of the science of genetics requires that quantitative and statistical procedures must often be used in all areas of this basic science. These become especially important as we deal with the organism as a unit which must, in the final analysis, be the major consideration of the plant and animal breeder as he utilizes genetics in his endeavors to improve the material with which he works. We cannot overemphasize the importance of the interpretation of our findings in terms of basic concepts of genetics which depend so heavily upon our understanding and utilizing of the knowledge which is being developed in all areas of the science. While we work to describe and understand the organism from the exterior, the biochemical geneticist and cytogeneticist, working at the genic and nuclear level, develop information and interpretations that extend to the outside. The meeting of these approaches will give us the understanding we require. Also, I am reasonably certain that the discussion here would convince the most skeptical that much productive thinking and labor is being devoted to all kinds of basic phenomena of plant growth and development. It can result in workable and correct hypothesis of the more complex phenomena, possibly offering more promise for applications in plant improvement than some "genic" approaches.

Since statistical genetics is equally dependent upon developments in mathematics and statistics, as well as information in all of the basic aspects of genetics, the study of quantitative inheritance as it applies to plant breeding is also a joint and mutual effort. Theory cannot evolve separately from experimentation. Neither can experimentation lead us far without a knowledge of theory. The two must be integrated.

We can now return to the final points given by Dr. Sprague in his opening address and evaluate some of the developments for the week as well as consider areas of emphasis for the future. While the deficiencies of our statistical genetic information have been indicated and emphasized, we have had provided summaries of many of our available procedures in theory and parameter estimation in a more uniform and understandable language. These have been presented by Kempthorne and Cockerham in a manner that has been needed and should remove much of the confusion for those who are to make a concerted effort to study these principles and procedures. Many examples have been cited where theory has been utilized in obtaining experimental estimates of genetic parameters. There has been far too limited application of theory in arriving at an

understanding of the magnitude of many of the genetic parameters needed in evaluation of breeding procedures. The summarization of both theory and experimental evidence in the proceedings of the symposium should be of immense value in insuring a greater utilization of the existing information.

With regard to the second conclusion by Sprague on the limitations of the existing statistical theory, these deficiencies have been indicated by many including Kempthorne, Henderson, Cockerham, Robertson, Dempster, and others. I am sure that the limitations of existing theory on such questions as methods of estimating the importance of epistatic gene action, the complex interaction of genotype and environment, linkage and the complications which it imposes in both estimation and selection procedures are, in general, of some consequence in all procedures that have been discussed. I am equally confident that we can expect a removal of these limitations as a result of the emphasis given to their seriousness. Contributions such as the one made by Dr. Schnell on the effect of linkage, and reported here, must be encouraged if we are to obtain the critical results required for an understanding of quantitatively inherited characters.

In developing the information in statistical genetics, it is important that the concepts be based on general population dynamics. We were very fortunate in having Dr. Wallace deal with the subject of reproduction and its various ramifications in the terms of the broader aspects of biology, for it is within this framework of population genetics that many of our assumptions in the theory of statistical genetics are based. We cannot divorce our thinking from the consequences of evolution and the methods of reproduction that have been important in leading to such structures in biological material as diploidy, polyploidy, self- and cross-fertilizers, apomixis, etc. The characters of our economic plants and animals with which we are most concerned; namely, yield and reproduction, have often been equated to fitness of the organism in population genetics.

In both population and quantitative genetics, more attention has been given to the various aspects of the unexplained phenomena of heterosis than any other topic. We are now converging upon this issue with approaches that I believe will lead, within the next few years, to a genetic explanation of heterosis which should be acceptable to all. The investigators of heterosis can profit from a fuller utilization of available information.

The plant breeder should be cognizant of developments in population genetics and become better acquainted with current research. In turn, the population geneticist can profit from findings by the plant breeder. Much of the literature on breeding is ignored, or its importance minimized, when considering theoretical problems in natural populations. An obvious need for better communication between the population geneticist, quantitative geneticist, and plant breeder was the equating of heterosis to overdominance by Wallace. Heterosis might better be defined as a phenomena and overdominance as a type of gene action.

Some of our procedures in statistical genetic investigations have limited population inferences. The schemes of diallel analyses in both theory and application, as contributed by Hayman, Mather, Griffing, and others, need further

attention if the results are to provide information for broader inferences. Both areas of genetics will profit from this approach. The usefulness of a development in quantitative inheritance will probably depend upon the extent to which we can generalize from the results it provides.

The area of genotype-environmental interaction is a problem of concern not only to the quantitative geneticist and plant breeder, but also to the population geneticist. This conference has provided a common meeting ground for those of us involved in studies of theoretical or experimental investigations which necessitate the application of mathematics to genetic problems. While the issues may be phrased in terms such as homeostasis, instability, coadaptation, general or restricted adaptability, they all are concerned with the differential response of the genotype to the varying environments.

The difficulties in bridging the gap between the statistical genetic parameters and the corresponding biological interpretations was demonstrated by Dickerson and others. In my opinion, the one area needing most attention is this biological interpretation of statistical genetic estimates. This extremely complex task requires the efforts of the most competent individuals in both genetics and statistics. When this gap is bridged the impact of information gained from studies concerned with population, statistical, and quantitative genetics will be realized. The plant breeder cannot disregard his responsibility here. If the training required in the basic sciences to integrate these disciplines is inadequate, then we must look to the future and provide proper training for future scientists.

Let us now focus our attention to the topics concerned with the nature of gene action and to the estimates of genetic parameters and relate these to problems of breeding. Many of our speakers, including Harris, Kempthorne, Cockerham, Henderson, Comstock, Hanson, Robertson, Matzinger, and others, have emphasized the importance of having unbiased estimates of genetic parameters, such as additive genetic variance, dominance variance, and epistasis, if we are to develop correct hypothesis and useful procedures. The repeated emphasis given to the use of the components of variance in developing an understanding of the inheritance of quantitative characters provides an indication of the progress made in this subject. This is very adequately demonstrated in our use and misuse of the concept of "heritability." The problems which the plant scientists have encountered and created with this concept have been indicated by Dr. Hanson. "Heritability" served a very useful purpose in the early years of quantitative genetic studies in the animal sciences. Since the individual animal was the basic unit of investigation, few of the problems which we encounter in our manipulations of plants were involved. We plant scientists must admit to much of the confusion which has resulted in our extensive and sometimes erroneous applications of this concept and, at the same time, argue for the beneficial effects of the information that have been derived. I think we are ready to move beyond the routine computations and reporting of heritability and give attention to variances that are involved in constructing heritability. As demonstrated by Gardner, Matzinger, and others, we are much more concerned with the magnitude of the

additive versus nonadditive action of the genes, expected progress from selection, and the comparison of the expected with realized progress. Although the concept of heritability is involved in many of these issues, there are more informative expressions that can be obtained from reliable estimates of the components of the genetic variance.

While the pioneers in statistical and quantitative genetics; namely, R. A. Fisher and Sewall Wright gave us, 40 years ago, the methods of petitioning and investigating our total genotypic variance, it is only in the last 20 years that we have made extensive use of these concepts. I think the reason for this delay can be traced to some extent to the lack of combined theoretical and experimental investigations moving in a joint attack on this subject. While certain of the theory had been developed, few experimental investigations were devoted to providing further stimulation for development of other theory and interpretation. As has been repeatedly demonstrated in this conference, it is the joint efforts of experimentation and theory proceeding on an integrated basis that have contributed to significant progress in our knowledge during the past 15 years. I feel we can look for further developments during the next decade.

Dr. Matzinger has emphasized the need for improving experimental designs for statistical genetics studies involving crops that do not cross-pollinate freely. Further refinements are certainly needed, particularly as investigations are expanded to include different kinds of biological material representing the range of methods of reproduction. This is not to imply that we have the optimum approaches that could be used in studying cross-fertilized crops, for we have a clear demonstration of this inadequacy in our recent attempts to measure the magnitude of epistatic variance in corn. The stimuli for new developments frequently come from the apparent inadequacy of existing methods which have been provided from the use of presently available procedures.

With regards to the status of information on the nature of gene action in corn, the earlier emphasis was given to the estimation of additive genetic and dominance variance, and we can now speak with greater confidence on these components. We are now accumulating information on genotype-environmental interaction, particularly the interaction of the additive genetic and dominance variance with environment. Also, studies on the estimation of epistasis, which are now underway, can be expected to provide at least an indication of the importance of the total epistatic variance, but these will be only the beginning of our development of an understanding of the inheritance of complex quantitative characters.

Some general conclusions can be indicated from results obtained for corn and other crop plants, and again these must be considered as tentative. These are:

(1) Additive genetic variance appears to be the component of genotypic variance of most importance in populations such as open-pollinated varieties of corn as well as, and probably more so, in many of our self-fertilizing crops.

(2) The dominance variance is appreciable, and while it has been indicated to be in the range of over-dominance with certain kinds of material, the

explanation of this finding appears to be the linkage bias which confound the estimates. It is emphasized, however, that we are estimating the average effects of genes over all loci, and no claim is made that there is not over-dominance at specific loci.

(3) Epistatis does not appear to be a major contributing factor in the inheritance of quantitative characters in corn. However, it is emphasized that very few reliable estimates of epistatic variance are available in the literature. I think that we can look for much greater emphasis to be given to the study of epistasis in the future and reliable results will be forthcoming from studies that are designed to provide meaningful and interpretable answers.

(4) Genotype-environmental interactions are of major concern in all of our quantitative genetic investigations and must be given consideration in the design and conduct of all studies in quantitative inheritance and plant breeding. The importance of genotype-environmental interactions is clearly demonstrated in the investigations with corn where it appears that the magnitude of this interaction may be approximately equivalent to that of the genetic variance itself. Our limited information does not provide a basis for a definite conclusion regarding the relative magnitude of environmental interactions involving additive, dominance, or any of the other genetic components of variance.

Dr. Griffing and Dr. Kojima have shown the importance of genotype-environmental interactions in plants and Drosophila, even under highly controlled environmental conditions. Griffing's suggestion that the heterosis in self-fertilizing plants may be greater under conditions of high temperatures is very interesting and needs further investigation in higher plants. However, it does not appear to me that we can expect as much importance to be associated with the high temperature variable in our consideration of F_1 versus parental performance as other environmental stresses; namely, moisture limitations and stresses during critical plant development periods. Emphasis needs to be given to the various environmental factors and genetic responses obtained under specifiable environmental conditions. The techniques of investigation being utilized by Dr. Grafius requires that an attempt be made use of information on environmental effects on the genotype and on the components of complex characteristics. This is a further refinement that must come in quantitative investigations if our results are to be interpretable with regard to the nature of the gene action involved. However, I should stress that we need to proceed cautiously in assuming that information from studies of components of a complex character can be used to predict the genetic expression of complex characters, such as yield.

Next, I would give attention to general problems of selection since this is probably of more concern to the breeder than any topic discussed at this symposium. While the plant breeder does not utilize the mathematical weightings of the selection index and the components of variance that must be available for constructing the index, he uses a type of index in phenotypic selection and therefore practices its application throughout the breeding program. We must, there-

fore, make better use of refinements and techniques which are available. Dr. Henderson has discussed, here and elsewhere, the joint consideration of traits in breeding and selection studies. The animal breeder has, of necessity, made more extensive use of the selection index than the plant breeder and can point to accomplishments from its application. The work of Manning stands as one of the few examples of the use of the selection index in a consistent and scientific manner to problems in plant breeding. We have no acceptable excuse, even though Dr. Henderson tried to provide us one, for not making more application of the selection index in plant work.

It would appear to me that valuable information for plant breeding could be derived from a study which provided comparisons between selection programs conducted for a single character, such as yield, and selection for two or more characters in combination with yield in the selection index. We need such experimental programs evaluating selection indices. Some of the problems that are likely to be encountered in the evaluation of the selection index can probably be orientated and investigated with selection studies conducted on highspeed computing machines as demonstrated by Dr. Harris. The selection work might involve an evaluation of various kinds of indices and a variety of parameters. This would necessitate the larger type computing facilities with a vast amount of storage capacity. It seems to me that this is only one of the many problems for which we may make use of these machines in a preliminary investigation of quantitative genetics situations.

The necessity of adequate control in selection studies has been demonstrated by Manning, emphasized by Kojima, and cannot be overstressed. In any selection study in which we intend to draw basic genetic inferences from the results, attention must be given to the nature of the control entry or entries, the number of control plots, and individuals or families to be used. If an adequate control is not used in the selection studies, then we have no basis for drawing valid conclusions for the progress achieved. Attention is being given to the use of control plots in our breeding and genetics studies from other standpoints. The information from properly arranged controls can provide the basis for a new approach in design and analysis of our biological experiments.

I think we can safely say from results of selection studies reported for plants in this symposium that few, if any, have been carried a sufficient number of cycles to permit any definite conclusions as to the rate of realized progress and the level at which we can expect the populations to be plateaued. Studies now underway are providing interesting trends, and results will become increasingly important with additional cycles. Emphasis should be given to procedures, such as mass selection, if the additive effects of genes are as important as has been suggested. Gardner's results with corn, where he has made what appears to be substantial progress through five cycles of mass selection, most certainly appear to confirm the expectations based on the magnitude of the additive genetic variance in the open-pollinated varieties. This alone gives ample reason for a reinvestigation of those populations from which the early maize workers; that is, 1900–1910, concluded that such a selection scheme would be futile, and turned their attention

to the inbred line and hybrid breeding procedure. It is my opinion that in many of our self- and cross-pollinated crops, considerable progress may be realized from a well-conceived and properly conducted mass-selection program in yield. Most certainly success should be realized for the more highly heritable and less complex agronomic characters. The major portion of the evidence presented by Matzinger in review of the situation in self-fertilized crops would substantiate the belief that we can expect further progress to result from selection programs, when well designed and modern techniques are used.

Penny has chosen to group several of the more complex selection procedures, principally those based on an evaluation for general and specific combining ability for the progenies, under the heading of "Recurrent Selection." He has pointed out that plans that have been proposed; namely, "Recurrent Selection for General Combining Ability" by Jenkins, "Recurrent Selection for Specific Combining Ability" by Hull, and "Reciprocal Recurrent Selection" by Comstock, *et al.* might be placed in the same grouping due to the similarity of having successive cycles of selection and recombination of a selected portion of the population. This is a common feature, but the critical differences in the schemes are based on the nature of the gene action involved in the population under selection. To me, this is a major criterion since the efficiency of the selection program must be determined on the basis of the nature of the gene action. The three procedures named above have different expectations with regard to the ultimate progress to be achieved, depending upon whether the majority of the genes show partiality to complete dominance, over-dominance, a mixture of the two, or other complexities such as epistasis, linkage, etc. These factors are not allucidated in Penny's proposal. However, the same general conclusions can be reached with regard to status of the evaluation of all of these procedures; namely, that experimental data simply do not exist to provide a valid evaluation of the relative merits of the three procedures. Our efforts must be continued to obtain this evaluation, and the plant breeders should be providing this information. I would urge you, as you design and carry out your breeding programs, to give attention to establishing selection studies with continuity over the necessary selection cylces. This will lead to compilation of results over a period of time that will be valuable, not only as a basis for descrimination among the various selection procedures, but in providing an understanding of the basic gene action which has led to the results. The incorporation of such basic research within the applied breeding program would be an appropriate change of emphasis in some of our efforts.

A most interesting evaluation of reciprocal recurrent selection compared to family selection is being provided in the laboratory studies with Drosophila reported by Dr. Kojima and Dr. Kelleher. Here again, the results are not conclusive, but it appears that a demonstration of the effectiveness of reciprocal recurrent selection versus family selection for a complex character in this organism may be conclusively demonstrated within the next few years. At the same time, information is being obtained on the variances that will possibly provide an explanation of the gene action involved. An excellent summary of the situation on the subject of selection has been provided by Dr. Sewall Wright in his

review and discussion of the symposium "Genetics and Twentieth Century Darwinism" held recently at Cold Spring Harbor. He stated, "Study of the effects of various patterns of selection in laboratory populations, in domestic animals, and cultivated plants still has far to go, and this is much more the case with the genetics of natural species. We may anticipate surprises that will require re-adjustments all along the line. The present symposium supplies many new data, largely at the level of actual populations which must now be digested." The same can be said here, even to the extent of including the words "the present symposium."

Before leaving the subject of selection studies, re-emphasis should be given to the importance of information that can be derived from laboratory studies as illustrated by Drs. Griffing, Kojima, and Kelleher. Unfortunately, selection studies with higher organisms present some problems. However, there is much to be gained from pilot investigations with laboratory organisms, even though we must exercise caution from the outset that direct transposition of information cannot be made from the laboratory studies to economic plants and animals. A greater utilization of laboratory studies and rapidly reproducing organisms will probably lead the plant breeder to the same conclusion as that given by Alan Robertson in his discussion of laboratory breeding experiments at the X International Genetics Congress where he closed his address with the following: "I hope that I have convinced you that those of us who devote part of our energies to Drosophila and mice are not wasting our time. Of one thing I am sure—that as a result of my work with Drosophila, I feel far more competent to discuss improvement of dairy cattle than if I had spent all my time analyzing milk records and perhaps breeding a few cattle."

Finally, I take this opportunity to summarize some of my own thoughts with regard to statistical genetics and plant breeding; these ideas relating principally to corn with which I have been concerned during the past 15 years. I think that our breeders have not made maximum use of the information provided from the inter-cross of the open-pollinated varieties and their potential value as breeding stocks. There is a renewed interest in this topic since considerable heterosis in inter-varietal crosses has been demonstrated and some crosses yield at a level approaching our best double cross hybrids. It would appear to me that this information may be of value, even in our advanced breeding program in this country, toward better utilizing the basic stocks from which to extract our inbred lines. This is certainly an important issue in countries where the double cross hybrid does not play a prominent role. The open-pollinated varieties and synthetics have had potential utility. The work of Dr. Lonnquist on synthetics provides important evidence on the utility of this suggestion, and Dr. Wellhausen has commented upon its immediate applicability in Mexico.

The available information with which I am familiar does not support the claim for a major amount of overdominance required for the explanation of the heterosis observed in corn. It appears that we have not provided a basis for discarding the early hypotheses for explanation of heterosis; namely, accumulation of dominant favorable alleles. I do not claim that the total gene action fits this hypothesis, or that heterozygosity *per se* can account for the heterosis. It is

suggested that genetic diversity existing between the parental stocks and partial-to-complete dominance of the genes may be the major factors contributing to heterosis in characters such as yield.

Another point is concerned with the nature of the stocks to which I think we should give attention in breeding programs and in quantitative genetic studies. Since it appears that genetic diversity is of great importance in making further progress and realizing maximum heterosis, greater effort should be given to bringing a wider diversity and a broader base to the germ plasm. I would suggest that we may have reached secondary peaks in the breeding and selection for many characters in our germ plasm pool as was suggested by Wright, and there is little likelihood of further improvement until we regress to a new route which will lead to still higher levels of performance. This requires the introduction of new germ plasm to broaden the genetic base. In corn, there is a wealth of material contained in the exotics in Latin America which may be useful for widening of the genetic base. It is not an easy and obvious task to incorporate this germ plasm into our present material and develop rapidly a product of greater economic importance. We must devote much attention to methods of utilizing this material and from this will come a myriad of problems. While attention is being given to methods of immediate utilization of the germ plasm, I would suggest the development of large panmictic pools of the various genetic stocks. Here, the many generations required for genetic mixing of the germ plasm could be taking place. We must then call upon other areas of genetics to provide the many techniques and approaches that will be required in the manipulation of the material in the breeding programs. New approaches must be taken to insure recombinations of genes and to attain linkage equilibrium before the material can be subjected to normal breeding uses. It is my opinion that linkage restrictions may, with our usual genetic stocks and certainly with introduction of exotics, impose far greater limitations than our existing genetic theory seems to indicate.

Finally, we must not hold to the old, but look to the new procedures and ideals in our goals in breeding. In corn, we have already seen indications that the plant types for which we have strived may be one of our greatest limitations. We must be ready to discard conformity and prejudices in at least a part of our programs of research and seek new and higher levels of performance which may very well come through radical changes in the form of the final product. A simple example would be that substantial increases in yield of corn may come, not from larger ears but from many smaller ears placed on a series of tillers. We know that this germ plasm exists in the primitive relatives of this plant. Radical approaches may be required to lead us to the new and higher peaks of performance to which Dr. Wright has referred. These ideas may all be worthless but quoting the words of Bessemer, the discoveror of a method of producing cheap steel, "I had an immense advantage over many others dealing with the problem inasmuch as I had no fixed ideas derived from long established practice to control and bias my mind, and did not suffer from the general belief that whatever is, is right."

Part II - Workshop

PART II—WORKSHOP

Foreword

THE workshop of the symposium was held March 27, 28, and 29 with about one-third of the participants remaining for these sessions. The objectives of the workshop were: (a) to give additional attention to certain topics discussed during the previous week, (b) to consider problems and questions raised by the participants, and (c) to develop plans and procedures, wherever possible, for both theoretical and experimental studies in statistical genetics.

Each morning, afternoon, and evening session was devoted to a single topic and introduced by a short contributed paper. The discussions following each presentation were not restricted to, nor necessarily concerned with, the results of the contributed paper. The lively discussions of these informal sessions did result in rather thorough coverage of the topics considered. Although many problems were faced which required further attention, the review of available information and the evaluation of existing procedures emphasized the limitations in present information and provided the basis for effective focusing on needed research.

The proceedings to follow are quite incomplete since most of the discussion was not available for publication. Certain contributed papers were omitted since they were prepared for publication elsewhere or represented reports of research still in progress. Contributed papers presented during the first week were also fitted into the proceedings. The true value of the workshop could be realized only by attending the sessions and participating in the discussions.—Editors.

Quantitative Genetic Concepts

Quantitative Genetics and Growth Analysis

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THE starting point of this contribution is a dissatisfaction with the static nature of so many of the models now in use for dealing with problems in quantitative genetics. I do not think it unfair to say that it would be hard to deduce from the internal evidence in many papers on quantitative genetics that growing organisms were being described at all. Since the capacity for growth and development is so characteristic of the organisms with which quantitative geneticists work, it seems reasonable to ask that the phenomenon of growth should be explicitly recognized in the models employed. How this might be done, and what help we can obtain from crop physiology and biometry in so doing, form the substance of this paper. A severe shortage of data on which to work compels the treatment to be more speculative than is desirable, but if its publication encourages the collection of suitable data to test the sort of models envisaged, this may be sufficient justification.

It is important to establish at the begining the scope, limitations and uses of the theory to be discussed. This may be done by considering its position relative to two extreme kinds of experiments and their associated theories.

At one extreme lies a practical plant-breeding project. This is a technological problem having as its aim, say, the improvement of yield. Methods of attack include crossing, making of polyploids, irradiation, etc., with of course selection applied to the populations generated. The extent of relevant theory here is debatable but presumably includes Mendelian genetics, selection theory, and various additive variance component theories. The relative usefulness of these different aspects of genetical theory would be a matter of considerable disagreement among plant breeders.

At the other extreme lie certain kinds of experiments on the biochemistry of micro-organisms, characteristically showing a very high degree of experimental control and often using the mathematical apparatus of physical chemistry with its array of differential equations, rate constants, and so on. Models for this situation have been explored by Hinshelwood (10) and others.

The gap between the biochemical description of plant metabolism and the prediction of plant yield is so great at the moment as hardly to need comment. However, it seems worth considering whether the construction of models lying somewhere between these extremes would be useful. Such models would relate to the description of growth on a macro-scale and would inevitably

have a high empirical content; however, if they were to be valuable they would also have to be of sufficient generality to improve prediction in technological experiments and also to provide a basis for improving the collection of data in such experiments (This second condition implies not only the reduction of random errors by improvement in experimental design etc., but also and much more importantly, the giving of guidance to the technologist on what kind of data he should collect in order to obtain maximum insight into the behaviour of his experimental material). These two requirements of improving prediction and increasing experimental efficiency, impose certain restraints on the models, of which two aspects in particular need further discussion.

GENERAL PROPERTIES OF SUITABLE MODELS

The place of random elements

Any random element in a model must be defined over a population, and it has predictable properties in the mass, but no predictions can be made for its behaviour outside the population unless we can relate the parameters of the distribution of the random element to some other measurable quantities. Consider, for example, the population of micro-environments producing individual differences in a genetically homogeneous population of plants. We may be able to measure the mean environment with some accuracy and to relate the mean growth of the plant population to that mean. This introduces a measure of prediction into the behaviour of the population mean without our necessarily being able to predict, for instance, the variance of individual plant growth. If no interest attaches to such individual differences but only to the population mean, the use of random elements to represent them in the type of model we are considering is unobjectionable. But we must be careful not to introduce random elements in cases where the variation concerned is of importance, since such action is equivalent to an assertion of irremediable ignorance and the models we are interested in are supposed to help dissipate such ignorance. Genotype-environment interactions are of this type, and also genotype-genotype interactions in a competitive situation. The expression of these in a model purely in terms of variance components has almost no predictive value.

The choice of plant characters

It is a platitude to say that a "final" character such as yield of grain in a cereal represents the final result of interactions of many systems inside the plant. In technological experiments there is some force in the argument that if final yield is what we are interested in then the genetics of final yield is what we should study. That is to say, genes are to be regarded as acting on this particular character, irrespective of the pathway by which they have their effect, e.g., through affecting tiller number, number of ears, number of grains per spikelet, etc. In the kind of theory discussed here, however, such an attitude cannot be maintained and we must attempt to isolate the pathways by which effects on such characters as final yield are produced. Such analysis falls into two parts;

in the first part we can consider, for example, the separation of yield in tomatoes into components such as number of trusses, numbers of fruit per truss, and mean size of fruit. Such component analysis is familiar in the literature from such work as that of Griffing (9), Quisenberry (14), and Smith (15), to mention only a few examples. The use of components of yield can introduce important simplifications into the genetic description of complex characters, as has been shown by Williams, Watkin (21); thus, heterosis in an F_1 for yield may result from independent additive gene action on two components whose product gives that yield. Again, heterosis in different crosses may be the result of quite different changes in the various components, and failure to include such differences in a model must lead to loss of predictability.

This first analysis into components still has the disadvantage of being static in nature. It gives only the pattern at the end and cannot say anything about the pathways by which the final pattern was reached. Without information on these pathways it becomes very difficult to interpret such quantities as genetic correlation coefficients since the same final figure can arise from any of several distinct physiological causes. The second stage of the analysis must involve therefore, the analysis of growth rates as well as that of final sizes.

AN APPROACH VIA CROP PHYSIOLOGY

An excellent account of work on growth as it affects heterosis has been given by Whaley (20). The scarcity of this type of analysis when compared to the size of the output on genetics as a whole is very striking. Some developments in other fields in recent years suggest that it may be time to reconsider such physiological approaches as that made by Ashby (1, 2, 3, 4) in the 1930's to the problem of heterosis and the physiological basis of genetic effects as a whole. Two developments in particular are of interest here; the work on crop physiology initiated by Professor F. G. Gregory and his school and developments in statistics by Box and others concerning the fitting of differential equations to chemical processes. For a useful general account of the former see Watson (16), and for the work of Box and his collaborators see (5, 6, 7).

To Professor Gregory's school we owe the introduction of such concepts as net assimilation rate (NAR) and leaf-area ratio (LAR). These represent a division of the relative growth rate $W^{-1}\ dW/dt$ where W is the total weight of the plant per unit area into two components $NAR = L^{-1}\ dW/dt$ where L is the total leaf area per unit area (or more generally an index of effective photosynthetic area) and $LAR = L/W$, i.e., the leaf area per unit weight of plant. The splitting of the relative growth rate into such components represents an attempt to isolate quantities having a readily interpretable biological meaning. Early hopes that NAR would prove to be invariant over a wide range of environments and plant species have been dashed by recent work, however. The reasons for this are certainly complex, but one important possibility to be considered is that the variation has arisen from the interaction between parts of the plant, e.g., between a storage organ such as is found in a carrot and the leaves supplying it,

or between the individual leaves of a plant. In this connection recent work by Gaastra (8) is of interest; he has shown how the photosynthate-light intensity relation for a whole plant is modified when a single leaf in a plant is exposed to the light, the remainder being darkened. The results indicate that variation in illumination of different leaves produces non-additive effects on the carbohydrate production of the whole plant.

Two papers by Watson and collaborators, one (17) on the origin of the yield increases in modern barley varieties and the other (18) on the growth patterns of wild beet and cultivated sugar beet, attack problems of direct interest to plant breeders. In (17) although the growth analysis did not produce a clear-cut solution, it showed where the critical stage occurred in the origin of yield differences and, what is just as important, indicated periods of growth where the old and new varieties showed little or no differences. The analysis of the wild and cultivated beet suggested the importance of plant geometry, typified by the special arrangement of leaves, in limiting growth. All this work indicates clearly the necessity of extending the ideas of the crop physiologists to take account of interaction between parts of the plant.

THE USE OF DIFFERENTIAL EQUATIONS

The description of biological systems by sets of differential equations has attracted increasing interest in recent years, particularly since the advent of electronic computers has made possible the large-scale computing which is the inevitable consequence of their use. Lucas (11) has recently attempted a general formulation of problems of pasture growth along these lines, and in the related field of animal populations, a most useful paper by Watt (19) describes the practical approach to the construction of models using differential equations. Watt stresses the unsatisfactory nature of multiple regression and associated linear models for the description of systems almost always characterised by the presence of asymptotes in the growth of their components.

In order to discuss the properties of models involving differential equations in a reasonably concrete fashion, we consider now the construction of a highly oversimplified model for vegetative growth in plants, based on certain fairly well attested characteristics of plant growth.

As a starting point we may take the allometric relation which is so often found to hold between different parts of the same plant or between a part of a plant and the whole. This gives the relation

$$\log w_1 = a + b \log w_2 \qquad \text{(i)}$$

where w_1 and w_2 are the weights (or sizes, etc) of the two parts concerned. The linearity may only be satisfactory if the range of weights involved is not too large or if growth is considered during the early exponential period only. Differentiating (i) with respect to t we have

$$\frac{1}{w_1}\frac{dw_1}{dt} = b\,\frac{1}{w_2}\frac{dw_2}{dt},$$

i.e., the relative growth rates (r.g.r.) of w_1 and w_2 are proportional. In the simple case of exponential growth the corresponding growth equations would be given by

$$\frac{1}{w_i}\frac{dw_i}{dt} = a_i$$

where the a_i are constants. This step embodies an important assumption, because it is equivalent to saying that the growth of any part is primarily limited by demand and not supply, that is to say the ability of w_i to increase depends first on the size of w_i, and not on the other w's. Thus, to take a simple case of the tops (w_1) and swollen root (w_2) of a carrot; if it is supposed that the growth rate of w_2 depends primarily on the supply of photosynthate from the tops and if this supply is divided among the tops and roots in proportion to their sizes, then it is easily shown that b in the allometric relation must be unity. Thus, supply-limited growth cannot easily produce b's with values other than unity; demand-limited growth has no such restriction. Since values of b other than unity are common, the demand-limited model seems preferable and is implied in the next stages of the argument. To extend the model to allow variable r.g.r.'s we must make the right hand side functions of w_i. Firstly, we may note if we put

$$\frac{1}{w_i}\frac{dw_i}{dt} = a_i + f_i(w_1, w_2 \ldots\ldots,)$$

where $f_i \to 0$ as all $w_i \to 0$ and if the a_i are not too small, then for a period when the w_i are small, a_i will be large compared to f_i, so that growth will be approximately exponential and allometric in these early stages. Secondly, we may note that the growth of a single w is frequently sigmoid and approximates to the logistic form

$$\frac{1}{w}\frac{dw}{dt} = a - bw.$$

This suggests a form $f(w_1, w_i \ldots\ldots\ldots) = b_1 w_1 + b_2 w_2 + \ldots$
Finally, we note that if in the early stages

$$\frac{1}{w}\frac{dw}{dt} = a,$$

then

$$\frac{1}{w^\theta}\frac{dw^\theta}{dt} = \theta a$$

so that w^θ satisfies the same equation as w. Couple this with the fact that the growth of a single w frequently satisfies an equation of the form

$$\frac{1}{w^\theta}\frac{dw^\theta}{dt} = a - bw^\theta$$

rather than the logistic form with $\theta = 1$, and we arrive at the final form

$$\frac{1}{w_1^{\theta_1}} \frac{dw_1^{\theta_1}}{dt} = a - b_1 w_1^{\theta_1} - b_2 w_2^{\theta_2} - \ldots . \qquad \text{(ii)}$$

and similar equations for the other w's.

The introduction of the θ parameters allows us to deal with the situation in which the measured w_i are allometrically related to the "real" w_i. Equation (ii) is capable of representing a considerable variety of growth patterns. Thus, the w's need not all increase with time. The structure can be made hierachical, in which each w's growth depends only on itself and the w's above it. This might be useful in describing the joint growth of individual leaves where some w's are strictly non-existant at the beginning before the leaves have been initiated. However, an adequate approximation may be given by assuming the leaves present, but taking such small values of w as effectively not to disturb the growth equations for existing leaves. In equation (ii) the a's, b's and θ's are regarded as parameters dependent on the environment and the plant structure. There is some evidence from data on carrots (Austin and Nelder, unpublished) to indicate that the θ_i may be relatively independent of the environmental variables, but any such generalisation would be premature.

PRACTICAL DIFFICULTIES

The testing of such models in practice and the associated statistical problems concerned with the estimation of the parameters in them produce many difficulties which should not be underestimated. These are of three main kinds which can be classed under the headings of difficulties of (a) identification, (b) goodness-of-fit testing and parameter estimation, and (c) experimental technique. We consider each in turn.

Difficulties of identification

The model presupposes first that we can identify the relevant w_i and secondly that we can identify the external (environmental) variables affecting the parameters a_i, b_i and θ_i. Such information as will enable one to make a start must come from a general study of the results of experimental plant physiology. The omission of an important w_i is mathematically equivalent to a wrong choice of f_i in equation (i) plus the omission of a complete equation from the system. The choice of f_i leads to the question of the goodness of fit of the model and type (b) difficulties.

Testing goodness of fit, and parameter estimation

The problems involved here can be seen by writing the relative growth rate in (ii) as Y and the quantities $w_i^{\theta_i}$ as x_i, so that the equation is seen as analogous to a multiple regression model. Unfortunately, for the experimenter the parts of a plant tend to increase in size together, so that the x_i are highly positively correlated. This has two undesirable effects: Firstly, it makes it impossible to get a sensitive goodness-of-fit test for an *a priori* model, and secondly it makes the estimate of param-

eter values highly negatively correlated. The case of a single variable satisfying equation (ii) is discussed by Nelder (12), the general situation for several w_i will probably be worse.

The fitting of differential equations to empirical data has been developed chiefly in the field of chemical engineering. The method is that of least-squares and the parameters are almost always non-linear. The main difficulty arises through the frequently ill-conditioned nature of the sum-of-squares surface. The chemical engineer has the advantage over the biologist in that he is far more free to vary his initial conditions, and hence to choose a well-conditioned part of the parameter space to work in. Methods of ameliorating ill-conditioning, whereby the design of the plant may make it difficult for the experimenter to find out how it works, are obviously a necessity and will require considerable experimental cunning. Possible methods of breaking the correlations come under the next heading.

Experimental design and technique

With the model proposed one fact is clear: Early exponential growth of parts when the w_i are small will shed no light on functional relationships. For in this situation the a_i's form the dominant term on the right hand side of equation (ii), and the system behaves as if the parts were growing independently. We thus require data where the parts do not show this type of growth exclusively, and such data may be obtained in several ways. Firstly, relative growth of parts may change naturally; thus, work with carrots by Austin at Wellesbourne (unpublished) shows that the tops reach a plateau value at a time when the swollen root is still in a rapid phase of growth, and some information can be obtained in this situation about the relation between root growth and the amount of tops present.

Secondly, we may consider changing the environment. Thus, a particular temperature regime may be used to alter the relative growth rates of different parts, or the illumination of single leaves in a plant can be used to discover the interaction between leaves in respect of the production of photosynthate (as suggested by Gaastra's work). Quite a severe test of a model based on differential equations would be obtained by growing plants in a number of environments $E_1, E_2, E_3, \ldots\ldots\ldots\ldots$, chosen to give different relative sizes to the w_i, and then transfering them all to a common environment E_0 in which subsequent growth would be followed. A correct model would give common a, b, θ, at the second stage with different constants of integration.

Thirdly, we may consider the class of treatments obtained by surgery, e.g., partial defoliation, root pruning, or addition by grafting. The success of this class of treatment depends on not bringing into play new reactions following the surgical operation. Thus, in equations (ii) we have made the absolute growth rate dw_i/dt depend primarily on w_i. However, the growth of, say, the swollen root in carrot would be primarily limited by the tops if a severe enough defoliation were carried out; hence, the model would be changed and the treatment would have defeated its own purpose.

The actual technique of doing this sort of experiment is likely to need considerable development. The fact that the average of a number of individual growth curves of the same form, but with varying parameters, is not usually a member of the same family means that biases will be introduced unless the individual curves being averaged are all closely similar or unless the individual curves can be obtained and used, the latter necessitating non-destructive measurements. The wide variation in growth in the field, even between plants of a supposedly genetically uniform line, is a fact unpleasantly familiar to experimenters, and the development of methods of reducing such variability will be essential. The existence of this variability leads to another important question, that of a theory of errors for growth analysis.

Errors in growth models

So far, we have been concerned with an entirely deterministic situation in the model considered. However, individual plant variation being what it is makes it necessary to include error terms in models. When error components are very small, the actual causes of the errors are not important and the mere addition of '$+\epsilon$' to the mean may be sufficient. When error components are appreciable, this approach is less satisfactory particularly where averaging over growth curves may give rise to a curve which is not of the same form as the components. For this reason, it may be desirable to split errors into components identified with definite biological aspects of growth, such as those caused by differences in germination time, initial embryo differences, subsequent competition effects, and early relative growth rates. Models which merely accumulate random components without attempting to relate them to specific aspects of growth are unlikely to be very illuminating. Very little information appears to be available on the origin of variability at different stages of growth (see (13) for an investigation in relation to fruit trees) and much remains to be done.

DISCUSSION

The reader will be aware that not much has been said so far about quantitative genetics; however, the relevance of the approach considered here should be clear. The attempt to put the prediction of performance on a sound basis by considering not only the final yield components but also the pathways by which they are reached will inevitably be a long-term project—sufficient has been said above to indicate some of the many difficulties involved and others will undoubtedly be found. Nevertheless the change-over from a static to a dynamic analysis seems inevitable and recent advances in crop physiology, biometry, and computing facilities suggest that it is not too soon to start thinking seriously about what models and experiments for dynamic analysis are going to be like. In particular it seems that we are hardly likely to get much further using static models with the interpretation of yearly variation in yield, or with the wider problems on genotype-environment interaction and genotype-genotype interaction in competitive situations.

Several important aspects of growth and development are not covered by the model discussed above. Thus, no distinction is made between increase in cell number and increase in cell size as factors responsible for the increasing size of an organ. Also, nothing is said about flowering, its initiation, and subsequent effect on the general pattern of growth. The reason for these omissions is lack of data; however, a first attempt might be made to include the flowering phase using information obtained by dissection to fix its onset. In certain situations, such as the one where flower initiation prevents further leaf development, there might be some advantage in analyzing the final yield of a seed crop in terms of plant size when initiation took place, the latter being further referable to the initial conditions, early relative growth rate, and the plateau value of the growth curve for vegetative growth.

There is a place for growth analysis as a bridge between statistical genetics and plant breeding, two disciplines which sometimes seem further apart than the workers in either would like. The static nature of so many models in statistical genetics must be unappealing to the plant-breeder who can hardly avoid noticing that his plants grow and change, while the complexity of the characters in which the plant-breeder is interested are the despair of the geneticist. The thesis developed here is that both would benefit from a collaboration with the physiologist, biochemist, and statistician in a combined attack on the problems of developing dynamic models for plant growth.

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Genetic Homeostasis and the Theory of Canalization

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IN the experimental study of quantitative inheritance, the most challenging problems are those which have to do with the relationship between metric deviation and reproductive ability, for it is quite certain that the nature of quantitative genetic variation must ultimately be understood in terms of its immediate evolutionary history. An excellent introduction to the ideas which have been developed in this sphere has recently been given by Falconer (4).

The phenomenon of genetic homeostasis, defined by Lerner (12) as the ability of a random mating population "to equilibrate its genetic composition and to resist sudden changes," can be observed experimentally in respect of each quantitative character showing additive genetic variation in the population concerned. The genetic equilibrium can be disturbed by artificial selection over a period of generations, and observations can be made of the subsequent change in the mean on relaxation of selection. From such a set of observations, a quantitative measure can be obtained which reflects the genetic homeostatic properties of the particular quantitative character, and which can be used as a basis for comparison of characters with different genetical properties.

The recent development of a satisfactory technique for measuring reproductive fitness in *Drosophila* (8) has made possible an examination of the validity of the limited theoretical framework relating homeostatic behaviour to the effects of natural selection and has, in addition, opened the way to a quantitative attack on problems arising from theories of the evolution of genetic complexity. The results to be discussed in this paper are of interest from both of these points of view.

The two quantitative characters chosen for study represent markedly different genetic systems: Abdominal hair number has been used because of the statistical simplicity of the genetic variance shown in wild-type populations, and scutellar bristle number was selected as an example of a highly canalized developmental pattern. In this way, the predictions arising from the mathematical theory of genetic homeostasis can be tested for applicability to two quite different sorts

of genetic equilibria. A comparison of the genetic homeostatic properties of the two characters can be expected to throw further light on some of the problems posed by Waddington's theory of the canalization of development.

THE MATHEMATICAL THEORY OF GENETIC HOMEOSTASIS

A most useful concept, due to Haldane (6), is that of the intensity of natural selection for a metric character. It is defined as the natural logarithm of the ratio of the fitness of the optimal phenotype to that of the whole population, but can often be determined from frequency distributions without information as to the actual fitness values of the members of the population. It is worthwhile to interpret this measure in terms of three different genetical models which have so far been examined.

Robertson (17) has explored the consequences of a model of genetic homeostasis in which extreme deviants are less fit than intermediates, not because they have extreme phenotypic values for the character in question, but because they are more homozygous than individuals close to the population mean. If the reduction in fitness due to segregation at the *ith* locus is denoted by S_i, it follows from Robertson's analysis that the mean fitness of the population is given approximately by

$$\bar{w}_0 = \phi\,(0) - \tfrac{1}{2}\,\bar{S}h^2 \qquad \text{(i)}$$

where $\phi(0)$ denotes fitness at the optimal phenotype (assumed to approximate to the population mean), $\bar{S}$ is the mean value of the S_i, weighted according to the contribution of the locus concerned to the additive genetic variance in the metric character, and h^2 is the heritability. Haldane's intensity of natural selection for the character is then

$$I = \log_e\left[1 + \frac{\tfrac{1}{2}\,\bar{S}h^2}{\pi_i(1 - S_i)}\right] \qquad \text{(ii)}$$

$$= \tfrac{1}{2}\,\bar{S}h^2 \qquad \text{approximately,}$$

provided the individual S_i values are small and the number of loci segregating for the metric character is sufficiently small for the term $\pi_i(1 - S_i)$ to be little different from unity.

Kimura (7) has considered a more general model in which it is assumed only that the fitness of a genotype is determined independently of its contribution to the metric character. He applied the resulting formulas to the situation in which, at each locus affecting the quantitative character, a mutant gene is maintained in equilibrium by the opposing influences of mutation pressure and natural selection. If the selective disadvantage of a mutant heterozygote is denoted by s_i, and θ represents the harmonic mean of the s_i, each reciprocal being weighted by the contribution to the additive genetic variance, the intensity of natural selection for the metric character can be written

$$I = \log_e\,(1 + \tfrac{1}{2}\,\theta\,h^2) \qquad \text{(iii)}$$

$$= \tfrac{1}{2}\,\theta\,h^2 \qquad \text{approximately.}$$

The third model which has been explored is that in which natural selection favors individuals with phenotypic values close to the population mean, because of the adaptive significance of the metric trait in question (9); all loci contributing to variation in the character are assumed to influence fitness solely through their effects on the character itself. If it is assumed that reproductive fitness declines with deviation x from the population mean as

$$\phi(x) = \exp(-\tfrac{1}{2}\, x^2/\sigma_f^2) \qquad \text{(iv)}$$

(analogous to postulating a normal distribution of the variable in the surviving population), it is clear that the parameter σ_f^2 is related to the intensity of natural selection for the optimal value. σ_f^2 is small if natural selection permits only those individuals close to the mean to reproduce, and infinite if all individuals have equal fitness. Haldane's definition of the intensity of natural selection leads to the intuitively acceptable expression

$$I = \tfrac{1}{2} \log_e (1 + \sigma_p^2/\sigma_f^2) \qquad \text{(v)}$$

which equals $\tfrac{1}{2}\dfrac{\sigma_p^2}{\sigma_f^2}$ approximately, for low intensities of selection, where the phenotypic variance of the quantitative character is denoted by σ_p^2.

