EVALUATION OF SINGLE-CROSS SELECTION METHODS WITH SIMULATED POPULATIONS

Thesis for the Degree of Ph. D.
MICHIGAN STATE UNIVERSITY
BAHMAN EHDAIE
1970

This is to certify that the

thesis entitled

Evaluation of Single-Cross Selection Methods with Simulated Populations

presented by

Bahman Ehdaie

has been accepted towards fulfillment of the requirements for

Ph.D degree in Agronomy

Charles E. Cress
Major professor

Date February 10, 1970

O-169

ABSTRACT

EVALUATION OF SINGLE-CROSS SELECTION METHODS
WITH SIMULATED POPULATIONS

By

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Three methods of breeding, namely, top-cross, reciprocal recurrent selection (RRS), and the Hallauer method, were evaluated and compared under various genetic situations. Since genotypic-environment interaction was not in the scope of this study, environmental variation was a random normal variable.

Genetic models used were additive (A), complete dominance (CD), pure overdominance (OD), optimum number (ON), additive by additive initial variance at gene frequencies 0.5 (AA), and additive by dominance initial variance at gene frequencies 0.5 (AD). A range of starting gene frequencies in population A and B were studied for each genetic model. Mild and strong selection intensities were practiced in the generated experiments to find the effect of selection intensity on the rate of progress. Ten cycles of selection were performed for the (RRS) experiments, eight for the "Hallauer" experiments, and four for the top-cross experiments. Progress in the hybrid population was the primary objective for study for each breeding method. Thirty independently segregating loci, each with two alleles, were simulated to determine a single character.

Greater responses were observed in the hybrid population when stronger selection was practiced except for the situations where the equilibrium gene frequency was present in the parental populations with (RRS) and the top-cross methods.

The top-cross method was competitive with the Hallauer and (RRS) method with regard to progress made in the hybrid population for a wide range of gene effects except for the case when over-dominant gene effects or selected epistatic effects were present. The top-cross tester was a completely recessive inbred line. When additive genetic variance was important, improvement in the hybrid population was similar for the Hallauer and (RRS) breeding methods. As non-additive genetic variance became notable, the Hallauer method was superior to the (RRS) method as well as the Top-cross method.

Under some genetic models, (RRS) was ineffective in advancing the mean of the hybrid populations when mild selection was practiced. Relatively small improvement was seen when stronger selection was practiced. In contrast, the Hallauer method improved the hybrid population means significantly under these genetic models. The Hallauer method seemed to be an effective way of producing superior single-cross hybrids under most, if not all, genetic situations. The recommendation was made that strong selection intensity be practiced in the first two or three cycles with little or no further testing until the lines are completely inbred.

No inter-locus selection effects were found for the inbred populations in the absence of epistasis for the Hallauer method. Intra-locus as well as inter-locus selection effects were observed for the hybrid population with the complete dominance and over-dominance models. With epistatic models, such as optimum number and additive by additive, both intra- and inter-locus selection effects were found for the inbred populations and hybrid population.

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A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Department of Crop and Soil Sciences

1970

This thesis is dedicated to my late parents, Mr. Hamdan Ehdaie and Mrs. Robab Ehdaie (Tabib), for their sincere support throughout my educational career.

ACKNOWLEDGEMENTS

The author expresses his sincere appreciation to Dr. C.E. Cress for his encouragement and guidance throughout the study.

Thanks are due to the committee members for their helpful suggestions and to Dr. C.M. Harrison for his critical appraisal of manuscript.

I express my deepest gratitude to my wife, Soraya, daughter, Suzan, and son, Sasan, for their patience and devotion during my years of study.

Finally, I thank the Iranian Government and the National Science Foundation for providing financial assistance (grant GB 6646) which made this study possible.

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I. INTRODUCTION

Shull (1909) described and outlined the pure-line breeding method for corn (Zea mays L.) which introduced a new era of plant breeding.