Artificial Selection and Relaxation

The behaviour of an additive genetic metric character under artificial selection and subsequent relaxation has been deduced by Robertson (17) on the basis of the model of heterozygote superiority for fitness. Following a shift in the mean of the character through g additive genetic standard deviations, it is to be expected that the mean reproductive fitness of the population will have declined to a level $\bar{w}$ (relative to that of the base population) given by

$$(-\log_e \bar{w})/g^2 = \tfrac{1}{2}\,\bar{S}. \qquad \text{(vi)}$$

On relaxation of selection, the return of the mean towards the unselected level in the first generation is expected to be a proportion $\bar{S}$ of the progress initially made. The parameter, $\bar{S}$, which appears throughout the calculations, has been suggested by Robertson as an appropriate measure of the *homeostatic strength* of the metric character. We have also seen that $\bar{S}$ is closely related to Haldane's parameter I (equation ii).

From an experimental point of view then, if we denote the proportional return to the mean of the base population in the first generation of relaxation by R_1, these results would lead us to expect the following relationship to hold:

$$\frac{(-\log_e \bar{w})/g^2}{R_1} = \tfrac{1}{2}. \qquad \text{(vii)}$$

The consequences of artificial selection followed by relaxation have not yet been explored for the model of deleterious genes maintained solely by mutation pressure, but the following results have been deduced for the model of natural selection for phenotypic intermediates (9). Using the same notation as

before (equations iv and v), after a shift in the mean of the metric character through g additive genetic standard deviations, the fitness of the population is expected to have declined to a level $\bar{w}$ (relative to that of the base population), given by the relationship

$$(-\log_e \bar{w})/g^2 = \tfrac{1}{2}\, h^2\, \sigma_p^2/\sigma^2 \qquad \text{(viii)}$$

where $\sigma^2 = \sigma_p^2 + \sigma_f^2$. On relaxation of selection, the change in the mean of the selected population in the first generation is expected to be a proportion $h^2\sigma_p^2/\sigma^2$ of the progress previously made. The model, therefore, leads us to expect equation vii to hold, though the underlying genetic mechanism is quite different from that of heterozygote superiority for fitness previously discussed.

The magnitude of R_1 also bears a straightforward relationship to Haldane's intensity of natural selection on the model of natural selection for phenotypic intermediates. It is a simple matter to show that R_1 is approximately equal to $2\ h^2I$, provided the intensity of natural selection is low.

The σ^2_{AA} Effect

It has been shown by Griffing (5) that the existence of additive × additive genetic interaction (σ^2_{AA}) between loci contributing to variation in a metric character leads to a regression of the population mean on relaxation of artificial selection, which will be confounded with that due to the effects of natural selection. From a descriptive point of view, it seems reasonable that this effect should be considered as much a component of the phenomenon of genetic homeostasis, as is the stabilizing action of natural selection. From the quantitative angle, however, the matter is complicated by the fact that the proportional return of the selected population in the first generation following relaxation of selection, due to the σ^2_{AA} effect, is not independent of the preceding number of generations of artificial selection. In the absence of any effects of natural selection, the expected magnitude of R_1, following n generations of artificial selection, can be shown to be

$$R_1 = \tfrac{1}{2}\left[1 + \frac{n(\sigma^2_A/\sigma^2_{AA})}{1 - (\tfrac{1}{2})^n}\right]^{-1}. \qquad \text{(ix)}$$

It can be seen from the expression that the expectations embodied in equation vii are not likely to be seriously disturbed, provided σ^2_{AA} is small relative to σ_A^2, and the magnitude of R_1 is measured after something like 10 generations of artificial selection.

EXPERIMENTAL OBSERVATIONS

The average reproductive fitness of an array of genotypes can logically be defined in terms of three major components: the probability of survival to breeding age *(S)*, the mating ability of adult males *(M)*, and the fecundity of mature females *(F)*. If the probability of survival to sexual maturity is the same for both sexes, the average fitness of the set of genotypes is given as $\Phi = \tfrac{1}{2}S(M+F)$. An elegant technique has recently been devised by Knight and Robertson (8)

for the measurement of competitive ability in *Drosophila melanogaster* under laboratory conditions, and extensive use has been made of the technique in studies of changes in reproductive ability due to inbreeding and to artificial selection for metric characters (11).

In terms of the three major components of reproductive fitness, the "competitive index" is a measure of *MFS*, each component being expressed relative to the standard tester stock, and it has been pointed out by Knight and Robertson that differences between lines in the competitive index will in general be greater than the corresponding differences in reproductive fitness. However, a simple extension of the competition test has since been suggested (10) which provides an estimate of $\frac{1}{2}S^*(M+F)$, where S^* denotes the mean probability of survival of the genotypes resulting from cross-mating between the wild-type line under test and the standard marked tester stock. An additional test can be made to estimate the ratio S/S^*, and the two combined to provide an estimate of Φ.

The Characters Studied

The experimental observations to be discussed have been made in the course of selection programs involving two quantitative characters, abdominal hair number, and scutellar bristle number, chosen to represent markedly contrasting genetic systems. The number of hairs on the fourth and fifth abdominal sternites has been used extensively in laboratory experiments with *Drosophila*, and the nature of the genetic variation displayed in wild-type populations is well understood (2). Inbreeding has little average effect on the mean of the character, and analyses show the genetic variation at equilibrium to be mainly additive. The means of crosses between selected lines and the base population are not widely different from the means of the parental values, though the observed mean is generally somewhat closer to that of the base population.

Scutellar bristle number on the other hand, is a metric character which has not been studied closely, due primarily to its discontinuous and almost invariant mode of expression. Payne's early experiments (13) have shown that although the number of macrochaetae on the scutellum is almost invariably four in wild-type individuals, one can breed from the occasional female with an extra bristle, to produce a population with an increased number of aberrant individuals. In fact, by directional selection Payne was able to increase the mean bristle number in the population to 9 in 30 generations. More recently, Rendel (15) has shown the relationship between gene dosage and bristle number to be highly complex, and has produced evidence of extensive canalization around the normal level of expression.

In my own work with this character, I have selected for increased bristle number in a wild-type population (Canberra), breeding from approximately 20 pairs of individuals per generation. Under this regime the progress plotted against the accumulated selection differential is extremely regular, but markedly non-linear. By the use of probit transformations, the discontinuous nature of the character can be shown to be responsible for only a small part of the non-

linearity, the principle factor being the curvilinear relationship between gene dosage and bristle number. Of even more interest has been the finding that crosses between selected lines and the base population depart markedly from the means of the parental values. On the probit scale, however, the response to selection is something close to a linear function of the accumulated selection differential, and crossing to the original population brings the mean on this scale approximately half-way back to the base level. It is apparent that we are here dealing with a metric character of considerable genetic complexity, in contrast to the relatively simple genetic situation underlying variation in abdominal hair number in wild populations. It is, therefore, of great interest to compare the homeostatic properties of the two systems.

Abdominal Hair Number in the Kaduna Population

An elaborate series of selection experiments involving abdominal hair number has been carried out by Dr. Alan Robertson and his co-workers in Edinburgh, using the Kaduna population. In earlier work, no measurements of competitive ability were made, but it is worthwhile for our present purposes to summarize the behavior of the selected lines on relaxation of artificial selection (2). Following five generations of mass selection at an intensity of 20/100 in each sex, five replicate high lines and five low lines were maintained under crowded conditions for a period of six generations. In both sets of lines, an average of 35 per cent of the initial response was lost during the period. We can reasonably estimate the proportion of the response lost in the first generation of relaxation as $R_1 = (1/6)\log_e (100/65) = 0.072$. Similar lines maintained under optimal conditions changed very little by comparison, and we can be confident therefore that the σ^2_{AA} effect played, at most, only a minor role in these lines.

In later work with the same population (11), duplicate high and low hair number lines were selected at an intensity of 10/50 in each sex, and the competitive indices determined after 5 and 10 generations for comparison with those of four control lines, maintained with 10 randomly selected pairs of parents each generation. The behavior of the selected lines on relaxation of selection at generations 5 and 10 was also recorded, the lines being maintained under crowded conditions. As discussed elsewhere (11), there are grounds for believing that at the latter point genetic fixation had become an important factor limiting the extent to which the means of the selected populations could change under natural selection. We shall therefore restrict ourselves to the results obtained after five generations of selection (Table 1).

The value of R_1 (0.037) is somewhat less than that calculated from the earlier study; it does not seem likely that the higher rate of inbreeding in the 10/50 lines could be wholly responsible for this discrepancy, and it is quite possible that the genetic situation in the cage population gradually changed during the 100-generation interval between the commencement of the 2 experiments. The corresponding value of $(-\log_e \bar{w})/g^2$ (where $\bar{w}$ refers to the mean competitive index of the selected lines relative to that of the controls) is 0.6 times the value

TABLE 1.—MEASURES OF THE DECLINE IN FITNESS WITH SELECTION AND OF GENETIC HOMEOSTATIC STRENGTH.

Population	Character	$(-\log_e \bar{W})/g^2$	Homeostatic strength (R_1)	Ratio
Kaduna	Abdominal hair number	0.022 ± 0.003^1	0.037	0.6
Canberra	Abdominal hair number	0.005 ± 0.006^2	0.004	1.1
Canberra	Scutellar bristle number	0.017 ± 0.006^2	0.042	0.4

[1]Based on measurements of the competitive index.
[2]Based on measurements of relative fitness.

of R_1, by comparison with the theoretical expectation of ½ (equation vii). The agreement is as good as one could expect in view of the bias associated with the competitive index as a measure of relative fitness, and the possibility that R_1 has been underestimated due to the effects of genetic fixation.

Abdominal Hair Number and Scutellar Bristle Number in the Canberra Population

In the hair number studies with the Kaduna population, replicate lines selected in the same direction at an intensity of 10/50 were found to differ quite markedly in the degree to which the competitive index changed under artificial selection. In addition, interpretation of the observations of homeostatic behavior was complicated by the problem of genetic fixation (11). In subsequent studies, a larger breeding population was used to minimize these disturbing effects. In the abdominal hair number selection, in both the high and low lines, a selection intensity of 10/20 was imposed in each of five cultures, the selected groups of males and females being mated randomly among cultures each generation. Each line, therefore, had a total of 50 pairs of breeding individuals per generation. The same rigid procedure could not be adopted in selection for increased scutellar bristle number, due to the discontinuous nature of the character, but roughly 20 pairs of parents were used each generation. The technique of measurement of competitive ability was also modified in the Canberra population studies to give unbiased estimates of relative fitness (10).

Selection for abdominal hair number gave a surprising result: in 10 generations of artificial selection, the mean of the population had been moved through an average of 4.8 additive genetic standard deviations, yet no significant decline in reproductive fitness could be detected. The behavior of the selected populations on relaxation of artificial selection gave independent evidence to the same effect (Table I). These results present a very different picture from those previously described for the Kaduna population, and possible explanations of the contrast in behavior of lines from the two populations will be considered in detail in the following section.

Ten generations of artificial selection ($\Sigma\, \bar{i} = 10.42$) for increased scutellar bristle number moved the Canberra population mean from 4.09 to 6.44, averaging over both sexes. At this point, 100 per cent of females and 93 per cent of males had more than the normal complement of four macrochaetae. On the probit scale this amounts to a total response of 6.0 additive genetic standard deviations at a heritability of 38 per cent. The mean reproductive fitness of the genotypes so produced was estimated to have been only 54 per cent of that of the array of genotypes in the control population, and the value of $(-log_e \bar{w})/g^2$ is therefore 0.017 ± 0.006. The corresponding value of R_1, measured on relaxation of selection for a period of 14 generations, was 0.042. Once again the ratio of these two quantities is as close to the theoretical value of ½ as one could expect.

DISCUSSION

The reduction in reproductive fitness which accompanies artificial selection results from two types of change in gene frequency: directional changes due to the selection pressure imposed and random changes in gene frequency due to genetic sampling at loci other than those contributing to the advance under selection. In this work, the fitness of selected lines has been given relative to that of control lines maintained under a comparable regime, so that the direct effects of restricted population size have been excluded. However, Robertson (18) has recently pointed out that the rate of inbreeding under artificial selection is expected to be greater than in a random-bred control, due to variation among progeny groups in the mean of the character under selection. His analysis has indicated that under selection for a character of high heritability, the effective number of breeding individuals may be considerably reduced.

These indications are difficult to reconcile with some of the experimental observations which we have made. For instance, one of the lines from the Kaduna population selected for increased abdominal hair number, has been shown by measurements of the competitive index and its components not to differ significantly in fitness from the random-bred control lines, despite the fact that restricted population size in the latter caused a 20 per cent reduction in fitness over the period (11). Two lines from the Kaduna population, which were selected for a period of 25 generations for increased sternopleural hair number, had progressed to a plateau situated a little over 5 phenotypic standard deviations from the base level, yet they were shown to be only 12 per cent less fit than the controls, a non-significant difference. Over the same period, the control lines had shown a decline of 40 per cent in the competitive index (11). It seems unlikely, therefore, that the increase in inbreeding due to artificial selection has been a serious source of bias in this work with Drosophila.

A Comparison of the Populations

Let us consider the behavior of the Kaduna and Canberra populations under selection for abdominal hair number. Had the selection regimes been identical in the two studies, we would have no alternative but to conclude that

the two populations differ intrinsically in their homeostatic properties, but we must consider the fact that the intensity of selection, the rate of inbreeding, and the measure of competitive ability differed in the two experiments. We can most easily exclude the last-mentioned as a source of confusion by recalculating the value of $(-\log_e \bar{w})/g^2$ for the Canberra population using the competitive index: the value comes out to be 0.005 as before.

Regarding the different rate of inbreeding involved, it is only the increase in inbreeding due to artificial selection which is relevant, and I have suggested this is probably not an important source of bias. However, quite apart from the reduction in fitness which may have been brought about in this way during selection, the phenomenon cannot account for the difference in behavior in the two populations on relaxation of artificial selection, for the heightened rate of inbreeding has its effect primarily on the background genotype, while the regression of the mean on suspension of selection is due to the subset of loci governing variation in the metric character.

We come now to the difference in selection intensity; 10/50 in the work with the Kaduna population, and 50/100 in the Canberra studies. The possibility exists that artificial selection at a lower intensity allows greater play to the opposing forces of natural selection, thereby reducing the realized response, the decline in fitness with selection, and also the regression of the mean on relaxation of artificial selection. However, the early work with the Kaduna population demonstrated the minor role played by natural selection under the optimal conditions of the selection process (2), so that we can discard this possibility as an explanation of the difference in behavior between the two populations.

As a result of recent work in Edinburgh, a reasonable hypothesis can be suggested to explain the contrast in homeostatic behavior. Experiments with the Kaduna population have been designed to measure the residual genetic variance in abdominal hair number, after a high theoretical level of inbreeding had been reached in populations inbred at different rates. The early results reported by Clayton (1) showed that at slower rates of inbreeding, considerably more additive genetic variance was retained than in the more rapidly inbred lines; however, it has since been found that most of the lines are segregating for inversions (3). Presumably then, in selection from the Kaduna base population, we have been dealing with alternative chromosome segments which differ in their effects on abdominal hair number and form heterozygotes superior in reproductive fitness to either homozygote. The marked genetic homeostatic properties which have been observed in respect of abdominal hair number in this population may well be due to the effects of these chromosome segments, rather than to the properties of individual loci.

If this is the case, we can consider the inversions as major "genes" which are overdominant for fitness, and give some indication of the magnitude of the heterozygote advantage. On the basis of Robertson's theory summarized earlier, we can estimate the value of $\bar{s}$ to be approximately 0.04 from the results in Table 1. Since the heterozygote advantage at individual loci is weighted by the con-

tribution of the locus to the genetic variance in abdominal hair number, the average inversion heterozygote superiority must be greater than 8 per cent, to an extent depending on the contribution of other loci to the variance. It will be interesting to see how this order of magnitude compares with that necessary to explain the segregation of the inversions in the long-term inbred lines studied by Clayton and Robertson.

A Comparison of the Characters

In the Canberra population studies with abdominal hair number, we are probably getting closer to a measure of the effects of the individual loci promoting variation in the character. We can estimate the value of $\bar{s}$ to be roughly 0.005, and the average degree of overdominance for fitness at the loci concerned to be of the order of 1 per cent. It is likely, therefore, that most of the genes involved are effectively neutral in their effects on reproductive fitness, and that the balance between forward and back mutation pressures largely determines the extent of the variability shown in equilibrium populations. Robertson (16) has suggested this as the reason for the statistical simplicity of the genetic variance shown by the character, and we have convincing data which support his contention.

We come now to the homeostatic properties of scutellar bristle number in the Canberra population. We know very little about the nature of the genetic variation displayed by this character. From the response to selection, the heritability of the character measured on the underlying probit scale has been estimated to be 38 per cent, but we have no information on the relative importance of σ^2_A and σ^2_{AA} in their contributions to this estimate. Future work can be designed to throw some light on this question. In experiments on relaxation of selection we can compare lines maintained under crowded conditions with those kept under optimal conditions, and we can deliberately minimize the effects of natural selection in the "optimal" lines by equalizing the numbers of offspring contributed by each pair of parents. We would expect to observe the σ^2_{AA} effect in the optimal lines, and the effects of natural selection plus the σ^2_{AA} effect in the crowded lines.

Despite this reservation, we are justified in concluding from the data in Table 1 that the homeostatic properties of scutellar bristle number and abdominal hair number in the Canberra population differ markedly, and the evidence clearly implicates differential reproduction and survival as a major contributing factor.

The interpretation of the scutellar bristle data rests, to some extent, on an understanding of the biological nature of the character, and on the implications of Waddington's theory of the canalization of development (20). It is important to stress that the formation of the macrochaetae on the thorax of normal individuals is an extremely regular affair. "The new adult epidermis, which in the young pupa replaces the old larval epidermis, first consists of a sheet of many similar cells. Then a few of these cells, at separate specific places, enlarge themselves and division occurs. One of the products of the ancestral cell transforms itself into the sensory nerve cell; the other divides once more, the two daughter

cells becoming the socket and bristle forming cells" (19). Four such organs are formed on the scutellum in fixed specific locations, each with "a sensory nerve cell whose one short nervous process ends near the base of the bristle, and whose other long nerve fibre leads to the central nervous system." When we use scutellar bristle number as a quantitative character, we automatically include the mechanism responsible for the maintenance of a definite pattern of phenotypic expression. Artificial selection based on the preservation of individuals with additional bristles leads not only to a gradual increase in the number of bristles on the whole structure, but to a modification of the embryonic field responsible for normal development. The nature of this modification is also predetermined by the characteristics of the field itself, the additional bristles falling into a pattern almost as marked as that of the four basic bristles.

It is just such an orderly developmental process which one would expect to show canalization, and Rendel's elegant experiments (14) have demonstrated its insensitivity to genetic influences. He has confirmed the existence of potential genetic variation underlying the uniform phenotypic appearance of wild-type individuals, by means of artificial selection in the presence of a mutant gene. Waddington's theory has, in fact, proposed that natural selection against deviation from the optimum will tend to produce greater stability, not by eliminating genetic segregation, but by rendering the individual less sensitive to its effects. As a consequence, one expects some characters to be less variable than others, those with the least variation being the ones for which deviation from the norm leads to the greatest reduction in fitness. Waddington has himself stressed the difficulties of testing this hypothesis experimentally, because of the lack of a logical basis for comparing the variability of different quantitative characters (20). There is, however, no difficulty in comparing the fitness cross-section of a character showing no evidence of canalization with that of a highly canalized developmental process.

There is an important distinction yet to be drawn, for we have reason to believe that the reduction in reproductive fitness measured in the laboratory has not been due to the presence of the extra scutellar bristles as such, but to genetically correlated secondary responses to the artificial selection imposed. This inference can be drawn from the observation that despite the presence of sufficient genetic variation for a complete return to the base level the experimental lines, under the influence of natural selection, have stabilized at means much removed from that of the base population. In Waddington's own terms, we have obtained information as to the nature of the "spurious" fitness cross-section of the character. However, I am not prepared to accept Rendel's suggestion that scutellar bristle formation is canalized simply because "development of bristles is somehow caught up in development of the thorax" (14). I believe it is reasonable to hold that canalization of the developmental processes leading to bristle formation has been due to the adaptive significance of these organs, and to the necessity for a precise arrangement in view of the suggested role they may play in registering fluctuations of air pressure during flight (19).

If this is the correct view, then we have no information as to the magnitude of the forces of natural selection which Waddington would hold responsible for the evolution of the canalization mechanism. The measurements we have made are concerned with the *secondary* effects of genetic segregation to which the primary developmental process has become insensitive—variation which is in fact sheltered from the direct effects of natural selection. We have shown the underlying genetic variation to be far from neutral in its effects on reproductive capacity, due no doubt to the rigidity of the relationships between the primary developmental path and those associated with it. It seems we can interfere with an equilibrium involving a peripheral character, such as abdominal hair number, without greatly affecting any associated developmental processes, so that no great reduction in fitness results, and genetic homeostatis is not marked. In general, we can perhaps expect to find that gene substitutions affecting highly canalized systems have far more extensive side-effects of a disruptive nature, leading in turn to reduced reproductive ability, and to pronounced homeostatic behavior on relaxation of selection.

SUMMARY

Predictions arising from the mathematical theory of genetic homeostasis have been tested under laboratory conditions, using *Drosophila melanogaster* as the experimental organism. The two quantitative characters chosen for study represent markedly different genetic systems. Abdominal hair number has been used because of the statistical simplicity of the genetic variance shown in wild-type populations, and scutellar bristle number was selected as an example of a highly canalized developmental pattern.

Within the limits of accuracy imposed by available techniques, the quantitative relationship between the change in reproductive fitness under artificial selection, and a subsequent measure of homeostatic behaviour on relaxation of selection, was found to be in accord with available theory. It has become clear, however, that future experiments of this nature must be designed to distinguish between homeostatic behavior due to natural selection, and that due to the disequilibrium of gametes brought about by epistatic effects.

Of perhaps greater interest is the contrast in genetic homeostatic properties exhibited by the two characters. As far as abdominal hair number is concerned, the evidence suggests that most of the individual genes have virtually no effects on reproductive fitness, so that mutation pressures must largely determine the extent of the variability in equilibrium populations. On the basis of Lerner's model of heterozygote superiority, the average degree of overdominance for fitness at the loci concerned can be estimated to be of the order of 1 per cent.

A genetic equilibrium such as that shown by abdominal hair number can evidently be disturbed under artificial selection without greatly affecting associated developmental processes, but the situation is very different when we deal with a canalized character such as scutellar bristle number. It has been shown that genetic segregation, against which the primary developmental path is buf-

fered, may be far from neutral in its over-all effect on reproductive capacity. We can infer also that gene substitutions affecting such a system will in general have extensive side-effects on secondary developmental processes, leading to a marked reduction in reproductive efficiency as progress is made under artificial selection, and to pronounced homeostatic behavior on relaxation of selection.

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The Covariance Between Relatives in the Presence of Linkage

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FOLLOWING basic results derived by Fisher (4) and Wright (11), the genotypic variance of a random mating diploid population which is in linkage equilibrium can be partitioned into the additive genetic variance, the dominance variance, and the epistatic (or interaction) variance. The epistatic variance can be subdivided further into various component variances as defined by Cockerham (1) and Kempthorne (5). The covariances between relatives with any degree of relationship can then be given as linear expressions of those partitions.

Even though the population is in linkage equilibrium, linkage may show up in the coefficients of certain components of the covariance between relatives. Cockerham (2), who was the first to investigate this case for linkage effects, found that the covariances of some relatives are affected, whereas others are not, and that only epistatic components involving sets of linked loci are concerned, the effect being always to increase the coefficients of the respective components. He also gave some such coefficients for the covariances between half sibs and full sibs, respectively, under the assumption of interference being absent, but he did not discover a simple method by which any desired coefficient could be ascertained. On the other hand, we may cite the following challenging remark from Matzinger and Kempthorne (8): "A formulation of the general effects of linkage is one of the outstanding problems in the whole area of quantitative inheritance."

The present paper exposes a general method for describing the effects of arbitrary linkages on the covariances between non-inbred relatives. The assumptions to be made include: (a) relatives being derived without selection from a random mating diploid population which is in linkage equilibrium, (b) absence of position effects on genotypic values, and (c) relative frequencies of gametes being not affected by changes of either genotype or environment. The approach makes use of some recent proposals (Schnell, 9) concerning notation and basic concepts which will briefly be recapitulated in the first three sections of this paper.

SET NOTATION

Whenever reference is to be made to individual loci, this will be done by means of indices such as i, j, k, etc. For the sake of generality, however, we shall

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often have to refer to sets of loci without specifying those loci individually. In such cases the following system of notation will be used.

Variable sets of loci are symbolized by capital letters, while the number of loci comprised within such a set is denoted by the corresponding lower case letter. The total set of loci involved in the inheritance of a quantitative trait is symbolized by N. Other letters having special meanings are R and S, which represent subsets of N referred to for additive effects and dominance effects, respectively.

The sign $\subset$ means "contained in." For instance, the condition $P \subset Q$ indicates that P is any subset of set Q, or in other words, that P varies within Q. The remaining subset, $(Q - P)$, is referred to as $\bar{P}$. The sign $\sum_{P \subset Q}$ indicates summation over all possible subsets P within a particular set Q, i.e., over 2^q items, as there are 2^q different ways of dividing set Q into two subsets, P and $\bar{P}$. For example, if set Q consists of the loci i, j, k, subset P must be either empty or one of the following sets: (i), (j), (k), (ij), (ik), (jk), or (ijk).

If not otherwise stated, subsets represented by distinct capitals are supposed to vary independently of each other within sets to be indicated. The subset of loci which is common to two sets, M and P, is denoted by MP, while $c(MP)$ stands for the number of loci comprised within subset MP. Furthermore, a capital followed by an asterisk, such as M^*, refers only to those sets M in which the number of loci involved is either zero or even.

The convention will be made throughout that $0^0 = 1$.

GAMETIC FREQUENCIES AND LINKAGE VALUES

We shall employ two different systems of parameters for describing the linkage relations existing within a given set of loci, namely *gametic frequencies* and *linkage values*, both of which are categories of probabilities supposed to be not influenced by either genotype or environment.

Gametic frequencies will be written in a general form such as $\gamma_{Q(P)}$, which symbolizes the probability that a gamete transmitted by an individual to its progeny carries maternal genes at the loci of a subset P contained in set Q, and paternal genes at the loci of the remaining subset $\bar{P}$. With respect to a given set of loci, Q, there are 2^q gametic frequencies of that sort, which must add up to unity, i.e.,

$$\sum_{P \subset Q} \gamma_{Q(P)} = 1. \tag{i}$$

Note that in the special case $q = 0$ there exists one gametic frequency, which is equal to unity. In the case $q = 1$ we have two gametic frequencies, both of which are equal to $\frac{1}{2}$ as a result of the general symmetry relation,

$$\gamma_{Q(P)} = \gamma_{Q(\bar{P})}. \tag{ii}$$

The general form of the linkage values is λ_{M^*}, where M^* refers to the set of loci involved. A linkage value, λ_{M^*}, can be defined in terms of the gametic frequencies belonging to any set Q which comprises M^* as a subset, the definition being,

$$\lambda_{M^*} = \sum_{P \subset Q} (-1)^{c(M^*P)} \gamma_{Q(P)}. \qquad \text{(iii)}$$

Formula (iii) implies the existence of linkage values referring to any set of loci the number of which is zero or even. For example, the gametic frequencies of a set Q which consists of the loci i, j, k, and l, can be used for defining the following eight linkage values: $\lambda_{()}$, λ_{ij}, λ_{ik}, λ_{il}, λ_{jk}, λ_{jl}, λ_{kl}, and λ_{ijkl}, where $\lambda_{()}$ stands for a linkage value referring to zero loci, which is obviously always equal to unity. A linkage value is zero, if the corresponding recombination fraction amounts to 50 per cent, and unity with recombination being absent. Generally we have the connexion,

$$\lambda_{M^*} = 1 - 2\rho_{M^*}, \qquad \text{(iv)}$$

where ρ_{M^*} is that recombination value in an extended system of such parameters which corresponds to a particular linkage value λ_{M^*}. Finally, we mention that Cockerham (2) in his linkage study used a quantity δ which is in fact the square of a linkage value referring to two loci.

The following relations between gametic frequencies and linkage values can be derived from formulas (ii) and (iii): Any gametic frequency is expressible as a linear function of appropriate linkage values, which is easily written down from the general formula,

$$\gamma_{Q(P)} = \left(\frac{1}{2}\right)^q \sum_{M^* \subset Q} (-1)^{c(M^*P)} \lambda_{M^*}. \qquad \text{(v)}$$

The expressions (v) of the 2^q gametic frequencies belonging to any given set Q are completely orthogonal with regard to the terms λ_{M^*} involved. Owing to this orthogonality, which is not met with in corresponding expressions in terms of recombination values, we have the simple relation,

$$\sum_{P \subset Q} \lambda^s_{Q(P)} = \left(\frac{1}{2}\right)^q \sum_{M^* \subset Q} \lambda^s_{M^*}. \qquad \text{(vi)}$$

As to special cases, formula (v) reduces to

$$\gamma_{Q(P)} = \gamma_{Q()} = \left(\frac{1}{2}\right)^q \sum_{M^* \subset Q} \lambda_{M^*}, \qquad \text{(vii)}$$

where $\gamma_{Q(Q)}$ denotes the frequency of that gamete which carries maternal genes at all the loci of set Q, and $\gamma_{Q()}$ similarly refers to the gamete carrying only paternal genes at those loci.

Formulas (v) to (vii) are basic to our approach, inasmuch as we shall have to give general formulations in terms of gametic frequencies, and then must turn to linkage values in order to perceive what actually happens in particular cases.

THE FUNCTION OF INBREEDING

A second basis of the present approach is the concept of the *function of inbreeding*, ϕ_Q, which is defined to be the probability that the two gametes possessed by an individual are identical by descent with respect to a given set of loci, Q.

The inbreeding function forms a generalization of Wright's (10) coefficient of inbreeding, F, if the latter quantity is defined on a probability basis, as has been done by Malécot (7) and Kempthorne (6). Apparently, the probability ϕ_Q is equal to F in the special case $q = 1$. The general relation between both sorts of probabilities may be written in the form,

$$\phi_Q = F^q + \text{(linkage effects)}. \tag{viii}$$

The effects of linkage, which can only show up with $q > 1$, must always be positive, except recombination is in excess of 50 per cent. Note that even with $F = 0$ the value of ϕ_Q is unity in the case $q = 0$, according to the convention that $0^0 = 1$.

In any given instance, the value of ϕ_Q depends on three things, viz.: (a) the system of inbreeding employed, (b) the number of loci contained in Q, and (c) the specific linkage relations existing between those loci. All the information regarding the two latter items is provided by the set of gametic frequencies pertaining to Q. Thus, ϕ_Q is a function of the gametic frequencies belonging to set Q, the type of that function being determined by the mating system employed. The more complex a system of mating is, the more difficult it will be to formulate a general expression of the resulting function of inbreeding. However, if a particular function ϕ_Q is expressible in general terms, its quantity applying to any specific set of loci can be deduced, using either gametic frequencies or linkage values.

For the purpose of illustration, we consider inbreeding by means of one generation of selfing. Regarding a given set of loci, Q, the two gametes of an offspring will be identical by descent if, and only if, both of them have arisen from the same gametic type formed by the parent. Hence the function ϕ_Q is in this case merely the sum of the squared gametic frequencies belonging to set Q, i.e.,

$$\phi_Q = \sum_{P \subset Q} \gamma^2_{Q(P)}, \tag{ixa}$$

which according to (vi) may also be written in the form,

$$\phi_Q = \left(\frac{1}{2}\right)^q \sum_{M^* \subset Q} \lambda^2_{M^*}. \tag{ixb}$$

From (ixb) we deduce with respect to specific sets of loci,

$$\phi_i = \frac{1}{2},$$

$$\phi_{ij} = \frac{1}{4}(1 + \lambda^2_{ij}),$$

$$\phi_{ijk} = \frac{1}{8}(1 + \lambda^2_{ij} + \lambda^2_{ik} + \lambda^2_{jk}),$$

$$\phi_{ijkl} = \frac{1}{16}(1 + \lambda^2_{ij} + \lambda^2_{ik} + \lambda^2_{il} + \lambda^2_{jk} + \lambda^2_{jl} + \lambda^2_{kl} + \lambda^2_{ijkl}),$$

and so on. Note that in these expressions the linkage value referring to zero loci, λ_0, has been replaced by its numerical value, viz., unity.

The utility of the concept of the inbreeding function with regard to the covariances between relatives will become apparent below.

KEMPTHORNE'S BASIC FORMULA

We now turn to our subject, viz., allowing for linkage in the covariance between relatives with an arbitrary degree of relationship. As we want to include the case of inbred parents, but to exclude the case of inbred relatives, we shall suppose that two relatives, X and Y, are somehow related through their respective dams *and/or* through their respective sires, but not otherwise. Putting a similar case, Kempthorne (5) derived a general formula, which will form the starting-point for the development below.

In reporting Kempthorne's basic result, we shall deviate slightly from his notation. The symbol Θ will stand for the probability that at a given locus the two genes transmitted to individuals X and Y by their respective dams are identical by descent. The probability Θ' in the same way refers to the two genes transmitted by the respective sires of those relatives. Thus, Θ and Θ' correspond to the symbols ϕ and ϕ', respectively, in the notation introduced by Malécot (7). We do not follow that notation here, because it seems to be desirable to reserve the symbol ϕ for denoting the function of inbreeding mentioned previously.

As to the components of the genotypic variance of the population studied we have to refer to the usual partitions, viz.

$$\sigma^2_A = \sum_i \sigma^2_{a_i},$$

$$\sigma^2_D = \sum_i \sigma^2_{d_i},$$

$$\sigma^2_{AA} = \sum_{\substack{i,j \\ i<j}} \sigma^2_{a_i a_j},$$

$$\sigma^2_{AD} = \sum_{\substack{i,j \\ i\neq j}} \sigma^2_{a_i d_j},$$

$$\sigma^2_{DD} = \sum_{\substack{i,j \\ i<j}} \sigma^2_{d_i d_j},$$

$$\sigma^2_{AAA} = \sum_{\substack{i,j,k \\ i<j<k}} \sigma^2_{a_i a_j a_k},$$

and so on, where

$\sigma^2_{a_i}$ = variance due to the additive effects at locus i,

$\sigma^2_{d_i}$ = variance due to the dominance effects at locus i,

$\sigma^2_{a_i a_j}$ = variance due to the interaction "additive effects at locus i × additive effects at locus j",

$\sigma^2_{a_i d_j}$ = variance due to the interaction "additive effects at locus i × dominance effects at locus j",

and so on. We shall use the general form $\sigma^2_{A^r D^s}$ for denoting that partition term which contains r A's and s D's in its designation. Such a term is the sum of all the variances involving additive effects at r loci, and dominance effects at s loci, the summation running over all possible distinct sets of r and s loci.

Written in the above notation, Kempthorne's result derived in the paper cited is as follows: The covariance between relatives X and Y with regard to a partition term $\sigma^2_{A^r D^s}$ is given by

$$(\Theta + \Theta')^r (\Theta\Theta')^s \left(\frac{1}{2}\right)^r \sigma^2_{A^r D^s}.$$

Owing to the convention $0^0 = 1$, the foregoing also applies when either Θ or Θ' is zero, as for instance is the case with the covariance between half sibs. Thus, the covariance between relatives X and Y has the general form,

$$\begin{aligned}\mathrm{Cov}_{(X,Y)} = {} & \frac{1}{2}(\Theta + \Theta')\,\sigma^2_A + \Theta\Theta'\,\sigma^2_D + \frac{1}{4}(\Theta + \Theta')^2\sigma^2_{AA} \\ & + \frac{1}{2}(\Theta + \Theta')\,\Theta\Theta'\,\sigma^2_{AD} + (\Theta\Theta')^2\sigma^2_{DD} + \frac{1}{8}(\Theta + \Theta')^3\sigma^2_{AAA} + \ldots.\end{aligned}$$

A more condensed expression is provided by the formula,

$$\mathrm{Cov}_{(X,Y)} = \sum_{r,s} (\Theta + \Theta')^r\,(\Theta\Theta')^s \left(\frac{1}{2}\right)^r \sigma^2_{A^r D^s}, \qquad \text{(x)}$$

where $r,s = 0, 1, 2, \ldots, n$; and $(r + s) = 1, 2, 3, \ldots, n$.

It should be noted that the definitions and formulas given in this section are generally valid with regard to any random mating diploid population which is in linkage equilibrium. In particular, they apply for an arbitrary number of loci segregating, and an arbitrary number of alleles per locus. The covariance formula, however, is derived under the assumption of linkage being absent.

THE GENERAL PRINCIPLE OF ALLOWING FOR LINKAGE

If linkage is to be allowed for, we have first to envisage the fact that the covariance between relatives can no longer be specified in terms of the usual partitions inasmuch as the epistatic variance is concerned. Consider for instance the partition term,

$$\sigma^2_{AAD} = \sum_{\substack{i,j,k \\ i \neq j \neq k \\ i<j}} \sigma^2_{a_i a_j d_k}.$$

In case of no linkage each of the component variances $\sigma^2_{a\,ia\,jd\,k}$ enters the covariance between X and Y with the same coefficient, $\frac{1}{4}(\Theta + \Theta')^g\Theta\Theta'$, whereas the respective coefficients may have different values when adjusted for linkage.

The principle of allowing for linkage is best demonstrated for an example such as one of the aforementioned variances, $\sigma^2_{a\,ia\,jd\,k}$, which apart from linkage contributes to the covariance in the amount of

$$(\Theta + \Theta')^g\,(\Theta\Theta')\left(\frac{1}{2}\right)^g\sigma^2_{a\,ia\,jd\,k}.$$

On expanding, the coefficient becomes a sum of products, in which each factor Θ (or Θ') refers to the probability of a certain event, viz. that two genes are identical by descent at a given locus. Indicating the respective loci by means of indices, we may put the foregoing expression in the form,

$$(\Theta_i\Theta_j\Theta_k\Theta'_k + \Theta_i\Theta'_j\Theta_k\Theta'_k + \Theta'_i\Theta_j\Theta_k\Theta'_k + \Theta'_i\Theta'_j\Theta_k\Theta'_k)\left(\frac{1}{2}\right)^g\sigma^2_{a\,ia\,jd\,k}.$$

Now each product such as $\Theta_i\Theta_j\Theta_k\Theta'_k$ specifies the probability of a compound event regarding the loci involved, and allowing for linkage means accommodating the products to the fact that probabilities referring to different loci inherited from the dams may not be independent of each other, and the same concerns loci inherited from the sires. With linkage, therefore, the above expression should be written as

$$(\Theta_{ijk}\Theta'_k + \Theta_{ik}\Theta'_{jk} + \Theta_{jk}\Theta'_{ik} + \Theta_k\Theta'_{ijk})\left(\frac{1}{2}\right)^g\sigma^2_{a\,ia\,jd\,k},$$

where Θ_{ijk} is the probability that the gametes transmitted to X and Y by their respective dams are identical by descent regarding the loci of set (ijk), and the other symbols have similar meanings.

To generalize our result, we define Θ_Q to be the probability that the gametes transmitted to X and Y by their respective dams are identical by descent regarding the loci of set Q, while Θ'_Q is similarly taken to refer to gametes transmitted by the respective sires. It will be necessary to assume that both Θ_Q and Θ'_Q are equal to unity in the case $q = 0$. We then consider any variance term, σ^2_{aRdS}, which is due to the interaction of additive effects at the loci of a given set R, and dominance effects at the loci of a set S. Neglecting linkage, this variance contributes to the covariance in the amount of

$$(\Theta + \Theta')^r\,(\Theta\Theta')^s\left(\frac{1}{2}\right)^r\sigma^2_{aRdS}.$$

Now we expand the coefficient into a sum of products, replace the power of Θ in each product by a probability Θ_Q referring to the appropriate set Q, substitute similarly for the powers of Θ', and we get an expression which may be written in the form.

$$\sum_{P \subset R} \Theta_{(P+S)}\, \Theta'_{(\bar{P}+S)} \left(\frac{1}{2}\right)^r \sigma^2_{a_R d_S},$$

where $\Theta_{(P+S)} = \Theta_Q$ for $Q = (P + S)$, etc. The covariance between relatives X and Y is found by summing over all the variance terms involved, i.e.,

$$\mathrm{Cov}_{(X,Y)} = \sum_{R,S} \sum_{P \subset R} \Theta_{(P+S)}\, \Theta'_{(\bar{P}+S)} \left(\frac{1}{2}\right)^r \sigma^2_{a_R d_S}, \tag{xi}$$

where $\sum_{R,S} \ldots$ is short for $\sum_{R \subset N} \sum_{S \subset \bar{R}} \ldots$ with $(r + s) \neq 0$.

Formula (xi) then represents the appropriate generalization of formula (x) for the case of arbitrary linkages.

Finally we are faced with the question of how to get particular values of the probabilities Θ_Q and Θ'_Q for a certain system of relationship between individuals X and Y. Let us imagine that the two gametes transmitted to X and Y by their respective dams, say, would not go that way but would unite, therewith giving rise to some individual Z. It is obvious that the function of inbreeding, ϕ_Q, of individual Z would be equal to the probability Θ_Q we are interested in. Thus, the probability Θ_Q, being in fact the inbreeding function of some hypothetical zygote, is a certain function of the gametic frequencies belonging to set Q, and the type of this function depends on the mating system employed. The same, of course, concerns the probability Θ'_Q.

The covariance between X and Y can therefore be specified if general expressions of the appropriate functions Θ_Q and Θ'_Q are available in terms of gametic frequencies. From those expressions the quantities applying to specific sets of loci can be deduced in terms of linkage values. Such quantities may be inserted for the respective factors Θ_Q and Θ'_Q in an expanded expression of formula (xi) to find the coefficient of any desired variance component.

COVARIANCES BETWEEN HALF SIBS AND FULL SIBS

For the purpose of illustration we first consider the covariances between half sibs and full sibs, assuming the parents of the relatives to be non-inbred.

Regarding a given set of loci, Q, the two gametes transmitted to a pair of half sibs by their common parent will be identical by descent if, and only if, both of them have arisen from the same gametic type formed by the parent. Thus, taking the maternal parent to be in common, the appropriate function Θ_Q is equal to the inbreeding function for one generation of selfing, as shown in formula (ix), viz.,

$$\Theta_Q = \sum_{P \subset Q} \gamma^2_{Q(P)} = \left(\frac{1}{2}\right)^q \sum_{M^* \subset Q} \lambda^2_{M^*}. \tag{xii}$$

Concerning specific sets of loci we have,

$$\Theta_i = \frac{1}{2},$$

$$\Theta_{ij} = \frac{1}{4}(1 + \lambda^g_{ij}),$$

$$\Theta_{ijk} = \frac{1}{8}(1 + \lambda^g_{ij} + \lambda^g_{ik} + \lambda^g_{jk}),$$

$$\Theta_{ijkl} = \frac{1}{16}(1 + \lambda^g_{ij} + \lambda^g_{ik} + \lambda^g_{il} + \lambda^g_{jk} + \lambda^g_{jl} + \lambda^g_{kl} + \lambda^g_{ijkl}),$$

and so on. As the respective sires of the half sibs would be unrelated, the function Θ'_Q is in this case,

$$\Theta'_Q = 0^q, \tag{xiii}$$

whence Θ'_Q is unity for Q being empty, and zero otherwise. With full sibs, formula (xii) applies to both sides of parents.