Jones (1918) suggested a procedure in which high-yielding single-crosses were used as parents to produce a double-cross with sufficient hybrid seed for commercial production.

In recent years there has been renewed interest in the commercial production of single-cross hybrids. This is due in part to the availability of more productive inbred lines, better field husbandry in seed production, and a better understanding of the gene action involved in heterosis.

As the productivity of single-cross and double-cross hybrids reached production limits, several other selection methods, top-cross, recurrent selection, and reciprocal recurrent selection (RRS), were developed which replaced the pure-line method. Recently, Hallauer (1967a) has suggested a selection scheme which produces single-cross rather than direct production of inbred lines or improved source material (i.e. reciprocal recurrent selection). The corn breeders, as well as other breeders, are interested in a selection method which produces the most productive material possible with the least amount of time, effort, and expense. This study was undertaken to evaluate the efficiency of the Hallauer method, top-cross method, and reciprocal recurrent selection (RRS) methods of

breeding.

In comparing the efficiency of different selection procedures, three different approaches have been used.

The first was to apply the various schemes for a period of time on the same biological materials such as plants and animals under similar conditions. Efficiency, then, was measured by the productivity of the end materials relative to the base material for a selection method. This system of comparing different methods of selection was not precise enough to make totally reliable conclusions since the amount of biological materials are restricted in the first place. In the second place, both biological material and environmental factors are subjected to much variability and take a long period of time to make valid conclusions about the efficiency of the various selection methods.

The second technique was concerned with the mathematical and statistical theory of selection procedures. In this case, if the selection methods were not mathematically complicated, the genetic gain or advance for only one cycle of selection was predicted for each selection method. The relative size of the genetic advances predicts which selection method is the best. In most of the mathematical developments some simplifying assumptions were made for sake of simplicity.

Some of these assumptions are:

(1) The populations were assumed to be infinite, so as to have a Mendelian population with its properties (Dobzhansky 1955).

(2) The genotypic values were assumed to follow a normal distribution.

(3) The gene effects were assumed to be very small relative to the genotypic variance.

(4) Selection was slow in the sense that the genotypic variance and its components did not change under selection.

(5) Inter-allelic interactions were assumed to be of low order.

This way of comparison is, therefore, inadequate for predicting changes in population means under different selection schemes after an arbitrary number of generations or cycles of selection.

A rigorous mathematical and stochastical treatment is required to handle the joint effect of inbreeding depression, epistasis, change in gene frequencies, and linkage on the mean of a finite size population under selection pressure. The construction and treatment of a model which contains all of these parameters is complicated and extremely tedious from a mathematical and stochastical point of view.

The third way of comparing selection schemes which has recently been used is the Monte Carlo technique of population simulation on high speed computers. Monte Carlo techniques not only handle the mathematically complicated selection models but also eliminate some of the simplifying assumptions restricting the biometrical theories. However, simulation techniques have some obvious disadvantages as well as merits.

No mathematical theory has been developed for the Hallauer procedure of selecting superior single-cross hybrids due to the mathematically complicated nature of simultaneous selfing, inbreeding and selection.

In the present study the Monte Carlo techniques have been used to empirically compare the method of Hallauer with the topcross and the reciprocal recurrent selection (RRS) methods. Since the classical works of Fisher, Wright, and Haldane, who founded the probabilistic basis of natural and artificial selection, thousands of experimental as well as natural selection experiments have been conducted on both plants and animals. The subsequent documentation of artificial selection, which may relate to this study, is so extensive that only selected papers were discussed. Primary emphasis was placed on corn (Zea mays L.) literature because of the origin of the selection methods simulated.

II. REVIEW OF LITERATURE

In the present study, only certain areas of theoretical and experimental selections on corn (Zea mays L.) will be reviewed. Improvement in corn has undoubtedly taken place since the earliest date of its cultivation, both through natural selection and objective selection by man.

A - Pure-line Method

The suggestion for a hybridization method in corn breeding was made by Morrow and Gardner (1893, 1894). They presented sufficient results to warrant the suggestion.

Shull (1908) reached the following conclusions:

a - In an ordinary field of corn the individuals are generally very complex hybrids produced by the combination of numerous elementary species (biotypes or pure-lines);

b - The deleterious effects of self-fertilization is due to the gradual build-up of homozygosity in the genetic make-up of the individual; and

c - The goal of the corn breeders should not be to find the best pure-line but to find and maintain the best hybrid combination to take advantage of the hybrid vigor (heterosis) phenomena manifested in F_1 progenies.

In the following year, 1909, three articles were published by three different authors about corn hybridization, different from that suggested by Morrow and Gardner. These three authors were Shull, East, and Collins. Collins' method of corn hybridization was in some respects similar to that proposed by Morrow and Gardner in which it was required to search and look for a new variety or strain each year, instead of going back to the same relatively inbred strains for each successive crop as suggested by Shull and East. Shull's method was more attractive to the corn breeder than East's. Shull (1909) in his classical article outlined the pure-line method of corn breeding, whereas East (1909) pointed out the possibility of a line-breeding method while trying to explain that decrease in vigor but not degeneration of character is usually the sole effect of inbreeding.

A new era of corn breeding began when Shull described the process of pure-line corn breeding. Shull (1909) recognized that inbred lines have an advantage over open-pollinated varieties in that they were homozygous and could be counted on not only to reproduce themselves with great precision, but also to produce hybrids of exactly the same genotypes year after year.

Shull's proposal was to use single-crosses for the commercial planting. These single-crosses to be made between pairs of inbred lines selected for their superior performance in combination with each other.

The double-cross hybrids, proposed by Jones (1918), made hybrid maize economically feasible.

However, a practical problem with the pure-line method of corn breeding was recognized when the number of productive inbred lines increased.

Considering that $\binom{n}{2} = \frac{n!}{2!\,(n-2)!}$ different single-cross hybrids can be made from n inbred lines (ignoring reciprocal crosses), it is apparent why this system of producing and testing inbred lines broke down when a substantial number of lines became available for testing. For instance, with only fifty inbred lines to be tested, this direct method of testing requires measurement of the yielding ability of 1225 F_1 hybrids or single-crosses, preferably repeated in more than one season and location. To overcome this handicap, top-cross or inbred by variety method of testing the inbred lines was adopted.

B - Top-cross Method

Davis (1927) first suggested the use of inbred x variety top-crosses to measure the general combining ability of the inbreds under test. General combining ability (GCA) may be defined as the comparative ability of a group of inbreds to combine with a tester or group of testers (Sprague and Tatum 1942). Only the inbreds with superior top-cross progeny performance are retained for further crossing and testing. These inbreds were expected to have high GCA. The inbreds with high GCA are combined in all possible single-cross combinations. The following season the hybrids are grown to measure the specific combining ability of the inbreds. Specific combining ability (SCA) may be defined as the deviation in performance of a specific single-cross from the performance expected on the basis of GCA (Sprague and Tatum 1942).

The most comprehensive data relating to the value of the top-cross method were reported by Jenkins and Brunson (1932). Their procedure was to compare the ranking of inbreds as determined by performance in inbred-variety crosses with average performance of the same inbreds in a number of single-crosses. Inbred lines that produced a low yield in top-crosses were found to produce low-yielding single-crosses. They concluded that on the basis of inbred x variety top-crosses, it should be possible to discard 50% of the inbred lines without danger of losing any really superior material. The remaining 50% may be given a more careful test in combination with other inbred lines for SCA.

Sprague (1939) demonstrated that if the variety is used as the seed parent it is recommended that no less than ten plants be used to sample the gametes of the variety.

Testers for GCA and SCA

As the top-cross parent, Jenkins and Brunson (1932) suggested the use of either the parent variety from which the inbred lines were derived, or if the new inbred lines are intended for crossing with inbred lines of another variety, they could be crossed with the variety from which those lines originated.