Now we can derive detailed expressions of the covariances in question. The covariance between half sibs turns out to have the convenient form,

$$\mathrm{Cov}_{(\mathrm{HS})} = \frac{1}{4}\sum_i \sigma^g_{a\,i} + \frac{1}{16}\sum_{\substack{i,j \\ i<j}} (1 + \lambda^g_{ij})\,\sigma^g_{a\,ia\,j} + \frac{1}{64}\sum_{\substack{i,j,k \\ i<j<k}} (1 + \lambda^g_{ij} + \lambda^g_{ik} + \lambda^g_{jk})\,\sigma^g_{a\,ia\,ja\,k} \tag{xiva}$$

$$+ \frac{1}{256}\sum_{\substack{i,j,k,l \\ i<j<k<l}} (1 + \lambda^g_{ij} + \lambda^g_{ik} + \lambda^g_{il} + \lambda^g_{jk} + \lambda^g_{jl} + \lambda^g_{kl} + \lambda^g_{ijkl})\,\sigma^g_{a\,ia\,ja\,ka\,l} + \ldots$$

The covariance between full sibs is less simple, since it involves dominance effects too. The first terms are given by

$$\mathrm{Cov}_{(\mathrm{FS})} = \frac{1}{2}\sum_i \sigma^g_{a\,i} + \frac{1}{4}\sum_i \sigma^g_{d\,i} + \frac{1}{4}\sum_{\substack{i,j \\ i<j}} \left(1 + \frac{1}{2}\lambda^g_{ij}\right)\sigma^g_{a\,ia\,j} + \frac{1}{8}\sum_{\substack{i,j \\ i\neq j}} (1 + \lambda^g_{ij})\sigma^g_{a\,id\,j}$$

$$+ \frac{1}{16}\sum_{\substack{i,j \\ i<j}} (1 + \lambda^g_{ij})^g \sigma^g_{d\,id\,j} + \frac{1}{8}\sum_{\substack{i,j,k \\ i<j<k}} \left(1 + \frac{1}{2}\lambda^g_{ij} + \frac{1}{2}\lambda^g_{ik} + \frac{1}{2}\lambda^g_{jk}\right)\sigma^g_{a\,ia\,ja\,k}$$

$$+ \frac{1}{16}\sum_{\substack{i,j,k \\ i\neq j\neq k \\ i<j}} \left(1 + \frac{1}{2}\lambda^g_{ij} + \lambda^g_{ik} + \lambda^g_{jk} + \frac{1}{2}\lambda^g_{ik}\lambda^g_{jk}\right)\sigma^g_{a\,ia\,jd\,k}$$

$$+\frac{1}{32}\sum_{\substack{i,j,k\\ i\neq j\neq k\\ j<k}}(1+\lambda^2_{ij}+\lambda^2_{ik}+2\lambda^2_{jk}+\lambda^2_{ij}\lambda^2_{jk}+\lambda^2_{ik}\lambda^2_{jk}+\lambda^4_{jk})\sigma^2_{a\,id\,idk} \tag{xva}$$

$$+\frac{1}{64}\sum_{\substack{i,j,k\\ i<j<k}}(1+\lambda^2_{ij}+\lambda^2_{ik}+\lambda^2_{jk})^2\sigma^2_{d\,id,jdk}+\frac{1}{16}\sum_{\substack{i,j,k,l\\ i<j<k<l}}\left(1+\frac{1}{2}\lambda^2_{ij}+\frac{1}{2}\lambda^2_{ik}\right.$$

$$\left.+\frac{1}{2}\lambda^2_{il}+\frac{1}{2}\lambda^2_{jk}+\frac{1}{2}\lambda^2_{jl}+\frac{1}{2}\lambda^2_{kl}+\frac{1}{8}\lambda^2_{ijkl}+\frac{1}{8}\lambda^2_{ij}\lambda^2_{kl}+\frac{1}{8}\lambda^2_{ik}\lambda^2_{jl}+\frac{1}{8}\lambda^2_{il}\lambda^2_{jk}\right)$$

$$\sigma^2_{a\,ia\,jaka\,l}+\ldots$$

Each coefficient in the foregoing formulas is easily separated into that part which is due to linkage, and the residual.

It is also possible to obtain more condensed expressions of the above covariances by inserting the appropriate general functions into formula (xi). For example, the covariance between half sibs reduces to

$$\mathrm{Cov}_{(\mathrm{HS})}=\sum_{R}\sum_{M^*\subset R}\lambda^2_{M^*}\left(\frac{1}{2}\right)^{2r}\sigma^2_{a_R}, \tag{xivb}$$

where the summation of R is over all the sets $R \subset N$ except $r = 0$. Likewise, the covariance between full sibs may be written as

$$\mathrm{Cov}_{(\mathrm{FS})}=\sum_{R,S}\sum_{P\subset R}\sum_{M^*\subset(P+S)}\lambda^2_{M^*}\sum_{L^*\subset(\bar{P}+S)}\lambda^2_{L^*}\left(\frac{1}{2}\right)^{2r+2s}\sigma^2_{a_R d_S}, \tag{xvb}$$

where the summation over R,S is the same as in formula (xi). Expressions (xivb) and (xvb) are both not very elucidatory. Yet, they can be used for deriving any particular component.

COVARIANCES BETWEEN ANCESTOR AND OFFSPRING

With non-inbred parents there is another category of covariances between relatives having some practical importance, viz., the covariances between ancestor and offspring.

Cockerham (2) stated for a population of the kind studied in this paper that covariances between relatives where one is an ancestor of the other are not affected by linkage. This statement does not hold in such generality, though it proves true for a special case. Let t be the number of generations which are intercalated between the respective generations of ancestor and offspring. For instance, we have $t = 1$ regarding grandparent and grandchild. Linkage then takes no effect in the case $t = 0$ only, i.e., with the covariance between parent and offspring.

The general formulas (x) and (xi) given previously are not applicable to the covariances between ancestor and offspring, since both of the parental gametes of the ancestor are related to but one of the two gametes giving rise to the offspring. If an ancestor and its offspring are separated from each other by t intercalated generations, their covariance is given by

$$\mathrm{Cov}_{(A,O)t} = \sum_{r}\left(\frac{1}{2}\right)^{rt+r}\sigma^2_{A^r} \qquad \text{(xvi)}$$

under the assumption of no linkage. It can be seen that the corresponding formula allowing for linkage is expressible as

$$\mathrm{Cov}_{(A,O)t} = \sum_{R}\left[\gamma_{R(R)}\right]^t\left(\frac{1}{2}\right)^r\sigma^2_{a_R}. \qquad \text{(xviia)}$$

Owing to (vii) this may be written in the form,

$$\mathrm{Cov}_{(A,O)t} = \sum_{R}\left[\sum_{M^s \subset R}\lambda_{M^s}\right]^t\left(\frac{1}{2}\right)^{rt+r}\sigma^2_{a_R}. \qquad \text{(xviib)}$$

Formulas (xvi) and (xvii) obviously coincide in the case $t = 0$, i.e., for the covariance between parent and offspring, by reducing to

$$\mathrm{Cov}_{(P,O)} = \sum_{r}\left(\frac{1}{2}\right)^{r}\sigma^2_{A^r} = \sum_{R}\left(\frac{1}{2}\right)^{r}\sigma^2_{a_R}. \qquad \text{(xviii)}$$

It will be of interest to consider the case $t = 1$, i.e., the covariance between grandparent and grandoffspring. From formula (xviib) this covariance is found to be

$$\mathrm{Cov}_{(GP,GO)} = \sum_{R}\sum_{M^s \subset R}\lambda_{M^s}\left(\frac{1}{2}\right)^{2r}\sigma^2_{a_R}, \qquad \text{(xixa)}$$

which on expanding becomes,

$$\begin{aligned}\mathrm{Cov}_{(GP,GO)} = {} & \frac{1}{4}\sum_{i}\sigma^2_{a_i} + \frac{1}{16}\sum_{\substack{i,j\\ i<j}}(1+\lambda_{ij})\sigma^2_{a_ia_j} \\ & + \frac{1}{64}\sum_{\substack{i,j,k\\ i<j<k}}(1+\lambda_{ij}+\lambda_{ik}+\lambda_{jk})\sigma^2_{a_ia_ja_k} \\ & \frac{1}{256}\sum_{\substack{i,j,k,l\\ i<j<k<l}}(1+\lambda_{ij}+\lambda_{ik}+\lambda_{il}+\lambda_{jk}+\lambda_{jl}+\lambda_{kl}+\lambda_{ijkl})\sigma^2_{a_ia_ja_ka_l}+\cdots\end{aligned} \qquad \text{(xixb)}$$

Let us compare these formulas to those which were derived for the covariance between half sibs, viz., formulas (xivb) and (xiva), respectively. There is a perfect corresponding between both types of covariances regarding every term involved, except that all the linkage values are squared in the covariance between half sibs, whereas they are not in the covariance studied here. Thus, the covariance between grandparent and grandchild is even more affected by linkage than the covariance between half sibs.

If both the covariance between grandparent and grandchild and the covariance between half sibs could be obtained experimentally, their difference would form an estimate of the net effects of linkage, with a certain weighing according to the respective intensities of recombination.

RELATIVES WITH INBRED PARENTS

We now propose to discuss the case of covariances between relatives the parents of which are inbred.

Even though we assume the relatives to be non-inbred, they may have inbred parents, at least when there is relationship only through the respective dams *and/or* the respective sires. Equation (xi), forms the appropriate general formula for this category of covariances between relatives. We shall restrict our view to the covariances between half sibs, and full sibs. If the parents themselves have a certain function of inbreeding, ϕ_Q, the suitable function Θ_Q for deriving the covariances in question can be shown to be

$$\Theta_Q = \sum_{P \subset Q} \sum_{K \subset Q} \gamma_{Q(K)} \gamma_{Q(\bar{K}P + K\bar{P})} \phi_P, \tag{xxa}$$

which after turning to linkage values becomes

$$\Theta_Q = \left(\frac{1}{2}\right)^q \sum_{P \subset Q} \sum_{M^* \subset Q} (-1)^{c(M^*P)} \lambda^g_{M^*} \phi_P. \tag{xxb}$$

As to specific sets of loci we have,

$$\Theta_i = \frac{1}{2}(1 + \phi_i),$$

$$\Theta_{ij} = \frac{1}{4}[(1 + \lambda^g_{ij})(1 + \phi_{ij}) + (1 - \lambda^g_{ij})(\phi_i + \phi_j),$$

$$\begin{aligned}\Theta_{ijk} = \frac{1}{8}[&(1 + \lambda^g_{ij} + \lambda^g_{ik} + \lambda^g_{jk})(1 + \phi_{ijk}) \\ &+ (1 - \lambda^g_{ij} - \lambda^g_{ik} + \lambda^g_{jk})(\phi_i + \phi_{jk}) \\ &+ (1 - \lambda^g_{ij} + \lambda^g_{ik} - \lambda^g_{jk})(\phi_j + \phi_{ik}) \\ &+ (1 + \lambda^g_{ij} - \lambda^g_{ik} - \lambda^g_{jk})(\phi_k + \phi_{ij})], \text{ etc.}\end{aligned}$$

For a concrete example let us suppose the parents to have arisen from one generation of selfing. In this case the inbreeding function of the parents, ϕ_Q, is that one given in formula (ix). Hence, formula (xxb) receives the form,

$$\Theta_Q = \left(\frac{1}{2}\right)^q \sum_{P \subset Q} \sum_{M^* \subset Q} (-1)^{c(M^*P)} \lambda^g_{M^*} \left(\frac{1}{2}\right)^p \sum_{L^* \subset P} \lambda^g_{L^*}, \tag{xxi}$$

from which we deduce with regard to specific sets of loci,

$$\Theta_i = \frac{3}{4},$$

$$\Theta_{ij} = \frac{1}{16}(9 + 2\lambda^g_{ij} + \lambda^4_{ij}),$$

$$\Theta_{ijk} = \frac{1}{64}(27+6\lambda^2_{ij}+3\lambda^4_{ij}+6\lambda^2_{ik}+3\lambda^4_{ik}+6\lambda^2_{jk}+3\lambda^4_{jk}-2\lambda^2_{ij}\lambda^2_{ik}-2\lambda^2_{ij}\lambda^2_{jk}-2\lambda^2_{ik}\lambda^2_{jk}),$$

and so on. The covariance between half sibs is now derived as

$$\text{Cov}_{(\text{HS})} = \frac{3}{8}\sum_i \sigma^2_{a_i} + \frac{9}{64}\sum_{\substack{i,j \\ i<j}}\left(1 + \frac{2}{9}\lambda^2_{ij} + \frac{1}{9}\lambda^4_{ij}\right)\sigma^2_{a_i a_j} + \ldots \qquad \text{(xxii)}$$

And the covariance between full sibs is found to be

$$\text{Cov}_{(\text{FS})} = \frac{3}{4}\sum_i \sigma^2_{a_i} + \frac{9}{16}\sum_i \sigma^2_{d_i} + \frac{9}{16}\sum_{\substack{i,j \\ i<j}}\left(1 + \frac{1}{9}\lambda^2_{ij} + \frac{1}{18}\lambda^4_{ij}\right)\sigma^2_{a_i a_j} \qquad \text{(xxiii)}$$

$$+ \frac{27}{64}\sum_{\substack{i,j \\ i\neq j}}\left(1 + \frac{2}{9}\lambda^2_{ij} + \frac{1}{9}\lambda^4_{ij}\right)\sigma^2_{a_i d_j} + \frac{81}{256}\sum_{\substack{i,j \\ i<j}}\left(1 + \frac{2}{9}\lambda^2_{ij} + \frac{1}{9}\lambda^4_{ij}\right)^2\sigma^2_{d_i d_j} + \ldots$$

As was noted by Cockerham (1), linkage influences the covariance between relatives having inbred parents twice, viz., first in producing the parents, and then again in producing the relatives. The present approach takes care of both influences simultaneously. To realize this we may neglect the linkage effects with the selfing stage in the above example by putting

$$\phi_Q = F^q = \left(\frac{1}{2}\right)^q.$$

The resulting probabilities Θ_Q are

$$\Theta_i = \frac{3}{4},$$

$$\Theta_{ij} = \frac{1}{16}(9 + \lambda^2_{ij}),$$

$$\Theta_{ijk} = \frac{1}{64}(27 + 3\lambda^2_{ij} + 3\lambda^2_{ik} + 3\lambda^2_{jk}),$$

and so on. We observe in this case that the linkage effects are now nearly halved as compared to the corresponding values found from (xxi) for the correct method.

We may also point to the fact that the function Θ_Q shown in formula (xxi) is equal to the function of inbreeding, ϕ_Q, of an individual resulting from two generations of selfing.

PARENTS REPLACED BY THEIR SELFED PROGENIES

At last, we shall study the covariances between half sibs, and full sibs, in a more peculiar case involving parental inbreeding.

Sometimes the relatives are produced not directly from the parents but from

progenies obtained by selfing those parents, each individual relative originating from outcrossing a different member of the selfed progeny of the respective parent. Matzinger and Kempthorne (8) as well as Cockerham (3) suggested this procedure as a means for making diallel crosses with non-multiflowered plants, where the parents may have an arbitrary degree of inbreeding. Let the parents arise from a mating system leading to a certain function of inbreeding, ϕ_Q. Then the appropriate function Θ_Q is expressible as

$$\Theta_Q = \sum_{P \subset Q} \sum_{K \subset Q} \sum_{H \subset Q} \gamma_{Q(H)} \gamma_{H(HK)} \gamma_{\bar{H}(\bar{H}K)} \sum_{G \subset Q} \gamma_{Q(G)} \gamma_{G(G\bar{K})} \gamma_{\bar{G}(\bar{G}\bar{K})} \phi_P, \qquad \text{(xxiv)}$$

where $\bar{K} = (\bar{K}P + K\bar{P})$. Though being indeed somewhat complex, formula (xxiv) may be used for deriving the probabilities Θ_Q applying to any given function ϕ_Q of the parents.

To have a simple example we suppose the parents themselves to be non-inbred. In this case formula (xxiv) reduces to

$$\Theta_Q = \sum_{K \subset Q} \left[\sum_{H \subset Q} \gamma_{Q(H)} \gamma_{H(HK)} \gamma_{\bar{H}(\bar{H}K)} \right]^2. \qquad \text{(xxva)}$$

Turning to linkage values we may use the expression

$$\Theta_Q \leqq \left(\frac{1}{2}\right)^q \sum_{M^* \subset Q} \lambda^2_{M^*} \left(\frac{1}{2} + \frac{1}{2}\lambda_{M^*}\right)^2, \qquad \text{(xxvb)}$$

which, however, is exact only up to three loci, while certain terms arising with four or more loci are neglected. The resulting probabilities Θ_Q, such as

$$\Theta_i = \frac{1}{2},$$

$$\Theta_{ij} = \frac{1}{4}\left[1 + \lambda^2_{ij}\left(\frac{1}{2} + \frac{1}{2}\lambda_{ij}\right)^2\right],$$

$$\Theta_{ijk} = \frac{1}{8}\left[1 + \lambda^2_{ij}\left(\frac{1}{2} + \frac{1}{2}\lambda_{ij}\right)^2 + \lambda^2_{ik}\left(\frac{1}{2} + \frac{1}{2}\lambda_{ik}\right)^2 + \lambda^2_{jk}\left(\frac{1}{2} + \frac{1}{2}\lambda_{jk}\right)^2\right],$$

lead to the covariances in question, viz.,

$$\mathrm{Cov}_{(\mathrm{HS})} = \frac{1}{4}\sum_i \sigma^2_{a\,i} + \frac{1}{16}\sum_{\substack{i,j \\ i<j}} \left[1 + \lambda^2_{ij}\left(\frac{1}{2} + \frac{1}{2}\lambda_{ij}\right)^2\right]\sigma^2_{a\,i\,a\,j} + \ldots \qquad \text{(xxvi)}$$

$$\mathrm{Cov}_{(\mathrm{FS})} = \frac{1}{2}\sum_i \sigma^2_{a\,i} + \frac{1}{4}\sum_i \sigma^2_{d\,i} + \frac{1}{4}\sum_{\substack{i,j \\ i<j}} \left[1 + \frac{1}{2}\lambda^2_{ij}\left(\frac{1}{2} + \frac{1}{2}\lambda_{ij}\right)^2\right]\sigma^2_{a\,i\,a\,j} \qquad \text{(xxvii)}$$

$$+\frac{1}{8}\sum_{\substack{i,j\\ i\neq j}}\left[1+\lambda^2_{ij}\left(\frac{1}{2}+\frac{1}{2}\lambda_{ij}\right)^2\right]\sigma^2_{a\,i\,d\,j}+\frac{1}{16}\sum_{\substack{i,j\\ i<j}}\left[1+\lambda^2_{ij}\left(\frac{1}{2}+\frac{1}{2}\lambda_{ij}\right)^2\right]^2\sigma^2_{d\,i\,d\,j}+\ldots$$

We may compare these formulas to those given in items (xiva) and (xva), respectively, in order to perceive what happens to the linkage effects if in producing the relatives each parent is replaced by the whole of its selfed progeny. As a result of this procedure, each linkage term referring to two loci, λ^2_{ij}, is multiplied by the factor $\left(\frac{1}{2}+\frac{1}{2}\lambda_{ij}\right)^2$, which amounts to one fourth for $\lambda_{ij}=0$, and unity for $\lambda_{ij}=1$. Thus, the effects of loose linkages are lessened at a higher rate than are those of relatively tight linkages. Such an outcome is of course to be expected as a consequence of the recombination taking place with the selfing stage. If only one of two relatives is produced from a selfing of the parent, while the other one is made from the same parent directly, this results in each term λ^2_{ij} being multiplied by $\left(\frac{1}{2}+\frac{1}{2}\lambda_{ij}\right)$.

It will be obvious from the above that the two procedures, viz., using the parents directly, and replacing them by their selfed progenies, can be applied in various combinations to the same population for the purpose of gathering estimates of the effects of linkage involving different kinds of weighing.

DISCUSSION

In summation, there remains but little to say concerning the present approach to the effects of linkage on the covariance between relatives. What is now available, is a body of fairly general formulas, which apply to a variety of important cases and may be extended to other genetical situations. It does not appear as if the practical utility of the method were in any way exhausted by the few examples here considered.

On the other hand, it cannot be denied that the present approach suffers from the rapidly increasing complexity of its formulations with more intricate systems of mating. It seems to be self-evident, however, that complicated situations in nature will require a more involved manner of representation. We consider it essential that the exact coefficient of any variance component can be specified in terms of linkage values, if wanted. Admittedly, such expressions in terms of linkage values do not tell us very much about their eventual size in a given case, if they involve more than two or three loci. But, as may be seen from the literature, covariances between relatives are only seldom specified over and above the terms involving two or three loci even though linkage is assumed to be absent.

It is hoped, after all, that the present method will prove useful for the genetical interpretation of experimental estimates of covariances between relatives. Of course, linkage is not the only problem of such interpretation. Hence, the above approach

cannot be more than just one step in the long way of removing unrealistic assumptions from the models used in quantitative genetics.

SUMMARY

Linkage may affect the epistatic components of covariances between relatives even if the basic population is in linkage equilibrium. A method is presented by which the exact coefficient of any component can be specified in terms of a system of parameters, named linkage values. Explicit formulas are given for several cases of the covariances between half sibs and full sibs, respectively, including parental inbreeding, and for the covariance between grandparent and grandoffspring.

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Problems in Selection

Qualitatively Different Responses to Selection in Opposite Directions

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IT IS very difficult to find out anything about the gene frequencies at the loci responsible for responses to selection, and in the absence of any evidence to the contrary it is natural to suppose that the genes responsible are at more or less intermediate frequencies in a random breeding population; or if they are not at intermediate frequencies, to suppose that the plus-acting alleles are all at more or less the same frequencies. I want to present briefly some results which I think disprove these simple suppositions.

Selection was made in both directions for the character 'litter size' in mice, litter size being measured as the number of live young born in first litters. Figure 1 shows the generation means over 31 generations (for details, see Falconer, 1960). Progress was made in both directions, but it probably ceased in both

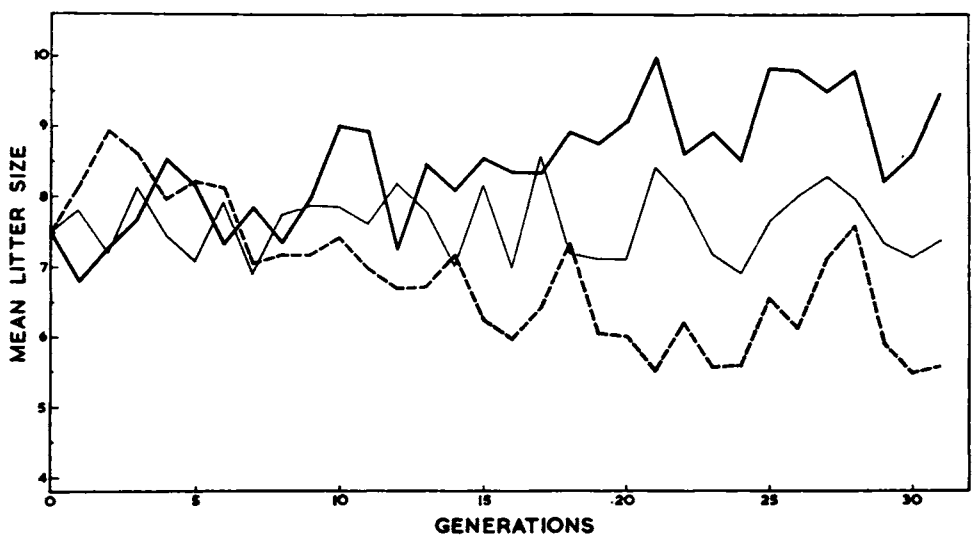

FIGURE 1. *Progress of selection for litter size.*

[1]Assisted by a Travel Grant from the Wellcome Trust.

lines after about 20 generations. An additional 10 generations are available for assessing the total progress made. An unselected control was kept which permitted a reliable comparison of the responses in the two directions. The total responses were equal in the two directions although the realized heritabilities showed the asymmetry commonly found in two-way selection experiments. The results were as follows:

	Upwards	*Downwards*
Total response	1.6 young	1.6 young
Realized heritability	8%	23%

The next step was to analyse the final character 'litter size' into its causative components, in order to see how these had been changed by the selection. The number of young born in a litter can be broken down into two main component characters: (1) the ovulation rate and (2) the embryonic survival rate. The second of these can be further subdivided into (a) the proportion of eggs that get fertilized and implant successfully in the uterus and (b) the proportion of implanted embryos that survive until birth. These components can be relatively easily measured by dissections of females. The ovulation rate can be reliably measured by counting the eggs in the fallopian tubes shortly after ovulation. (Most mice mate during the night and mated females carry a copulation plug in the vagina which can be found on examination in the morning. Dissections are made within a few hours of finding the plug.) Alternatively, the ovulation rate can be estimated, though less reliably, from the number of corpora lutea in the ovaries of pregnant females. If dissections are made at about 16 days of pregnancy (gestation lasts 19–20 days), then all three components of litter size can be assessed simultaneously. The implanted embryos leave a mark on the uterus even though they die very soon after implantation.

Egg counts were made on females of the 32nd generation of both the selected lines and the control line. These egg counts, which have already been reported (1), showed that the increased litter size of the high line could be fully accounted for by an increased ovulation rate, but the reduced litter size of the low line could not be attributed to a change of ovulation rate. This finding necessitated complete embryo counts in order to trace the fate of the eggs in the low line. These counts were made in mice of the 33rd generation. The results of the egg counts and embryo counts are given in Table 1. One of the points to be settled was whether the loss of the low-line eggs or embryos was a feature of the genotype of the embryos themselves or the genotype of the mothers. Accordingly, the low-line females were divided into two groups, one mated to low-line males and the other mated to control-line males. About 30 females were dissected in each of these mating groups and in the high and control lines. The results of the dissections show unequivocally that the reduced litter size in the low line resulted from deaths of embryos after implantation and that this loss was a fea-

TABLE 1.—EGG COUNTS AND EMBRYO COUNTS IN MICE OF THE 33RD GENERATION OF SELECTION.

Measurement	High	Control	Low	Low ♀ x Control ♂
Ovulation rate:				
Eggs	13.7	8.9	10.3	—
Corpora lutea	13.1	9.1	10.2	9.7
Mean loss:				
Preimplantation (% of corpora lutea)	18.5	11.3	16.9	11.5
Postimplantation (% of implants)	16.4	11.0	33.5	34.6
Mean no. of live embryos	8.8	7.1	5.4	5.7
Comparable mean litter size	9.2	7.6	6.0	—

ture of the genotype of the low-line females and not the genotype of the embryos. Figure 2 depicts the history of the litters in the three lines from ovulation to birth, in terms of the mean numbers surviving at successive stages. The post-

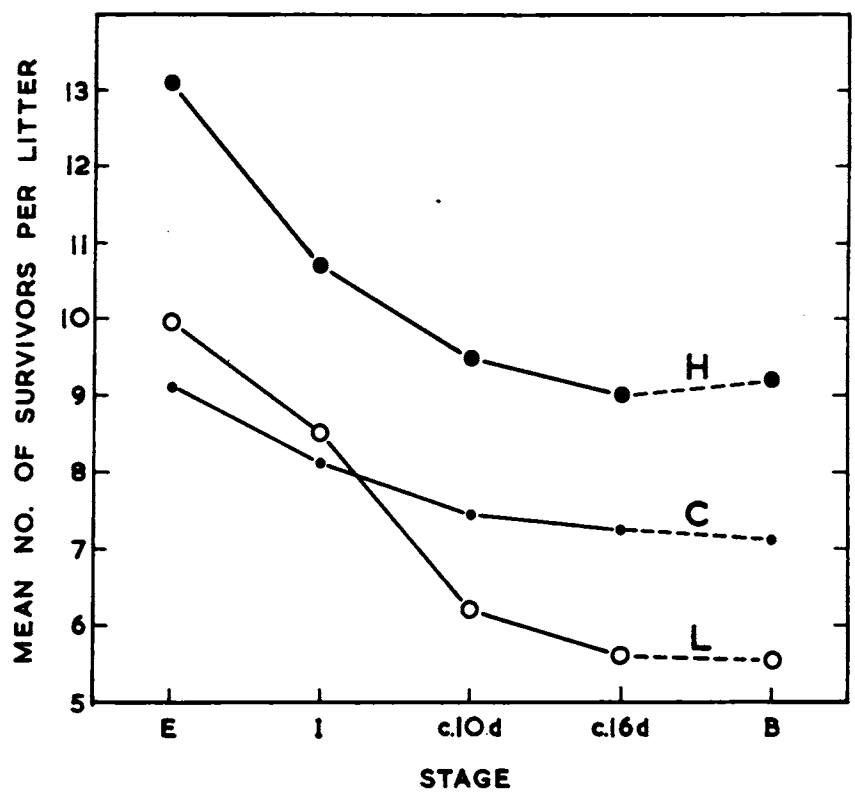

FIGURE 2. *Mean numbers of survivors at successive stages of gestation. H, C, and L are the high, control, and low lines respectively. The stages are: E = eggs shed; I = implantation; B = litter size at birth.*

implantation deaths here have been divided into early and late, corresponding to deaths before or after about 10 days of gestation. The difference between the low line and the others is almost entirely in the early post-implantation losses. The comparable litter sizes at birth are the means of the lines over the last 10 generations and do not, of course, refer to the same females as provided the data for the embryonic stages.

This analysis of the final character 'litter size' into its components brings to light a puzzling, if not paradoxical, situation: Selection in opposite directions produced qualitatively different responses. How can we account for the fact that ovulation rate responded to upward selection but not to downward selection, while the ability of females to sustain their implanted embryos responded to downward selection but not to upward selection? I think we must postulate that the genetic variation of the two components was caused by different genes and that these genes were at different frequencies in the base population. Rare alleles that are favored by selection will contribute much to the response, but rare alleles that are selected against will contribute little to the response. It is reasonable to suppose that genes affecting the physiology in such a way as to increase prenatal losses would have been at low frequencies in the base population, because the loss of embryos must be unconditionally disadvantageous under natural selection. Selection for small litter size would achieve a response through the increase of the frequencies of these genes, but selection for large litter size would gain little in response from a reduction of their frequencies. The differences of response in the two directions would be even more marked if the low frequency alleles were recessive, which would be another reasonable assumption to make, because, in general, deleterious alleles tend to be recessive. The unidirectional response in prenatal mortality is thus fairly easily understood. That of the ovulation rate, however, is more difficult. If one could suppose that alleles causing a high ovulation rate had been at low initial frequencies, there would be no difficulty, but this is not an acceptable supposition because it would require natural selection to have favored a low ovulation rate. It is more likely that an intermediate ovulation rate is optimal. Failure of the ovulation rate to decline in the low line may perhaps be explained in part by supposing that in the low line the segregation of the genes causing prenatal losses largely masked the variation of ovulation rate.

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The Influence of Errors of Parameter Estimation Upon Index Selection[1,2]

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THE magnitude of sampling errors and the resulting inaccuracies of estimation of genetic and phenotypic parameters have been discussed in the earlier papers and discussion of this symposium. The theory of selection indexes as developed by Smith (5) and Hazel (2) is such that with knowledge of certain parameters, the gain from selection can be maximized. However, in practice, these parameters are not known and estimates are used in their place for the calculation of index coefficients. The study to be discussed here was aimed at determining the influences of errors of parameter estimation upon the resulting progress and the estimation of the resulting progress when index selection is carried out.

THEORY OF INDEX SELECTION

The selection of individuals will be considered here but the theory of variety selection is quite similar, differing only in the definition of certain quantities of interest. Conceptually, an additive genetic value for net worth, symbolized by the letter H, exists for each individual in the population. However, since the H value for a particular individual will not be known, selection is carried out on an index,

$$I = \sum_{i=1}^{n} b_i X_i$$

where X_i is the phenotypic value of the individual for the *ith* trait and there are n traits of interest. In this derivation each phenotypic value is considered to be

$$X_i = G_i + E_i$$

where G_i represents the additive genetic contribution to the phenotypic value of the individual for the *ith* trait

and E_i represents the contribution due to environmental influences and to dominance and epistatic effects.

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[2]The author expresses his appreciation to Mr. Howard Jesperson for the vast amount of time and effort spent in development of the IBM 650 program for this study.

It is further assumed that $Cov(G_i,E_j)$ is equal to zero for all i and j. The coefficients of the index, the b_i values, are chosen so as to maximize the improvement in H when selection is based upon the I values for the individuals. When the regression of H upon any linear function of X_i values is linear, the improvement in H will be $B_{HI}\, i_s\, \sigma_I$

where B_{HI} is the coefficient of regression of H on I,

σ_I is the standard deviation of I values,

and i_s is the selection differential expressed in standard units.

Considering i_s as being a constant, which it will be for truncation selection of normally distributed I values and for other possible situations, the index which will result in the maximum attainable progress is $I = \sum_{i=1}^{n} b_i X_i$ where the b_i values are defined by the simultaneous equations

$$\sum_{i=1}^{n} b_i P_{it} = G_{tW} \text{ for } t = 1, 2, \ldots, n$$

where $P_{it} = \mathrm{Cov}(X_i, X_t)$

and $G_{tW} = \mathrm{Cov}(G_t, H)$.

Actually, any set of index coefficients which is a constant multiple of this set of b_i values will result in the maximum attainable progress. It is of interest to note that the b_i values defined above, which maximize

$$i_s\, B_{HI}\, \sigma_I = i_s \frac{\mathrm{Cov}(I, H)}{\sigma_I},$$

also maximize the correlation between I and H and minimize the sum of squares of differences between $(I-\mu_I)$ and $(H-\mu_H)$. The maximum attainable progress, which shall be symbolized by ΔH, will be

$$i_s \frac{\mathrm{Cov}(I, H)}{\sigma_I} = i_s \frac{\sum_i b_i G_{iW}}{(\sum_{ij} b_i b_j P_{ij})^{1/2}} = i_s \left(\sum_i b_i G_{iW}\right)^{1/2}$$

when the b_i values are defined by the simultaneous equations given above.

PROGRESS FROM CALCULATED INDEXES

However, in actual practice the population parameters, the P_{ij} and G_{iW} values, will not be known and estimates of these will have to be used to obtain the coefficients for an index. These coefficients, symbolized by $\hat{b}_i$, are obtained from the simultaneous equations

$$\sum_{i=1}^{n} \hat{b}_i \hat{P}_{it} = \hat{G}_{tW} \text{ for } t = 1, 2, \ldots, n$$

where the circumflex ($\hat{}$) over the symbol for a population parameter indicates an estimate of that parameter. Thus, the $\hat{b}_i$ values are estimates of the optimum b_i

values and since these estimates will differ from the optimum values by an amount dependent on the closeness of the $\hat{P}_{ij}$ and $\hat{G}_{iW}$ values to the P_{ij} and G_{iW} values, progress resulting from selection on this calculated index will be something less than the maximum attainable progress. Symbolizing the progress from selection for a particular calculated index,

$$\hat{I} = \sum_{i=1}^{n} \hat{b}_i X_i,$$

by $\Delta H'$, it is found that

$$\Delta H' = i_s \frac{\sum_i \hat{b}_i G_{iW}}{(\sum_{ij} \hat{b}_i \hat{b}_j P_{ij})^{1/2}}.$$

This expression is the progress which would result if selection was carried out in an infinite population and ignores sampling errors of selection due to finiteness of the selected population. The fact that $\Delta H'$ will always be less than or equal to ΔH, is seen from the identity pointed out by Hanson and Johnson (1) that the correlation between values for the optimum index and the values for a particular calculated index is equal to $\frac{\Delta H'}{\Delta H}$. Since correlation coefficients are bounded by $+1$ and -1, it follows that $\Delta H'$ varies between ΔH and minus ΔH. It must be realized that each of repeated estimations will result in a different set of $\hat{b}_i$ values and thus a different $\Delta H'$ value and, therefore, we see that a "population" of $\Delta H'$ values exists which will be distributed within these limits. Of course, with more accurate estimation, the population of $\Delta H'$ values will be distributed closer to the ΔH value.

Associated with each $\Delta H'$ value will be an estimate of the progress from selection which might be made from the estimates of the population parameters. These estimates of progress, which shall be symbolized by $\hat{\Delta} H$, are obtained by substituting the estimates for the parameters in the previously presented equation for ΔH to obtain

$$\hat{\Delta} H = i_s (\sum_i \hat{b}_i \hat{G}_{iW})^{1/2}.$$

When H is defined to be a linear function of the additive genetic values for the n traits of interest, i.e., $H = \sum_{i=1}^{n} a_i G_i$, and where the a_i values representing the relative economic weights for each trait are considered to be constants,

G_{tW} is found to be equal to $\sum_i a_i G_{it}$ and $\hat{G}_{tW}$ equals $\sum_i a_i \hat{G}_{it}$,

where $G_{it} = Cov(G_i, G_t)$ and $\hat{G}_{it}$ is an estimate of G_{it}.

Imposing this definition of H, the three values given above are altered as follows:

$$\Delta H = i_s (\sum_{ij} a_i b_j G_{ij})^{1/2},$$

$$\Delta H' = i_s \frac{\sum_{ij} a_i b_j G_{ij}}{(\sum_{ij} b_i b_j P_{ij})^{1/2}},$$

$$\text{and } \hat{\Delta H} = i_s (\sum_{ij} a_i b_j \hat{G}_{ij})^{1/2}.$$

The two considerations of primary interest in this study were the closeness of the distribution of $\Delta H'$ values to the ΔH value and the effectiveness and accuracy of $\hat{\Delta H}$ values as estimates of the corresponding $\Delta H'$ values. Measures of these two considerations will differ depending upon the combination of true parameters involved, upon the procedure of estimating the parameters, and upon the amount of data used for estimation.

ESTIMATION OF PARAMETERS

The population parameters, the phenotypic and additive genetic variances and covariances of the traits of interest, may be estimated from several types of analysis, which, in general, involve the relationships of traits in related individuals. Primary consideration in this study was upon the estimation procedure resulting from the analyses of variance and covariance for the traits of interest where the individuals observed are arranged in paternal-half-sib groups. When the population is considered to be mating at random, the usual estimates of the additive genetic variances or covariances may be expressed as

$$\hat{G}_{ij} = \frac{4}{m}\left[\frac{\text{"sire" sum of products}}{s-1} - \frac{\text{"within sire" sum of products}}{s(m-1)}\right]$$

where s is the number of sire groups, and m is the number of offspring for each sire.

The "sire" sum of products may be expressed as

$$\sum_k \frac{(\sum_h X_{ikh})(\sum_h X_{jkh})}{m} - \frac{(\sum_{kh} X_{ikh})(\sum_{kh} X_{jkh})}{sm}$$

and the "within sire" sum of products may be expressed as

$$\sum_{kh} X_{ikh} X_{jkh} - \sum_k \frac{(\sum_h X_{ikh})(\sum_h X_{jkh})}{m}$$

where X_{ikh} represents the phenotypic value for the *ith* trait of the *hth* offspring of the *kth* sire in the sample of data which is being used for estimation. Of course, when the subscripts i and j represent the same trait, these values become sums of squares. This estimation procedure seems to have been first used by Hazel and Terrill (3).

It can be shown that when there are equal numbers of offspring per sire and when the basic data is normally distributed, P_{ij} is more accurately estimated by

$$\hat{P}_{ij} = \frac{\text{total sum of products}}{sm-1}$$

where the total sum of products can be expressed as

$$\sum_{kh} X_{ikh} X_{jkh} - \frac{(\sum_{kh} X_{ikh})(\sum_{kh} X_{jkh})}{sm},$$

even though this estimate is biased, than by the more commonly used estimate resulting from the sum of the estimates of the variance or covariance components, and, thus, this estimate of the phenotypic variances and covariances was considered in this study.

SIMULATION OF ESTIMATION

This estimation procedure, when two traits are involved, was simulated on the IBM 650 Data Processing System of the Statistical Laboratory at Iowa State University. This "Monte Carlo" simulation follows from the representation of the phenotypic values for the two traits as

$$X_{1kh} = \lambda_1 c_k + \lambda_2 e_{kh}$$
$$\text{and } X_{2kh} = \lambda_3 c_k + \lambda_4 s_k + \lambda_5 e_{kh} + \lambda_6 f_{kh}$$

where c_k, s_k, e_{kh}, and f_{kh} are random independent variables, the λ-values are constants, $k = 1, 2, \ldots, s$, and $h = 1, 2, \ldots, m$ for all k. For this study, normally and independently distributed variables with means of zero and unit variances were generated for the random independent variables. These values were generated by first obtaining 10-digit uniformly distributed variables by the power residue method as outlined in IBM Reference Manual; Random Number Generation and Testing (4) and then transforming these to normal variables (except for rounding) by a table look-up procedure using a table for the cumulative normal distribution with with a mean of zero and a variance of unity.

The additive genetic variances and covariances and the phenotypic variances and covariances for traits simulated in this manner are functions of the λ-values. These parameters are

$$G_{11} = 4\lambda_1^2,\ G_{12} = 4\lambda_1 \lambda_3,\ G_{22} = 4\lambda_3^2 + 4\lambda_4^2,$$
$$P_{11} = \lambda_1^2 + \lambda_2^2;\ P_{12} = \lambda_1 \lambda_3 + \lambda_2 \lambda_5$$
$$\text{and } P_{22} = \lambda_3^2 + \lambda_4^2 + \lambda_5^2 + \lambda_6^2.$$

Thus, various combinations of additive genetic and phenotypic parameters were simulated by choosing the set of λ values to use with the random variables. This simulation technique is quite similar with only minor differences to the procedure worked out by Dr. L. D. Van Vleck at Cornell University and discussed in a paper by Wadell and O'Bleness (6).

In an effort to simulate the usual modifications of unreasonable estimates, the following operations were incorporated into the program:

1. if an estimate of additive genetic variance was negative, this estimate and the estimate of the additive genetic covariance was set equal to zero for further calculations,
2. if an estimate of additive genetic variance was greater than the corresponding estimate of the phenotypic variance, the estimate of the pheno-

typic variance was substituted for the additive genetic variance estimate in the future calculations, and

3. if the absolute value of the estimate of the additive genetic correlation was greater than unity, $\hat{G}_{12}$ was set equal to $\pm (\hat{G}_{11}\ \hat{G}_{22})^{1/2}$ retaining the original algebraic sign for $\hat{G}_{12}$.

Fifteen different combinations of the true population parameters were simulated in this study. These were the combinations of G_{11} and G_{22} both taking on the values of .2, .5, or .8, with the genetic correlation,

$$r_{G_1G_2} = \frac{G_{12}}{G_{11}^{1/2}\, G_{22}^{1/2}},$$

taking on the values of −.5, zero, .2, .5 or .8. For all combinations of the parameters, λ values were chosen such that P_{11} and P_{22} were equal to unity and the environmental correlation,

$$r_{E_1E_2} = \frac{P_{12} - G_{12}}{(P_{11} - G_{11})^{1/2}\,(P_{22} - G_{22})^{1/2}},$$

was equal to zero. The relative economic values, a_1 and a_2, were both chosen to be unity for all combinations of parameters. These combinations of true parameters shall be termed "population types." The 15 sample size types which were simulated were those representing the combinations for s equal to 50, 100, 200 or 400 and m equal to 5, 10, 20, or 40 with the exception of the $s = 400$, $m = 40$ combination.

The calculations were carried out in such a manner that each set of random variables for a particular sample size type was combined with each of the 15 sets of λ-values. This confounding of the observations on the various population types for a particular sample size type was not completely desirable because it led to difficulties in interpreting the trends among the results, but this procedure allowed a much larger number of observations on the different combinations of sample size types and population types than would have been possible without this confounding for the same amount of computing time.

This simulation procedure was carried out 19 times for each combination of sample size type and population type. From each set of estimates, $\hat{G}_{11}$, $\hat{G}_{12}$, $\hat{G}_{22}$, $\hat{P}_{11}$, $\hat{P}_{12}$, and $\hat{P}_{22}$, index coefficients, $\hat{b}_1$ and $\hat{b}_2$, were calculated. From these values and the true parameters, the values for $\Delta H'$ and $\hat{\Delta} H$ were calculated using the equations already presented.

RESULTS AND DISCUSSION

From the 19 Monte Carlo observations of $\Delta H'$ and $\hat{\Delta} H$ for each combination of sample size type and population type and the ΔH value for the population type the following values were calculated:

$$\frac{\Delta H - \frac{1}{19}\sum \Delta H'}{\Delta H} \text{ which estimates } \frac{\Delta H - E\,[\Delta H']}{\Delta H},$$

$$\frac{1}{19\,\bar{I}_s}[\Sigma\,\hat{\Delta}H - \Sigma\,\Delta H'] \text{ which estimates } \frac{E[\hat{\Delta}H] - E[\Delta H']}{\bar{I}_s},$$

$$\text{and } \frac{1}{19\,\bar{I}_s^2}\Sigma\,(\hat{\Delta}H - \Delta H')^2 \text{ which estimates } \frac{E[(\hat{\Delta}H - \Delta H')^2]}{\bar{I}_s^2}.$$

The Monte Carlo estimates for four of the population types are presented in Table 1. The first of these values represents the average fractional decrease in selection progress from the maximum attainable progress. This decrease results from the errors of estimation of the true parameters. The second value is a measure of the tendency to over- or under-estimate the progress for a particular index. The third value, which is the mean squared difference between the estimates and the true progress values for the calculated indexes, is a measure of the accuracy of estimation of genetic progress from selection.

Although the numerical values presented in the tables seem to involve quite large sampling errors, certain conclusions regarding the magnitude of these values and the trends among them are warranted for the population types considered. The influences of sampling errors seem to be most pronounced when $G_{11} = G_{22} = .2$ and $r_{G_1G_2} = -.5$. For this population type, a sample of more than 1,000 individuals (50 sires with 20 offspring each of 100 sires with 10 offspring each) seems to be necessary in order to obtain an index that will result in average progress 80 per cent as large as the maximum attainable progress. When the genetic correlation is positive,

TABLE 1A.—MONTE CARLO ESTIMATES OF FUNCTIONS OF $\hat{\Delta}H$, $\Delta H'$, AND $\Delta H = .1491\ I_s$ WHEN $G_{11} = G_{22} = .2$, $r_{G_1G_2} = -.5$, $r_{E_1E_2} = 0$ AND $P_{11} = P_{22} = 1.0$ FOR VARIOUS COMBINATIONS OF s AND m.