Hull (1947a) made a statement that theoretically the most efficient tester would be a homozygous recessive at all loci and that homozygosity for the dominant alleles at any locus should be avoided.

Green (1948) tested Hull's hypothesis with respect to lodging resistance. He used a relatively high-yielding, lodging-resistance, double-cross hybrid, and a relatively low-yielding,

lodging susceptible, open-pollinated variety as top-cross tester parents in crosses with 83 plants of each of three single-cross F_2 progenies. The data obtained indicated conclusively that the susceptible tester provides greater opportunity for selection among the segregates with which it was crossed.

Keller (1949) carried out an experiment in which a related and an unrelated single-cross were used as the tester parents in evaluating a group of selected F_2 plants of maize.

Different estimates of variability were obtained for the agronomic characters studied. In none of the comparisons was the difference large. Keller rejected Hull's hypothesis on the basis of the data obtained. He reasoned that if the hypothesis is correct, the component of variance due to the interaction of lines with testers would be less for high combining testers than for low combining testers.

Hull's hypothesis was supported theoretically by considering the constant parent regression method of analyzing the single-crosses developed initially by Hull (1947b) and amplified by Griffing (1950). The regression of performance of offspring on the performance of the variable parent was shown to be largest when the gene frequency of the character for the constant parent was zero. The regression coefficient was zero when the gene frequency was one for complete dominance or at equilibrium gene frequency for overdominance.

Matzinger (1953) conducted a study in which 16 randomly chosen inbred lines were involved. The variance component estimates of the interaction of inbred testers x lines, single-cross testers

x lines, and double-cross testers x lines for yield in bushels per acre were 17.22, 11.90, and 6.46, respectively. The relative magnitude of the variance component estimates of the tester x line interaction indicated that as the genetic variation within a tester parent increased the tester x line interaction component was decreased. He emphasized that when the object of an experiment is to determine a replacement for an existing line in a certain combination, SCA is of prime importance and the most appropriate tester is the opposite single-cross parent of the double cross or its component inbred lines. When a group of new lines were to be tested without any predetermined plan, then the ranking of lines with respect to GCA could be accomplished most economically by employing a heterozygous and heterogeneous tester.

Sprague (1955) reached the same conclusion based on a series of experiments conducted at Iowa.

Grogan and Zuber (1957) performed a study to compare single-crosses with double-crosses when used as top-cross parents for measuring new lines for GCA and SCA.

They concluded:

a - A tester closely related to the lines being tested should not be used as a top-cross parent when desiring information on GCA.

b - Information on GCA can be obtained more economically and with as much validity by using double-crosses rather than the average information from single-crosses.

c - A top-cross tester with a low value for GCA is more suited for measuring the average performance of a group

of lines than one having a high value for GCA.

d - A single-or a double-cross, related or unrelated to the lines, could be acceptable as the top-cross parent when the agronomic characters under consideration are controlled only by a few genes. Marked differences may be found between the testers when the traits are controlled by many genes.

Sprague (1959) stated that a suitable tester for GCA could be obtained by synthesizing a number of inbreds most widely used within a maturity zone.

Thompson and Rawlings (1960) carried out an experiment to evaluate four single-cross testers of different ear heights when used as top-cross parents for measuring yield and ear height of corn. A slight advantage was indicated for the two lowest yielding testers for yield evaluation which was in agreement with Hull's hypothesis.

Rawlings and Thompson (1962) further considered the role of average gene frequency of the tester in selection for GCA in maize. They defined a "good" tester to be one which classified correctly in a relative sense the entries under selection, and discriminated efficiently among the material in the test. Considering the theoretical aspects of the experiment, they showed the following expression as the genetic variance among test cross progenies, half-sibs, for the ith locus.

$$\tfrac{1}{2}\, p_i(1-p_i)(1+F)[1 + (1-2q_i)a_i]^2\, u_i^2 \qquad [1]$$

where

p_i = average gene frequency at the ith locus of the material under test (test population),

q_i = average gene frequency at the ith locus of the material used as the tester (tester population),

u_i = half the distance between two homozygetes at the ith locus,

$a_i u_i$ = difference between the heterozygote and the average of the two homozygotes when a_i is a measure of the degree of dominance at the ith locus, and

F = coefficient of inbreeding of the material under test (test population).