Sample size s	type m	$\frac{\Delta H - E[\Delta H']}{\Delta H}$	$\frac{E^{1/2}[(\Delta H' - \Delta H)^2]}{\Delta H}$	$\frac{E[\hat{\Delta}H] - E[\Delta H']}{\bar{I}_s}$	$\frac{E[(\hat{\Delta}H - \Delta H')^2]}{\bar{I}_s^2}$
50	5	.4487	.5692	.0726	.0244
50	10	.1698	.2622	.1152	.0237
50	20	.2875	.3945	.0282	.0042
50	40	.0977	.1455	.0161	.0025
100	5	.3082	.4307	.1393	.0403
100	10	.2471	.3919	.0465	.0088
100	20	.0410	.0655	.0283	.0036
100	40	.0357	.0550	.0107	.0017
200	5	.2333	.3386	.0676	.0156
200	10	.0375	.0679	.0441	.0089
200	20	.0270	.0429	.0073	.0008
200	40	.0160	.0271	.0008	.0006
400	5	.1939	.3226	.0582	.0086
400	10	.0656	.1301	.0144	.0034
400	20	.0154	.0223	−.0054	.0008

TABLE 1B.—MONTE CARLO ESTIMATES OF FUNCTIONS OF ΔH, $\Delta H'$, AND $\Delta H = .4045\, I_s$ WHEN $G_{11} = G_{22} = .2$, $r_{G_1G_2} = .5$, $r_{E_1E_2} = 0$ AND $P_{11} = P_{22} = 1.0$ FOR VARIOUS COMBINATIONS OF s AND m.

Sample size s	type m	$\Delta H - E[\Delta H']$ / ΔH	$E^{1/2}[(\Delta H' - \Delta H)^2]$ / ΔH	$E[\hat{\Delta}H] - E[\Delta H']$ / I_s	$E[(\hat{\Delta}H - \Delta H')^2]$ / I_s^2
50	5	.2915	.4325	.0321	.0526
50	10	.0324	.0523	.0792	.0363
50	20	.0364	.0618	−.0563	.0195
50	40	.0162	.0279	−.0421	.0103
100	5	.0722	.1281	.1200	.0635
100	10	.0238	.0373	.0036	.0221
100	20	.0049	.0073	.0421	.0101
100	40	.0033	.0047	.0063	.0069
200	5	.0379	.0537	−.0009	.0195
200	10	.0062	.0122	.0358	.0123
200	20	.0037	.0060	.0012	.0030
200	40	.0018	.0033	.0001	.0040
400	5	.0290	.0508	.0222	.0169
400	10	.0058	.0085	−.0052	.0076
400	20	.0021	.0031	−.0140	.0025

TABLE 1C.—MONTE CARLO ESTIMATES OF FUNCTIONS OF ΔH, $\Delta H'$, AND $\Delta H = .4082\, I_s$ WHEN $G_{11} = G_{22} = .5$, $r_{G_1G_2} = -.5$, $r_{E_1E_2} = 0$ AND $P_{11} = P_{22} = 1.0$ FOR VARIOUS COMBINATIONS OF s AND m.

Sample size s	type m	$\Delta H - E[\Delta H']$ / ΔH	$E^{1/2}[(\Delta H' - \Delta H)^2]$ / ΔH	$E[\hat{\Delta}H] - E[\Delta H']$ / I_s	$E[(\hat{\Delta}H - \Delta H')^2]$ / I_s^2
50	5	.1733	.2808	.0476	.0436
50	10	.0772	.1518	.1178	.0416
50	20	.0689	.1153	−.0264	.0120
50	40	.0353	.0537	.0060	.0109
100	5	.0808	.1446	.0856	.0454
100	10	.0372	.0658	.0116	.0138
100	20	.0105	.0153	.0312	.0100
100	40	.0132	.0203	.0104	.0045
200	5	.0385	.0578	.0249	.0184
200	10	.0098	.0175	.0541	.0143
200	20	.0075	.0112	.0126	.0022
200	40	.0071	.0115	−.0035	.0021
400	5	.0199	.0390	.0209	.0147
400	10	.0093	.0162	.0126	.0050
400	20	.0029	.0048	−.0072	.0028

TABLE 1D.—MONTE CARLO ESTIMATES OF FUNCTIONS OF $\hat{\Delta}H$, $\Delta H'$, AND $\Delta H = .9487\, i_s$ WHEN $G_{11} = G_{22} = .5$, $r_{G_1G_2} = .5$, $r_{E_1E_2} = 0$ AND $P_{11} = P_{22} = 1.0$ FOR VARIOUS COMBINATIONS OF s AND m.

Sample size s	type m	$\Delta H - E[\Delta H']$ / ΔH	$E^{1/2}[(\Delta H' - \Delta H)^2]$ / ΔH	$E[\hat{\Delta}H] - E[\Delta H']$ / i_s	$E[(\hat{\Delta}H - \Delta H')^2]$ / i_s^2
50	5	.0632	.1483	−.0331	.1396
50	10	.0157	.0259	.1289	.0808
50	20	.0142	.0269	−.1187	.0664
50	40	.0105	.0163	−.0895	.0410
100	5	.0191	.0314	.1346	.1215
100	10	.0094	.0144	.0201	.0594
100	20	.0019	.0026	.0652	.0335
100	40	.0022	.0037	.0181	.0224
200	5	.0111	.0170	−.0089	.0247
200	10	.0032	.0064	.0481	.0254
200	20	.0019	.0027	.0053	.0116
200	40	.0012	.0025	.0023	.0146
400	5	.0051	.0096	.0209	.0261
400	10	.0019	.0027	−.0006	.0146
400	20	.0010	.0014	−.0163	.0081

this amount of data will yield indexes resulting in progress which will, on the average, be more than 95 per cent as large as the maximum. Similar trends for decreases in the magnitude of the average fractional decrease in progress are associated with increases in the additive genetic variances, and thus the heritability values, with increases in the number of sire groups used for estimation, or with increases in the number of offspring per sire group.

The mean difference between the estimates of progress from selection and the true progress values for particular calculated indexes seems to be slightly positive for most combinations of the number of sires and number of offspring per sire. This indicates that, in these cases, there is a slight tendency for over-estimation of the progress from index selection.

The mean squared difference between the estimated progress and the true progress for calculated indexes seems to be fairly large for all situations considered here, indicating that even with indexes based upon 8,000 individuals the accuracy of predicting the progress which will be attained will not be really good. A tendency is noted for this function to increase as the additive genetic variances for the two traits increase and as the genetic correlation between the two traits increases. These increases in the mean squared difference are associated with increases in ΔH, the maximum attainable progress. For a particular combination of the true parameters the mean squared difference tends to decrease somewhat as either the number of sires or the number of offspring per sire increases.

Generalizations upon these observed trends are somewhat hazardous at the present time because the combinations of true parameters which were studied here do not include situations where the environmental correlation between the two traits is non-zero, where the heritability values for the two traits are unequal, or where the two traits have unequal economic importance. However, it is hoped that the present work with the desired future extensions will lead to a deeper understanding of index selection and its relationships to estimation procedures.

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Effect of Selection on the Components of Genetic Variance

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IN a random mating population genetic advance under selection is proportional to the additive component of genetic variance, but selection almost always affects genetic variance as well as the population mean. It is, therefore, important to know how genetic variance changes under continued selection. Genetic variance can be partitioned into components and the interrelationship among these components is also of great interest. Nevertheless, there are no studies on this problem except those by Lush (9) and Kimura (5). They both examined a very special case, that is, the case of additive gene action with no dominance. This seems due to the fact that general treatment of this problem is beset with tremendous complexity in mathematical handling. If, however, we make certain assumptions, which are not necessarily unreal, the problem becomes less difficult and the effect of selection on the genetic variance can be evaluated. The purpose of this paper is to present the results of the investigation based on these simplifying assumptions.

ASSUMPTIONS

The assumptions are as follows:

1. Original population is in linkage equilibrium.
2. Linkage disequilibrium due to selection is negligible.
3. Change in gene frequency in each selection cycle is small.
4. Selection is followed by at least one generation of random mating.

Assumption 1 is satisfied in a population which has undergone several generations of random mating without selection. If, however, natural selection operates, a considerable amount of linkage disequilibrium can be built up under some particular epistatic gene actions, as shown by Lewontin and Kojima (8). In these situations the following theory does not hold. Another difficulty is that selection almost always affects linkage equilibrium and the resulting linkage disequilibrium causes mathematical handling to be very complicated. Assumption 2 is made in order to avoid this difficulty. The validity of this assumption has been examined in the Appendix, and it will be seen that if assumptions 3 and 4 are fulfilled, this generally holds true at least for those genes which are

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independent or loosely linked. Assumption 2 is probably reasonably well satisfied for quantitative characters controlled by a large number of genes, especially when heritability is low. Assumption 3 could be satisfied in many selection experiments by appropriate design.

GENERAL TREATMENT

In a random mating population in linkage equilibrium, genetic variance is a function of gene action and gene frequency. Thus, symbolically,

$$\sigma_G^2 = f(g, p)$$

where σ_A^2, σ_D^2, σ_{AA}^2, ---, respectively stand for additive genetic variance, dominance and gene frequency. Under the assumptions we have made the change in genetic variance due to one cycle of selection is given by

$$\Delta\sigma_G^2 = \frac{d\sigma_G^2}{dp}\Delta p. \tag{i}$$

Following Cockerham (1) or Kempthorne (4), the genetic variance can be partitioned in the following way:

$$\sigma_G^2 = \sigma_A^2 + \sigma_D^2 + \sigma_{AA}^2 + \sigma_{AD}^2 + \sigma_{DD}^2 + \cdots,$$

where σ_A^2, σ_D^2, σ_{AA}^2, ---, respectively stand for additive genetic variance, dominance variance, additive × additive epistatic variance, and so on. The changes in the components of genetic variance can be obtained as follows:

$$\Delta\sigma_A^2 = \sum_a \sum_i \frac{\partial\sigma_A^2}{\partial p_{ia}}\Delta p_{ia}, \tag{iia}$$

$$\Delta\sigma_D^2 = \sum_a \sum_i \frac{\partial\sigma_D^2}{\partial p_{ia}}\Delta p_{ia}, \tag{iib}$$

$$\Delta\sigma_{AA}^2 = \sum_a \sum_i \frac{\partial\sigma_{AA}^2}{\partial p_{ia}}\Delta p_{ia}, \tag{iic}$$

etc.,

where a and i stand for locus a and allele i, respectively, in a system of multiple loci and multiple alleles. If gene action is specified, $\frac{\partial\sigma_A^2}{\partial p_{ia}}$ and Δp_{ia} are easily obtained. The general formula for Δp_{ia} under truncation selection is (2, 12):

$$\Delta p_{ia} = \frac{p_{ia}(1 - p_{ia})}{2}\frac{\delta}{\sigma^2}\frac{\partial\bar{Y}}{\partial p_{ia}}, \tag{iii}$$

where $\bar{Y}$, δ, and σ^2 are respectively mean phenotypic value, selection differential, and phenotypic variance. Following Wright (12), the frequencies of all alleles of locus a are expressed in the form

$$p_{ja} = r_{ij_a}(1 - p_{ia})$$

in $\bar{T}$ before differentiation. Here, r_{ij_a} is given by $p_{ja}/(1 - p_{ia})$. Thus, using formulas (ii) and (iii), the change in components of genetic variance can be determined for any type of gene action. In the following, we will consider the four types of gene action most often referred to in quantitative genetics. This will be done in terms of either one locus with two alleles, or two loci each with two alleles, since the cases of more than two loci are not essentially different. The selection scheme which will be considered is mass selection.

SOME SPECIAL GENETIC MODELS UNDER MASS SELECTION

Additive gene action with dominance.

The additive genetic variance and dominance variance for a pair of alleles are given by

$$\sigma_A^2 = 2pq\,[a + (1 - 2p)d]^2 \text{ and}$$
$$\sigma_D^2 = 4p^2q^2d^2,$$

where a, d, and $-a$ denote the genotypic values of AA, Aa, and aa, respectively. The changes in these components of genetic variance under one cycle of selection are

$$\Delta\sigma_A^2 = 4pq\,[a + (1 - 2p)d]^2\,[(1 - 2p)a + (1 - 8pq)d]\,\frac{\delta}{2\sigma^2}$$
$$= 2\sigma_A^2\,[(1 - 2p)a + (1 - 8pq)d]\,\frac{\delta}{2\sigma^2} \text{ and} \qquad \text{(iva)}$$
$$\Delta\sigma_D^2 = 16\,p^2q^2\,(1 - 2p)\,[a + (1 - 2p)d]d^2\,\frac{\delta}{2\sigma^2}$$
$$= 4\sigma_D^2\,(1 - 2p)\,[a + (1 - 2p)d]\,\frac{\delta}{2\sigma^2}, \qquad \text{(ivb)}$$

where

$$\Delta p = 2pq\,[a + (1 - 2p)d]\,\frac{\delta}{2\sigma^2}. \qquad \text{(v)}$$

Some values of (iva) and (ivb) under different specifications regarding dominance are

TABLE 1.—AMOUNTS OF THE CHANGE IN GENETIC VARIANCE DUE TO ONE CYCLE OF MASS SELECTION WHEN GENE ACTION IS ADDITIVE.[1]

	p	.0	.1	.2	.3	.4	.5	.6	.7[2]	.8	.9	1.0
	d = 0	.00	.29	.38	.34	.19	.00	−.19	−.34	−.38	−.29	.00
σ_A^2	d = a	.00	1.52	.51	−.46	−.98	−1.00	−.69	−.33	−.09	−.01	.00
	d = 2a	.00	3.32	.14	−2.65	−3.09	−2.00	−.69	−.06	—[2]	—	—
σ_D^2	d = a	.00	.09	.20	.20	.12	.00	−.08	−.08	−.05	−.01	.00
	d = 2a	.00	.14	.27	.26	.14	.00	−.06	−.03	—	—	—

[1]All values should be multiplied by $\delta a^3/2\sigma^2$.

[2]The population under selection reaches a stable equilibrium point at p = .75.

given in Table 1. It is interesting that in the case of no dominance, $\frac{d\sigma_A^2}{dp}$ is small when Δp is large and large when Δp is small. Consequently, $\Delta\sigma_A^2$ has a similar value for a wide range of values of p(.1–.4 and .6–.9). Δp is maximum when p is at .5 and becomes small as p goes to either 0 or 1. The pattern is similar for other levels of dominance, and also for $\Delta\sigma_D^2$, though the range of p is not so wide as in the case of no dominance. If overdominance is involved, Δp becomes 0 when $p = (a + d)/2d$. Hence, $\sigma_A^2(= 0)$ and σ_D^2 remain constant as long as the population is under the same selection pressure.

Complementary gene action.

The genotypic values in complementary gene action can be written as follows:

	BB	Bb	bb
AA	i_c	i_c	0
Aa	i_c	i_c	0
aa	0	0	0,

and the components of genetic variance are

$$\begin{aligned}
\sigma_{A1}^2 &= 2p_1q_1^3p_2^2(1 + q_2)^2i_c^2,\\
\sigma_{A2}^2 &= 2p_2q_2^3p_1^2(1 + q_1)^2i_c^2,\\
\sigma_{D1}^2 &= p_1^2q_1^2p_2^2(1 + q_2)^2i_c^2,\\
\sigma_{D2}^2 &= p_2^2q_2^2p_1^2(1 + q_1)^2i_c^2,\\
\sigma_{AA}^2 &= 4p_1q_1^3p_2q_2^3i_c^2,\\
\sigma_{AD}^2 &= 2p_1q_1^3p_2^2q_2^2i_c^2,\\
\sigma_{DA}^2 &= 2p_1^2p_2^2p_2q_2^3i_c^2, \text{ and}\\
\sigma_{DD}^2 &= p_1^2q_1^2p_2^2q_2^2i_c^2,
\end{aligned} \tag{vi}$$

where subscripts 1 and 2 refer to loci A and B, respectively. The changes in components of genetic variance are

$$\begin{aligned}
\Delta\sigma_{A1}^2 &= \frac{\partial\sigma_{A1}^2}{\partial p_1}\Delta p_1 + \frac{\partial\sigma_{A1}^2}{\partial p_2}\Delta p_2\\
&= 2q_1^2p_2(1 + q_2)\,[(1 - 4p_1)p_2(1 + q_2)\Delta p_1 + 4p_1q_1q_2\Delta p_2]\,i_c^2,\\
\Delta\sigma_{D1}^2 &= 2p_1q_1p_2(1 + q_2)[(1 - 2p_1)p_2(1 + q_2)\Delta p_1 + 2p_1q_1q_2\Delta p_2]\,i_c^2,\\
\Delta\sigma_{AA}^2 &= 4q_1^2q_2^2[(1 - 4p_1)p_2q_2\Delta p_1 + p_1q_1(1 - 4p_2)\Delta p_2]\,i_c^2,\\
\Delta\sigma_{AD}^2 &= 2q_1^2p_2q_2[(1 - 4p_1)p_2q_2\Delta p_1 + 2p_1q_1(1 - 2p_2)\Delta p_2]\,i_c^2, \text{ and}\\
\Delta\sigma_{DD}^2 &= 2p_1q_1p_2q_2[(1 - 2p_1)p_2q_2\Delta p_1 + p_1q_1(1 - 2p_2)\Delta p_2]\,i_c^2,
\end{aligned} \tag{vii}$$

where

$$\begin{aligned}
\Delta p_1 &= 2p_1q_1^2p_2(1 + q_2)i_c\frac{\delta}{2\sigma^2} \text{ and}\\
\Delta p_2 &= 2p_2q_2^2p_1(1 + q_1)i_c\frac{\delta}{2\sigma^2}.
\end{aligned} \tag{viii}$$

Formulas for $\Delta\sigma_{A_s}^2$, $\Delta\sigma_{D_s}^2$, and $\Delta\sigma_{DA}^2$ are the same as $\Delta\sigma_{A_I}^2$, $\Delta\sigma_{D_I}^2$, and $\Delta\sigma_{AD}^2$, respectively, except for appropriate changes in subscripts. Calculations similar to those given in Table 1 can be made with these formulas but will be omitted because of limitations of space.

Duplicate gene action.

The genotypic values are as follows:

	BB	Bb	bb
AA	i_d	i_d	i_d
Aa	i_d	i_d	i_d
aa	i_d	i_d	0.

The additive and dominance components of genetic variance are

$$\sigma_{A1}^2 = 2p_1q_1^3q_2^4i_d^2 \text{ and}$$
$$\sigma_{D1}^2 = p_1^2q_1^2q_2^4i_d^2. \tag{ix}$$

The epistatic variances are the same as those in complementary gene action, if i_e^2 is replaced by i_d^2. Thus,

$$\Delta\sigma_{A1}^2 = 2q_1^2q_2^3[(1 - 4p_1)q_2\Delta p_1 - 4p_1q_1\Delta p_2]\, i_d^2 \text{ and}$$
$$\Delta\sigma_{D1}^2 = 2p_1q_1q_2^3[(1 - 2p_1)q_2\Delta p_1 - 2p_1q_1\Delta p_2]\, i_d^2, \tag{x}$$

and the changes in gene frequencies are

$$\Delta p_1 = 2p_1q_1^2q_2^2i_d \frac{\delta}{2\sigma^2} \text{ and}$$
$$\Delta p_2 = 2p_2q_2^2q_1^2i_d \frac{\delta}{2\sigma^2}. \tag{xi}$$

Optimum model gene action.

The mean value of optimum model proposed by Wright (10) is given by Kojima (7),

$$\bar{Y} = -[(\bar{S} - \phi)^2 + V],$$

where Y and S are the values of secondary and primary characters, respectively; ϕ is the optimum value; and V is the total genetic variance in the primary character. Thus,

$$\bar{S} = \sum_{i=1}^{n} P_i, \qquad P_i = p_i^2a_i + 2p_iq_id - q_i^2a_i, \text{ and}$$

$$V = \sum_{i=1}^{n} [p_i^2a_i^2 + 2p_iq_id_i^2 + q_i^2a_i^2 - P_i^2].$$

The components of genetic variance can be obtained by using Kojima's (6) method, giving

$$\sigma_A^2 = 2\Sigma p_iq_i[(d_i^2 - a_i^2)(1 - 2p_i) + 2\{a_i + (1 - 2p_i)d_i\}(\bar{S} - P_i - \phi)]^2,$$
$$\sigma_D^2 = \Sigma p_i^2q_i^2[2(d_i^2 - a_i^2) + 4d_i(\bar{S} - P_i - \phi)]^2,$$

$$\sigma_{AA}^2 = 16\Sigma p_i q_i p_j q_j [a_i + (1 - 2p_i)d_i]^2 [a_j + (1 - 2p_j)d_j]^2, \quad \text{(xii)}$$
$$\sigma_{AD}^2 = 32\Sigma p_i q_i p_j^2 q_j^2 [a_i + d_i(1 - 2p_i)]^2 d_j^2, \text{ and}$$
$$\sigma_{DD}^2 = 64\Sigma p_i^2 q_i^2 p_j^2 q_j^2 d_i^2 d_j^2.$$

There are no epistatic variances higher than the second order in the optimum model regardless of the number of loci involved, so long as the primary scale is determined by additive gene action with dominance. Note also that the epistatic variances are all independent of optimum value, i.e., ϕ.

There are many possibilities of specifying the parameters in the optimum model. Different levels of dominance in the primary character can produce different types and magnitudes of genetic variance in the secondary character. Number of genes and optimum value are also the factors which change the magnitudes of genetic variance. Here we will consider only a case where two genes with no dominance are involved in the primary character. $\phi = a_1 = a_2 = a$ is also assumed. In this case the components of genetic variance are

$$\sigma_{A1}^2 = 2p_1 q_1 [4q_2 + (1 - 2p_1)]^2 a^4,$$
$$\sigma_{D1}^2 = 4p_1^2 q_1^2 a^4, \quad \text{(xiii)}$$
$$\sigma_{AA}^2 = 16p_1 q_1 p_2 q_2 a^4,$$

and $\sigma_{AD}^2 = \sigma_{DD}^2 = 0$. These components are the same as those given by Wright (10), although he did not partition the epistatic variance into σ_{AA}^2, σ_{AD}^2, and σ_{DD}^2. The changes in components of genetic variance are

$$\Delta\sigma_{A1}^2 = 2[4q_2 + (1 - 2p_1)][\{4(1 - 2p_1)q_2 + (1 - 8p_1q_1)\}\Delta p_1 - 8p_1q_1\Delta p_2]a^4,$$
$$\Delta\sigma_{D1}^2 = 8p_1q_1(1 - 2p_1)a^4\Delta p_1, \text{ and} \quad \text{(xiv)}$$
$$\Delta\sigma_{AA}^2 = 16[(1 - 2p_1)p_2q_2\Delta p_1 + p_1q_1(1 - 2p_2)\Delta p_2]a^4,$$

where

$$\Delta p_1 = 2p_1q_1[4q_2 + (1 - 2p_1)]a^2\frac{\delta}{2\sigma^2} \text{ and}$$
$$\Delta p_2 = 2p_2q_2[4q_1 + (1 - 2p_2)]a^2\frac{\delta}{2\sigma^2}. \quad \text{(xv)}$$

NUMERICAL CALCULATIONS FOR REPEATED SELECTION

The formulas of the preceding section make it possible to examine the change in genetic variance under repeated selection under various specifications concerning initial gene frequencies, gene effects, and selection intensity. Gene frequencies are rarely known in open-pollinated populations. In populations derived from crosses between two highly inbred lines, $p = .5$ can be assumed for all segregating loci. Hence, in the following calculations we take the initial gene frequency to be .5 for all genetic models. The evaluation of gene effects is also very difficult. In the case of additive gene action, however, we can estimate the average gene effect in standard units ($\bar{a}/\sigma$, not average effect of gene substitution) if heritability and number of genes are known. The average gene effect in standard units is one-half of Falconer's (3) "Proportionate effect." He evaluated the

proportionate effect for a number of characters in Drosophila (abdominal bristles, etc.) and mice (body weight) and got approximately .2 for every character despite several limitations in his procedures. We take $a/\sigma = .1$ as a reasonable estimate for many characters for the additive case, although this value may well be high for yield in plants and animals. Since σ is the phenotypic standard deviation, a/σ is expected to change as the selection cycle proceeds. If, however, many genes govern the character in question and heritability is sufficiently low, then the change in a/σ must be very small (note that σ is less variable than σ^2). Consequently, we assume a/σ constant in all generations. In other cases we assume the following values for gene effect:

Complementary	$i_c/\sigma = .1$
Duplicate	$i_d/\sigma = .1$
Optimum model	$a^2/\sigma = .01$

For selection intensity we shall assume that the extreme 1/20 of the population is retained. Thus, the selection differential in standard units δ/σ is 2.06 for a large sample. Our parameter $\delta/2\sigma$ is, therefore, $1.03 \doteq 1.00$.

The results of some computations made under these assumptions are illustrated graphically in Figures 1–4. In the case of additive gene action (Figure 1) the change in genetic variance is dependent on the degree of dominance. Under no dominance, σ_A^2 decreases slowly in early generations of selection. The rate of the change gradually increases until the eighth generation, after which it again decreases. The rate of change in σ^2_A for early generation becomes progressively larger as the degree of dominance increases. On the other hand, the dominance variance remains fairly constant irrespective of generation or degree of dominance.

When complementary gene action is involved (Figure 2), σ_A^2 is the largest component of genetic variance and twice the dominance component at $p_1 = p_2 = .5$. The rate of change in this component is so large that after about 10 cycles of selection, σ_A^2 and σ_D^2 have almost the same value, σ_D^2 increases in the first seven generations and then begins to decrease gradually. The epistatic components which decrease as selection progresses are very small compared with the additive and dominance components in all generations. With duplicate gene action (Figure 3) σ_A^2 again decreases rapidly, σ_{AA}^2 being the next rapidly changing component. σ_{DD}^2 is almost constant for 20 generations. In the optimum model (Figure 4) σ_A^2 decreases most rapidly as before, but σ_{AA}^2 and σ_D^2 show very little change.

Summing up all cases it appears that σ_A^2 is more affected by selection than other components of genetic variance and that σ_{DD}^2 is the least affected. More generally the genetic components associated with additive effects change more rapidly than those associated with dominance. This is true even if the initial gene frequency is not .5, although, of course, if the initial frequency is less than .5, it is possible that all the components increase in the early generations of selection. If, for example, the initial gene frequency is .2 and the model is one of additive gene action with no dominance, σ_A^2 at first increases almost linearly until

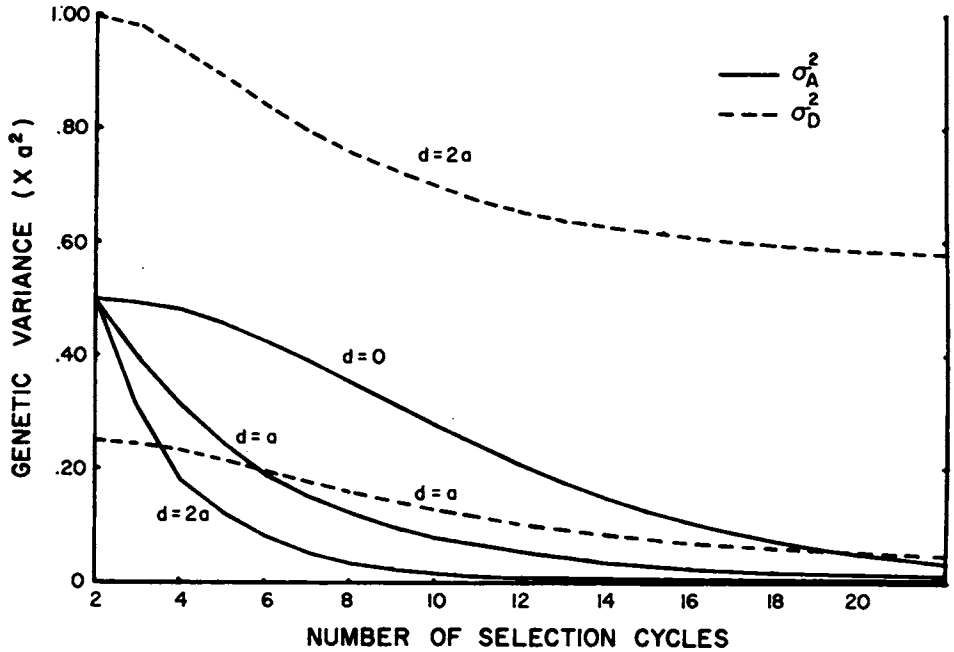

FIGURE 1. *Changes in the components of genetic variance under 5% truncation selection with additive gene action.*

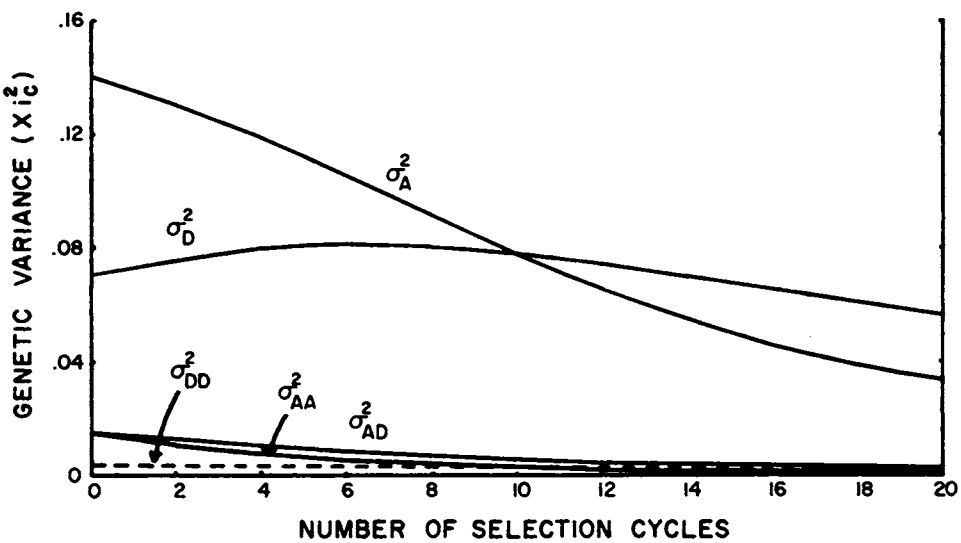

FIGURE 2. *Changes in the components of genetic variance under 5% truncation selection with complementary gene action.*

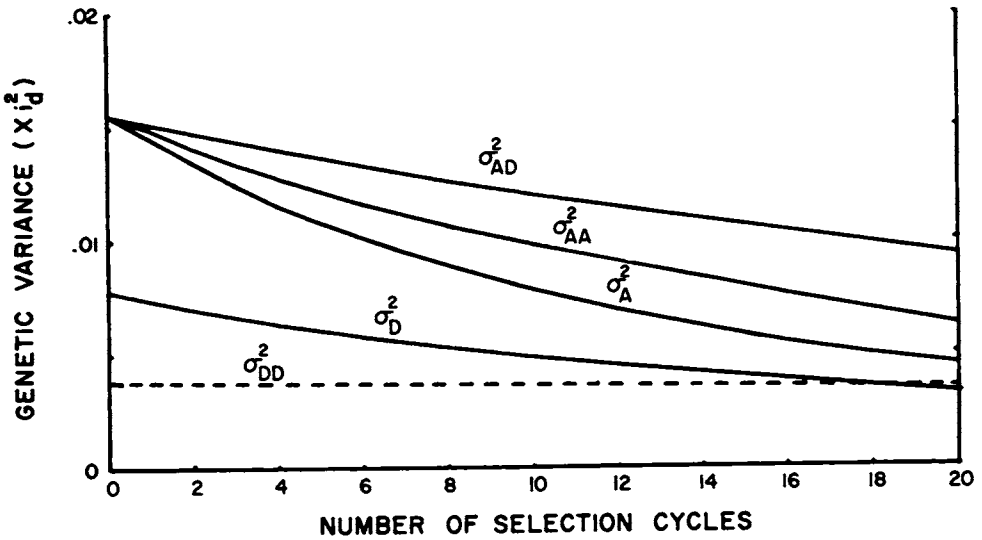

FIGURE 3. *Changes in the components of genetic variance under 5% truncation selection with duplicate gene action.*

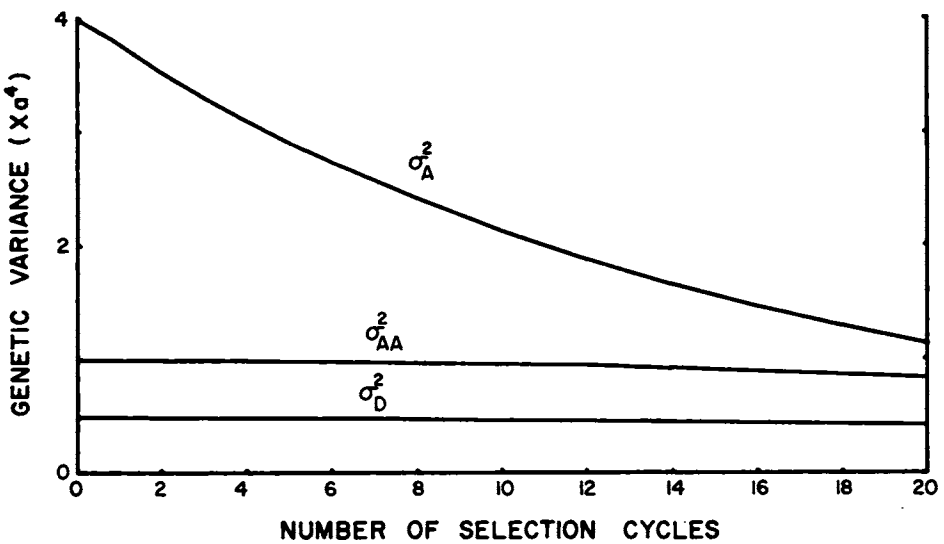

FIGURE 4. *Changes in the components of genetic variance under 5% truncation selection with optimum model gene action.*

p becomes approximately .4, and after p reaches .5 it begins to decrease following the pattern described above. In the case of complete dominance σ_A^2 increases until p reaches .25 and then decreases. The maximum values for σ_A^2 when d = 2a are attained at p = .204 and .922. On the other hand, the magnitude of σ_D^2 is maximum at p = .5 for any degree of dominance and the change in σ_D^2 is milder than σ_A^2.

In the case of complementary gene action ($p_1 = p_2$), σ_A^2 increases until p reaches .447. The maximum values for σ_D^2, σ_{AA}^2, σ_{AD}^2, and σ_{DD}^2 are attained at $p = .610$, .250, .375 and .500, respectively. If $p_1 \neq p_2$, the gene frequencies from which the components of genetic variance begin to decrease are obtained by equating (vii) to 0 and solving for p_1 and p_2. In this connection note that Δp_i is always proportional to the additive effect of gene A_i.

In the case of duplicate gene action ($p_1 = p_2$), σ_A^2 and σ_D^2 increase until p approaches .125 and .250, respectively. The epistatic components follow the same pattern as in complementary gene action, although Δp_i is generally smaller in this case. In the optimum model the maximum values of σ_A^2 are at $p = .120$ and .947, the minimum point being at $p = .833$ where $\sigma_A^2 = 0$. $p = .833$ is an equilibrium point, but this equilibrium is not stable (cf. Kojima, 7). The maximum values for σ_D^2 and σ_{AA}^2 are attained both at $p = .500$.

Finally, experimental geneticists may be interested in discriminating between different types of gene action by examining changes in genetic variances. But, as we have seen, there are many factors which determine the change in genetic variance, so that such discrimination is probably not practicable. One possible method might be to use the population derived from a cross between two inbred lines after several generations of random mating in order to reduce linkage disequilibrium. Even in this case, however, care would be required to recognize the effects of negative correlations between characters, or natural selection which might operate counter to artificial selection.

SUMMARY

The effect of selection on various components of genetic variance was examined assuming four different models with respect to type of gene action. It was found that the variance components associated with additive effect are more affected by selection than those associated with dominance but that differences are not sufficiently distinctive to be helpful in discriminating among different types of gene action.

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APPENDIX

In a random mating population the genotype frequencies for two loci, each with two alleles, can be expressed in terms of gamete frequencies as shown in Table 2. In this table P_{11}, P_{10}, P_{01}, and P_{00} stand for the frequencies of gametes AB, Ab, aB,

TABLE 2.—SELECTIVE VALUES FOR NINE GENOTYPES.

	BB	Bb	bb	
Frequency	P^2_{11}	$2P_{11}P_{10}$	P^2_{10}	
Selective value	W_{22}	W_{21}	W_{20}	AA
Complementary	1	1	$1-s$	
Duplicate	1	1	1	
Frequency	$2P_{11}P_{10}$	$2(P_{11}P_{00}+P_{10}P_{01})$	$2P_{10}P_{00}$	
Selective value	W_{12}	W_{11}	W_{10}	Aa
Complementary	1	1	$1-s$	
Duplicate	1	1	1	
Frequency	P^2_{01}	$2P_{01}P_{00}$	P^2_{00}	
Selective value	W_{02}	W_{01}	W_{00}	aa
Complementary	$1-s$	$1-s$	$1-s$	
Duplicate	1	1	$1-s$	

and *ab* in the parental population, respectively. If selection operates according to the selective values as given in Table 2, the change in gamete frequencies after selection and random mating will be (8)

$$\Delta P_{11} = \frac{P_{11}(W_{AB} - \bar{W}) - rW_{11}D}{\bar{W}},$$

$$\Delta P_{10} = \frac{P_{10}(W_{Ab} - \bar{W}) + rW_{11}D}{\bar{W}},$$

$$\Delta P_{01} = \frac{P_{01}(W_{aB} - \bar{W}) + rW_{11}D}{\bar{W}}, \text{ and}$$

$$\Delta P_{00} = \frac{P_{00}(W_{ab} - \bar{W}) - rW_{11}D}{\bar{W}},$$

where W_{AB}, W_{Ab}, W_{aB}, and W_{ab} are the average selective values of gametes *AB*, *Ab*, *aB*, and *ab*, respectively, $\bar{W}$ being the over-all mean selective value, and r the recombination value between loci *A* and *B*. D is a measure of linkage disequilibrium and given by $P_{11}P_{00} - P_{10}P_{01}$. If a population is in linkage equilibrium, then D is zero and the gamete frequencies are given by

$$P_{11} = p_1p_2,\ P_{10} = p_1q_2,\ P_{01} = q_1p_2,\ P_{00} = q_1q_2,$$

where p_1, q_1, p_2, and q_2 are the frequency of *A*, *a*, *B*, and *b*, respectively. In the following we assume that the original population is in linkage equilibrium, that is, $D^{(0)} = 0$.

The linkage disequilibrium after one cycle of selection will then be

$$D^{(1)} = \begin{vmatrix} P_{11}^{(0)} + \Delta P_{11}^{(0)} & P_{01}^{(0)} + \Delta P_{01}^{(0)} \\ P_{10}^{(0)} + \Delta P_{10}^{(0)} & P_{00}^{(0)} + \Delta P_{00}^{(0)} \end{vmatrix}$$

$$= \frac{P_{11}^{(0)}\,P_{00}^{(0)}}{\bar{W}}(W_{AB} - W_{Ab} - W_{aB} + W_{ab}) + (\Delta P_{11}^{(0)}\,\Delta P_{00}^{(0)} - \Delta P_{10}^{(0)}\,\Delta P_{01}^{(0)})$$

$$= \frac{P_{11}^{(0)}\,P_{00}^{(0)}}{\bar{W}}\,\alpha_{AB} - \Delta p_1^{(0)}\,\Delta p_2^{(0)}, \qquad \text{(i)}$$

where α_{AB} is additive × additive epistatic comparison, while $\Delta p_1^{(0)}$ and $\Delta p_2^{(0)}$ are the amounts of change in p_1 and p_2, respectively and given by (11)

$$\Delta p_i^{(0)} = \frac{p_iq_i}{2\bar{W}}\frac{\partial \bar{W}}{\partial p_i}.$$

In the case of additive gene action with dominance α_{AB} is 0, so that $D^{(1)}$ is

$$D^{(1)} = -\Delta p_1 \Delta p_2. \qquad \text{(ii)}$$

$D^{(1)}$ must, therefore, be very small, because Δp_1 and Δp_2 have been assumed to be sufficiently small. In the case of complementary gene action $D^{(1)}$ is given by (cf. Table 2)

$$D^{(1)} = \frac{p_1q_1^2p_2q_2^2s}{\bar{W}} - \Delta p_1\Delta p_2 = \frac{p_1q_1^2p_2q_2^2s(1-s)}{\bar{W}^2}. \quad \text{(iii)}$$

The maximum value of $D^{(1)}$ is .0023 at $p_1 = p_2 = .322$, if $s = .1$ as assumed in the numerical calculation in the text. Thus, the linkage disequilibrium is again negligible.

When duplicate gene action is involved, $D^{(1)}$ will be

$$D^{(1)} = -\frac{p_1q_1^2p_2q_2^2s}{\bar{W}} - \Delta p_1\Delta p_2 = -\frac{p_1q_1^2p_2q_2^2s}{\bar{W}^2}. \quad \text{(iv)}$$

The maximum value of this quantity is $-.0023$ at $p_1 = p_2 = .324$ if $s = .1$. In the optimum model we have considered in the text, the linkage disequilibrium will be

$$D^{(1)} = -\frac{2p_1q_1p_2q_2s}{\bar{W}} - \Delta p_1\Delta p_2, \quad \text{(v)}$$

which shows that $D^{(1)}$ is large unless the selection coefficient s is small. But if the additive effects of genes in the primary characters are almost the same as those of the case of additive gene action, as may be commonly the case, then s is usually small. In the case of $s = .01$ and $p_1 = p_2 = .5$, it will be $-.0014$.

There are too many types of gene action to be examined here. In general, however, the linkage disequilibrium due to one cycle of selection is negligible except the case of disruptive selection, which occurs rarely in either nature or breeding programs.

However, the situation changes when we turn to repeated selection for a number of generations. Repeated selection accumulates linkage disequilibrium, while the random mating after selection will reduce the disequilibrium. The amount of reduction in the linkage disequilibrium due to random mating increases as the disequilibrium is accumulated, so that there must be a limit for the increase of the disequilibrium. Let us now examine how much the disequilibrium is accumulated by the repeated selection.

If we put

$$P_{11}^{e1} = (p_1 + \Delta p_1)(p_2 + \Delta p_2),\ P_{10}^{e1} = (p_1 + \Delta p_1)(q_2 - \Delta p_2),$$
$$P_{01}^{e1} = (q_1 - \Delta p_1)(p_2 + \Delta p_2), \text{ and } P_{00}^{e1} = (q_1 - \Delta p_1)(q_2 - \Delta p_2),$$

then we have

$$P_{11}^{(1)} = P_{11}^{e1} + D^{(1)},\ P_{10}^{(1)} = P_{10}^{e1} - D^{(1)},$$
$$P_{01}^{(1)} = P_{01}^{e1} - D^{(1)}, \text{ and } P_{00}^{(1)} = P_{00}^{e1} + D^{(1)}.$$

Thus, the gamete frequencies after the second cycle of selection will be

$$P_{11}^{(2)} = P_{11}^{e1} + (1-r)D^{(1)} + \Delta P_{11}^{(1)},$$
$$P_{10}^{(2)} = P_{10}^{e1} - (1-r)D^{(1)} + \Delta P_{10}^{(1)},$$
$$P_{01}^{(2)} = P_{01}^{e1} - (1-r)D^{(1)} + \Delta P_{01}^{(1)}, \text{ and}$$
$$P_{00}^{(2)} = P_{00}^{e1} + (1-r)D^{(1)} + \Delta P_{11}^{(1)}.$$

Hence, the linkage disequilibrium is

$$D^{(2)} = \begin{vmatrix} P_{11}^{(2)} & P_{01}^{(2)} \\ P_{10}^{(2)} & P_{00}^{(2)} \end{vmatrix} = (1 - r)D^{(1)} + \begin{vmatrix} P_{11}^{e1} + \Delta P_{11}^{(1)} & P_{01}^{e1} + \Delta P_{01}^{(1)} \\ P_{10}^{e1} + \Delta P_{10}^{(1)} & P_{00}^{e1} + \Delta P_{00}^{(1)} \end{vmatrix}$$

$$= (1 - r)D^{(1)} + D^{[2]}.$$

Following this procedure we can obtain the linkage disequilibrium after n cycles of selection and it will be

$$D^{(n)} = (1 - r)^{n-1} D^{(1)} + (1 - r)^{n-2} D^{[2]} + \cdots + D^{[n]}. \qquad \text{(vi)}$$

This is a mathematical representation of what Lush (9) mentioned in his mimeographed book "Genetics of Population." Here, if $D^{(1)} = D^{[2]} = \cdots = D^{[n]}$, then we have

$$D^{(n)} = \frac{1}{r}[1 - (1 - r)^n] D^{(1)}.$$

In reality, of course, the equality $D^{(1)} = D^{[2]} = \cdots = D^{[n]}$ rarely holds. However, if we put the maximum value of the linkage disequilibrium due to one cycle of selection, $D^{(1)}$ max, that can be obtained from all possible gene frequencies instead of $D^{(1)}$ for particular gene frequencies at which selection is initiated, the following expression will generally hold true,

$$D^{(n)} \leq \frac{1}{r}[1 - (1 - r)^n] D^{(1)} \text{ max.} \qquad \text{(vii)}$$

This formula shows that the linkage disequilibrium increases as the number of selection cycles gets large and recombination value becomes small. The values of $1/r[1 - (1 - r)^n]$ for the first eight generations and $n = \infty$ are given in Table 3. As will be seen from this table, assumption 2 of the text does not hold even though assumptions 3 and 4 are satisfied if r is small and n is large. If, however, r is larger than 10 per cent the linkage disequilibrium is not serious for a considerable number of selection cycles. Note that the values for $n = \infty$ in Table 3 are approximate assessments of the maximum bound for linkage disequilibrium. They are never the equilibrium values of linkage disequilibrium.

TABLE 3.—VALUES OF $[1 - (1 - r)^n]/r$.

r \ n	1	2	3	4	5	6	7	8	∞
.01	1	1.99	2.97	3.94	4.90	5.85	6.79	17.73	100
.1	1	1.90	2.71	3.44	4.10	4.69	5.22	5.70	10
.3	1	1.70	2.19	2.53	2.77	2.94	3.06	3.14	3.3
.5	1	1.50	1.75	1.88	1.94	1.97	1.98	1.99	2

DISCUSSION

K. KOJIMA: I would like to comment on the buildup of linkage disequilibrium in epistatic genetic systems. Letting W_{AB}, W_{Ab}, W_{aB}, and W_{ab} be the marginal means for the gametes AB, Ab, aB, and ab, respectively, we find that the amount of linkage disequilibrium after one cycle of selection is proportional to the additive × additive epistatic comparison defined by Cockerham (1). That is to say, $\Delta = C(W_{AB} - W_{Ab} - W_{aB} + W_{ab})$ where Δ is the build-up linkage disequilibrium, C a constant involving gametic frequencies, and $(W_{AB} - W_{Ab} - W_{aB} + W_{ab})$ is the additive × additive comparison. Under continuous selection program, the accumulation of linkage disequilibrium may turn out to be significant in considering the magnitudes and changes of genetic components of variance.

M. NEI: (At the time of the Symposium $D^{(1)}$ in (i) of the Appendix was given in a different form) Dr. Kojima's argument is true if the recombination value is small and selection is carried on for a large number of generations, although he neglected the linkage disequilibrium due to additive effect $(-\Delta p_1 \Delta p_2)$. The build-up of a considerable amount of permanent linkage disequilibrium under particular genetic models has been shown by Wright (1952; Quantitative Inheritance), Kimura (1956; Evolution 10), and Lewontin and Kojima (1960; Evolution 14). No one has, however, worked out the precise formula for $D^{(n)}$ and the formula developed here is still an approximation. Nevertheless, under the conditions discussed in the Appendix the linkage disequilibrium due to selection is negligibly small for a considerable number of generations.

Quantitative Genetic Studies With Polyploids

Quantitative Genetic Studies With Polyploids

INTRODUCTION

H. L. CARNAHAN, *Chairman*[1]

IN arranging for participants in this session, it was generally agreed that it would be desirable to begin with a brief review of disomic and tetrasomic inheritance and a statement of some of the problems associated with the study of quantitative inheritance in polyploids. I should like to emphasize first, however, that there are many agricultural plants which behave as autopolyploids or segmental allopolyploids. Many forage grasses fall into these categories (4) including such important species as *Dactylis glomerata, Phleum pratense, Bromus inermis,* and several *Agropyron* species. To these grasses we can add alfalfa, *Medicago sativa;* birdsfoot trefoil, *Lotus corniculatus;* potato, *Solanun tuberosum;* and coffee, *Coffee arabica.* In addition, induced autoploids have proved successful in such diploid crops as turnips, rye, alsike clover, and several floriculture crops (7).

It it hoped that the papers presented will stimulate an interest in the problems associated with the genetics of polyploids, and that some of the problems posed may be soon attacked jointly by breeders, cytogeneticists, and statistical geneticists.

BASIC PROBLEMS IN QUANTITATIVE GENETICS OF AUTOTETRAPLOIDS[2]

JOHN W. DUDLEY

The basic difference between autotetraploids and diploids is that autotetraploids have four chromosomes which can pair together instead of two. If these four homologous chromosomes form quadrivalents, double reduction can occur and gametes which carry two genes from the same original chromosome will form. The frequency of double reduction is measured by the parameter alpha, which varies with frequency of quadrivalent formation and the amount of crossing over between the gene and the centromere (3).

With four homologous chromosomes instead of two, there are with two

[1]Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, Reno, Nevada.

[2]Joint contribution from the Crops Research Division, ARS, USDA, and the Department of Field Crops, North Carolina Agricultural Experiment Station, Raleigh, North Carolina. Published as Paper No. 1306 of the North Carolina Agr. Exp. Sta. Journal Series.

alleles per locus five different possible genotypes *(AAAA, AAAa, AAaa, Aaaa, aaaa)* instead of three as in diploids. With this number of possible genotypes the within locus genetic variance can be divided into additive, digenic, trigenic, and tetragenic components (10). If 2 variable loci are considered, 10 distinct types of epistatic variance components are possible. Kempthorne (10) derived the covariances between various types of relatives in random mating populations in terms of this generalized description of genetic variances.

Production of homozygous inbred lines of autotetraploids is extremely difficult. In the putative natural autotetraploid species, such as alfalfa, birdsfoot trefoil, and orchardgrass, a relatively high degree of self-incompatibility prevents production of homozygous lines. Even if self-fertile autotetraploids were available, 3.80 times as many generations of selfing are necessary to produce the same degree of homozygosity in an autotetraploid as a diploid if random chromosome segregation is assumed (13). Thus, the possibility of utilizing homozygous lines in quantitative genetics studies of autotetraploids seems remote.

Two other complicating factors in the study of autotetraploids are a random mating population does not come to equilibrium for genotypic frequency after a single generation of random mating and if alpha is greater than zero, some inbreeding will occur with random mating.

Most species considered to be natural autotetraploids are probably at least partially differentiated so that they might better be considered segmental alloploids. For study of quantitative genetics, the effects of having some of the genes affecting a character carried on chromosomes behaving in a tetrasomic manner and others carried on chromosomes behaving in a disomic manner are not known.

Three major questions may be raised concerning quantitative genetics of autotetraploids. (a) What effect should presence of a predominance of tetrasomic inheritance have on selection of breeding procedures? (b) What types of experiments will most effectively assess the relative importance of the various types of genetic variances which are present? (c) What types of experiments can be devised to measure the relative importance of disomic and tetrasomic inheritance for genes affecting a given quantitative character?

THE GENETIC INTRA-CLASS CORRELATION AND MODE OF INHERITANCE IN TETRAPLOID ALFALFA

M. W. ADAMS[3]

The purpose of this note is to suggest a method of ascertaining mode of inheritance of quantitative traits in a tetraploid organism. The method is based on a comparison of theoretical with observed genetic correlations among members of the first selfed generation (S_1). The theoretical genetic intra-class correlation for S_1 families for the disomic case was shown by Wright (16), using

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the path coefficient method, to be 2/3; by an extension of Wright's method to the tetrasomic case, assuming random chromosomal assortment and additive gene effects in families produced by selfing of an initially non-inbred parent, the genetic intra-class correlation (r_I) is found to be 2/7 (1).

The r_I for S_1 families is obtained for any quantitative trait in terms of the ratio of the genic variance between families (σ_B^2) to the total genic variance; that is

$$r_1 = \frac{\sigma_B^2}{\sigma_B^2 + \sigma_W^2}$$, where σ_W^2 equals the genic variance within families (3).

As illustrative of the method data are presented (table 1) from the M. S. thesis of Mr. W. D. Dunlap (6); his calculations were based on data from 16 S_1 families of alfalfa, each family numbering 60 plants.

TABLE 1.—PROBABILITY LEVELS FROM T-TEST FOR SIGNIFICANCE BETWEEN THEORETICAL AND OBSERVED INTRA-CLASS CORRELATIONS.

		Theoretical r_1 values:	
		Disomic No Dominance 0.667	Tetrasomic No Dominance 0.286
Source	Observed r_1	Probability level	
1955:			
X_1 (Growth Habit)	0.767	0.20	0.01
X_3 (Leaf Score)	0.472	0.05	0.10
X_4 (Internode Length)	0.379	0.01	0.50
D (Discriminant Function)	0.500	0.10	0.10
P (Purple-Qualitative)*	0.450	0.02	0.20
P_q (Purple-Quantitative)*	0.390	0.01	0.40
Y_q (Yellow-Quantitative)*	0.250	0.01	0.50

*Refers to flower color scores.

The environmental errors were calculated from repeated measurements on the progeny plants, the errors being of the sampling type. Estimated r_I's are within the expected range of values, though due to the low number of families involved, the values are still subject to a sizable error of estimation.

I should like to emphasize that what is suggested here is not that alfalfa behaves heterosomically for the traits listed, but rather that here is a relatively uncomplicated method of inferring mode of inheritance of quantitative traits in a tetraploid organism.

In order to obtain reliable estimates of r_I one must observe the precaution of random sampling from the base population, taking a large number of plants to be selfed, and using an experimental design calculated to provide a high degree of error control.

POLYPLOIDS AND POLYGENES

L. DESSUREAUX[4]

Extending the methods of quantitative inheritance to polyploid systems presents numerous complex problems. An attempt has been made by Dessureaux (5) to adapt the diallel cross method of analysis to autotetraploid. For this purpose, he specified the autotetraploid genotypes in Mather's terminology (12) as follows:

Frequency	*Genotypes*	*Value*
α	AAAA	d
β	AAAa	$h + \lambda d$
γ	AAaa	h
ϑ	Aaaa	$h - \lambda d$
ϵ	aaaa	$-d$

Where λ is defined as $1/2 - 1/2\ h/d$ if $h \leqq d$ or as $1/2 + 1/2\ h/d$ if $h \leqq -d$. The above definition does not include over-dominance. The frequency of the genotypes is determined by the gene frequency $(p + q)^4$.

Using these genotypic values, the parent-offspring regression is examined briefly. With complete dominance, the regression of selfed progenies on their parents is nearer to unity with autotetraploid than with diploid. Epistasis, if complementary, decreases the regression coefficient and increases inbreeding depression. If a duplicate type of epistasis is involved, the regression coefficient approaches unity and inbreeding depression is slight.

Various expected statistics were calculated from the diallel table in the case of one-gene, two alleles autotetraploid model, assuming chromosome segregation, random mating, and equal gene frequency. The regression of the array covariance *(Wr)* on the array variance *(Vr)* was curvilinear (5). In the absence of epistasis, it is possible to estimate the additive and dominance variances and therefore to assess the average degree of dominance. A diallel table constructed on a two-gene model was used to examine the disturbances caused by two types of epistasis to the *Wr, Vr* graph and the changes in Griffing's general and specific combining ability (8). Complementary epistasis tends to inflate dominance estimate without affecting specific combining ability, whereas duplicate epistasis tends to underestimate dominance but increases the relative estimate of specific combining ability.

Experimental data from a 10×10 diallel cross within the DuPuits variety of alfalfa were given. The characters studied were mean number of cotyledonary leaves, mean number of unifoliate leaves per plant, length and breadth of the unifoliate leaf.

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GENE POOLS AND RECURRENT PHENOTYPIC SELECTION IN ALFALFA[5]

C. H. HANSON[6], R. R. HILL, JR.[7], and J. W. DUDLEY[7]

This selection experiment on alfalfa was initiated at Raleigh, North Carolina, in 1950. The objectives of the Raleigh breeding program, as well as those of most other programs in eastern United States, included resistance to many diseases and insect pests, in addition to desirable agronomic qualities. The occurrence of resistance to any one disease or insect was infrequent in foreign and domestic stocks tested, making it unlikely to find genotype combining even several of the characteristics needed. Undesirable linkages were expected, but proof of the existence of tight linkages of undesirable gene combinations is still lacking. Naturalized strains are nonexistent because rainfall pattern in the East is unfavorable for seed production.

Recurrent phenotypic selection, primarily for disease and insect resistance, was initiated in 1950 within each of two populations (A and B) by randomly intercrossing 400 plants within each. These individuals were selected during the previous 4-year period of introduction and testing. In the second and subsequent cycles, about 90 plants were selected from about 2,000 in each population on the basis of phenotype, and intercrossed within populations to provide seed for the next cycle. The effectiveness of this selection program is illustrated by the changes in mean rust and leafhopper-yellowing scores for populations A and B (Table

TABLE 2.—MEAN RUST AND LEAFHOPPER-YELLOWING SCORES FOR EACH OF 7 CYCLES OF RECURRENT PHENOTYPIC SELECTION IN ALFALFA POPULATIONS A AND B[1].

Cycle	Rust score[2]		Leafhopper-yellowing score[3]	
	A	B	A	B
2	6.5	5.6	6.1	6.5
3	6.4	4.5	6.2	5.9
4	6.5	3.8	5.9	6.2
5	3.6	2.7	5.7	5.6
6	2.6	2.4	5.2	5.4
7	2.9	2.5	5.1	4.8
8	2.8	2.1	5.0	4.5

[1]Each mean is the average of 14 replications of 10 plant plots grown in a randomized complete block design at Clayton, N. C.

[2]Caused by *Uromyces striatus*. Scored 1–9: 1 = no pustules observed, 9 = most leaves severely infected.

[3]Scored 1–9: 1 = no yellowing, 9 = severe yellowing.

[5]Joint contribution from Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture and Department of Field Crops, North Carolina Agr. Expt. Station, Raleigh, North Carolina.

[6]Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, Beltsville, Maryland.

[7]Crops Research Division, Agricultural Research Service, U. S. Department of Agriculture, Raleigh, North Carolina.

2). Significant changes in both rust and leafhopper-yellowing score have been made. Hill (9) studied the pooled within-plot variances and found a reduction in genetic variance of rust score for both populations with little change in variance for leafhopper score.

In addition to improved rust resistance and tolerance to leafhopper yellowing, greater resistance to crown and stem rots and certain leaf spot diseases over standard varieties has been observed in the material from the seventh cycle of selection from both populations. In North Carolina, population B yields about 10 per cent more forage in broadcast plantings than the standard varieties Atlantic and Williamsburg.

Recurrent phenotypic selection has been effective in these two broad genetic base populations where conditions were similar to those given in paragraph 1. The success of this selection procedure is probably due to relatively high heritability in the narrow sense of resistance to the diseases and insects involved and to the fact that the procedure provided optimum opportunity for genetic recombination. Other advantages are (a) convenience of preserving genetic variation for characters other than those being selected, (b) flexibility for instituting more complex breeding procedures aimed at improving characters such as yield, and (c) low cost of time and labor.

GENERAL VS. SPECIFIC COMBINING ABILITY FOR REACTION OF ALFALFA TO COMMON LEAF SPOT, PSEUDOPEZIZA MEDICAGINIS (LIB.) SACC.

H. L. CARNAHAN

Estimated components of variance for general and specific combining ability for common leaf spot reaction on alfalfa were derived from two replicates of 10 F_1 plants per cross per replicate as follows:

Set I—Nine leaf spot resistant heterozygous clones each crossed with each of six leafhopper resistant but leaf spot susceptible clones.

Set II—As in set I except eight clones were represented in each parental group.

Set III—A six-clone diallel among heterozygous clones selected for leaf spot resistance.

All F_1 crosses were produced by hand-pollination.

The estimated components of variance for general combining ability for sets I through III were 15.8, 2.3, and 2.8 times as large as the respective estimates for specific combining ability. None of the estimated components of variance for specific combining ability deviated significantly from zero.

The preponderance of general combining ability effects on common leaf spot reaction is in substantial agreement with previously published results (2, 14) and with breeding results (15).

Substantial progress in breeding for common leaf spot resistance was evidenced by a reaction of 1.45 for one single cross from resistant parents of the diallel as contrasted to 8.60 for the cultivar Buffalo.

ASSESSING THE PERFORMANCE OF INBRED LINES OF ALFALFA

J. L. FYFE[8]

In a program of alfalfa breeding making use of inbred lines, two of the problems requiring answers are:

1. What is the quantitative relation between yield and inbreeding coefficient? Alfalfa being an autotetraploid, unrelated crosses have one-third of the average inbreeding coefficient of their parents and so double crosses, for example, are less inbred than single crosses.

2. How important are general and specific combining ability in determining the yield and other attributes of crosses? The more important is general combining ability, the more the justification for early testing.

Taking inbreeding coefficients, (expressed as percentages,) as independent variable and yield (expressed as per cent of the check) as the dependent variable, there was good agreement to a linear relation, for two cases, with a slope somewhat steeper than −2. In a third case the agreement was fairly good and the slope less steep, even after some allowance had been made for accidental selfing involving certain parents.

General and specific combining ability were studied in complete sets of single and double crosses between six slightly inbred (F = 31%) parents. With attributes other than yield, the general combining abilities of the inbred parents gave a useful guide to the performance of both single and double crosses. With yield, however, the performance of single crosses was affected by specific combining ability and although the performance of double crosses was clearly related to the general combining abilities of their single cross parents, the latter bore little relation to those of the inbred grandparents. When the double crosses were grouped under common grandparents, the influence of the latter could just be detected.

In another experiment, comparing test-crosses of inbred parents, there were clearly significant effects of general combining ability in respect of yield.

SUMMARY COMMENTS

This section has been a joint contribution of authors to quantitative genetic studies with polyploids, being directed principally to alfalfa. Whether alfalfa behaves as an allotetraploid, a segmental allotetraploid, or an autotetraploid, one certainly would conclude from the presentations of Hanson, Carnahan, and Fyfe that populations (or synthetics) can be improved by simple mass or phenotypic recurrent selection, and that considerable progress can be made through improved synthetics. That such progress is possible has been demonstrated by plant breeders in developing improved varieties. Unfortunately, many of the quantitative genetic studies in alfalfa stem from crosses between selected clonal lines. It would seem that a much more fruitful approach would

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be to consider the problem in terms of population dynamics typical of an alfalfa variety or of populations such as those synthesized by Hanson. The variability which is transmissable to the progeny in such a population is pertinent information for a breeding program. At this level of thinking, the nature of ploidy in alfalfa is secondary.

It is apparent from these presentations that considerable information on inheritance and chromosome behavior in alfalfa would be required before information from studies on the nature of gene action can be properly interpreted. Analyses of some qualitative characters revealed tetrasomic inheritance. The predominantely two by two pairing is apparently not incompatable with the assumption that alfalfa is an autotetraploid, although not expected. However, sufficient evidence has not been presented here to warrant the assumption that alfalfa is an autotetraploid. Until additional data are available, it would appear that this species should be treated as a segmental allopolyploid, and the assumption of diploid inheritance would be as applicable as tetraploid inheritance. Certainly, additional data are required. The study of inbreeding depression as proposed by Adams has merit. Alternative designs should be examined as possible methods of estimating the extent of autotetraploid inheritance in quantitative characters in alfalfa. However, whether one chooses the procedure proposed by Adams or some alternative, the sampling must be made relative to some random mating population. Unless this is done the information on gene action may simply add to the confusion.—Editors

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DISCUSSION

S. G. STEPHENS: Would it be possible in those tetraploid species, from which two plants can be derived (potato), to study components of genetic variance at the diploid level and then extrapolate to the tetraploid case?

J. W. DUDLEY: I don't know. This is an interesting possibility which deserves consideration.

W. D. HANSON: (1) I would appreciate if you would expand upon the cytogenetic information (2 × 2 pairing) and the autotetraploid. Where on the scale (allo—auto) would you place alfalfa? Since it appears to be intermediate, why not use allopolyploid assumption? (2) What information (experimental) is available on inbreeding in alfalfa as contrasting diploid vs. tetraploid inbreeding depression?

J. W. DUDLEY: (1) I would place alfalfa close to the autopolyploid end of the scale since most of our genetic information indicates autopolyploid behavior. (2) Very few good data are available on inbreeding depression in alfalfa. Results obtained have been interpreted as indicating inbreeding depression more typical of diploids than of autotetraploids.

R. E. COMSTOCK: For leaf-hopper score you showed estimates of genetic variance but not non-genetic. Can you give us the latter? Do you know selection differentials? In view of rather consistent progress it would be interesting to compare predicted and observed progress both because you have a tetraploid and because your estimatic of genetic variance may be biased upward by G-E interaction variance.

J. W. DUDLEY: I do not have the estimates of non-genetic variance with me. Selection differentials are not known because of the way in which the material was handled during the cycles of selection.

O. NISSEN: Will a transformation (for instance of scores) affect the relative values for general and specific combining ability? If so, how can this be explained in a biological way?

H. L. CARNAHAN: It is my understanding that transformation of score data may have no effect on the relative proportion of general to specific combining ability or that the transformation, in some instances, will diminish the specific combining ability component. In the study I reported the specific combining ability component of variance was small and not significant with non-transformed data; therefore, it seemed unnecessary to repeat an analysis with transformed data. Your questions are well taken, however, and I should like to hear further comment on the need and/or desirability of transforming such score data where the scores seem to correspond with a "natural" classification as was the case with alfalfa common leaf spot infection scores.

H. L. CARNAHAN (to *R. E. COMSTOCK):* To the extent that scaling or transformation will largely remove non-additive genetic variance, how much, if any, consideration should be given to using this removable non-additive variance as a basis in choice of breeding method?

R. E. COMSTOCK: I presume you have in mind transformations like the logarithmic or square root where the distance on the transformed scales becomes progressively longer (or shorter) relative to distance on the original scale as value on the latter increases. With this qualification, I would say that amount of removable non-additive variance deserves attention in choices that would be made in terms of relative amounts of additive and non-additive variance. For example, in a case where the additive variance was small relative to total genetic variance using one scale but large using another I would choose the action to be favored when additive variance is large regardless of which scale would be used in ordinary observation.

Another way of expressing my opinion is to say that I believe your "removable non-additive" variance offers essentially the same potential as additive variance for any selection method that is effective in the presence of additive variance.

I must say, however, that I have some doubt that the removable non-additive variance is likely to be very large when additive variance is small. Nevertheless, I suppose there could be enough of it to affect ones decision if the answer I've given is accepted.

W. ADAMS: Regarding the use of transformation of scale, I have done this in a selected population which was skewed in gene frequency for reaction to leafspot in alfalfa. Perhaps the log transformation was the wrong one to use, but, at any rate, it made no difference so far as detecting residual variances was concerned.

G. E. DICKERSON: All that transforming of scores can accomplish is to expand the observed differences in some portion of the distribution (range) relative to those vs. others. It will increase the proportion of the variation due to additive gene and environmental effects, if the untransformed data contains some type of systematic interaction of gene $\times$ environmental

effects. The common example is the threshold type of interaction, where a given gene (or environmental) difference has a substantially smaller effect as the ceiling or floor is approached. The transformation merely eliminates part of the real interaction present in the biological observations.

It should be emphasized, however, that transformation is of little use in making selection more effective. A transformation cannot change the *order* of the phenotypes and hence would change nothing if selection were solely for the transformed trait. It could help only if selection were directed toward improvement of several traits. In this case, use of the *untransformed* data has the desirable feature that a given gene effect on susceptibility automatically will be penalized more heavily by a *linear* selection index in a gene-environmental background which produces serious levels of disease than in one which produces minimal levels of disease. Transforming the data on susceptibility scores to eliminate threshold type of interaction effects sacrifices the advantages of automatic (curvilinear) heavier emphasis in selection, as the level of susceptibility increases.

C. H. HANSON: The Griffing modification of the diallel cross technique for estimating components for general and specific combining ability is frequently used on alfalfa. How does choice of parents, as well as polyploidy, affect the inferences one can make from the data?

B. GRIFFING: There are at least two sorts of inferential problems for which the diallel can be used: obtaining information on specific crosses of highly selected material and estimating population parameters for a conceptual population from which the diallel material may be considered a random sample.

In the first case, the parents and crosses constitute the entire population about which inferences are to be made. The objective is to compare the average performance of parents, and, more particularly, to compare the performance of specific crosses. Thus, the problem is to estimate effects and their standard errors.

In the second case, the diallel system is used to generate a random sample from a conceptual population. Inferences are not to be made about the individual parents and crosses but about the parameters (usually covariances among relatives) in the conceptual population.

In my early paper (1), I used homozygous lines as parents. Under the appropriate assumptions, the combining ability components estimate the following population parameters:

$$\sigma^2 \text{ g.c.a.} = \text{Cov (PO)}, \text{ and}$$

$$\sigma^2 \text{ s.c.a.} = [\sigma_G^2 - 2\text{Cov(PO)}],$$

where,

Cov(PO) = parent-offspring covariance in the equilibrium random mating population, and

σ_G^2 = total genotypic variance.

Matzinger and Kempthorne (3) considered the consequences when the parents are subjected to varying degrees of inbreeding. Of particular interest is the situation where the parents, themselves, are non-inbred elements from the random mating population. Under this assumption, the combining ability components estimate the following:

$$\sigma^2\text{g.c.a.} = \text{Cov(HS) and}$$

$$\sigma^2\text{s.c.a.} = [\text{Cov(FS)} - 2\text{Cov(HS)}],$$

where

Cov(HS) = Covariance of half-sibs, and

Cov(FS) = Covariance of full-sibs in the equilibrium random mating population.

Assuming no epistasis and diploid inheritance, the combining ability variance components (for the two extreme sorts of diallels) estimate the following genotypic variance components:

	Homozygous parents	Randomly mated parents
σ^2g.c.a.	$\frac{1}{2}\sigma_A^2$	$\frac{1}{4}\sigma_A^2$
σ^2s.c.a.	σ_D^2	$\frac{1}{4}\sigma_D^2$

where

σ_A^2 = additive genetic variances, and

σ_D^2 = dominance variance.

This, then, represents the first obvious difference due to choice of parents.

Further complications arise when the parents are chosen from heterozygous material. For example, the progeny resulting from the cross of two, non-inbred parents are full-sibs, and differences among them are due to genetic segregation as well as environmental effects. Hence the expectation of the within plot mean square is

$$\sigma_f^2 + [\sigma_G^2 - \text{Cov(FS)}]$$

where σ_f^2 is the environmental component. This complication and others are discussed, excellently, by Kempthorne (2).

It should be pointed out that for the combining ability components to provide unbiased estimates of the population parameters, as indicated above, the analyses should not include the parents. Also, if the inheritance is not diploid, the above relationships between combining ability components and covariances among relatives still hold, but the genetic interpretations of the covariances depend on the nature of inheritance, i.e., the level of ploidy (2).

One of the main problems of interpretation arises when the breeder uses somewhat selected material, rather than a strictly random sample, for the parents of the diallel. For example, consider a mass selection program starting with a random mating population in equilibrium. The population is truncated and at least some of the surviving plants are used as parents in a diallel. The question arises as to how much disturbance does such a procedure generate in the utilization of the variance estimates for predicting genetic advance? It would seem that the answer is determined largely by the intensity of selection together with the magnitude of the heritability. I should suppose that if the selection intensity is weak to moderate, the heritability small, and if a fairly large number of plants are used to form the breeding material for the next generation, the bias generated by use of selected material would not be excessively great.

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Interplant Competition

A Mathematical Interpretation of Interplant Competition Effects

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A PRIMARY consideration in the study of quantitative inheritance and selection for quantitative characters is the separation of genetic and non-genetic variation. It is generally assumed that reduction to a minimum of the environmental variation influencing individuals in a population is desirable in order that variation due to genetic effects may be measured with a reasonable degree of efficiency. Beyond the knowledge that uniformity is desirable, relatively little has been established concerning the levels of various factors in the environment, which may be to the advantage of the geneticist and plant breeder.

Competition, whether between individual plants or between rows, is a factor in the environment usually encountered in genetic and plant breeding experiments. While investigations of competition phenomena have shown some rather consistent effects, it is clear that much remains to be done to clarify our concepts concerning them. Several investigations have established that the relative survival of cereal varieties in mixed plantings has been found not to be a sound criterion of the yielding ability of the separate varieties (2, 7, 8, 12, 13). It has also been shown that genotypic vigor and competitive ability are sometimes negatively correlated. On the other hand, vigor resulting from advantage in seed size contributes to both superior independent performance and competitive ability (1, 5). The differential nature of inter-genotypic competition has been demonstrated both between plants within a row (1, 10, 14), and between rows (3, 4, 5, 6). Differential ability to compete for soil nutrients has been offered as an explanation of varietal differences in competitive ability; yet, competition effects have been shown to increase with higher levels of soil fertility (11), and competitive differences have been demonstrated for varieties grown in a hydroponic medium (15). This limited review of investigations of competition effects is presented only to illustrate some of the complexities of competition phenomena.

It is the purpose of this paper to present a simple procedure for the interpretation of one category of competition effects, and to demonstrate the application of this procedure to two types of experiments.

MATERIALS AND METHODS

Field Experiment

The initial experiment was concerned with determining the magnitude of competition effects produced by two seed sizes and three genotypes. A standard method was used in planning this experiment, such that comparisons could be made between plots seeded separately to different types of seed and plots seeded to the same two types in competition with one another. In this experiment, the competing types were alternated within the row. The competitive effect was measured by the excess of difference between the paired seed types over the difference between the same types seeded separately.

The basic plot type in this experiment consisted of 3 rows spaced 6 inches apart, with 36 plants spaced 2 inches apart within the row. The center row of each plot was used for all determinations. Seven replications were used with complete randomization of plots within each. The genotypes used were three varieties of barley; Parkland, Brandon 3902, and Herta. Small and large seed lots of each variety were obtained by screening, followed by hand-picking to remove broken, diseased or otherwise abnormal seeds. The small and large seed lots weighed approximately 20 grams and 45 grams per 1,000, respectively. For the determination of yield and kernel weight, plants from the center row of each plot were bulked. In rows consisting of two seed types alternated in competition, each type was bulked and considered as a half-plot.

An analytical procedure appropriate to this experiment was used by Christian and Grey (1). It consisted of a direct analysis of variance, but with two errors calculated, one being appropriate to comparisons of material grown in separate plots, the other to comparisons of material grown within the same plot (i.e., in competition). The data obtained were initially analyzed by this method, but it was found rather cumbersome with the number of comparisons required in this experiment. A procedure was therefore devised which was convenient for this experiment and which would be applicable to many kinds of competition studies. The main objective of the procedure is to provide a reliable measure of the general competitive influence of each type under study. The term "competitive influence" is used deliberately to denote a distinction from "competitive ability." "Competitive influence," or the capacity of a type to exert competition on its neighbors, is the phenomenon generally measured. Competitive ability, on the other hand, is the capacity of a type to withstand competition from its neighbors; it is more difficult to measure as an entity separate from the inherent vigor of the type.

The analytical procedure used is based on treating the categories of types being measured as factors, with the individual types within categories as levels of the factors, thus making up a typical factorial analysis. The procedure is best illustrated by an example in which the factor measured is variety, with the individual varieties as levels. Taking three levels designated as varieties V_1, V_2, and V_3, to be compared for competitive influence, the varieties are seeded alone, and in all combinations of two varieties competing, making six plots in

all. Since each competition plot provides two sources of data, that from the competing variety and that from the tested variety, nine determinations are obtained for any one character.

Taking yield as the criterion and denoting *Yij* as the yield of the *ith* variety when grown in competition with the *jth* variety, the measurements obtained can be arranged as in Table 1, in which the first subscript of each

TABLE 1.—ARRANGEMENT OF NINE DETERMINATIONS OBTAINED FROM THREE VARIETIES GROWN SEPARATELY AND IN COMPETITION.

Type of Competition	Tested Material			
	V_1	V_2	V_3	Total
V_1	Y_{11}	Y_{21}	Y_{31}	$Y_{.1}$
V_2	Y_{12}	Y_{22}	Y_{32}	$Y_{.2}$
V_3	Y_{13}	Y_{23}	Y_{33}	$Y_{.3}$
Total	$Y_{1.}$	$Y_{2.}$	$Y_{3.}$	$Y_{..}$

refers to the number of the tested variety and the second to the number of the competing variety. The following statistical model then describes the yield of the *ith* variety grown in competition with the *jth* variety:

$$Y_{ij} = m + y_i + c_j + c_{ij} + e_k$$

in which:

m is the over-all mean.

y_i is the yielding ability of the *ith* variety.

c_j is the competition that the *jth* variety offers to an adjacent variety.

c_{ij} is the competition offered by the *jth* variety to a specific *ith* variety.

e_k is the error associated with the *kth* plot from which the Y_{ij} measurement was obtained.

Comparison of the column totals $Y_{1.}$, $Y_{2.}$, and $Y_{3.}$ will estimate the relative yielding abilities of the three varieties, whereas comparison of the row totals $Y_{.1}$, $Y_{.2}$, and $Y_{.3}$ will estimate the relative competitive influence of the varieties. In this example the eight degrees of freedom available can be allocated as follows: 2 D.F. for each of yielding ability and competitive influence and 4 D.F. for the interaction.

In the field experiment, three varieties were used with two seed sizes within each. The treatments involved were:

V—tested variety; 3 levels.

V_1—competing variety; 3 levels.

S—tested seed size; 2 levels.

S_1—competing seed size; 2 levels.

The 36 treatment combinations possible may be regarded as a $3 \times 3 \times 2 \times 2$

factorial. The 35 degrees of freedom available between treatments may be assigned as shown in Table 2.

Competitive influence was measured by the difference between plants competing with one type and those competing with another, the sum of other contributing factors being taken as equal for each type. To illustrate, the difference in competitive influence of large and small seeds was estimated by

TABLE 2.—ALLOCATION OF DEGREES OF FREEDOM IN A 3 x 3 x 2 x 2 FACTORIAL COMPETITION EXPERIMENT.

Source of variation	Degrees of freedom
Varieties	2
Seed sizes	1
Competition due to varieties	2
Competition due to seed sizes	1
First-order interactions	13
Second-order interactions	12
Third-order interactions	4
Total treatments	35

TABLE 3.—EFFECT OF SEED SIZE DIFFERENCE IN THREE VARIETIES.

Characteristic	Manner Sown	Difference: Large over Small		
		Parkland	Br. 3902	Herta
Early tillers	Separately	0.93**	0.39	1.00**
	Competing	0.57**	0.64**	1.25**
Final tillers	Separately	1.78**	0.71	1.66**
	Competing	2.36**	2.61**	6.56**
% fertile culms[1]	Separately	−1.1	0.0	0.0
	Competing	0.3	−0.2	−1.6
Plant height (ins.)	Separately	3.54*	2.13	3.46**
	Competing	0.96	3.73**	2.43*
Kernels per head	Separately	1.98	0.51	0.77
	Competing	0.34	5.80**	1.84
Kernel weight (mgms.)	Separately	0.98	1.99*	0.07
	Competing	2.46**	2.57**	0.46
Yield (gms.)	Separately	2.61**	1.37	1.74*
	Competing	4.24**	4.87**	4.27**

*Significant at the 5% level.
**Significant at the 1% level.
[1]Retransformed data.

summing appropriate measurements of all plants competing with small seed and subtracting the sum of comparable measurements of plants competing with large seed.

Seven characteristics were used as criteria in this experiment and they are listed in Table 3.

Greenhouse Experiment

The objective of the greenhouse experiment was to determine the effect of plant spacing and depth of seeding upon competition due to seed size in one variety, Parkland. The average weight of the large and small seeds used was 47.7 and 26.5 milligrams respectively. The factors studied and the levels of each were: (a) depth of seeding—1.50, 2.75 and 4.00 inches; (b) plant spacing—$2 \times 2 \times 4 \times 4$ and 6×6 inches; and (c) seed size—large seeds only, small seeds only, and large and small seeds sown alternately. A split-plot arrangement in four replications was used, the nine combinations of sowing depths and seed sizes forming the main plots, the three spacings the sub-plots. Effects were measured in terms of days to emergence, seedling height 11 days after sowing and 10 days after emergence, tiller number 25 days after sowing and at maturity, tiller number, cumulative culm height, and total plant weight (Seed weight was considered unreliable because of some sterility of florets).

The experiment was analyzed as a $2 \times 2 \times 3 \times 3$ factorial, based on considering seed size as two factors, direct seed size effect and the competition effect of seed size, each at two levels.

RESULTS AND DISCUSSION

The purposes of this presentation can be served without using all of the information obtained from the experiments. The data presented have, therefore, been chosen with a view to illustrating applications of the method described.

Field Experiment

Data from the field experiment were analyzed both by the method used by Christian and Grey (1) and by the factorial procedure. Table 3 is presented to illustrate the type of information and interpretation obtainable from the first procedure. The critical comparisons are those between separate plantings of large and small seeds and competing plantings of the seed sizes. For cases in which the advantage of large seed was highly significant in competing plots but not significant where the sizes were separated, the importance of competition effect was clearly indicated. This situation was encountered in five of the seven characteristics measured in Br. 3902. The interpretation is not so readily made in instances where the effect was significant both in separate and competing plots, although greater in the latter; e.g., final tillers and yield in Parkland and Herta. Individual "t" test comparisons are possible between differences, but with any considerable number of types included in the experiment these would be rather cumbersome.

The information obtained concerning the main effects in the field experiment through the factorial type of analysis is shown in Table 4. For the sake of clarity, only the significance levels attained are shown. The comparisons represent the over-all effect produced by the types being compared. The competition effects were assessed by comparing the average of all materials competing with one type with the average of all those competing with the other type concerned in the specific comparison being made. The determinations, therefore, represent the general competitive influence of the types under consideration over all the factors involved in the experiment. Evaluation of interaction effects provided more specific information concerning variations in the general pattern. In this experiment only 8 first-order interactions out of 210 possible for all 7 characteristics exceeded the 5 per cent level of significance. Of these, five were concerned with tillering and involved the variety Herta. This variety tillers more profusely than the others tested. Only two of the significant interactions involved competition effects. While few of the interaction effects were of consequence in this experiment, it is conceivable that they might be a major consideration in other competition studies. A more precise evaluation of such effects is possible by a further breakdown of the analysis into individual degrees of freedom.

TABLE 4.—SIGNIFICANCE OF DIFFERENCES OBTAINED FOR THE FOUR MAIN EFFECTS IN THE FIELD EXPERIMENT.

Category	Comparison	Early tillers	Final tillers	Fertile tillers %	Plant height	Kernels per head	Kernel weight	Yield
Varieties	P–B[2]	*	**		**	**	–**	**
	P–H	–**	–**	**	**	**	–**	**
	B–H	–**	–**	**	**	**		
Seed size L–S[1]	Over P & B	**	**	–**	**		**	**
	Over P & H	**	**	–*	**			**
	Over B & H	**	**		**			
Varietal competition[3]	/P–/B				*			
	/P–/H							–*
	/B–/H							
Seed size competition /L–/S[3]	Over P & B		–**					–**
	Over P & H		–**					–**
	Over B & H		–**					–**

*Difference positive and significant at the 5% level.
**Difference positive and significant at the 1% level.
-*Difference negative and significant at the 5% level.
-**Difference negative and significant at the 1% level.
[1]L = large seed, S = small seed.
[2]P = Parkland, B = Br. 3902, H = Herta.
[3]/ = those competing with.

Greenhouse Experiment

The analysis of variance for four characteristics studied in the greenhouse experiment is presented in Table 5. In this analysis depth of sowing and plant spacing are factors in the experiment in the usual sense, each at three levels, with seed size and competition due to seed size treated as additional factors, each at two levels.

TABLE 5.—ANALYSIS OF VARIANCE OF CERTAIN AGRONOMIC CHARACTERISTICS IN EXPERIMENT COMPARING SEED SIZES AT VARIOUS DEPTHS AND SPACINGS.

Source of Variation	Degrees of Freedom	Mean Square			
		Days to Emergence	Early Tillers	Final Tillers	Plant Weight at Maturity
Depth of sowing (D)	2	62.44**	8.18**	0.15	8.39
Seed size (S)	1	0.49	7.80**	22.16**	23.90
Competition (C)	1	0.36	0.51	4.92	54.72**
S × C	1	0.92	0.11	0.96	0.32
D × S	2	0.27	0.84	1.61	5.92
D × S	2	0.90	0.53	4.09	4.85
D × S × C	2	2.24	0.13	4.39	1.30
Plant spacing (P)	2	1.39	18.60**	90.57**	506.34**
P × D	4	0.66	0.23	2.26	18.67*
P × S	2	0.51	0.29	0.57	5.42
P × C	2	0.45	0.01	0.02	2.08
P × S × C	2	0.00	0.05	0.94	9.08
P × D × S	4	0.38	0.04	2.62	7.55
P × D × C	4	0.32	0.24	2.67	4.89
P × D × S × C	4	0.46	0.27	7.46*	28.32**
Main plot error	33	2.15	0.27	1.54	7.07
Sub-plot error	72	0.51	0.20	2.11	7.49

*Significant at the 5% level.
**Significant at the 1% level.

Although provision was made for uniformity of soil and watering, conditions in the greenhouse were somewhat less than ideal for such an experiment. Floret sterility was considerable throughout the experiment, probably due to poor temperature-light relationships at certain phases of development. The individual plot size of six plants may have been smaller than desirable. At any rate, the coefficients of variability were generally high for all characteristics, ranging from 11 to 42 per cent.

In spite of these limitations some definite information could be derived from the data. Depth of seeding had an effect only at early stages of development. Seed size had no effect on emergence, but affected tillering at an early stage as well as increasing the ultimate tiller production. Competition due to seed size was shown to be significant in final plant weight only. Plant spacing affected early tillering, final tillering, and plant weight to a highly significant degree.

With few exceptions, the interactions were not shown to be significant,

and those which were significant were difficult to interpret. This may have been due in part to the high coefficients of variability encountered in the experiment. Differences between spacing treatments were large, and a breakdown of the error terms to their components gave evidence of non-homogeneous errors among spacings. Therefore, the experiment was reanalyzed for the harvest data within each spacing. The effect of seed size and competition due to seed size at each spacing were of particular interest. The significance of these effects is shown in Table 6. The results suggest that both seed size influence and interplant competition diminished as spacing between plants was increased. The effect of spacing upon competition and environmental variance requires more thorough evaluation over a wider range before definite conclusions can be drawn. While increased spacing diminished competition in this experiment, it also increased the coefficient of variability, a fact of considerable importance if found to be of general occurrence.

TABLE 6.—SIGNIFICANCE OF SEED SIZE EFFECTS AT THREE PLANT SPACINGS.

Comparison	Spacing	Tillers	Plant Weight
Seed size directly.....	2 × 2 ins.	**	**
	4 × 4 ins.	**	N.S.
	6 × 6 ins.	N.S.	N.S.
Competition of seed size.....	2 × 2 ins.	*	**
	4 × 4 ins.	N.S.	*
	6 × 6 ins.	N.S.	N.S.

*Significant at the 5% level.
**Significant at the 1% level.
N.S. Did not reach the 5% level of significance.

GENERAL DISCUSSION

The analytical procedure described achieves a similar purpose to the procedure used by Christian and Grey (1), but there are important differences. Both methods are designed to determine the extent of competitive influence of one type in association with another. The method of Christian and Grey (1) measures competition based on the difference between two differences; i.e., $(Y_{1'} - Y_{2'}) - (Y_1 - Y_2)$, where $(Y_{1'} - Y_{2'})$ refers to types in competition and $(Y_1 - Y_2)$ refers to the corresponding types sown separately. This can be shown algebraically to be equivalent to the comparison between the row totals $(Y_1 + Y_{2'})$ and $(Y_{1'} + Y_2)$ obtained when the four measurements concerned are arranged:

Competing Seed Type	Tested Seed Type 1	Tested Seed Type 2	Total
1.....	Y_1	$Y_{2'}$	$Y_1 + Y_{2'}$
2.....	$Y_{1'}$	Y_2	$Y_{1'} + Y_2$

Comparisons between such row totals form the basis for measuring interplant competition by the factorial procedure. Hence, the two methods are equivalent when only two types are measured.

The factorial method has the advantage in flexibility. It provides an estimate of the general "competitive influence" of the types tested, but at the same time can be used to separate out specific effects. It is particularly useful when the types can be classified into a number of categories, e.g., species, varieties, seed size, etc., in providing information on the competitive influence of levels within each category. It is also useful in studies such as the greenhouse experiment described, in which competition is considered as a main effect to be evaluated in conjunction with spacings, depths or similar factors. Significant competitive effects reveal the general competitive influence of a type over all other factors in the experiments. When significant interactions with competitive influence are encountered they can be evaluated by comparisons between the individual treatment means concerned.