The following assumptions were made for the derivation of [1] with respect to the ith locus:

1 - The test population is initially at Hardy-Weinberg equilibrium,

2 - Each individual from the test population is pollinated by a random sample of pollen from the tester population, and

3 - no epistasis.

The total genotypic variance was obtained by summing over all loci. All genetic variance of half-sib progeny means were additive. This was shown by regressing the performance of half-sib progeny means on the number of + genes of the individuals selected from the random mating test population (Comstock et al 1949, and Cress 1965).

The effect of gene frequency of the tester population, q, is apparent. In the absence of dominance for all loci, a = 0, the

total genotypic variance of half-sib test cross progeny is independent of tester gene frequency. The amount of genetic variance is proportional to

$$[1 + (1-2q_i)a_i]^2. \qquad [2]$$

The quantities in [2] are always positive and p_i, a_i, u_i, and F are constant for a particular set of material being tested. The homozygous recessive tester, $q_i = 0$, has an increasing advantage as a_i increases.

Rawling and Thompson also discussed the situation where overdominance was large relative to partial and complete dominance and gene frequency in the tester population was relatively high. With several overdominant loci, a tester with high gene frequencies could lead to more genetic variation among test cross progenies than a tester with somewhat lower gene frequencies. From the trends in the data, they concluded that there were differences among the testers studied which favor poor performing testers for GCA. The striking difference expected from the theory developed did not appear in the data. One possible explanation was that the assumption of no epistasis was inadequate.

Hays (1963) concluded, from his own experiments and other studies, that in tests for GCA for the first isolation of inbred lines, the tester should be genetically diverse from the lines to be tested, adapted to the region where the inbreds are to be used in crosses, and should consist of material that has not previously been selected for high combining ability.

Early generation testing for GCA was suggested by Sprague (1946) in which S_o individuals or individuals selfed for a few generations were crossed with the top-cross parent. On the basis of a top-cross progeny test a large number of individuals or segregates were discarded from further testing. Hays (1963) mentioned that lines proved to be high or low combiners in a top-cross test made in S_o or S_1 material, were not necessarily homozygous for this condition, but might in many cases, segregate for combining ability during the process of self-fertilization. Therefore, on the average, visual selection during inbreeding might be expected in the majority of cases to lead to an improvement in GCA of the resultant inbred lines.

C - Reciprocal Recurrent Selection (RRS) Method

Comstock et al (1949) suggested the use of foundation material from two sources that are genetically diverse and which combined well together to give a desirable hybrid. The sources for ease of presentation might be referred to as A and B, and the material from these sources should each be heterozygous. Individual plants of source A were selfed and at the same time pollinated by a random sample of pollen from source B. The same procedure was repeated for individual plants of source B. Thus B used as a tester to select plants from source A that combine more satisfactorily with source B and vice versa. The selected S_1 lines of A were intercrossed randomly to produce a synthetic. The same procedure produced a synthetic for B. At this stage a cycle of reciprocal recurrent selection (RRS) was completed. After completion of as many cycle as desired, or at the end of each cycle,

selfing and selection could be practiced, with the intention eventually of producing single-cross hybrids of the type (A × B), where the inbreds A were obtained from the A source and the B inbreds from the B source. Cyclic selection could be followed as long as there was genetic variability.

Numerous experiments were conducted by different people using Hull's (1945) and Comstock et al's methods not only on maize but on many other crop and animal species.

The results of many of these studies were discussed by Cress (1965). Dickerson (1952) compared the two methods of recurrent selection theoretically. Schnell (1961) discussed some aspects of (RRS). Griffing (1962) developed, theoretically, all possible combination of recurrent selection in which one or two random mating populations might be employed as source materials. Recently, Cress (1966, 1967) reviewed and discussed various aspects of recurrent selection methods, their uses and advantages in breeding programs.

The selection methods described previously were developed many years ago and are successfully used by breeders. A method was recently proposed by Hallauer (1967a) and is in the primary stages of testing. This method of single-cross hybrid selection is the primary objective of the present study.

D - Hallauer Method

Hallauer (1967a) proposed a method for corn breeding to use all genetic variance for improving a polygenic character. He was impressed by an increasing body of experimental evidence indicating the involvement of non-additive gene effects in the

expression of polygenic characters and the mathematical article by Cockerham (1961) in which the relative genetic gains due to selection were computed for different types of hybrids. As a background for the Hallauer method, some aspects of Cockerham's paper and some experimental evidence concerning non-additive gene effects in maize will be discussed.

Cockerham (1961) considered components of genetic variance among unrelated single-, three-way-, and double-crosses, and relative gains that can be expected from selecting among these hybrids. Using the concept of identity of genes by descent developed by Malécot (1948) and defining F, the inbreeding coefficient of a line, as the probability of two random alleles of the line being identical by descent, Cockerham demonstrated, mathematically, that variation among the three types of hybrids would always be in the order of single-crosses greater than three-way and three-way greater than double crosses. The relative advantages would be a minimum of 1 to 3/4 to 1/2 when all of the genetic variance is additive and when the parents of the hybrids were completely inbred, F = 1.0. The relative advantages of selecting among the hybrids increased in favor of the single-crosses if dominant and epistatic gene effects (nonadditive gene effects) were important. If only additive effects were important, selection among single-crosses would be twice as effective as selection among double-crosses. If much of the genetic variance was nonadditive, selection among single-crosses would be four times as effective as among double-crosses.

Cockerham (1961) assumed that the lines involved in the production of the three types of hybrids had an equal but arbitrary degree of inbreeding and were a random sample derived from a random mating population. The last assumption was necessary as a base reference for making comparisons among the three types of hybrids. He also assumed regular diploid individuals or lines having simple Mendilian inheritance with no linkage between the loci.

Non-additive gene effects in corn population

Additive genetic variance has been shown to exist, at least in moderate amounts, in most corn populations [see Gardner (1963) for review]. Dominance variance and degree of dominance have varied in relative magnitude for various types of corn populations, and the relative importance of the degree of dominance in heterosis is an unsettled issue.

Although only a limited amount of data has been obtained, epistatic variance appears to contribute little to the total genetic variance of corn populations (Eberhart et al 1966, and Stuber et al 1966). However, evidence is accumulating for the presence of epistasis in specific combinations of inbred lines of maize.

Bauman (1959) used 2 corn inbreds and the single-cross between these 2 inbreds onto an inbred tester to detect the possibility of epistatic gene effects in determining yield, ear height, and kernel row number in corn. If performance of the single-cross x tester (3-way-cross) deviated significantly from the average performance of the two inbred x tester single-crosses, then epistatic gene effects were indicated. Epistatic gene effects were found to

be involved in the expression of the agronomic characters considered. However, significant epistasis x year interactions were found in some cases. The method employed proved to be relatively ineffective in detecting epistasis.

Gorsline (1961) extended Bauman's method of detecting epistatic gene effects for yield, grain moisture, silking, stalk quality, plant height, ear node height, percent ear node length, ear length, ear diameter, and ear length/diameter ratio. Epistasis was established for all ten characters. Yield and ear length exhibited fewer instances of epistasis than the other eight characters. Epistatic gene effects appeared to be of general importance in maize performance for the ten characters studied, and epistasis x environment interaction was expected to be common and important. Sprague et al (1962) also used Bauman's concept to provide estimates of the influence of epistatic gene effects on corn yield. Estimates were obtained from comparisons involving balanced sets of single- and three-way-crosses and between observed and predicted three-way-cross hybrids. Significant differences in yield were observed indicating that epistasis might be a factor of some importance in the populations from which the inbred lines were selected for the study.