The statistical model adopted assumes homogeneity of errors for within and between plots, the inter- and intra-plot errors being pooled as the testing error. The assumption of homogeneity need not hold true under all conditions. In case of great deviation between inter- and intra-plot errors, information might be sacrificed for reliability by using the larger of the two for tests of significance.

The factorial procedure described is primarily useful for the kind of investigations used for illustration, i.e., to detect and measure the competitive influence of various types upon one another in various circumstances. Undoubtedly the model used could be extended, but other methods would be more appropriate in many instances. As an example, the method developed and used by Sakai (9) has many applications. In this procedure various types are seeded in mix-planted and separate comparative populations. Competition is measured by the extent to which the intra-population variance in the mix-planted lots exceeds the sum of the environmental and genotypic variances. The variance of the mixed populations can be partitioned in this manner:

$$Vm = Vg + Ve + Vc,$$

where *Vm* stands for the variance of the mixed populations, and *Vg*, *Ve* and *Vc* for the genotypic, environmental, and competitional variances respectively.

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DISCUSSION

F. W. SCHNELL: No doubt the difference between the arrangement by Dr. Helgason and a mixture (random arrangement) should be evaluated experimentally. However, should it not be expected that the effects in question would be maximized by the former arrangement as compared to the latter one?

S. B. HELGASON: This could be considered a reasonable assumption, but I have no data bearing on this problem.

R. J. MIRAVALLE: Is the competition effect measured for given spatial arrangement in any way related to the competition effect for another spatial arrangement?

S. B. HELGASON: One experiment was concerned with competition due to seed size and spatial arrangement. The direction of the effect was constant, only the magnitude being changed. Whether this is true of varietal competition needs further investigation.

G. E. DICKERSON: Is it correct to consider interplant competition as degree of adversity of environment for individual plants, consisting of such elements as spacing and genetic character of the surrounding plants? If so, would

not the first step be determination of the operating range in level and type of interplant competition which is likely to include the optimum yield per unit of land area for the genetic material under study, considering annual variation in rainfall, etc.?

A second question is whether there are real differences in ranking of *varieties* depending upon the level of plant competition effects? Is this not just another form of genetic environmental interaction...except that the environment can be nearly completely controlled? One then can deliberately use the optimal (range of) environment for selection among genetic stocks?

S. B. HELGASON: Considering competitive ability as tolerance to adversity is a worthwhile concept, and as such need not be considered a separate entity from inherent vigor. The main reason for separating the two is the peculiar fact, demonstrated by several workers, that vigor and competitive ability are independent or even negatively correlated. This obviously has important implications in measuring quantitative characters in a genetically diverse population grown in competition. However, in the breeding of crops in which mixed populations are the end product, the basic problem is to develop constituents which combine vigor and competitive ability, each in the highest compatible degree possible. The second question raised bears on this last point. Presumably the optimal environment for selection would be one in which competition effects are included on some systematic basis.

W. D. HANSON: I would like to make an additional comment to Dr. Dickerson's second question. Genotypes which are relatively high yielding under competition with other genotypes or under wide spacings are not necessarily the higher yielding genotypes when grown in pure stands under normal commercial production. In fact, I have data for a soybean line which indicate that based on nonbordered, single-row yield tests it would be selected as an outstanding line, yet under bordered yield tests it would be quickly discarded as undesirable.

Interplant Competition Between Barley Genotypes

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INTRODUCTION

THE problem considered is the interplant competition between barley plants of specific genotypes. The characters studied are yield of grain and in turn its three components, heads per unit area, number of kernels per head, and kernel weight. The effect of competition between genotypes was measured in the F_2, $F_=$, F_3, F_4, and $F\infty$ generations and the data obtained were compared with each other and with the performance of the genotypes in pure stands. The results obtained are discussed in relation to selection under competitive conditions. For a review of the literature as it relates to the problem considered, the reader is referred to papers by Christian and Gray (1), Sakai (7, 8), Gustafson (3), Suneson and Ramage (10), Helgason (6), and Hanson (4).

MATERIALS AND METHODS

The barley genotypes used were derived by continued self-fertilization and selecting in each generation the heterozygous type *Vv*. Thus, after 20 generations the desired homozygotes *VV* and *vv* should be isogenic except for genes closely linked with the marker locus. The line used in this study is designated as 16–*Vv*–20, the original parents being Manchuria C.I. 2330 (*vv*, 6-row) and Kolter C.I. 987 (*VV*, 2-row). The heterozygote *Vv* and the two homozygotes *VV* and *vv* can be readily distinguished one from another. The process of isogenesis consists of selecting a heterozygous *Vv* plant in each generation to produce the progeny of the next generation under a system of self-pollination, which is the normal means of reproduction in barley. The mean genetic length of marked chromosome segments remaining intact (as in the parents) during isogenesis by selfing has been computed by Hanson (5), and for advanced generations is approximately $1/(n-1)$, where n refers to the filial generation.

A large population of plants segregating for the *VV*, *Vv*, and *vv* genotypes was grown in the 20th generation. At harvest, seed of each type was placed in a separate pool. From these pools the appropriate number of seeds were drawn to construct test populations for the F_2, $F_=$, F_3, F_4, F_∞ and the parental lines,

16–*VV*–20 and 16–*vv*–20, as shown in Table 1. The system chosen is one where it is assumed that each genotype has the same reproductive rate. Thus, the plan provides a means for comparing the data obtained on the basis of a predetermined theoretical model. The synthesis of the F_2 to F_∞ generations in the manner shown can be justified by stating that at this advanced generation of inbreeding there is very little change in any of the genotypes with each succeeding generation like the 21st, 22nd, etc. Furthermore, the plan adopted allowed for the testing of all generations and parental lines each year in a single experiment.

The data reported on are from tests grown at Aberdeen, Idaho, in 1955 and 1956. The seeds used for growing each population were thoroughly mixed and sown at random in rows 1 foot apart and 10 feet long, with a cone-type seeder. The seeding rate of two seeds per inch was the same for all populations. Each plot consisted of four rows of which the center two only were used for data. The over-all scheme was one using randomized blocks with 10 replications in 1955 and 12 in 1956. At harvest time, a 2-foot section was taken from one of the two center rows of each plot and these were used to get measurements on the yield components as given by Grafius (2). The tests were grown under irrigation and were normal for the years and area. There was no lodging, and diseases were absent.

EXPERIMENTAL RESULTS

The yield of grain per plot of the parental lines and the five populations for the two years is given in Table 2. There is a significant difference in yield between the parental lines, but none between the different populations or between the mean yield of the parental lines and the different populations. There also is no trend in the yield level as one goes from the F_2 to the $F\infty$ generation. The data show that interplant competition within a population did not affect total yield. The relative yields of the component genotypes of a population behave differently, however, as will be shown later.

Since the seeds were sown at random in linear order down each row, it is

TABLE 1.—PLAN OF SYNTHESIS FOR POPULATIONS USED IN STUDY.

Parental line or generation	Proportionate number of seeds drawn from each genotype pool			Resulting population		
	VV	Vv	vv	VV	Vv	vv
F_2	0	4	0	1	2	1
$F=$	1	4	1	1	1	1
F_3	2	4	2	3	2	3
F_4	6	4	6	7	2	7
F_∞	1	0	1	1	0	1
P_{VV}	1	0	0	1	0	0
P_{vv}	0	0	1	0	0	1

TABLE 2.—AVERAGE YIELD OF GRAIN IN GRAMS PER PLOT FOR PARENTAL LINES AND GENERATIONS.

Parental line or generation	Year		Average
	1955	1956	
	gr.	gr.	gr.
P_1,16-VV-20	746.3	933.2	839.7
P_2,16-vv-20	871.1	1264.0	1067.6
Ave. $P_1 + P_2$	808.7	1098.6	953.7
F_2	869.7	1092.9	981.3
$F_{=}$	—	1113.5	—
F_3	812.2	1100.7	956.5
F_4	785.0	1172.4	978.7
F_∞	800.7	1109.6	955.2

possible to estimate the adjacent genotype associations that occur in each population. These associations are given in Table 3, and the data can be looked upon as a rough index of the degree of competition that exists. Competition can be separated into two parts; that between like genotypes as *VV–VV*, *Vv–Vv*, and *vv–vv* and that between unlike genotypes as *VV–vv*, *VV–Vv*, and *Vv–vv*. With regard to the phenomenon of competition, the writers can only say that it exists. They are unable to define it explicitly or to describe its biological mode of action. Furthermore, it is not known if the competition between like genotypes is identical in every way to that between unlike genotypes. In the present experiment, only the competition between unlike genotypes is subject to measurement. In Table 3, it is seen that the unlike associations range from a maximum of 66.7 per cent in the $F_{=}$ to 50.0 per cent in the $F\infty$. It also is of interest that the F_3 has a higher value than either the F_2 or F_4.

TABLE 3.—ADJACENT GENOTYPE ASSOCIATIONS ALONG THE ROW FOR GENOTYPES AND GENERATIONS SHOWN.

Genotype	Generation				
	F_2	$F_{=}$	F_3	F_4	F_∞
	Pct.	Pct.	Pct.	Pct.	Pct.
VV–VV	6.25	11.11	14.06	19.14	25.00
vv–vv	6.25	11.11	14.06	19.14	25.00
Vv–Vv	25.00	11.11	6.25	1.56	.00
Total	37.50	33.33	34.37	39.84	50.00
VV–vv	12.50	22.22	28.13	38.29	50.00
VV–Vv	25.00	22.22	18.75	10.94	.00
Vv–vv	25.00	22.22	18.75	10.94	.00
Total	62.50	66.66	65.63	60.17	50.00

The experiment included three identifiable genotypes, thus making it possible to separate these at harvest time and to obtain data on yield and the yield components for each. These data are shown in Table 4 and Figures 1 to 4. The scale chosen for the abscissa in the figures measures the per cent of the *Vv* genotype in each population.

TABLE 4.—TWO-YEAR AVERAGE MEASUREMENTS FOR YIELD AND YIELD COMPONENTS OF GENOTYPES IN F_2, F_∞, F_3, F_4, F_∞ AND IN PURE STANDS.

Genotype	Generation					Pure Stand
	F_2	F_∞	F_3	F_4	F_∞	
	Yield—deviation from expectation—per cent					
VV	−5.19	−2.48	−1.15	− .08	+4.05	−6.83
Vv	+2.48	+2.52	+1.94	+2.73	—	—
vv	+2.71	− .02	− .79	−2.65	−4.05	+6.83
	Heads per unit area—deviation from expectation—per cent					
VV	−1.03	+2.28	+3.87	+5.29	+8.25	+1.46
Vv	+1.91	+1.60	+1.52	+2.02	—	—
vv	− .87	−3.86	−5.38	−7.30	−8.24	−1.46
	Kernels per head—number					
VV	19.81	20.29	20.51	20.90	21.55	19.50
Vv	39.66	40.58	39.69	40.90	—	—
vv	49.05	47.64	48.32	46.71	46.03	50.15
	Kernel weight—mg.					
VV	47.6	48.1	48.1	47.7	48.2	48.4
Vv	29.1	28.5	28.8	28.8	—	—
vv	26.7	26.7	26.5	26.9	26.7	26.2

The effect of competition in altering the relative yield of the 3 genotypes in the F_2 to F_∞ generation is shown in Table 4 and Figure 1. The slope of the regression lines *VV* and *vv* is highly significant, whereas that of the line *Vv* is not. The relative yields of the *VV* and *vv* genotypes in advanced generations, like F_4 and greater, are reversed from their performance in pure stand. The relationship of this reversal to selection for yield will be discussed later. The higher yield of *vv* plants over *VV* plants in pure stand has been amply confirmed by additional tests with these 2 lines and by 24 similar pairs of diverse origins. These tests were made in the United States, in Canada, and in Europe during a period of several years. The performance of the *Vv* genotype in Figures 1 to 4 will be discussed later.

The yield components, heads per unit area (1 square foot), number of kernels per head, and kernel weight, were studied separately. The data for heads per unit area are given in Table 4 and Figure 2. The slope of the regression lines *VV* and *vv* is highly significant, indicating the effect of competition on this component. The slope of the *Vv* regression line is not significant. The *VV* and *vv*

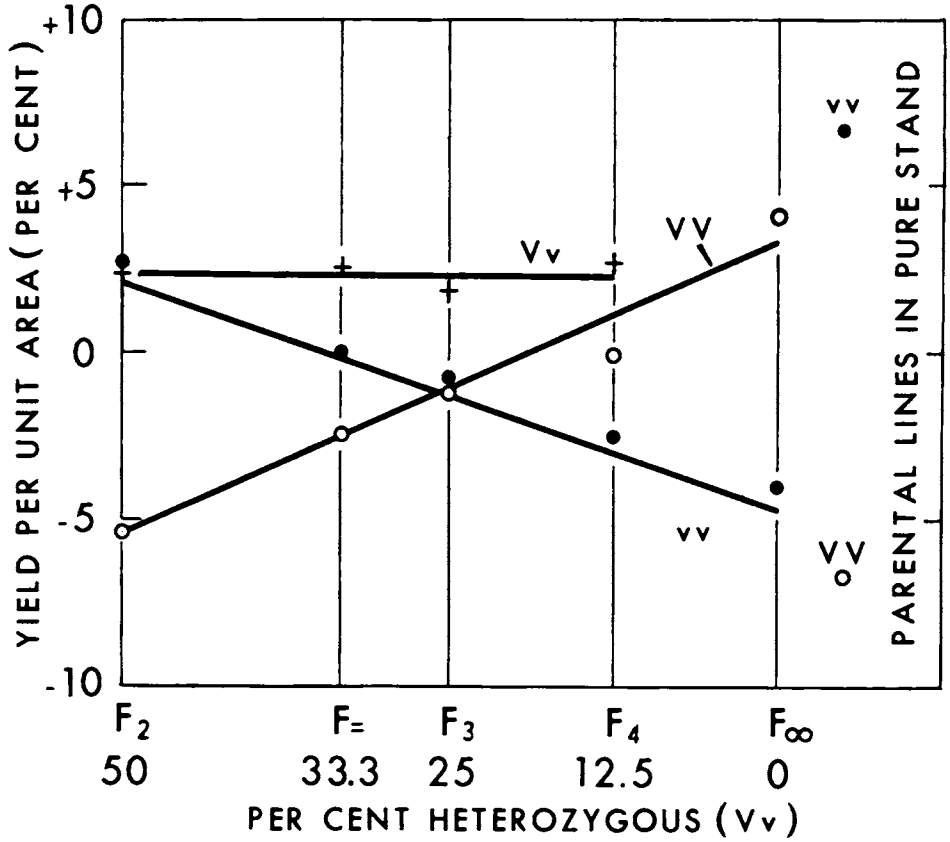

FIGURE 1. *Yield of grain per unit area (deviation from expectation) for component genotypes of F_1 to F_∞ and for parental lines in pure stand.*

genotypes agree in the sign of their difference in pure stand and in the populations, but the magnitude of this difference increases markedly as the competition between these two types is intensified. Since the seeding rate was constant for all populations, the adjustments in the heads per unit area were brought about through the tillering character.

The effect of competition on the number of kernels per head is given in Table 4 and Figure 3. The slope of the regression lines *VV* and *vv* is significant, indicating an effect of competition on this component. The slope of the *Vv* regression line is not significant. The number of kernels per head for the *VV* and *vv* genotypes in pure stand is similar to that in the populations. The agreement is better in this case than for the two previous characters of yield and heads per unit area.

The last component studied was kernel weight and the data are given in Table 4 and Figure 4. The slope of all three regression lines is nonsignificant. There also is very good agreement between the performance of this character in

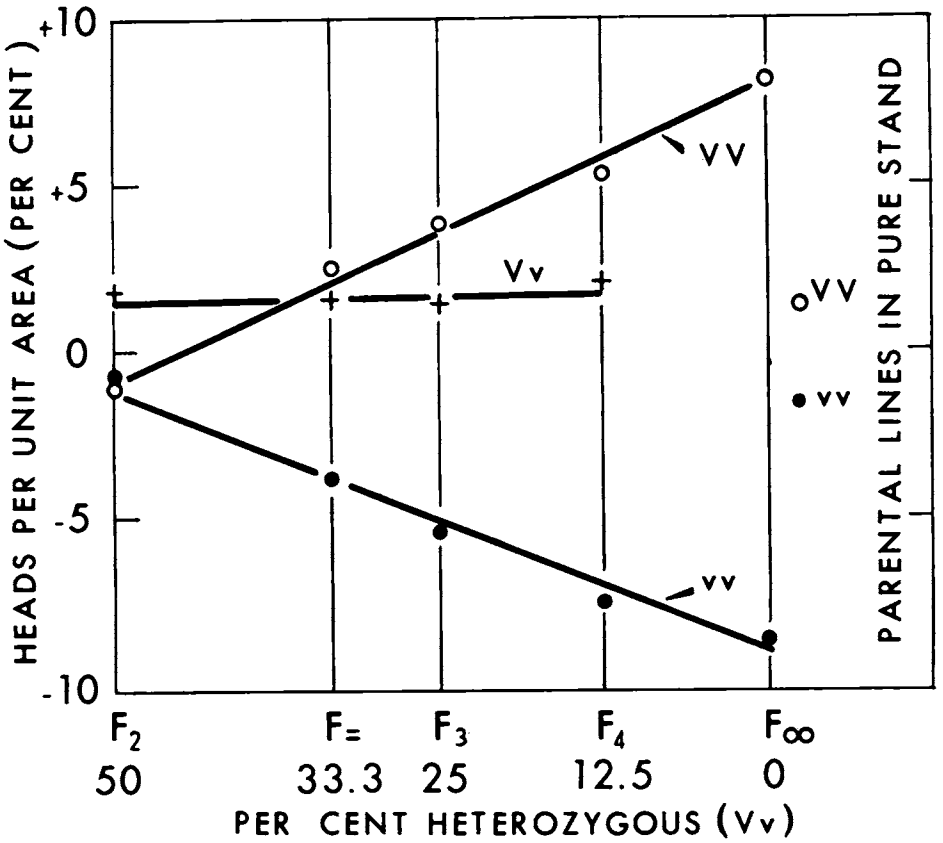

FIGURE 2. *Heads per unit area (deviation from expectation) for component genotypes of F_2 to F_∞ and for parental lines in pure stand.*

pure stand and in the populations. It is concluded that kernel weight was not affected by competition in this experiment. This conclusion is in agreement with numerous other studies where it has been shown that under normal conditions kernel weight is a relatively stable character.

The data for the *Vv* genotype on yield and the three components of yield have been given in Table 4 and Figures 1 to 4. Unfortunately, no data are available for the pure stand performance of this genotype because seed in the amount needed was difficult to get. The average value of the *Vv* genotype for the four populations in which it appears shows it to be superior in yield to both *VV* and *vv* genotypes, to be above average but below *VV* in heads per unit area, to be above average but below *vv* in kernels per head, and to be below average but above *vv* in kernel weight. In comparisons of *Vv* with *VV* and *vv* in pure stand, *Vv* is found to be above average but below *vv* in yield, to be superior to both *VV* and *vv* in heads per unit area, to be above average but below *vv* in kernels per head, and to be below average but above *vv* in kernel weight.

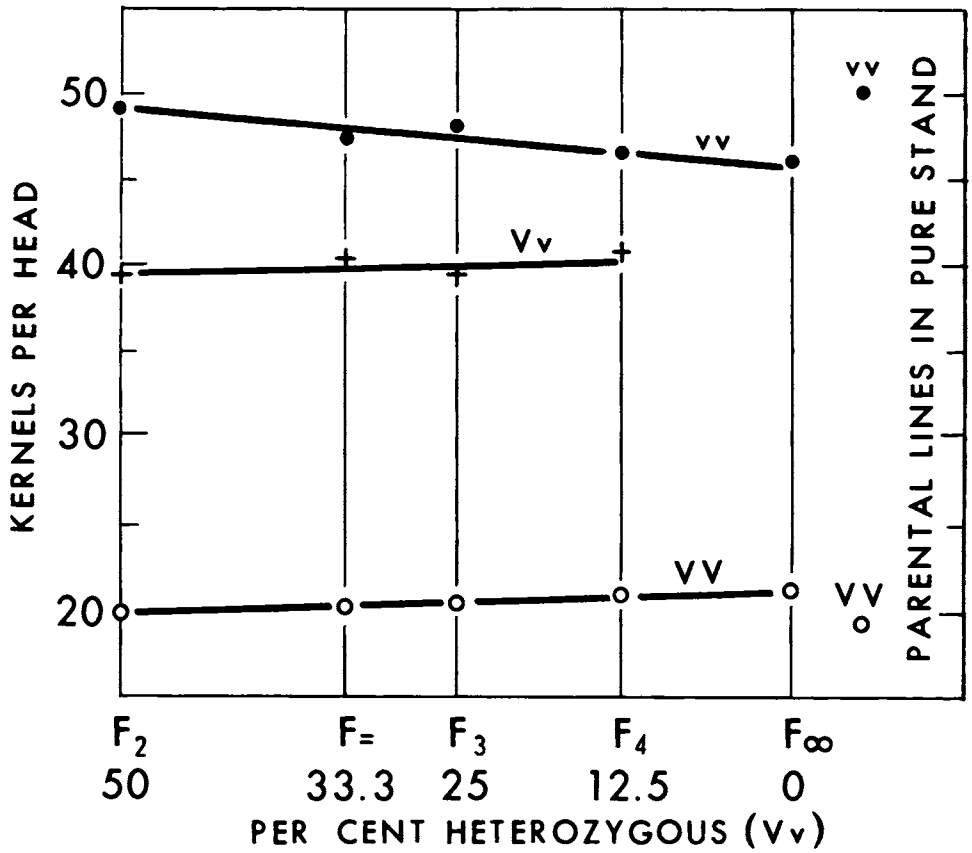

FIGURE 3. *Number kernels per head for component genotypes of F_1 to F_∞ and for parental lines in pure stand.*

The higher yield of the *Vv* genotype raises the question—is this heterosis? This question cannot be answered for two reasons. Firstly, the proportion of *Vv* plants in the four populations is slightly greater than expected. This is a chance deviation since seeds for this genotype must come from F_1 plants. Secondly, the yield of *Vv* plants may be enhanced through competition with the *VV* and *vv* plants in the same population. The presence or absence of this influence cannot be confirmed since no data are available on the yield of *Vv* plants in pure stand.

The zero slope of the *Vv* regression lines in Figures 1 to 4 is of considerable interest. The design of the genetic structure of the four populations in which *Vv* plants occur is such that in each population the *Vv* plants are balanced against an equal number of *VV* and *vv* plants. This balanced relationship could give the results observed. A similar relationship does not exist when one considers *VV* plants in relationship to the other two, and similarly for *vv*. The idea that *Vv* plants are better buffered than either *VV* or *vv* plants is an attractive one. The fact that *Vv* plants hold a relatively constant position in all populations and for all factors investigated tends to give support to this idea.

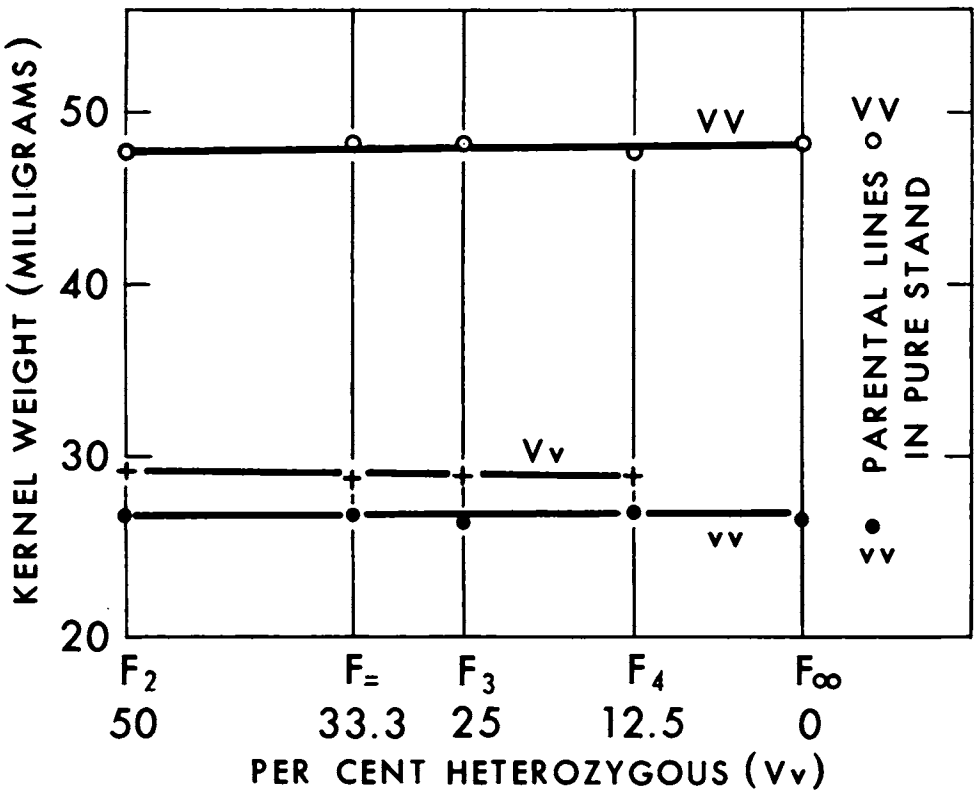

FIGURE 4. *Kernel weight for component genotypes of F_2 to F_∞ and for parental lines in pure stand.*

DISCUSSION

The barley lines used in this study can be considered as being highly isogenic after 20 generations of selfing. Therefore, the three genotypes used have a common background, and the effects observed can be related directly to the genotype in question. It cannot be stated categorically, however, that the effects are due to a single gene locus since the calculated genetic length of the segment under consideration is 5.26 crossover units. The number of heterozygous loci residing in this segment in addition to the single locus *Vv* is not known since this number will depend on the particular parents crossed to initiate the lines.

The results obtained show that competition is a major factor in affecting the performance of barley genotypes grown in a mixture. For yield of grain the effect is great enough to reverse the relationship when pure stands and mixed populations are compared. Major shifts also occur in the mixed populations for number of heads per unit area and number of kernels per head. Kernel weight is undisturbed.

The sign and magnitude of the shifts observed should caution the investigator in interpreting any results obtained from the use of conventional statistical

procedures in the analysis of data from characters where competition plays a major role.

The reversal in yield performance of the same genotype in pure stand vs. in a mixture is an important consideration when a population is approached for selection. Where high yield is the criterion selected for, say in the F_6, and the selection is intended for use in pure stands, then the instructions from the present study are that one should save the poorest plants from the F_6 rather than the good ones. This is a paradox to the plant breeder. On the other hand, if the rule shown has a degree of universality, it may explain why breeding for increased yield has progressed so slowly. Additional studies need to be conducted in other environments and with other plant material to determine how universal this rule may be.

The results obtained with isogenic lines in the present study suggest that statistical methods could be applied to similar cases in order to get estimates of genetic variances. A study of a short segment of the genome in a common background should increase the resolving power for defining the kinds of gene action involved. Biologically, it is possible to develop a series of isogenic lines which would cover segment by segment the entire genome of an organism. Each segment would involve linkage, and the degree of linkage would be related to segment length as determined by the amount of selfing. It also is possible to develop lines such that two or more segments, each on a different chromosome, could be studied simultaneously. Here, linkage would be zero for all inter-segment classifications.

Another technique for developing material for partial genome analysis is the chromosome substitution line as described for wheat by Sears (9) and Unrau, Person, and Kuspira (11). This technique makes use of a nullisomic line and the backcross in such a way as to substitute one entire exotic chromosome for study in an otherwise common background. In such a case the statistical analysis would have to consider both linked and unlinked genes but be confined to a single chromosome. The substitution technique can be extended to include two or more chromosomes for study simultaneously.

With techniques available for providing biological material suitable for the segmental study of a genotype, it would appear that a statistical analysis of such material should be less complicated and more directly interpretable as to the kinds of gene action involved.

SUMMARY

The three genotypes *VV*, *Vv*, and *vv* from an advanced isogenic line of barley contrasting the 6-row vs. 2-row head character were grown in pure stand and in F_2, $F_=$, F_3, F_4, and $F\infty$ populations.

Interplant competition between these three genotypes was measured for yield and the three components of yield—heads per unit area, number of kernels per head, and kernel weight.

Significant shifts due to competition were found for yield, heads per unit area, and number of kernels per head, whereas kernel weight was unaffected. The sign and magnitude of the shifts observed were of a degree to caution the investigator in interpreting the results obtained by the use of conventional statistical procedures in the analysis of characters greatly affected by competition.

Significant reversals in relative yield were found to exist in comparisons between the same genotype, *VV* or *vv*, when grown in pure stand and in an advanced generation, thus indicating that the poorest plants should be saved from an advanced hybrid population rather than the good ones when yield is the criterion for selection. If this phenomenon has a degree of universality, then it may explain why breeding for increased yield has progressed so slowly.

The application of statistical analyses to genome segments by use of isogenic and substitution lines for the purpose of more directly defining the kinds of gene action involved is discussed.

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DISCUSSION

D. R. KNOTT: Do you think it generally will be true that there is a good correlation between the yield of a genotype in pure stand and its yield as a single spaced plant?

G. A. WIEBE: There are very little critical data on this point. For the two homozygous genotypes used in this study, but in a different experiment, there was no change in their relative yields over a wide range of spacings, when grown in pure stands. In this test the competitive effect of unlike genotypes did not enter. More data are needed on the relation between the yield of single spaced plants, at a distance where competition is at a minimum, and in normal density stands. This type of information needs to be developed for a broad group of genotypes.

L. P. V. JOHNSON: Do you not consider that the 2-rowed, 6-rowed situation is a special case, since they are differently constituted with respect to the components of yield? Two-rowed varieties compensate for fewer seeds per spike by having larger seeds and a larger number of tillers per plant.

G. A. WIEBE: In some respects the 2-rowed *VV* vs. 6-rowed *vv* example considered here may be looked upon as a special case. Among world barleys one finds that these two types do differ rather consistently in their yield components. On the other hand, since approximately 25 per cent of the barleys in any world collection are 2-rowed, a cross of the type studied here would not be of unusual occurrence. In another study (unpublished) where blue vs. white aleurone was the distinguishing character used and the background was homozygous for 6-row, the same general results were obtained as for the 6-row vs. 2-row case in the present study in that the relative yields in pure stand were reversed from those in the mixture.

P. ROBINSON: In pure stands the yield $vv > VV$, in mixed stands $vv < VV$, but *VV* is taller than *vv* and in general the more vigorously growing plants will give a higher yield. Then is not the result (i.e., reversal) to be expected?

G. A. WIEBE: Yes, I think one would expect this result in the case of a mixture, but why does the type which shows up as more vigorous in a mixture give lower yields in pure stand? It seems to me we are lacking in basic knowledge of what competition is and its *modus operandi*. In the present case where the stand was dense in the mixture it is my opinion that competition was intense at an early stage and that the tillering character was heavily involved. I doubt that the difference in height had much influence on the results.

R. J. MIRAVALLE: The merit of mixtures of varieties, biotypes, genotypes, etc., may or may not be less than the components going into the mixture. For example, adaptation of a mixture to a wider range of environments than its components is supposed in cotton breeding.

G. A. WIEBE: The only comment I have is that the mixture of the genotypes tested in the present study yielded the same as the average of the components. No tests were made on adaptation of the mixture or the component genotypes over a range of environments. Conceivably, a mixture could yield significantly more or less than the average of the components grown separately. We lack critical data in this area and particularly so on criteria for selecting the component types so as to give superior yields when grown as a mixture.

W. D. HANSON: One of our problems in discussing plant competition arises from the lack of an acceptable definition. I consider it as the differential response of an experimental unit under different competing environments with reference to a base and a measurement criterion. To speak specifically of plant competition, we need to define the unit (such as a plant, a pot, or a single row plot), the competing population, and the measure. Consider that we wish to speak of competition with reference to a 16-foot yield row of soybeans. Competing conditions may arise from spacial arrangements, nutritional levels, genotypes, etc. If we further restrict our discussion to competition arising from a set of genetic types, for example, we can then describe a base competing population. With these restrictions and definitions we can develop a model for competition and design experiments to describe it. This approach was used by Sakai and also by myself (in a recent issue of Crop Science).

Diallel Analysis

Applications of the Diallel-Cross Techniques to Plant Breeding

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THE breeding of superior qualitative characters has long enjoyed effective genetic guidance and has prospered accordingly; but the breeding of superior quantitative characters has, to a large extent, been denied such guidance and has, therefore, been much less prosperous. The difficulty with quantitative characters is that they tend to be continuous in their variation. This means indistinguishable phenotypic classes and difficult or impossible applicability of classical Mendelian analysis.

Consider, for example, breeding for high yield. High yield is an important objective in most plant breeding projects; yet selection for it has come as a rather incidental, delayed-action step, taken in the final stages of the work when perhaps 99 per cent of the lines have been discarded on other grounds. For yielding capacity there has been no genetic information, no genetic guidance. Without genetic guidance, the plant breeder has had no rules to systematize selection of parents, to regulate the manipulation of progenies, or to permit prediction and isolation of superior lines.

It is not surprising, then, that the advent of the Fisher-Yates-Mather-Jinks-Hayman diallel-cross technique some 7 years ago was hailed by plant breeders as a long-overdue methodolgy for rationalizing the genetic study of continuous variation. And it would not be surprising if the utility of the new technique were subject to some degree of exaggeration.

Gilbert (2) has given a critical evaluation of the diallel-cross technique. He categorically criticizes the basic genetical assumptions of the technique and in so doing invokes eventualities, near and remote, and implies that the statistics involved must be inferentially valid. He concludes that the value of this technique is exaggerated and that information gained from it is little more than that obtainable from the parents themselves.

Many of the points raised by Gilbert are well taken, for the technique has many shortcomings. It appears, however, that he fails to appreciate fully that a statistical-genetic analysis must be based upon statistical assumptions and produce a statistical result. This consideration, coupled with the fact that a polygenic system is involved, makes it rather unfair, or even naïve, to expect that the diallel analysis will give results anything like those obtainable from classical

Mendelian analysis. And Gilbert fails to justify, genetically at least, his insistence on valid statistical inference. In Mendelian analysis we draw genetic conclusions about a certain character as exhibited by a certain hybrid. Any notion that the gene(s) involved might be of general occurrence comes from our knowledge of mutations, and of selection and transference of them, rather than from any thought of statistical inference. The fact that a method of analysis is statistical does not necessarily graft statistical inference onto the genetic conclusion. We are dealing with the same kind of genetic phenomenon. We are merely seeing it less directly.

Good plant breeders presumably have consciences. It has already been indicated that selection for high yield came as a weak and incidental phase performed on a very few hybrid lines originally selected for other agronomic characters. As far as yield was concerned, elimination had been random, unwitting, and of the order of 99 per cent. It does one's plant-breeding conscience little good to contemplate the enormous number of the very highest yielding lines unwittingly discarded during 50 years of modern plant breeding.

In 1954, the barley breeders at the University of Alberta conceived a breeding project in which yielding capacity was the primary character under investigation. Of first concern was the kind and number of parents to be used. We considered that they should be of diverse origin so as to provide differential genotypes. We considered using 10 to 20 parents in perhaps 50 to 100 crosses.

Fortunately, the first papers of Jinks (4) and of Hayman (3) came to our attention and revolutionized our plans. We saw in the diallel-cross technique two main advantages: experimentally, a systematic approach; and, analytically an over-all genetic evaluation that would be useful in identifying, in an early generation, crosses of best selection potential. Thus, our investigation took the form of a 15-parent, non-reciprocal diallel of 105 crosses, which, with the parents and one filler, were accommodated in an 11×11 simple repeated lattice design.

In considering the parents, we chose to disregard the rule that they be taken at random. The question of inferential validity was involved, and perhaps a relation to random mating; but we held these considerations less important than our practical knowledge of parental material at hand. We chose varieties Husky and Vantage because they were high yielding, Peatland because of possible good combining ability (both Husky and Vantage were derivatives of it), Jet because it was an exotic with presumably a highly differential genotype, and included a few random choices.

Yield was assumed to be a heritable, complex character comprising three components: number of heads per plant, number of kernels per head, and weight of seed. Expression of each component was presumed to be polygenically controlled, requiring separate analysis.

Analytically, we used the model of Hayman (3) which assumes:

1. parental homozygosity,
2. normal diploid segregation,
3. no difference between reciprocal crosses,

4. no multiple alleles,
5. no linkage, and
6. no non-allelic genic interaction.

The first three assumptions are usual ones and, in all probability, apply. Numbers 4 and 5 are made in the interests of simplicity and justified on the basis of probable unimportance. The last assumption is tested by the analysis as a null hypothesis.

In this paper we shall be able to deal with only a small part of the analytical results, which were reported at length by Johnson and Aksel (5). We shall consider certain results, first in terms of genetic information and second in terms of genetic guidance to plant breeding.

Table 1 gives the names and numerical designations of the barley varieties used as parents. Numbers 2, 3, 7, 8, and 13 are two-rowed varieties; the others are six-rowed.

TABLE 1.—NAME AND NUMERICAL DESIGNATIONS OF BARLEY VARIETIES USED AS PARENTS IN DIALLEL CROSSES.

Variety	No.	Variety	No.	Variety	No.
O.A.C. 21	1	Beecher	6	Peatland	11
Hannchen*	2	Sanalta*	7	Titan	12
Proctor*	3	Herta*	8	Jet*	13
Fjola	4	Velvon 11	9	Trebi	14
Plains	5	Husky	10	Vantage	15

*Two-rowed varieties, the remaining being 6-rowed.

Figure 1 shows a graphical analysis of the F_2 (1957) data for yield, based on an extracted 9 × 9 diallel (36 crosses).

The parabola, $W_r^2 = V_p V_r$, delimits the area in which coordinate data (W_r, V_r) may occur. The line of unit slope ($b = 1$) through the origin and $\bar{V}_r$, $\bar{W}_r$ ($\bar{V}_r = \bar{W}_r$ since $H = D$) is the line of complete dominance. Relative to the line of complete dominance, movement of the regression line of unit slope upwards ($\bar{V}_r < \bar{W}_r$ since $H < D$) would denote decreasing (partial) dominance, while movement downwards ($\bar{V}_r > \bar{W}_r$ since $H > D$) would denote increasing dominance (overdominance). The line represents the average response of all arrays. In the present case overdominance is indicated. The actual regression line (b = 0.635, not drawn) differs significantly from zero and from unity.

The relatively high variance of array 1 suggests non-allelic interaction, probably complementary. Such interaction tends to move the line to the right (as in increasing dominance) and to drop its slope below the expected value of unity.

The analysis was then repeated with array 1 excluded. Results are shown graphically in Figure 2.

It is now clear that array 1 must have contributed largely to the previous

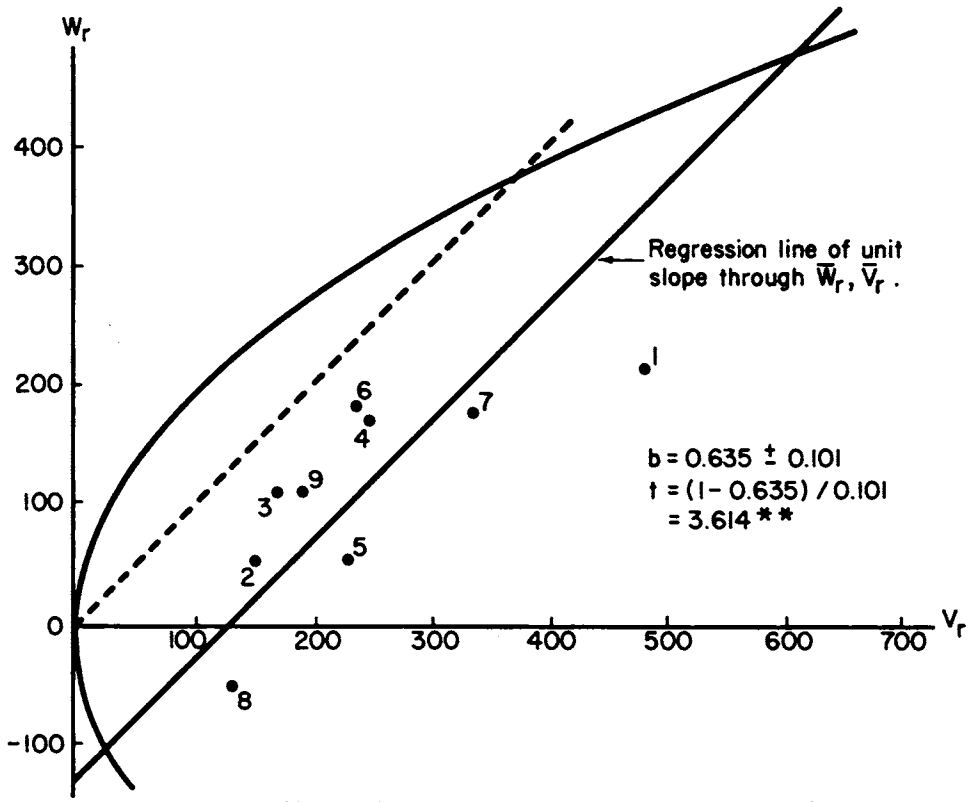

FIGURE 1. *Yield per unit area, F_2 (1957), arrays 1 to 9; V_r, W_r graph.*

deviation from unit slope. The regression line is now approximately of unit slope ($b = 1.087$).

Figure 2 provides an excellent linear example from which to discuss the order of dominance. Array 8, with its small W_r, V_r value, has the greatest excess of dominant alleles. Ascending the line, we meet arrays having increasing proportions of recessive alleles. Recessive alleles permit increased variability and larger variances.

From the analysis we see that the technique is sensitive to array expression of average degree of dominance and of non-allelic interaction.

Our investigation involved an unusual and interesting situation in that 6-rowed and 2-rowed parents are constituted differently with respect to components of yield. Six-rowed types have larger numbers of kernels per head; 2-rowed types compensate for fewer kernels per head by having larger kernels and more heads per plant. We shall see how this is reflected in the arrays of the F_2, grown in 1958. In this paper we shall deal only with number of kernels per head.

Figure 3A shows a remarkable relation between high number of kernels per head and degree of excess of recessive genes. The arrays of all 6-rowed parents

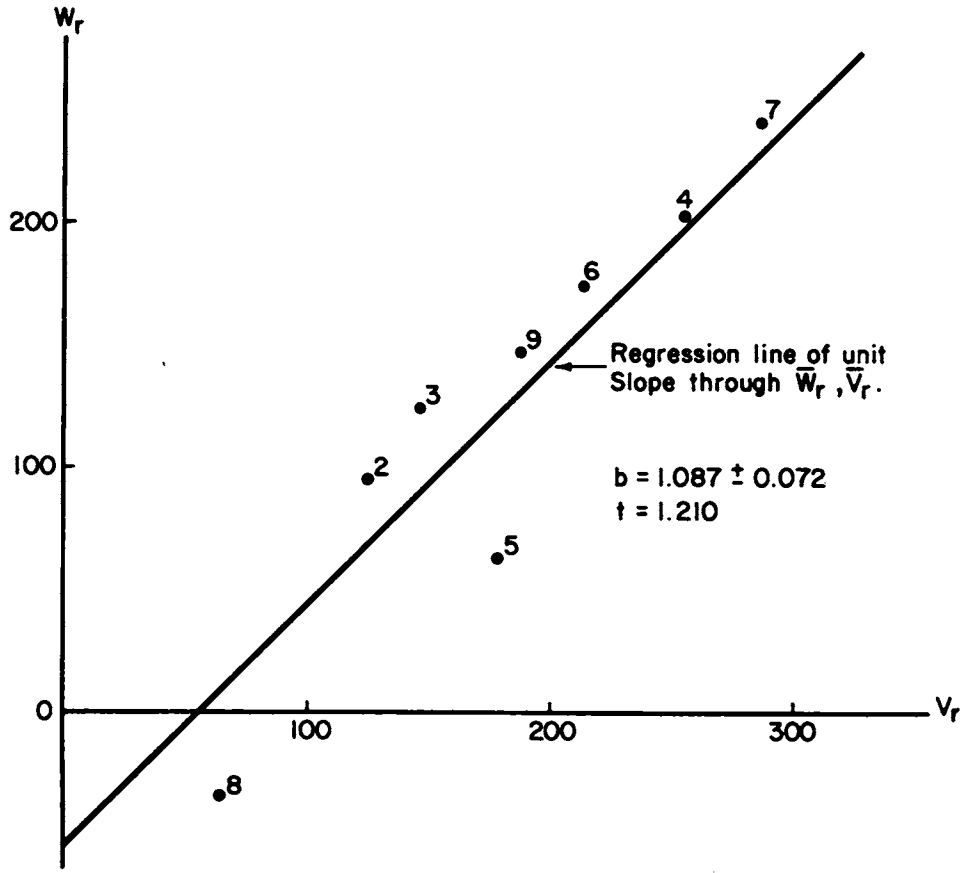

FIGURE 2. *Yield per unit area, F, (1957), arrays 2 to 9; V_r, W_r graph.*

are at the upper end of the line (excess of recessive alleles) except number 6, the Beecher array. (Beecher is a small-headed, six-rowed variety with a kernel number typical of two rowed varieties).

Figure 3B provides a direct examination of this relation. The standardized deviations of y_r, the parental measurements, and $(W_r + V_r)$, the order of dominance of the parents, were computed using the formula, $(x_i - \bar{x})/s$, where x_i is the value of the individual parent, $\bar{x}$ the mean of the parents, and s the standard deviation. The relation of quadrants to recessiveness and dominance and to high and low kernel numbers is indicated in the figure. The distribution of coordinate points and the correlation coefficient show a very close positive association between high numbers of kernels per head and an excess of recessive alleles, and between low numbers of kernels per head and an excess of dominant alleles.

The component, number of kernels per head, shows a strong, positive correlation with the complex character, yield. In this respect it is predominant over the other components.

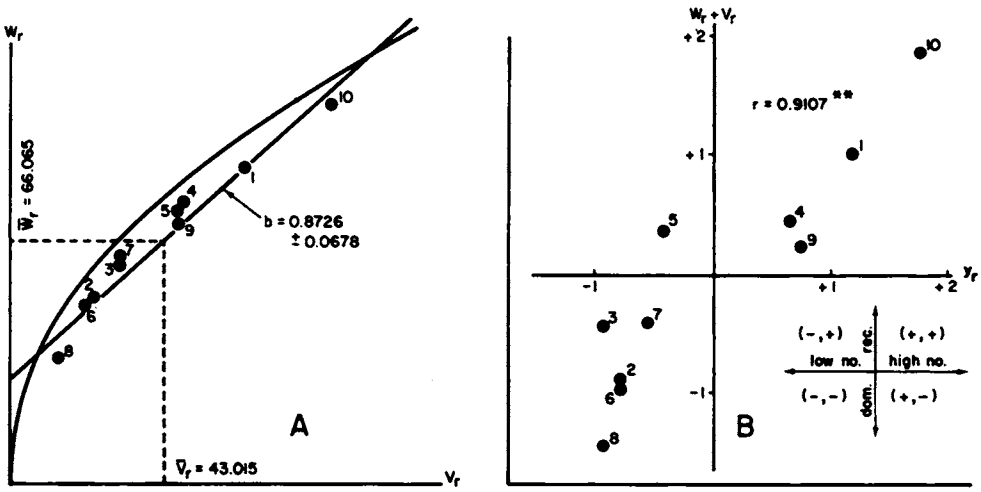

FIGURE 3. *Number of kernels per head, F_2 (1958). A. V_r, W_r graph. B. Standardized dev., y_r and $W_r + V_r$ graph.*

We have shown that the general diallel-cross analysis provides an over-all genetic and performance evaluation. This will enable the plant breeder to eliminate low yielding arrays on a reasonably sound basis, but he will wish to have every possible guidance in evaluating the selection potential of individual crosses. The higher-yielding crosses will have segregates of higher average yields, but the degree by which the highest yielding segregate deviates from the mean will depend upon the range of variability in the cross. This range may be measured by variance or standard deviation, but it is also reflected, and on a more strictly genetic basis, by scaling tests which detect non-conformance with the hypothetical assumption of independent action of non-allelic genes.

In Table 2 some of the crosses are evaluated by the scaling test, $\bar{F}_2 - (\frac{1}{2}\bar{F}_2 + \frac{1}{4}\bar{P}_1 + \frac{1}{4}\bar{P}_2) = 0$. The results point to the high selection potential of cross 2 × 8. This cross shows the highest average yield; it is most consistently high yielding, and its positive test value (denoting complementary gene action) is at the highest level of significance.

We have outlined a small part of the genetic analyses made on the 105-cross diallel (5). What advantages did this technique provide that were useful to the plant breeder? Let us enumerate them.

1. Compared to other methods available, the diallel-cross technique provided a more systematic approach to large-scale studies of continuous variation, and a better-disciplined analysis of the resulting data.

2. The over-all analysis provided reliable genetic information on dominance and recessiveness (averaged over-all arrays) and on complementary non-allelic interaction (averaged over-all crosses within an array). This information was obtained for yield and for the components of yield.

TABLE 2.—YIELDS OF INDIVIDUAL CROSSES (F_2 AND F_3, 1958) SHOWING SIGNIFICANT NON-ALLELIC INTERACTIONS BY THE SCALING TEST, $F_2 - (\frac{1}{2}\bar{F}_2 + \frac{1}{4}\bar{P}_1 + \frac{1}{4}\bar{P}_2) = 0$.

Cross	Scaling Test Values		Total Yield		Av. ($F_2 + F_3$)
	Sign	Degree of Signif.	F_2	F_3	
1 × 4*	+	0.01	737	1008	873
1 × 5	+	0.05	1037	1038	1038
1 × 8	+	0.05	759	962	861
2 × 4	+	0.10	849	999	924
2 × 8	+	0.01	1137	1125	1131
3 × 6	+	0.10	901	1026	964
3 × 8	+	0.05	1211	1048	1130
4 × 5	+	0.01	848	1042	945
4 × 8	+	0.05	984	1039	1012
5 × 7	+	0.10	809	909	859
5 × 8	+	0.01	800	980	890
5 × 9	−	0.05	1060	850	955
7 × 8	−	0.05	1089	856	973
9 × 10	−	0.10	1192	1033	1113
Highest yielding cross			1215 (3 × 7)	1139 (4 × 10)	—
Highest yielding parent			1233 (10)	1207 (10)	1220

*Parental numbers: 1. O.A.C. 21, 2. Hannchen, 3. Proctor, 4. Fjola, 5. Plains, 6. Beecher, 7. Sanalta, 8. Herta, 9. Velvon 11, 10. Husky.

3. The analysis demonstrated the primary importance of the yield component, number of kernels per head, a character that lends itself to practical selection techniques as a morphological reflection of yielding capacity.

4. The general analysis permitted genetically-sound elimination of a high proportion of arrays and crosses of low selection potential.

5. Scaling tests provided a more critical evaluation of the selection potential of individual crosses. Such tests detect crosses that are superlative in both highness of yield and significance of non-allelic interaction. Such crosses should have, as a theoretical probability, the highest yielding lines among their segregates.

Our experience in the project just outlined encouraged us to undertake a further and similar investigation in barley. A 12-parent diallel cross has been made with the objective of advancing knowledge on the inheritance of malting quality. The parents were selected for having, individually, high, low, or ideal levels and for having, collectively, all levels of the main components of malting quality. These components are barley nitrogen, wort nitrogen, malt extract, saccharifying activity, and alpha amylase, all in their varying amounts and proportions (see Table 3).

The parents, F_1, F_2, and F_3 of the 66 crosses will be grown in the field in 1961. To provide data for the analysis, malting tests will be made on samples

TABLE 3.—LEVELS OF MALTING QUALITY COMPONENTS IN PARENTAL VARIETIES.

Variety	Barley nitrogen	Malt extract	Wort nitrogen	Sacch. act.	Alpha amylase
O.A.C. 21	M	M	M	M	M
Parkland	M	H	M	M	M
Husky	M	M	L	L	M
U.M. 570	M	M	H	HH	H
Edda	M	H	H	H	—
Traill	M	L	L	M	M
York	M	H	LL	M	M
Pirkka	H	H	HH	H	HH
Wolfe	H	LL	M	LL	LL
H53-11	H	LL	M	LL	H
H53-505	M	H	M	M	M
Liberty	HH	LL	H	M	L
Ideal levels	L	HH	M	M	M

LL—Very low
L—Low
M—Medium
H—High
HH—Very high

from replicated plots of all parents and hybrids. An enormous number of segregates (say 50,000) will come under the scrutiny of this malting-test evaluation. Low-quality materials will be eliminated, first, on an array basis, later, on an individual-cross basis. The relatively few crosses retained will be tested on an individual-line basis in an effort to isolate highly superior malting types. It is hoped that all selection for malting quality may be made with sound genetic guidance.

Here, as in the former case, the diallel-cross technique permitted us to plan a large-scale investigation in a systematic way, and, again, we are able to look forward to a sound, over-all analysis of the resulting data.

Further analyses, now nearing completion, of the data from the 15-parent diallel cross (5) provide rather striking instances of the usefulness of the diallel technique in plant breeding. These studies, on sowing-to-heading and heading-to-ripening periods in barley and their relation to yield and yield components, were based on an extracted 10-parent diallel. Analyses are being carried out by Hayman's (3) method and by a single-array technique (1).

The results provide additional points toward the refutation of Gilbert's (2) statement that, for the plant breeder, the information gained from analysis of diallel crosses is little more than that obtained from the parents themselves. In the present instance, studies of parents would have revealed some information on correlations between the life-cycle periods and between these periods and yield or components of yield, information which is purely statistical or descriptive and entirely non-genetical. The diallel analysis, on the other hand, provided additional information on the genetic identity of several characters, on domi-

nance-recessive relations, on genic interaction, and on probable linkage associations. This information, greatly outweighing that obtainable from parental observations, will provide invaluable guidance in the plant breeding aspects of the investigation.

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DISCUSSION

J. L. FYFE: In cereal diallels at Cambridge it has never been the case that the analysis has indicated that one should not choose the cross with the highest mean (F_2 or F_3). This might not be the case in Dr. Johnson's 15 × 15 diallel, where the best cross in F_2 was Proctor × Herta. One of these parents is English and the other Scandinavian and it does not appear a likely cross from which to breed to get a variety for Canada. Did the analysis indicate this or did it indicate that it was worth breeding from?

L. P. V. JOHNSON: In our selection work, we look upon mean yield of a cross as one criterion of potential superiority. Other criteria are: range of variability, which indicates the degree by which the highest yielding segregate deviates positively from the mean, and the presence of complementary gene action, which may be expected to produce genotypes capable of expressing good combining ability. In choosing the cross of highest selection potential, we would look for the best balance between all three criteria.

As to the practical breeding value for Canada of parents of Scandinavian and English origin, I need only repeat that the cross Procter × Herta was one of the best. I would suggest that here superiority may have been due to complementary gene action which, in turn, may be attributed to the diverse origin of the parents.

W. D. HANSON: The point should be emphasized that the use of diallel approach in breeding program depends upon whether the crop is open-pollinated or selfed. Dr. Johnson has been dealing with a self-pollinated crop. The criterion of a good cross would be based on the value of homozygous lines generated by the cross. The variability associated with F_1 or F_2 in your diallel analysis is of value to you only as it reflects the potential of a cross to generate good homozygous lines. For this, you have no information. From soybean data which I have observed (and based on top yielding F_3 lines) I am led to conclude that a look at mid-parental values could serve as well as your diallel analysis for selecting potential crosses.

L. P. V. JOHNSON: We have emphasized our interest in assessing the variability within a cross because its range is a direct indication of the degree by which the higher yielding segregates deviate positively from the mean. Theoretically, the range of variability is also an indication, though less direct, of extremely-deviating homozygous lines. This becomes clear when one considers that homozygous genotypes occur in the proportion of $2^n/3^n$ of all genotypic classes and are well-distributed in the over-all segregation.

Mid-parental values, especially when used in scaling tests, may provide useful information on degrees of dominance and on non-allelic gene interaction. However, in a large diallel cross, it is unquestionably true that mid-parental values as treated in the complete analysis provide a more systematic and, probably, shorter procedure. Also, they provide a better over-all view of the genetic picture.

F. MORLEY: Claims are advanced for the diallel analysis which could be advanced for an array of alternate procedures. It is our work to evaluate alternative not to sell one technique or another to plant breeders or to each other.

L. P. V. JOHNSON: I have no doubt that Morley is right. As much might have been said for alternative procedures. But, we chose this particular method for our particular situation and, in reviewing our results, I have undertaken to make the best possible case for the diallel-cross technique. This has been done in the interests of promoting constructive discussion. Neither the time at my disposal nor my experience permit comparative evaluation of alternative procedures.

Notes on Diallel-Cross Theory

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THIS is a synthesis of some of my own ideas about the diallel cross with gleanings from the writings of Drs. Griffing, Jinks, and Kempthorne (see references below) and from memory of discussions with Drs. Breeze and Mather in Birmingham, England. However, none of these people are responsible for my interpretations of their work.

POPULATION THEORY

From a population point of view the diallel cross, or the set of all crosses within a set of inbred parent lines, comprises two populations, one being the parent lines themselves as reproduced by selfing and the other being the F_1 crosses. There is a two-way relation between the two populations. The F_1 population is the consequence of mating the parent population at random, and the parent population is a random sample from the F_1 population after inbreeding to homozygosity. The existence of these two populations and their interrelation means that information about the genetic system is lost either when one population is disregarded or when the two populations are treated as one. The original diallel analysis of Jinks and myself recognized the two populations and obtained the maximum information, although not quite in the manner presented here, but all analyses of variance of diallel tables (including 6) have lost information in one or other of these two ways. Analysis of variance of the parent and F_1 populations separately, together with their analysis of covariance, supply the full information.

STATISTICAL MODEL

The populations may be described by six statistical parameters as follows:

Parent population:	mean,	μ_0, and
	variance,	σ_0^2.
F_1 population:	mean,	μ_1,
	variance,	σ_1^2, and
	half-sib covariance,	γ_{11}.
Joint populations:	parent-offspring covariance,	γ_{01}.

The variation within and between the two populations is described by five parameters, $\mu = \mu_1 - \mu_0$ and the four second degree statistics. Griffing's (3) analysis of variance supplies unbiassed estimates of σ_1^2 and γ_{11} and Hayman (9) gives both unbiassed and maximum likelihood estimates of all the parameters (but note our γ_{11} and γ_{01} for Hayman's (9) c_{11} and c_{01}).

GENETICAL MODELS

The variation within the F_1 population can be expressed in terms of the variances of general and specific combining abilities:

$$\sigma_1^2 = 2\sigma^2_{gca} + \sigma^2_{sca} \text{ and}$$
$$\gamma_{11} = \sigma^2_{gca}.$$

Only the F_1 population is needed to estimate the variances of combining abilities. Evidently combining ability does not contain the maximum amount of information about the action of the genes by which the parents differ and, indeed, it is as much a statistical as a genetical, concept.

One satisfactory model of non-epistatic gene action was constructed by Mather (13). With d and h for additive and dominance effects and p and q for frequency of positive and negative alleles, the expressions of the statistical parameters in terms of genetical parameters (ignoring environmental variation) are

$$\begin{aligned}
\mu &= 4\Sigma p_i q_i h_i \\
&= h, \\
\sigma_0^2 &= 4\Sigma p_i q_i d_i^2 \\
&= D, \\
\sigma_1^2 &= 2\Sigma p_i q_i (d_i + (q_i - p_i)h_i)^2 + 4\Sigma p_i^2 q_i^2 h_i^2 \\
&= \tfrac{1}{2}D - \tfrac{1}{2}F + \tfrac{1}{2}H_1 - \tfrac{1}{4}H_2, \\
\gamma_{11} &= \Sigma p_i q_i (d_i + (q_i - p_i)h_i)^2 \\
&= \tfrac{1}{4}D - \tfrac{1}{4}F + \tfrac{1}{4}H_1 - \tfrac{1}{4}H_2, \text{ and} \\
\gamma_{01} &= 2\Sigma p_i q_i d_i (d_i + (q_i - p_i)h_i) \\
&= \tfrac{1}{2}D - \tfrac{1}{4}F
\end{aligned}$$

where

$$\begin{aligned}
h &= 4\Sigma p_i q_i h_i, \\
D &= 4\Sigma p_i q_i d_i^2, \\
F &= 8\Sigma p_i q_i (p_i - q_i) d_i h_i, \\
H_1 &= 4\Sigma p_i q_i h_i^2, \text{ and} \\
H_2 &= 16\Sigma p_i^2 q_i^2 h_i^2.
\end{aligned}$$

If the statistical parameters have been estimated unbiassedly then $\hat{D}$, $\hat{F}$, $\hat{H}_1$ and $\hat{H}_2$ derived from the above equations are also unbiassed. Two forms for the estimators of these genetical components are given by Hayman (9).

The estimators of F, H_1 and H_2 originally given by Hayman and Jinks were biassed and only accurate in large diallel crosses. If we denote Hayman's (7, p. 797) estimators by primes their expectations are

$$\epsilon D' = D,$$
$$\epsilon F' = F - 2F/n,$$

$$\epsilon H_1' = H_1 + (h^2 - H_2)/n, \text{ and}$$
$$\epsilon H_2' = H_2 + (h^2 + 4H_1 - 6H_2)/n + 6H_2/n^2$$

where n is the number of parents.

The proportional bias in the primed estimate of F is $2/n$ downwards. The biases in the primed estimates of H_1 and H_2 depend on h^2 as well as on H_1 and H_2. If the signs of the dominance deviations are balanced so that h is zero, the proportional bias in the primed estimate of H_1 is about $1/n$ downwards while for H_2 it is about $2/n$ downwards for large n with an upper limit of $1/6$ downwards for small n. If genes are coupled in repulsion, h^2 may be as large as kH_2, where k is the number of gene groups by which the parents differ. Since the number n of parents is about 2^k, it can then be shown that the bias in the primed estimates of H_1 and H_2 is upwards and decreases very slowly as n increases from two, from about 25 per cent for H_1 or from about 37 per cent for H_2.

It may appear from the estimates that h^2 is greater than kH_2. For instance, in Sprague's data quoted by Hayman (9) there were 10 parent lines so that k could not be greater than about three. Yet, the estimate of h^2 was 47 times the estimate of H_2. This indicates that Mather's model was not appropriate and indeed epistasis was known to be present in that data.

THE (V_r, W_r) GRAPH

The *rth* parent together with its offspring constitute the *rth* array of the diallel cross. If V_r is the variance of the *rth* array and W_r the covariance of the *rth* array with all the parents then, with Mather's model,

$$W_r - V_r = \tfrac{1}{4}(D - H_1)$$

so that $W_r - V_r$ is independent of r. The points (V_r, W_r) lie on that part of this straight line of unit slope within the limits $W_r^2 \leq V_r V_{OLO}$, where V_{OLO} is the variance of the parents. The constancy of $W_r - V_r$ is a criterion for the validity of Mather's model. Another criterion, mentioned above, is that the number of parents n should be greater than $2^{(h^2/H_2)}$. The assumptions in the model are that the parents are homozygous, that the genes are biallelic and that the genes act, and are distributed, independently.

The expected variance of $W_r - V_r$ depends on circumstances. The variance of $W_r - V_r$ between arrays is different from its variance between replicates. The latter in turn depends on whether replicates contain identical sets of genotypes (the usual circumstances) or are derived from independent samples of the parents. At present the only satisfactory test for variation in $W_r - V_r$ in small diallel crosses is an analysis of variance of $W_r - V_r$ (7). In large diallel crosses the theoretical variance(s) of $W_r - V_r$ may prove more useful.

If there is no evidence that $W_r - V_r$ is variable then the (V_r, W_r) graph exhibits the relative dominance properties of the parents (7, 10).

If $W_r - V_r$ is not constant, at least one of the assumptions of the model must be relaxed. The failure of each assumption characteristically distorts the (V_r, W_r) graph from a straight line of unit slope so that when $W_r - V_r$ is not constant this graph may indicate the more general model necessary to describe the genetical variation.

SMALL DIALLEL CROSSES

When the number of parents n is less than 10 none of the components of variation, either statistical or genetical, in the diallel cross can be significant estimates of population parameters. However, in this case, the individual parents and crosses are the main interest, and no population to which inferences might be made is envisaged. The experiment then lies in the domain of Eisenhart's (1) Model I, and an analysis of variance to test linear differences is appropriate. The information available from the small diallel cross is that there are certain differences between the parents, between the crosses, or between the general or specific combining abilities of the parents.

The over-all properties of the genes in the diallel cross can still be described from Eisenhart's suggestion that components of variance be estimated from a Model II analysis and that these be interpreted for the particular set of parents in the way that they would have been interpreted for a population when derived from a sufficiently large sample of parents. Three points require care here. Firstly, unbiassed estimation of the components is even more important with small diallel crosses than with large diallel crosses. Secondly, the errors of the components are derived from their empirical variation over replicates (14) and not from population sampling theory. In other words, the components are estimated separately from within each replicate and not from the usual analysis of variance over all replicates. Thirdly, the meaning of such definitions as

$$D = 4\Sigma p_i q_i d_i^2$$

should be realized clearly. In a diallel cross of eight parents, only three blocks of genes can differentiate them so that the above summation is restricted to the three corresponding block values of d_i. With four parents only two blocks of genes and two values of d_i are concerned. Similarly, H_1 and H_2 involve the measures of dominance, h_i, of only these two or three blocks of genes. The components D, F, H_1, and H_2 do not measure the variation potentially available from segregation. This third point applies to large diallel crosses, too, but it is much more serious to ignore it in small diallel crosses.

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DISCUSSION

F. W. SCHNELL: What is the justification for eliminating lines showing non-allelic interaction from the analysis, (a) concerning the possible breeding value of such lines and (b) from the standpoint of statistical theory?

B. I. HAYMAN: Parents showing non-allelic interaction are eliminated to reduce the set of parents to conform to the simple genetical model described above. The subsequent analysis provides no information about the eliminated lines. Elimination is justified in small diallel crosses because only particular parents are being investigated. Elimination is not justified in large diallel crosses whose parents were sampled from a population because it destroys the random nature of the sample and so destroys the basis of inference to the population. It could only be justified if the inference were shifted to the subpopulation containing no non-allelic gene differences.

The elimination of parents corresponding to the points in the (V_r, W_r) graph deviating most from the best-fitting line of unit slope is biassed by the skew distribution of V_r. Points to the right of the line (smaller $W_r - V_r$) are more likely to be selected by eye so that parents exhibiting the highest specific combining ability are eliminated. The remaining parents have lowered average specific combining ability. It is better to eliminate separately the parents corresponding to both the maximum and minimum $W_r - V_r$ even though the point corresponding to the former may not deviate much from the best line of unit slope (8, p. 351).

A. ROBERTSON: I am rather worried by the use of the diallel analysis technique for the detection of epistasis in a series of crosses. After all, what one finds when epistasis has in fact been claimed is merely that the experimental results do not fit in with the predictions made on the simple model, which of course is based solely on two alleles. Now this may be splitting hairs, but am I not allowed to say, when a particular cross is unexpectedly

good or unexpectedly bad, that this is because here we have two alleles at the same locus forming a combination which is otherwise unrepresented in this population of crosses? It seems to me that all we can really say is that the model is breaking down, and it seems to me unjustified to put the blame for this at the door of epistasis when it could equally well be ascribed to multiple alleles.

P. ROBINSON: We can obtain a weighted mean of $p \times q$, a "weighted" mean of d/a, and a "weighted" mean of $(p - q)$, for all genes. But, can one interpret these in any useful manner?

B. I. HAYMAN: The diallel analysis of Jinks and Hayman breaks the variances of general and specific combining abilities into parts that are not obtainable from a randomly mating population. This is to compare the additive, the dominant and to some extent the epistatic actions of the genes. If epistasis is absent H_1/D is an average of h^2/d^2 and so describes on the average the relative magnitudes of the additive and dominant actions of the genes. In particular, if H_1 is greater than D then at least one of the groups of genes by which the parents differ is over-dominant.

No such statements about gene action can be inferred from σ_A^2 and σ_D^2 although these contain all the genetical information necessary to predict the advance from selection in a randomly mating population. Both gene action and selection advance are of interest to geneticists and each is described by its appropriate set of statistics.

F. W. SCHNELL: To what extent would it be possible to interpret the set of parents as a random sample of a synthetic variety made by composing those parents?

B. I. HAYMAN: Such a synthetic variety would contain only a portion of the genotype of each parent. It would be more correct to interpret the synthetic variety as a random sample of the parents.

SEWALL WRIGHT: Ever since a rather extensive correspondence with Fred Hull a number of years ago, when he was developing tests for overdominance from diallel crosses, I have been much impressed with the advantages of this method at least from the standpoint of exploring the possibilities offered by inbred lines for producing a synthetic variety. Dr. Johnson's paper has very much reinforced this. I am, however, dubious on how far one can draw inferences with respect to anything but the lines themselves and their immediate crosses. Mr. George Rommel of the U. S. Bureau of Animal Industry started 23 lines of guinea pigs in 1906 and maintained them by exclusive brother-sister mating. When I took charge of them in 1915, six were already extinct in spite of much effort, others soon followed because of low fecundity or heavy mortality. The five best lines that remained would have been a good basis for producing a very good strain of guinea pigs (double crosses raised 80 per cent more young

per mating-year than these best inbreds), but statistics could hardly have been drawn from diallel matings among the latter that would have had any significance with respect to either the foundation stock or any synthetic derived strain. On the other hand, diallel crossing carried at least to F_2 fits in admirably with my philosophy of multiple selective peaks. The interaction components from analysis of a random breeding population indicates merely an obstacle to mass selection. The interactions indicated by diallel crosses tend to locate selective peaks and thus the opportunities for greater advance than possible from mass selection.

H. F. ROBINSON: I would like to comment further on the difficulty of providing random lines from an open-pollinated variety of corn. I wish merely to emphasize the point made by Dr. Wright that it is extremely difficult to produce random inbred lines that may represent, in proper frequency, the genotypes of the parent population. In two varieties of corn, starting with 300 S_0 plants, we have approximately 50 S_8 remaining in V_1 and 100 S_8 lines in V_2. A large scale study of these intra-variety F_1 line crosses, the reconstituted variety (F_1 crosses or a within-variety basis) is 4 per cent to 5 per cent higher yielding. One method of overcoming this difficulty is to use the reconstituted variety to compare with F_1's among the so-called "random" lines.

E. L. BREESE: The Jinks/Hayman diallel analysis developed as a quick means of recognizing different types of gene action in sets of inbred lines. The method has been used by Dr. Jinks to survey a wide variety of crop plants, and he was able to infer that in a majority of cases heterosis could be attributed to complementary gene-interaction and not, as hitherto postulated, to overdominance at individual loci. Thus, the technique has contributed greatly to our wider understanding of the genetic basis for heterosis.

It is not suggested that the method is a panacea for all plant breeding complaints. It can, however, provide a considerable amount of adjunct genetic information which could be of great value in formulating coherent plant breeding programmes. This is especially so when the information can be related to the past selective history of the inbred lines.

With regard to Dr. Comstock's comments, where a small set of inbred lines is to be regarded as a sample of our initial population, few people can be unaware of the dangers of unconditionally extrapolating the results.

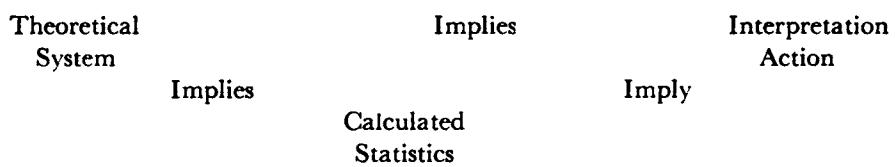
One further point: the removal of arrays in order to improve the regression is not an integral part of Wr/Vr analysis. This was suggested as a means of facilitating discovery of which parents contributed most to epistatic effects. Any inferences drawn were always substantiated by scaling and other tests.

B. I. HAYMAN: I agree with the comments of both Dr. Wright and Dr. Breese, except the latter's claim that Dr. Jinks has demonstrated that heterosis is usually attributable to complementary gene action. Epistasis seems to occur

in any highly heritable character if enough crosses are examined (8) but only in maize where there has been selection for heterosis is the epistasis positively correlated with the heterosis. As I have pointed out in my answer to Dr. Schnell's first question and previously (8), the determination of epistatically combining lines from the (V_r, W_r) graph can easily give a wrong impression of the relation between epistasis and heterosis.

Griffing's (5) careful investigation of epistasis between two genes shows that the advance of a randomly mating population under selection depends partly on additive variation and partly on additive × additive epistatic variation. On selection being relaxed, the additive part of the advance is maintained but the gene combinations reassort themselves to eliminate the epistatic part of the advance. In other words epistasis is orientated only while selection pressure is maintained and is randomly disposed in the absence of selection.

J. A. NELDER: The use of deductive systems involves the use of a triangle:



In practice, we use the indirect deduction through calculated statistics, and this can go wrong in at least two distinct ways. There may be over-robustness, in which case actual systems differing greatly from theoretical ones should produce different actions, but give calculated statistics giving the same action. There may be over-sensitivity, in which actual systems differing only slightly from a theoretical system give calculated statistics very different and hence different actions when they should give the same action. Gilbert has suggested that variance components may be over-sensitive in this terminology and perhaps that scaling tests may be over-robust. In putting forward any deductive system for actual use, it is desirable that it should not suffer from over-robustness or over-sensitivity.

B. I. HAYMAN: The weakness in Nelder's argument seems to be the tacit assumption of a rigid coupling between calculated statistics and consequent action. Knowledge of the parameters of the theoretical system is inferred from the calculated statistics and is in terms of confidence intervals or standard errors which specify not one action but a range of possible actions. Statistics (such as maximum likelihood estimators) with the most information about the theoretical system give the narrowest range of actions. Other statistics, correctly interpreted, give wider ranges of action. The important criterion is the information content of the statistics which is inversely related to the range of inferences and hence to the range of actions. I am not sure that consideration of robustness and sensitivity, as defined here by Nelder, is necessary in these circumstances.

Genetic Diversity, Heterosis, and use of Exotic Stocks

Genetic Diversity, Heterosis, and the use of Exotic Stocks in Maize in Colombia[1]

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THE cooperative corn improvement program of the Colombian Ministry of Agriculture and The Rockefeller Foundation was initiated in 1950 and is conducted at five experiment stations which, with their substations, represent elevations ranging from sea level to 8,500 feet. Since the program combines research and training, the day to day breeding work is carried out by Colombian agronomists. In addition, these agronomists conduct special research projects, the results of some of which are presented here.

At present, most of the corn produced in Colombia is used directly for human consumption. At high elevations, large grained flours and flints are preferred, while at lower elevations flints are favored. Dents are uniformly unpopular. With the growing importance of the animal industry, however, there are indications that this situation may be changing. The corn improvement program has therefore begun investigations of exotic materials, chiefly United States, Mexican, and Venezuelan dents, in the hope that heterotic effects will be found similar to those observed in flint-dent crosses in Cuba, the United States, and other countries. Other types of intervarietal crosses may also prove important, since experience in Colombia has shown that good breeding material tends to be of complex origin.

MAIZE COLLECTIONS

The "World Collection" of *Zea mays* maintained in the Western Hemisphere probably includes about 12,000 collections. The breakdown by areas of the available collections is shown in Table 1.

It will be noted that the collections from the United States and Canada represent only about 2.5 per cent of the total material. Furthermore, the great

[1]The studies and observations on which this paper is based were conducted under the auspices of the Department of Agricultural Investigations of the Colombian Ministry of Agriculture and The Rockefeller Foundation. Paper No. 137 of the Agricultural Journal Series of The Rockefeller Foundation. Paper was presented by Dr. William H. Hatheway.

[2]The author and the agronomists of the corn improvement program are grateful to Dr. William H. Hatheway and the members of the statistical program for advice and analysis of data.

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TABLE 1.—NATIVE STRAINS AND RACES OF MAIZE STORED IN THE GERM PLASM BANKS (2,3,5,7,8,9,10,12,13).

Collection center	Area	Number of collections	Races described
Mexico		4362	
	Mexico		25
	Cuba		7
	Central America		20
	West Indies		7
Colombia		4344	
	Colombia		23
	Bolivia		32
	Chile		19
	Ecuador		27 estimate
	Venezuela		25 estimate
	Perú		Unknown
Brazil		2508	
	Brazil and Eastern South America		52
United States		281	
	U.S. and Canada		4–6

bulk of investigations on corn have been with the Corn Belt Dent, a type of corn that has arisen from crossing and subsequent selection of only two races of maize which themselves represent less than 1 per cent of those described. This is certainly not a very large source population in regard to genetic diversity, nor does it constitute a very large source of potential heterosis. Brown (3) has stated that where hybrid corn breeding is of long standing, it has reached a "stage in its development where further significant increases in yield are difficult to achieve. When faced with this difficulty, the breeder then becomes particularly interested in new breeding techniques and new materials."

The Colombian program has had at its disposal the entire Andean corn collection as well as many of the collections from the Brazilian and Mexican germ plasm banks. On the whole, it has proved extremely difficult to obtain high-yielding hybrids from the inbred lines developed from native strains, even though a large number of these strains are fairly acceptable in plant and ear type, according to the usual conventions of corn breeders. The Colombian race Común, for example, is reasonably acceptable in plant and ear when judged as an indigenous type; yet, of the 154 collections of this race only 3 have been retained in the breeding program because of the poor yielding ability of the race.

Experience in recent years has shown that the best breeding material in Colombia usually originates from improved varieties or synthetics having complex origins. Examples of this type of material are the Cuban Yellow Flints; Tuxpeño from Mexico; Costeño and Puya Grande from Colombia; and the synthetics Venezuela 1 and Eto which were developed by Langham in Venezuela and Chavarriaga in Colombia. It has also been found that certain races of corn that are extremely undesirable on esthetic grounds as well as very low-yielding, exhibit a considerable amount of hybrid vigor when crossed.

All these types of corns—good and bad—make up the collections which are the world's only real source of material for the development of superior corn. The problem, however, is not simply one of screening 12,000 collections to find the best 10 or 20. Experience in the Colombian program suggests that the very superior corns—the Tuxpeños, Cuban Yellow Flints, Corn Belt Dents, and Etos—must be created. To appreciate the potentialities of the present collections for this purpose, we need only remember that Chavarriaga was working with relatively limited basic material when he produced Eto.

With the objective, therefore, of learning how to use the available collections of corn, the Colombian program has initiated preliminary studies on local-exotic crosses, intervarietal and inter-racial crosses, and genetic variances in several open-pollinated varieties.

LOCAL-EXOTIC CROSSES

Through the courtesy of a number of investigators, several exotic stocks have been obtained for planting in observation trials in Colombia. Beginning in 1957, crosses were made between Colombian material and these exotic stocks. Whenever possible, a cross that appeared promising as breeding material was carried to the F_2, F_3, or backcross generation.

The results of an experiment involving exotic crosses, which was planted at Palmira in 1960, are presented in Table 2. The design was a randomized block with four replications. The materials were as follows: Diacol H-205 and H-252 are yellow and white hybrids, respectively, and are recommended for the area in which the yield trial was conducted. Cuba 325 is a collection from Cuba of the Cuban Yellow Flint type. The West Indian Composite is made up of selected collections from the West Indies and the United States; it had been grown in Tennessee for 6 generations. Eto is a synthetic variety with germ plasm from Colombia, Venezuela, the Caribbean area, and, to a lesser extent, the United States. Eto Blanco was selected for desirable plant type from white segregates in Eto by means of numbered sibs. Zapalote-Corn Belt Synthetic is composed of Mexican races Zapalote Chico, Zapalote Grande, and U. S. Corn Belt material. Sintética Precoz is a synthetic made up of early maturing inbred lines, similar to the Caribbean and Cateto Flints. Blanco Común is the white component of the Colombian race Común. Nariño 330 Blanco is derived from a Colombian collection, a one-ear sample of yellow corn from which two rows were shelled and planted; white segregates were selected and increased to form this variety. Hays Golden, Cassel White, and Long Ear Synthetic are from the United States. The sample of Zapalote Chico is an advanced generation of strains collected by Dr. Edgar Anderson and the collecting group from the Mexican Germ Plasm Bank. These strains were crossed and maintained in Iowa.[4]

At first glance, about half the material listed in Table 2 appears to be of little value in Colombia. As shown in Table 3, however, yields of selected

[4]The Colombian program extends its thanks to Dr. W. L. Brown, of the Pioneer Hi-Bred Corn Company, who supplied stocks of Zapalote-Corn Belt Synthetic, Zapalote Chico, West Indian Composite, and Long Ear Synthetic.

TABLE 2.—YIELDS OF COLOMBIAN AND EXOTIC CORNS AND CROSSES. PALMIRA, 1960A.*

Pedigree**	Yield, bu./A. (15% moisture)	% of Blanco Común
Diacol H-252	101.2	146
Cuba 325 × West Indian Composite	93.7	135
Diacol H-205	92.7	134
Eto × West Indian Composite	91.8	133
Eto Blanco	88.5	128
Eto	87.1	126
(Zapalote-Corn Belt Syn.) × Eto[2]	85.7	124
Sin. Precoz × West Indian Composite	83.8	121
Zapalote Chico × Eto Blanco[2]	80.0	116
Long Ear Synthetic × Eto[2]	74.4	108
(Zapalote-Corn Belt Syn. × Eto)—#	73.4	106
Sintética Precoz	72.0	104
Blanco Común	69.2	100
West Indian Composite	63.1	91
(Eto × Hays Golden)—#—#	61.7	89
Nariño 330 Blanco	60.7	88
(Eto Blanco × Cassel White)—#—#	57.4	83
(Cuba 325 × Hays Golden)—#—#	55.1	80
(Eto Blanco × Zapalote Chico)—#	54.6	79
(Eto × Long Ear Synthetic)—#	47.5	69
(Nariño 330 Blanco × Cassel White)—#—#	46.6	67
Cuba 325	43.8	63
Zapalote Chico—#	32.5	47
(Zapalote-Corn Belt Syn.)—#	24.0	35
Long Ear Synthetic	20.2	29

L.S.D. 5% = 14.1 bu./A.
L.S.D. 1% = 18.7 bu./A.
*A = first planting season.
**Each—#—represents one sibbed generation.

crosses to Eto and other Colombian material are more encouraging. The first backcross of the Zapalote-Corn Belt and Long Ear synthetics to Eto approached the yields of the two recommended Diacol hybrids and possessed more acceptable market qualities than did the F_2's. The West Indian Composite, which is more closely related to Eto than are these two synthetics, exhibited some heterosis in the F_1. The most striking comparisons, however, concern the yields of crosses in relation, not to the yields of the parents or the recommended hybrids, but to the yield of the local native race. With the exception of the F_2 of the Eto × Long Ear Synthetic cross, all the yields shown equaled or exceeded that of the local race. While these data are from only one location and for only one planting season, they are nevertheless sufficient to illustrate that, although exotic maize may be grossly unadaptable and undesirable in appearance for a number of characters, the breeder's perseverance may be rewarded.

In Table 4, which presents similar data, the backcross and F_2 of the Eto Blanco × Zapalote Chico cross show some merit. Of particular interest, however, are the crosses of Cuba 325 and Sintética Precoz to the West Indian Composite.

TABLE 3.—YIELDS OF NATIVE AND EXOTIC VARIETIES AND CROSSES IN BUSHELS/ACRE AND IN PERCENTAGE OF YIELD OF PARENTS AND NATIVE VARIETY. PALMIRA, 1960A.

Pedigree	Yield, bu./A. (15% moisture)	Yield in percentage of		
		Parental mean	High parent	Native variety
Eto	87			126
F_1 × Eto	86	155	99	124
F_2	73	132	84	106
(Zapalote-Corn Belt Synthetic)—#	24			29
Eto	87			126
F_1 × Eto	74	138	85	108
F_2	48	89	55	69
Long Ear Synthetic	20			20
Eto	87			
F_1	92	123	106	133
West Indian Composite	63			
Diacol H-205	93			134
Diacol H-252	101			146
Blanco Común (native variety)	69			

L.S.D. 5% = 14.1 bu./A.
L.S.D. 1% = 18.7 bu./A.

Of these, the only locally adapted corn was Sintética Precoz. The yields of the other varieties were poor, but in the crosses high yields were obtained. The degree of heterosis over the higher-yielding parent is noteworthy: 149 per cent in the Cuba 325 × West Indian Composite cross and 117 per cent in the cross of Sintética Precoz × West Indian Composite.

Many of the best experimental double-cross hybrids now in tests in Colombia have one inbred line extracted from Cuba 325. Others include lines from Puerto Rico, Panama, and Venezuela, and other Cuban varieties. At Medellín, selected segregates of a cross involving a Colombian variety and 38–11 from the United States were bulked and then placed under selected sibbing. Experimental double-crosses incorporating this line have yielded 10 to 19 per cent more than the most recently released hybrid for that area.

One might question the practicality of using such exotic and unadapted material, particularly when the entire Andean corn collection as well as those from the Mexican and Brazilian germ plasm banks are available. Although the races from these three areas are extremely divergent phenotypically, there is nevertheless some question as to the genetic diversity among and within this material. It is known from both practical experience and intervarietal and interracial crosses that much of this material exhibits little heterosis, and this fact suggests that the material is rather closely related. Certain varieties and races, however, are excellent sources of high combining lines and exhibit a great deal of heterosis on a varietal as well as a line basis.

TABLE 4.—YIELDS OF NATIVE AND EXOTIC VARIETIES AND CROSSES IN BUSHELS/ACRE AND IN PERCENTAGE OF YIELD OF PARENTS AND NATIVE VARIETY. PALMIRA, 1960A.

Pedigree	Yield, bu./A. (15% moisture)	Yield in percentage of		
		Parental mean	High parent	Native variety
Eto Blanco	88			128
F_1 × Eto Blanco	80	133	91	116
F_2	55	92	62	79
Zapalote Chico— #	32			47
Cuba 325	44			63
F_1	94	176	149	135
West Indian Composite	63			91
Sintética Precoz	72			104
F_1	84	124	117	121
West Indian Composite	63			91
Diacol H-205	93			134
Diacol H-252	101			146
Blanco Común (native variety)	69			

L.S.D. 5% = 14.1 bu./A.
L.S.D. 1% = 18.7 bu./A.

INTERVARIETAL CROSSES

A number of studies concerning intervarietal crosses have been in progress for some time at the five breeding centers in Colombia. Torregroza (11) found that 7 crosses made up among 10 varieties exhibited an amount of heterosis that ranged from 1 to 20 per cent, with an average of 17 per cent. Some evidence of F_2 breakdown and epistatic effects was noted, although the population size was not large and genotype-environment interactions must be studied in more detail. In other experiments involving 12 highland varieties crossed diallelically, Torregroza and Varela (unpublished) obtained heterosis estimations in two locations which averaged 10 per cent over the higher-yielding parent.

Practical application of this type of study is illustrated by Table 5. These data on high-elevation varieties are selected from a randomized block of eight replications. The first cross, Cun. 365 × Ecu. 466, exhibited F_1 heterosis of 18 per cent over the higher-yielding parent. Although the isolated open-pollinated F_2 and F_3 generations did show some effect of inbreeding depression, the drop was small and yield still compared favorably with that of the widely grown native variety (Harinoso Mosquera). The F_1 of this intervarietal cross was released for commercial production as a "hybrid" in 1959. The cross of Blanco Rubi × Rocamex V-7 was also high yielding (16 per cent over the higher of the two parents), but the drop in the F_2 was more pronounced. The yield increase from the F_2 to the F_3 generation is noteworthy. Such increase, though often somewhat smaller, occurs in about 50 to 65 per cent of the family crosses that have been studied in Colombia.

TABLE 5.—YIELDS OF INTERVARIETAL CROSSES. TIBAITATÁ, 1960.

Pedigree	Yield, bu./A. (15% moisture)	Yield in percentage of		
		Parental mean	High parent	Control
Cun. 365	104			
F_1	126	123	118	117
F_2	113	110	109	101
F_3	119	116	114	106
Ecu. 466	101			
Harinoso Mosquera (control)	108			
Blanco Rubí	105			
F_1	121	121	116	121
F_2	107	102	107	102
F_3	120	120	115	120
Rocamex V-7	96			
Diacol V-551 (control)	100			

L.S.D. 5% = 7.9.
L.S.D. 1% = 10.3.

Table 6 is a summary of data from yield trials of eight varieties crossed in all possible combinations at three lowland locations. The low average yields are the result of extremely unfavorable conditions at the Montería station, where yields were about half those at Palmira and Medellín. Percentage of heterosis is presented as mean heterosis of all crosses involving any one variety. The lowest

TABLE 6.—AVERAGE YIELDS OF VARIETIES AND CROSSES AND AVERAGE PERCENTAGE OF HETEROSIS. MEDELLÍN, PALMIRA, MONTERÍA, 1957B*.

Variety	Yield, bu./A.	% Heterosis measured by	
		Parental mean	High parent
Nariño 330 Blanco	47.3	141	132
Nariño 330 Amarillo	50.6	138	129
Eto Blanco	67.7	123	108
Eto	64.9	117	104
Col. 2	57.5	126	116
Ven. 1	51.0	131	122
Ven. 305	48.0	137	128
Peru 330	41.0	152	134
Mean		131	122
Controls:			
Medellín Diacol H-251	75.4		
Palmira Diacol H-204	92.4		
Montería Diacol H-151	54.7		
Common Diacol H-203	66.5		
Common V-1	59.0		

*B = second planting season.

average amount of heterosis was 17 per cent, for Eto, and the greatest amount was that noted for Peru 330, 52 per cent over the mean of the parents. Mean heterosis for all varieties was 31 per cent. Yields of the F_1's exceeded those of the higher-yielding parents by an over-all average of 22 per cent. Mean heterosis for the varieties ranged from 4 to 84 per cent over the high-yielding parent. Lines of the varieties have been topcross tested against selected intervarietal crosses for reciprocal selection of lines to be used ultimately in double-cross hybrids.

At Palmira, a study is being made with the objective of replacing one of the program's highest-yielding commercial synthetics, Diacol V–101, which is not acceptable in the market because of its large-dented flour cap. Six varieties have been crossed in all possible combinations, increased through the F_2 and F_3 generations, and tested for two semesters. The cross of one of V–101's parents, a visually mass selected Tuxpeño from Mexico, with Nariño 330 Blanco yielded 22 per cent over the high parent in the F_1, 15 per cent over the high parent in the F_2, and 16 per cent over the high parent in the F_3. A cross of this same Mexican source with Eto Blanco outyielded the high parent by 34, 15, and 15 per cent in the F_1, F_2, and F_3, respectively. In addition, these entries outyielded V–101 by 9 to 35 per cent. It is possible that mass and visual selection for yield and grain type will result in even higher yields of corn with stronger market appeal.

Other types of selection may also prove successful. Cassalett (4) has reported that first cycle syn_2 yields of an intervarietal cross are about equal to the yield of the recommended hybrid in the Colombian lowlands. Additional data indicate that the syn_3 of this synthetic also equals the commercial hybrid in yield, and that the syn_2 and syn_3 generations of another synthetic derived from an intervarietal cross yield considerably more than the presently recommended variety.

GENETIC VARIANCES

The results obtained from intervarietal crosses leave little doubt that many of the varieties used in Colombia could be improved by recurrent or reciprocal recurrent selection. Before a large number of these studies is initiated, however, a more complete survey of the available material is needed, as well as more information about the genetic situations in some of the exceptionally good varieties. In order to study the types of selection and breeding program that can be used most advantageously with these materials, a series of Design I biparental progeny studies was begun in 1958.

Arboleda (1) has carried out Design I studies in Eto and Eto Blanco. Table 7 shows the analysis of variance of some of his data, and Table 8 presents components of variance, degree of dominance, and heritability. In Eto there was no apparent difference between additive and non-additive effects, but in Eto Blanco the genetic variance due to additive effects was very high. Although these results are for only one year, nevertheless they are in line with the behavior of these two varieties in the regular breeding program.

At the beginning of Arboleda's study, each male parent crossed to the four females was also self-pollinated. On the basis of the average performance of

each male family in 1958, S_1 seed of the highest yielding 10, 20, and 30 per cent of the male inbreds was bulked to form three synthetics for Eto Blanco (designated A, B, and C) and three synthetics for Eto (D, E, and F). Table 9 is a summary of the data from two seasons and five experiments for the yields of these synthetics in percentage of yield of the parent variety. Mean yield in bushels per

TABLE 7.—ANALYSIS OF VARIANCE OF GRAIN YIELDS OF 256 BIPARENTAL PROGENIES OF ETO AND ETO BLANCO. PALMIRA, 1958. (ADAPTED FROM ARBOLEDA)

Source of variation	d.f.	Mean Squares		M.S. Expectations
		Eto	Eto Blanco	
Blocks	15	0.3333	0.1516	
Replications in blocks	16	0.0687	0.0442	
Males in blocks	48	0.1086	0.1580	$\sigma^2 + 10\sigma^2p + 20\sigma^2f + 80\sigma^2m$
Females in males in blocks	192	0.0565	0.0588	$\sigma^2 + 10\sigma^2p + 20\sigma^2f$
Error	240	0.0309	0.3378	$\sigma^2 + 10\sigma^2p$
Within plots	459	0.0182	0.0224	σ^2
Total	511	0.0579	0.0338	

Data based on lbs. of grain/plant.

TABLE 8.—ESTIMATIONS OF COMPONENTS OF VARIANCE, DEGREE OF DOMINANCE, AND HERITABILITY OF GRAIN YIELD OF TWO RELATED VARIETIES. PALMIRA, 1958. (ADAPTED FROM ARBOLEDA)

	Variance due to plots	Variance due to female	Variance due to male	Additive genetic variance	Non-additive genetic variance	Grade of dominance	Heritability %	σ^2D/σ^2A
Eto	0.00127	0.00128	0.00065	0.00260	0.00253	1.385	12.18	0.97
Eto Blanco	0.00142	0.00125	0.00124	0.00496	0.00005	0.140	19.07	0.01

TABLE 9.—YIELDS OF SIX SYNTHETICS IN DIFFERENT GENERATIONS OF SYNTHESIS IN PERCENTAGE OF PARENT VARIETY. PALMIRA 1960A, 1960B.

Pedigree	Mean yield in bu./A. of parent variety	% yield of parent variety		
		Syn 1	Syn 2	Syn 3
Eto	104			
Eto I Syn D		119	106	118
Eto I Syn E		108	110	100
Eto I Syn F		112	107	107
Eto Blanco	112			
Eto Blanco I Syn A		111	106	113
Eto Blanco I Syn B		108	111	122
Eto Blanco I Syn C		109	108	118

acre for the parent varieties is also given. The improvement of yield in the Eto Blanco synthetics is noteworthy. Another series of synthetics will be made up on the basis of two-year means of the individual crosses, using selection pressures of 10, 20, and 30 per cent against the 256 individual crosses.

CONCLUSION

In this presentation of some of the research being carried out by the joint corn improvement program of the Colombian Ministry of Agriculture and The Rockefeller Foundation, the chief aim has been to illustrate the kind of work that can be done with the tremendously varied stocks of maize now available to investigators and to call to mind certain principles of applied evolution and genetics which have not been stressed during the past 30 years of hybrid corn breeding. Use of the many strains and races of maize available for study may shed new light upon the mechanisms of heterosis. It is also possible that, with modern field techniques, these new materials can be subjected to "old-fashioned" breeding schemes—intervarietal crosses, mass selection, and the like—with a high probability of success.

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DISCUSSION

C. H. HANSON: I am not clear as to the difference between what you call the F_2 generation of a variety cross and the syn_2 generation.

W. H. HATHEWAY: The nomenclature used in the Colombian corn program may be illustrated by the following example:

(Eto) I syn_3 means

first cycle (I) of a recurrent selection program third (3) synthetic generation, in the variety "Eto." (Eto) I syn_1 would refer to those plants growing from seed derived from crosses of selected lines of the variety "Eto."

K. KOJIMA: Exotic stocks have quite different evolutionary backgrounds, so the study of divergent genetic crosses in Drosophila species may help to set up a sound program for utilization of exotic germ plasm in plant breeding. Information relevant to this connection is (1) behavior of linkage—epistatis complex indicated in the F_1 heterosis and F_2 breakdown, (2) environments in which the programs are to be set up (e.g., high altitude or low; North America or South), and (3) recombination cycles prior to selection study, etc.

W. H. HATHEWAY: I agree that study of crosses of divergent stocks in Drosophila would be useful in helping us understand how exotic germ plasm affects the performance of native material. My feeling is basically this: (1) It has been shown that exotic material can in some cases raise grain yield in maize, (2) introduction of exotic germ plasm into active stocks is not difficult (intermediate breeding stations are not required), and (3) relatively small amounts of exotic germ plasm may be necessary. The last is pure conjecture, but could be checked cytologically. This would be especially easy in Drosophila. I certainly would like to know how introduction of small amounts of exotic germ plasm into a population affects the genetic variability of that population, if additive components are affected more or less than dominance components, and so forth. This whole question borders on the introgression problem: just what happens when widely divergent strains or species cross? May one expect to find surprising effects? And if so, what genetic mechanisms are involved?

R. H. MOLL: The cross of an adapted and an exotic variety out-yielded the cross of two adapted varieties indicating the potential utility of genes in exotic corns in certain combinations and suggests that the adaptability (reflected by relative yield) is not indicated by the adaptability of the two parents.

	Jarvis	Indian Chief	Diente de Cabello	Mayorbela
Jarvis	.510	.569	.528	.544
Indian Chief		.533	.617	.586
Diente de Cabello			.364	.317
Mayorbela				.374

W. H. HATHEWAY: I should say that the adaptability reflected by relative yield is not indicated by the *average* adaptability of the two parents. On the other hand, your data suggest that *at least one* of the two parents should be adapted. I should like to see the results of some backcrosses to Indian Chief. I should also like to know something about the genetic variances in populations derived from these crosses and backcrosses.

S. WRIGHT: I would like to comment on the role of overdominance in the multiple peak model. Multiple peaks depend on intermediate optima (with qualifications brought out by Kojima) and pleiotropy (or genetic correlation). Overdominance tends instead to reduce the number of selective peaks. Overdominance and multiple peaks have in common that they imply more or less non-additive genetic variance, but while utilization of the additive variance by mass selection leads to the best possible genetic system, permitted by the genes that are present if there is only one selective peak, this is not in general the case if there are multiple peaks, irrespective in both cases of overdominance. Even with only 5 or 10 per cent additive variance, maximal improvement of plants and animals would be a very simple matter if it were not for multiple peaks.

L. BAKER: Can estimates of genetic correlations between important traits in composites using exotics be meaningful relative to detection of when desirable or undesirable linkage relations might be present?

R. E. COMSTOCK: Distinction should first be made between (1) linkage of genes having primary effects on different characters and (2) linkage of genes with primary effects on the same characters. The first kind of linkage will contribute to genetic correlation between different traits. Genetic correlations with desired sign would suggest that linkages of the first kind were generally in the desirable phase. However, unless the correlations were quite high the evidence would not be compelling because genetic correlation reflects pleiotropy and the distribution in the chromating material of genes affect-

ing the two traits as well as linkage. The problem is lack of benchmarks. One could never say how high the correlation would be if a maximum proportion of linkages were in favorable phase or how low it would be if a maximum proportion were in unfavorable phase.

Finally, there seems no obvious way to deduce anything about linkage between genes affecting the same trait (second class of linkages) from genetic correlation between that trait and any other.

W. H. HATHEWAY: How important really is the recombination problem in using exotic material? Couldn't a single chromosome or part of one affect considerably the variability of a variety? This possibility could conceivably be checked cytologically at least in corn. This would involve chromosome knobs and other cytological markers. Thus, good lines derived from a (Col. 1 × 38–11) mixture could be examined for chromosomes or parts of them foreign to Col. 1 but present in 38–11. The best lines might actually contain only small amounts from 38–11.

R. E. COMSTOCK: What you propose might be found to be the case without, to my mind, demonstrating that "the recombination problem" is not important. The hypothetical finding you describe would indicate that a small amount of chromatin material from 38–11 had been effective for improvement of genetic material that originated otherwise from Col. 1. It would tell you nothing about further potential improvement not realized because other potentially useful genes in 38–11 were not freed by recombination from chromosome blocks composed largely of genes less favorable than their Col. 1 alleles.

W. D. HANSON: The average segment length of parental gene blocks following a mating procedure can be formulated as a function of a parameter, sf(m), where s is the characteristic genetic map length for a chromosome map and f(m) involves the mating procedure (Hanson, Genetics, 1959). For a species such as corn, one might expect about 60 per cent of the chromosome to be transmitted intact through a single meiotic division. In an adapted × exotic cross the chromosome homologies may be reduced. If this reduction in recombination frequency is of the order of .5 that expected, then one might expect about 80 per cent of the chromosome to be transmitted intact through a single meiotic division. It is not too difficult to see why one could recover essentially the adapted type when selection pressures are applied immediately following a cross between adapted and exotic types of corn. Further, if one has a measure of the reduction in recombination intensity for such crosses, he can at least formulate the results of intermating cycles.

Estimation of Genetic Variances and Heritability

Genetic Variability for Quantitative Characters in Alfalfa[1]

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WHEN a crop plant is selected for higher yield or some specific production character, estimates of genetic variability for the characters involved are of interest because they make possible a choice of the more efficient methods of selection, the prediction of the progress of the selection itself, and an estimate of the cost. Indeed it is well known that the success of a selection program is dependent mainly on the amount of genetic variability present in the selected populations and on the method of selection used. Moreover, the knowledge of genetic correlations among production characters and between production and other traits helps to improve the efficiency of selection by the use of favorable combinations of characters and to minimize the retarding effect of negative correlations. For these reasons, and to obtain data on some aspect of alfalfa breeding pointed out by studies on different ecotypes of this important fodder plant (1), a genetic study of characters of agronomical and botanical interest has been conducted. The type chosen for the experiment was strain L 99/100, developed by the Stazione Sperimentale di Praticoltura di Lodi (Milan), and known in culture as Florida variety.

ORIGIN OF THE STRAIN L 99/100

This type was selected a few years ago from material previously mass-selected during a period of about 25 years. The parental types probably came from the region of the Po Valley around Cremona and Lodi (Milan) and were adopted for strong stems, abundant and wide leaves, persistence in culture, and drought resistance.

Some hundred plants superior for leaf production and other agronomic traits were selected in 1948 and studied in single plant cultures for their behavior on dry as well as irrigated fields. The superior plants were selected and in groups of two were allowed to be pollinated by Bombus bees under isolation in cages. Plants within the progeny of these families were selected and again paired plants were pollinated under isolation. The subsequent progeny was tested under dry as well as irrigated culture conditions.

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The strain L 99/100 represents the progeny of one of the selected families which was found to be more or less satisfactory for all the characters considered.

This type can be described briefly as follows: vigorous plant with several erect and thin stems covered by leaves from the base; average height about 120 cm; leaves dark green with ovate-lanceolate shape; flowers from light to dark violet, occasionally also green or violet with green stripes.

CHARACTERS CONSIDERED IN THIS STUDY

Traits of agronomic interest

1. Earliness: the number of days from May 21 to the beginning of flower production.
2. Plant height, in cm, at the first cut.
3. Number of stems per plant at the first cut.
4. Weight of the stems in gr (taken as the average of two observations each made of three stems sampled at random at the first cut).
5. Weight of the leaves in gr (taken as the average of two observations like the weight of the stem).
6. Ratio of weight of stems to weight of the leaves.
7. Weight of the green plant in gr at the first cut.

Traits of botanical interest

Size of the leaves observed on a random sample of two subterminal leaves per crop:

8 and 9: length and maximum width of central leaflets in mm; average of two determinations.

10 and 11: length and maximum width of lateral leaflets in mm, average of four determinations of the two leaves sampled.

12 and 13: ratio of the average length to the average width for the central and the lateral leaflets.

Size of the flowers observed on a random sample of four flowers per plant:

14 and 15: length of the calicine tube and of the flower (calicine tube + vexillum).

EXPERIMENTAL PROCEDURE AND METHOD OF ANALYSIS

The experiment was initiated in April 1957, when a sample of 60 plants (genotypes) of L 99/100 were taken at random from a 2 year old alfalfa field. Each plant was subdivided into four propagules. As far as possible, the propagules were uniform for size of the root system and for the number of stems. They were transplanted into four experimental plots in rows 50 cm apart with a distance of 50 cm in the row. This was done according to a design which required one propagule per plant into each plot and complete randomization within plot. The four plots can be considered as four different random replications of all the 60 plants sampled.

Observations were made for the characters listed above in 1957 and repeated in 1958. Earliness (trait no. 1) was not observed in 1958, while the weight of the green plant (trait no. 7) was not taken in 1957.

Since the four replications were genetically identical propagules for each of the 60 sampled plants, a hierarchic analysis of variance can give an estimate of variance for differences between plants which may be considered due to genetic and environmental influences, and an estimate of variance for differences between propagules within plants which may be considered due to environmental influences only.

A general scheme of analysis of variance with p plants and r replications, and the expected and observed composition of variances, where y represents the mean number of propagules per plant, is given in Table 1.

TABLE 1.

Sources of variability	Degree of freedom	Sum of squares	Mean squares	Expected components	Observed components
Total	pr−1	D_T	—		
Between plants (genotypes)	p −1	D_P	V_P	$\sigma_E^2 + y\sigma_G^2$	Q + yG
Between propagules within plants	(pr−1)−(p−1)	D_C	V_C	σ_E^2	Q

Considering that phenotypic variance is made by a genetic and an environmental component, and assuming that phenotypic variance equals unity, it may be found that (2):

$$\sigma^2_P = \sigma^2_E + \sigma^2_G$$

and

$$\frac{\sigma^2_P}{\sigma^2_P} = \frac{\sigma^2_E}{\sigma^2_E + \sigma^2_G} + \frac{\sigma^2_G}{\sigma^2_E + \sigma^2_G} = e^2 + h^2 = 1,$$

where h^2 designates heritability, namely the genetic portion of variability when phenotypic variance is equal unity, and e^2 designates the environmental portion of phenotypic variability. h^2 and e^2 are obtained from the observed components of variance as follows:

$$h^2 = \frac{G}{Q + G} \text{ and}$$

$$e^2 = \frac{Q}{Q + G}.$$

Covariance analysis of data obtained for two traits, A and B, performed under the same scheme summarized for analysis of variance gives estimates of genetic

and environmental components of phenotypic covariance, namely G_{AB} and Q_{AB}. From these phenotypic correlation coefficients and the genetic and environmental correlation coefficients are obtained:

phenotypic correlation coefficient, $r_{AB} = \dfrac{Q_{AB} + G_{AB}}{\sqrt{(Q_A + G_A)(Q_B + G_B)}}$,

genetic correlation coefficient, $r_{G_AG_B} = \dfrac{G_{AB}}{\sqrt{G_A \times G_B}}$, and

environmental correlation coefficient, $r_{Q_AQ_B} = \dfrac{Q_{AB}}{\sqrt{Q_A \times Q_B}}$.

RESULTS

Genetic variability

Estimates of the mean of the phenotypic variance as well as of the genetic and environmental components of variance, of h^2 and e^2 obtained from the data collected in two subsequent years are given in Table 2.

1. *Earliness.* This character shows a rather high h^2 estimate. Selection applied with a suitable method should be efficient. It is important to stress here that earliness in alfalfa is very important for yield, being connected with the number and time of cuts, and for possible simultaneous production of seeds on all the plants.

2. *Plant height.* Heritability estimates are not very high, about 0.09 the first year and 0.04 the second year. The mean values for the two years show that in 1958 the clones reached a complete recovery from clonal multiplication. However, there is also an increase of phenotypic variability and particularly of the environmental portion which contributes to give less reliable data for selection purpose. These conclusions tend to weaken the importance of this character as a descriptive one for varieties.

3. *Number of stems per plant.* The mean number of stems per plant markedly increases from the first to the second year. Genetic variability which gives a very low h^2 value the first year cannot be estimated on the second year, since variance between plants is smaller than variance within plants.

4. *Weight of the stems.* The average weight of the stem was found to be constant in the two years, that is, it was found to be independent from effect of clone subdivision or aging. This aspect and the sufficiently high estimates of heritability from 0.11 to 0.20 stress the importance of this character for selection.

5. *Weight of the leaves.* A drop in the mean for this character is shown in the second year. At the same time phenotypic variance and its genetic part are also reduced giving a smaller estimate of h^2. With aging, environmental influences tend to mask the genetic variability and to decrease the possibility of judging the genotype from the phenotype. It should be noted, however, that

TABLE 2.—MEAN ($\bar{x}$), PHENOTYPIC VARIANCE (s^2_P), GENETIC (s^2_G) AND ENVIRONMENTAL (s^2_E) COMPONENTS OF PHENOTYPIC VARIANCE, h^2 (HERITABILITY) AND e^2 ESTIMATES FOR THE CHARACTERS STUDIED IN L 99/100 STRAIN OF ALFALFA.

Characters	Year	Mean ($\bar{x}$)	s^2_P	s^2_G	s^2_E	h^2	e^2
1. Earliness, days from May 21	1957	10.94 ± 0.49	54.02	8.54	45.48	0.158	0.842
	1958	(1)	—	—	—	—	—
2. Plant height, cm.	1957	80.86 ± 0.99	228.05	19.76	208.29	0.087	0.913
	1958	114.76 ± 1.27	371.18	13.72	357.46	0.038	0.962
3. Number of stems	1957	8.79 ± 0.31	23.19	1.33	21.86	0.057	0.943
	1958	48.67 ± 0.96	(2)	(2)	—	—	—
4. Weight of the stems, gr.	1957	5.27 ± 3.40	11.74	1.26	10.48	0.107	0.893
	1958	5.38 ± 3.10	9.60	1.91	7.69	0.199	0.801
5. Weight of the leaves, gr.	1957	4.79 ± 3.25	43.86	34.34	9.52	0.783	0.217
	1958	3.15 ± 1.86	3.18	0.55	2.63	0.173	0.827
6. Weight of stems/weight of leaves	1957	1.21 ± 0.02	0.2872	0.0153	0.2719	0.053	0.947
	1958	1.81 ± 0.04	0.5306	0.1791	0.3515	0.337	0.663
7. Weight of the green plant, gr.	1957	(1)	—	—	—	—	—
	1958	309.92 ± 10.71	27372.94	1737.12	25635.82	0.063	0.937
8. Length of the central leaflet, mm.	1957	20.09 ± 3.10	9.58	0.06	9.52	0.006	0.994
	1958	21.67 ± 3.32	10.96	2.07	8.89	0.189	0.811
9. Width of the central leaflet, mm.	1957	5.66 ± 1.24	1.5454	0.0044	1.5010	0.003	0.997
	1958	7.59 ± 1.84	3.3890	0.2734	3.1156	0.081	0.919
10. Length of lateral leaflets, mm.	1957	17.32 ± 2.66	7.10	0.06	7.04	0.009	0.991
	1958	18.42 ± 3.39	11.44	0.60	0.84	0.052	0.948
11. Width of lateral leaflets, mm.	1957	4.65 ± 0.99	(2)	—	—	—	—
	1958	6.13 ± 1.61	2.55	0.23	2.32	0.091	0.909
12. Length/width of the central leaflet	1957	3.72 ± 0.09	1.92	0.01	1.91	0.005	0.995
	1958	2.93 ± 0.03	0.2600	0.0288	0.2312	0.111	0.891
13. Length/width of lateral leaflets	1957	3.89 ± 0.04	(2)	—	—	—	—
	1958	3.09 ± 0.03	0.2101	0.0732	0.1369	0.348	0.652
14. Length of the calicine tube, mm.	1957	2.41 ± 1.24	(2)	—	—	—	—
	1958	2.77 ± 0.31	(2)	—	—	—	—
15. Length of the flower, mm.	1957	10.12 ± 4.18	(2)	—	—	—	—
	1958	10.12 ± 2.32	(2)	—	—	—	—

(1) not observed.
(2) variance between plants smaller than variance between clones within plants.

on the second year h^2 still remains high enough (0.17) to indicate a character for which good progress by selection can be expected.

6. *Ratio of weight of the stems to the weight of the leaves.* Low h^2 estimate has been obtained for the first year, while for the second year the h^2 estimate is high, 0.34. No practical conclusions seem to be suggested at present by this character for breeding purpose.

7. *Weight of the green plant.* This trait has received much attention from alfalfa breeders because it is thought to combine different production characters such as plant height, number and weight of the stems, and weight of the leaves. From the data herein, however, it appears that the complex aspect of the character results in a high phenotypic variance connected with a limited genetic portion of variability. This means that the genotype cannot be evaluated satisfactorily from the phenotype and that the breeder can make little progress selecting for the gross character.

Also, characters 8 to 13 involving size and shape of the leaves seem of little interest for selection, at least for the alfalfa type considered in this research. The size of the leaves is certainly larger in the second year than in the first. This may be due either to a complete recovery from clonal subdivision or to a gross environmental influence.

Heritability estimates for length and width of the central and lateral leaflets (characters 8 to 11) are small in the two years with the exception of the length of the central leaflet which gives an h^2 estimate of 0.19 for 1958.

The average ratios between length and width of the leaflets (characters 12 and 13) are found smaller the second year with respect to the first year. Genetic variability is either not detectable or gives a very small h^2 estimate on the first year, while it exhibits higher h^2 estimates in the second year.

The characters observed on the flowers (14 and 15) showed similar estimates of the means for the two years, but no estimate of h^2 was obtained from the data collected.

Concerning the results obtained on the strain L 99/100 in relation to alfalfa breeding, only the following characters, among all those studied, were found to be suitable for immediate improvement under mass selection:

1: earliness

4: weight of the stems

5: weight of the leaves.

Other characters may be considered for selection, namely (2) plant height, (3) number of the stems, and (7) weight of the green plant. However, progress under mass selection is likely to be limited, because of the low heritability estimates found.

The problem of description of types may also be considered on the basis of the above results, and from the conclusions reached during a cooperative program for the study of different ecotypes in alfalfa described by Haussmann (1). Plant height, number of stems per plant, the ratio of weight of the stems to the leaves, and leaf sizes were unsuitable for a description of types, because the

variability of differences shown at subsequent cuts, different locations, and years was too high. Similarly, the results presented herein show that variations of the same traits are largely dependent on environmental influences. Production characters like weight of the stems and of the leaves were, on the contrary, found to be more suitable for a description of alfalfa types in different locations and years since their variation was shown to be mainly dependent on the genetic background.

CORRELATIONS BETWEEN CHARACTERS

Correlations between the different characters is another aspect which should be kept in mind for better planning of selection programs for improving production characters.

Selection for one character will result in a progress for all positively correlated but in a regress of all negatively correlated characters. These relations suggest the possibility of taking advantage of relations between characters considering a scheme of selection for more than one character at the same time, or minimizing the negative influence of negative correlations between characters using a suitable index of selection.

For the above reasons a study of phenotypic, genetic, and environmental correlations has been performed for the characters which gave estimates of genetic variability, using the data collected in 1958. The various correlation coefficients between the characters studied are given in Tables 3, 4, and 5.

These tables show that production characters are correlated with each other and one may assume that such associations are due to a common genetic background acting in the same direction on all the characters. Also some of the environmental correlation coefficients reach the point of significance for P 5 per cent or 1 per cent, indicating that environment is exerting a common influence on such characters.

No significant correlation coefficient is found for the association between plant height and the morphology of the leaflets, measured by their length, width, and the ratio of length to width.

Negative genetic correlation coefficients are found for the association between the weights of stem and leaves and the width of central and lateral leaflets. Such correlations seem of importance because improvement in yield is associated with narrow leaflets.

The length-width ratio of leaflets is positively associated with production traits, because of the negative correlation between production and width of the leaflets.

Length and width of the leaflets are positively correlated with each other; the width of central and lateral leaflets is negatively correlated with the length-width ratio. Highly significant positive correlation coefficients are also found between the length-width ratios of central and lateral leaflets.

The correlation data given in tables 3, 4, and 5 are important for a selection program intended to increase the yield in alfalfa. It is indeed possible to improve different yield characters by selection applied for one character only,

TABLE 3.—PHENOTYPIC CORRELATION COEFFICIENTS (r_{AB}) BETWEEN THE CHARACTERS STUDIED ON L99/100 ALFALFA TYPE.

Characters	h^2	4. Weight of the stems	5. Weight of the leaves	6. Weight of stems/ weight of leaves	7. Weight of the green plant	8. Central leaflet, length	9. Central leaflet, width	10. Lateral leaflets, length	11. Lateral leaflets, width	12. Central leaflet, l/w	13. Lateral leaflets, l/w $h^2=0.35$
2. Plant height	0.04	+0.263**	+0.185**	+0.094	+0.545**	(1)	(1)	(1)	(1)	(1)	(1)
4. Weight of the stems	0.20		+0.797**	—	+0.369**	(1)	−0.187**	(1)	−0.175**	+0.186*	+0.187*
5. Weight of the leaves	0.17			—	+0.370**	(1)	−0.189**	(1)	−0.175**	+0.705**	+0.143*
6. Weight of stems/ weight of leaves	0.34				−0.007	(1)	(1)	(1)	(1)	(1)	(1)
7. Weight of the green plant	0.06					−0.073	−0.114	−0.097	−0.138*	+0.006	+0.001
8. Central leaflet, length	0.19						+0.789**	+1.090**	+0.796**	—	(1)
9. Central leaflet, width	0.08							+0.685**	+0.935**	—	−0.653**
10. Lateral leaflets, length	0.05								+0.724**	(1)	—
11. Lateral leaflets, width	0.09									−0.505**	—
12. Central leaflet, ratio length/ width	0.11										+0.910*

*Above P 0.05 level of significance: 0.132.
**Above P 0.01 level of significance: 0.173.
(1) Covariance between plants smaller than covariance between clones within plants.

TABLE 4.—GENETIC CORRELATION COEFFICIENTS ($r_{G_AG_B}$) BETWEEN THE CHARACTERS STUDIED ON L 99/100 ALFALFA TYPE.

Characters	h^2	4. Weight of the stems	5. Weight of the leaves	6. Weight of stems/ weight of leaves	7. Weight of the green plant	8. Central leaflet, length	9. Central leaflet, width	10. Lateral leaflets, length	11. Lateral leaflets, width	12. Central leaflet, l/w	13. Lateral leaflets, l/w $h^2=0.35$
2. Plant height	0.04	+0.555**	+0.312*	+0.407**	+0.535**	(1)	(1)	(1)	(1)	(1)	(1)
4. Weight of the stems	0.20		+1.014**	—	+0.782**	(1)	−0.519**	(1)	−0.447**	+0.817**	+0.531**
5. Weight of the leaves	0.17			—	+0.517**	(1)	−0.607**	(1)	−0.480**	+0.990**	+0.520**
6. Weight of stems/ weight of leaves	0.34				+0.270	(1)	(1)	(1)	(1)	(1)	(1)
7. Weight of the green plant	0.06					−0.093	−0.020	−0.067	−0.601**	+0.027	0.000
8. Central leaflet, length	0.19						+0.396**	+0.500**	+0.316*	—	(1)
9. Central leaflet, width	0.08							+0.767**	+0.967**	—	−0.679**
10. Lateral leaflets, length	0.05								+0.654**	(1)	—
11. Lateral leaflets, width	0.09									−0.834**	—
12. Central leaflet, ratio length/ width	0.11										+0.721**

*Above P 0.05 level of significance: 0.250.
**Above P 0.01 level of significance: 0.325.
(1) Covariance between plants smaller than covariance between clones within plants.

TABLE 5.—ENVIRONMENTAL CORRELATION COEFFICIENTS ($r_{E_AE_B}$) BETWEEN THE CHARACTERS STUDIED ON L 99/100 ALFALFA TYPE.

Characters	h^2	4. Weight of the stems	5. Weight of the leaves	6. Weight of stems/ weight of leaves	7. Weight of the green plant	8. Central leaflet, length	9. Central leaflet, width	10. Lateral leaflets, length	11. Lateral leaflets, width	12. Central leaflet, l/w	13. Lateral leaflets, l/w $h^2=0.35$
2. Plant height	0.96	+0.245**	+0.179*	+0.061	+0.546**	(1)	(1)	(1)	(1)	(1)	(1)
4. Weight of the stems	0.80		+0.748**	—	+0.325**	(1)	−0.141	(1)	−0.135	+0.077	+0.038
5. Weight of the leaves	0.83			—	+0.360**	(1)	−0.134	(1)	−0.132	+0.037	+0.021
6. Weight of stems/ weight of leaves	0.66				−0.060	(1)	(1)	(1)	(1)	(1)	(1)
7. Weight of the green plant	0.94					−0.073	−0.122	−0.108	−0.100	+0.004	+0.002
8. Central leaflet, length	0.81						+0.870**	+1.187**	+0.878**	—	(1)
9. Central leaflet, width	0.92							+0.681**	+0.941**	—	−0.697**
10. Lateral leaflets, length	0.95								+0.731**	(1)	—
11. Lateral leaflets, width	0.91									+0.469**	—
12. Central leaflet, ratio length/ width	0.89										+1.010**

*Above P 0.05 level of significance: 0.153.
**Above P 0.01 level of significance: 0.202.
(1) Covariance between plants smaller than covariance between clones within plants.

and it is possible to increase the response to selection for one character, for example, the weight of leaves, by selecting at the same time for another character more easily detectable, such as plant height.

The negative association found between yield characters and the width of the leaflets points to the need for considering this trait when selecting for higher production. A combined selection for both yield characters and large leaflet would indeed give much less response than would be expected on the basis of the genetic variability available for both characters and the selection pressure applied.

SUMMARY

Hierarchic analysis of variance of data collected from cuts of several plants (genotypes) was used to give estimates of genetic and environmental variances for many production and morphological characters in strain L 99/100 of alfalfa, grown as variety Florida. Phenotypic, genetic, and environmental correlation coefficients between characters have also been obtained by using covariance components from covariance analysis.

Heritability estimates suggest that a few characters may be improved by mass selection: namely, earliness, weight of the stems, and weight of the leaves. Other traits can be improved by selection, but a limited response will be expected; namely, plant height, number of the stems, and weight of the green plant.

The estimates of the genetic correlation coefficients show that production characters are positively correlated with each other. It is thus possible to increase the efficiency of selection for one character by simultaneous selection for other production characters. The negative genetic correlation coefficients found between production characters and width of the leaflets emphasize the point that selection for larger leaflets must be avoided when selection is aimed to increase yield.

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DISCUSSION

F. MORLEY: Unless the plant yields were taken very early or very late in the growing season, are not they meaningless in relation to agricultural production? Moreover, what about viruses in these cuttings?

R. E. SCOSSIROLI: As indicated, all the yield traits have been observed at the first cut, that is at the time in which they are really meaningful for agricultural production.

For what is concerning the second point, we were aware about the possible influence of viruses on production traits and on variability components. For this reason we accurately checked all the plants for the presence of viruses and we did not consider for the analysis an entire group of clones from the same plant when they showed virus symptoms. Incidence of viruses however was very low.

R. E. COMSTOCK: A point has been made that the heritability estimates found in this study tend to be low. The size of the heritability estimate must be judged in the light of the fact that the estimate here is on the single plant basis. For single plant estimates they really cannot be judged as low though some unknown amount is probably genetic difference in recovery to subdivision of plants.

Heritability: A Second Look

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IN any research program involving the estimation of heritability it is essential at the outset to know exactly why such an estimate is required. This is a truism, but in many instances it would appear that the estimation of heritability is the prime object of the experiment, rather than a link in the chain of research. Unfortunately, this is a criticism which can be leveled against many statistical techniques; they come to be regarded as an end in themselves, rather than a means to an end. Instead, they should, of course, be regarded merely as tools—albeit useful, and often powerful, tools—in the hands of the research worker.

Several reasons have been put forward for requiring an estimate of heritability. Lush (5), for example, lists the following four points:

1. When heritability in the narrow sense is high, reliance should be placed mainly on mass selection, and as heritability becomes lower more emphasis should be placed on pedigrees, sib tests, and progeny tests.
2. If the epistatic variance is relatively high, more reliance should be placed on selection between families, and linebreeding.
3. If overdominance is prominent, the breeding plan should turn toward inbreeding, with the object of producing hybrids for the commercial market.
4. If the variance due to interactions between heredity and environment is relatively large, the breeding plan tends more toward producing a separate variety for each ecological region.

The following point might also be added:—

5. Heritability in the narrow sense may be used to estimate expected improvement due to selection.

It will be noticed that heritability is mentioned specifically only in points 1 and 5; estimates of variance components are required when consideration is given to the other points. Heritability itself is defined in terms of variance components, and this is where more emphasis should be placed; i.e., on the separation of the total observed variation (V_t) into that portion which is due to genetic factors (V_g), subdivided into that which is due to additive effects (V_a), that which is due to non-additive effects of gene action, and that portion which is due to non-genetic factors (V_e). Heritability in the narrow sense is merely the name given to the proportion V_a/V_t. It is well known that proportions are difficult to deal with

statistically, and that there is a loss of information when one considers a single number, i.e., the ratio, as opposed to its two components. Fisher (2) has criticized the use of heritability on these grounds.

In spite of this, it is a useful notation expressing the importance of genetic factors in influencing a particular trait. It would be of considerable advantage to the research worker if he were able to say that, in general, the heritability of a particular character was, say, 70 per cent. In many cases this is possible; for example, in work where the environment can be reasonably controlled, as in the laboratory or in growth chambers or in situations where the genetic content of the various populations does not vary appreciably. Unfortunately, the plant breeder working under field conditions cannot control the environment to any large extent, and in addition, different breeders work with different genetic material. In animal breeding experiments, on the other hand, the environment can be controlled to a much greater extent, in addition to which, the animal itself can exercise some control on its environment by moving to more suitable conditions. There is, therefore, often a marked difference between plant and animal breeding experiments in the ease with which environmental variability can be controlled.

There are also other differences between the two areas of research which limit the use of heritability estimates more severely in plant breeding. One of these is that the animal breeder has a well defined unit, the individual animal, with which to work, whereas the unit in plant breeding is often the "plot," which has no fixed size. Size of plot affects variability and therefore heritability. Further, the plant density within the plot will also affect heritability, particularly if density has a direct effect on the character being studied, such as leafiness. It is also possible in some plant experiments to define heritability on a replication basis, as well as on a single plot basis. By increasing the number of replications it is possible, theoretically, to increase this estimate of heritability to as close to unity as we please.

With heritability depending so much on the choice of plot size, planting density, and number of replications, it is obvious that heritability estimates must be treated with some caution, and the comparison of estimates for a particular character obtained by different workers is of doubtful utility.

Even if all these factors could be standardized, the variability encountered in the field militates against the general use of a mean estimate of heritability. If the mean obtained were, say 70 per cent, a research worker would know that, in general, he could use a program of mass selection, but he would still have to obtain an estimate from his own data in order to be satisfied that this was the correct approach. Frey and Horner (3), for example, give estimates of heritability (based on regression coefficients) of date of heading for 22 crosses of oats which varied from 12 per cent to 102 per cent in one year. The mean heritability obtained was 43.7 per cent, and the standard deviation was 21.4. With this type of variation it would appear that the research worker is chasing a will-o'-the-wisp if he hopes to establish a mean heritability estimate for general use.

In order to reduce the variation, Frey and Horner suggest an estimate of heritability "in standardized units." This change increased the mean to 61.5 per cent, but the standard deviation was reduced only slightly to 17.4. This estimate is equivalent to using the correlation coefficient between parent and offspring instead of the regression coefficient. There can, of course, be an appreciable difference between the two coefficients, and the question then arises as to which is the better estimate of heritability. It is well known that if the X-values (in this case, the parental values) are selected, the correlation coefficient is biased, whereas the regression coefficient is not. Another reason for suggesting the use of the correlation rather than the regression coefficient is that the former is always less than (or equal to) unity, whereas the latter is not. Theoretically, heritability cannot exceed unity, but estimates sometimes do. In such cases, either the statistical or the genetic model is wrong. Unfortunately, it is difficult to separate the causes, but often a transformation to obtain a more normal distribution seems to help. This procedure is probably better than trying to cover up errors in the model by using the correlation coefficient.

Modifications, such as this, to the definition of heritability seem to confuse the issue, rather than helping, and the use of heritability "in the broad sense" and "realized heritability" add to the confusion. It would be of considerable benefit to restrict usage of the term to heritability in the narrow sense, as some authors already do (1). Heritability in the broad sense may be regarded as an estimate of the upper bound of heritability in the narrow sense, and should not be used if the latter is available. It has been claimed (4) for example, that, with clonal material, heritability in the broad sense may be used to estimate expected improvement from selection. The argument is based on the fact that plants are vegetatively reproduced, and therefore total genetic variability is of interest, not merely the additive portion. If clones are to be selected for vegetative reproduction, the improvement may be estimated directly from clonal means. If clones are to be selected for crossing in order to establish new lines, then heritability in the narrow sense should still be used.

Finally, one might legitimately ask, if an estimate of heritability is as restricted in its application as indicated here, and since a ratio is not as informative as a knowledge of its two components, is there any point in estimating heritability? In many cases, a selection program can be decided upon from an examination of mean squares in an analysis of variance. However, a meaningful estimate of heritability is of use in estimating expected progress from adopting that program, and it is also a very useful concept in determining the relative importance of genetic effects which may be passed on to offspring, even in cases where it would be difficult to extrapolate to other populations.

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DISCUSSION

W. D. HANSON: I would like to relate this presentation to that given last week. Even though the unit (animal) is well defined in animal work, one still finds considerable confusion in the use of the statistic, heritability. In plant work the confusion is magnified. In addition to problems introduced by modes of reproduction, a measurement taken on a field plot is an expression of a family of genotypes for many cases. These ramifications led to a consideration of relative genetic variability in terms of selection concepts. The pertinent question is whether we should continue to use the term heritability for such modified cases.

F. MORLEY: One must extrapolate in the real world, and one must use estimates of heritability derived by someone else, especially with new crops in new environments. Therefore, it is important to specify exactly how published estimates were obtained in order that others may extrapolate.

P. ROBINSON: The dangers of extrapolation in research work are generally well known, but do not appear to be sufficiently stressed in plant breeding work under field conditions. With a complex character such as yield, which is influenced by a large number of factors—both genetic and environmental—it is unlikely that all of these factors will remain relatively constant from one set of conditions to another. With less complex characters, influenced by only a few factors, the relevant conditions may be more easily standardized. In the former, then, extrapolation should be made with extreme caution. As Dr. Morley points out, it is important to specify exactly how published estimates of heritability were obtained—both as regards methods of calculation, and also as regards techniques of collecting the data, and conditions under which parents were selected and the plants grown. With this detailed information a research worker may be able to judge how closely his own conditions relate to those in which other estimates were obtained.

In the laboratory or the growth chamber environmental conditions are more easily controlled, and extrapolation will not involve the same dangers, although even here caution must be exercised.

W. D. HANSON: Certainly we need to know the background of a heritability estimate. However, I do not attribute a uniqueness to any one estimate due to problems already discussed. As data become available, a relative variability concept among characters for a crop evolves. With recommended testing procedures with F_3 soybean lines; for example, I know that I should realize a gain of about 20–40% for yield, 50–65% for protein, 60–70% for oil, and 70–80% for maturity of the selection difference. This information is valuable and can be used in planning breeding programs.

SEWALL WRIGHT: There has evidently been considerable drifting in the meanings of the term heritability and the symbol h^2. I think that I introduced the latter in a paper in 1920 as the degree of determination by heredity. It was intended to contrast with the degree of determination by environmental variability (e^2) and thus was in the broad sense. The analysis of total variability into such components is of course still older. R. A. Fisher made such an analysis of human characters in 1918. I analyzed variability in an array of inbred strains into that within and between strains in 1918. Weinberg in 1910 was clear about such an analysis. I think that Lush introduced the term heritability and the narrow sense of the additive component. I disagree with Dr. Robinson that h^2 should not be used comparatively. The whole point of my 1920 paper was the comparison between $h^2 = 0$ within an inbred strain and $h^2 = .40$ in the random bred control stocks. Both derived from parent-offspring correlations.

P. ROBINSON: The above remarks also have a bearing on Dr. Wright's comment. It is of course possible to make comparisons of heritability estimates under properly controlled conditions. Very often, however, comparisons are made, with no real basis for such comparisons. One could draw a parallel with comparisons of means. Only under certain circumstances is it possible to compare, say, the mean yield of treatment A in experiment I with the mean yield of treatment B in experiment II, where the two experiments are conducted at different times or in different locations.

R. SCOSSIROLI: I would like to make a proposal with the goal to have a clear terminology. We have already been using h^2 to indicate heritability estimates from single individuals, h^2_{fa} = heritability estimate obtained on the basis of family means, and in such a sense we used h^2_D to indicate heritability estimates from full-sib family, h^2_S from half-sib family and $h^2_{2(D+S)}$ as a combined estimate. I would like to propose that a series of subscripts might be used as follows:

h^2 = heritability on individual basis on a broad sense,

h^2_{fa} = as above, the same for h^2_S, h^2_D, and $h^2_{2(D+S)}$,

h^2_A = heritability on the basis of additive variance only (it may include also the realized heritability),

h^2_{A+D} = heritability on the basis of additive + dominance variances,

h^2_{A+D+I} = heritability on broader sense, including interaction from epistasis. The subscript I can have I_{AA}, I_{AD}, and so on to indicate the type of epistatic interaction involved.

P. ROBINSON: Several research workers, e.g., Falconer, are already using the term heritability and the notation h^2, with no qualifying phrases or subscripts, to denote heritability in the narrow sense. This seems to be a logical usage because it is heritability in the narrow sense which is of prime interest in determining the degree of inheritance of a quantitative character. Some standardization of notation and terminology is certainly required for heritability defined in other senses, and possibly something along the lines suggested by Dr. Scossiroli would help to clarify the position.

S. WRIGHT: It seems to me that the essential thing in using the term heritability is to specify clearly in every case the nature of the character and the unit (individual plot, etc.) and the nature of the total population (including environment). A mere list of heritabilities of some undefined character (.1, .3, .5, etc.) is meaningless without this information, even for action.

R. E. COMSTOCK: I agree wholeheartedly. Dr. Wright has put his finger on a vital issue. I remember a paper in which two quite different estimates of heritability for the same character were reported. The author was puzzled by the difference having failed to distinguish that the unit was in one case a single plant observation and in the other a family mean based on two or more plot values.

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