Gamble (1962a, 1962b) outlined a procedure to separate six genetic parameters, namely, mean, additive, and dominance gene effects, and three types of digenic epistatic effects (additive x additive, additive x dominance, and dominance x dominance) which might affect genetic variation of a quantitative trait. Estimates of the parameters were obtained using the population means of two

inbred lines, their crosses, and progeny from subsequent selfing and crossing. The estimates of gene effects indicated that dominant gene effects were quite important in the inheritance of yield. Estimates of additive gene effects were of low magnitude and in many cases were non-significant. Epistatic gene effects were considered to be more important than additive gene effects in the inheritance of yield in the crosses studied. The additive x additive and additive x dominance gene effects were relatively more important than the dominance x dominance effects. Hallauer and Russell (1962) estimated the additive, dominance, and epistatic gene effects from six population means or six generations. They noted the relatively greater importance of some of the espitatic components for the agronomic characters studied.

Eberhart et al (1964) developed a method to predict the performance of double-cross hybrids of maize when epistasis was present. Epistatic gene effects were detected for some of the double-cross hybrids derived from the six inbred lines examined.

Eberhart et al (1966), from a comprehensive experiment, obtained full-sib and half-sib covariances in two open-pollinated varieties of maize. These full- and half-sib covariances provided estimates of additive, dominant, and certain estimable functions of epistatic variances which were useful for investigating the relative importance of the different types of genetic variation in the two varieties. Seven characters were studied in both varieties. The possibility of epistatic variance was reported for yield of one of the varieties.

Stuber et al (1966) investigated the genetic variability and interrelationship of six economic characters in the crosses of two maize populations. An evaluation of the epistatic components of variation received primary consideration. However, significant epistatic variability was not detected.

Because of Cockerham's conclusions that theoretically greater gains could be made by selecting among single-cross hybrids rather than double-cross hybrids or three-way-cross hybrids, and the evidence of non-additive gene action in maize coupled with the renewed interest in the commercial production of single-crosses, Hallauer (1967a) described and outlined a breeding method that isolates and tests single-cross hybrids during the inbreeding process. The essential features of the method follows (quoted from Hallauer):

> Phase 1. Crosses are made between individual S_o plants. The plants used in the crosses are also self-pollinated to maintain the plant's genotype. The hybrids produced by crossing the S_o plants are evaluated in yield trials, and the selfed seed (or S_1) of each S_o plant is stored for future use. From the results of the yield tests, the top 30 to 50% high yielding crosses are selected. Since the crosses cannot be tested extensively because of insufficient seed, a mild selection intensity is suggested.
>
> Phase 2. The pairs of S_1 lines which represent the selected S_o plant crosses are planted ear-to-row. The same procedures outlined for making the crosses and selfs between S_o plants are used between plants of the pairs of S_1 progenies. Since segregation occurs upon selfing an S_o plant, it is suggested that four to six crosses be produced within each pair of S_1 progenies. This affords selection for yield with S_1 progenies, some of which may be due to favorable epistatic combinations. A relatively low selection intensity (30 to 50%) is recommended.
>
> Phase 3. The S_2 seed of the selected entries is planted ear-to-row in pairs that correspond

to the original S_o plant crosses. Crossing and selfing between S_2^o plants is continued. Yield evaluations of the crosses are made and selections are made for continued crossing and selfing between plants of the S_2 progenies.

Phase n. The procedure is repeated until the selfed progenies of the plants used in the selected crosses are homozygous and homogeneous. At this time, one will have a group of selected single crosses that have been tested for yield in each generation of inbreeding. If favorable epistatic combinations for yield were present, there would have been an optimum opportunity for their selection.

The Hallauer method was developed primarily to isolate effectively single-cross hybrids for their SCA. This way, one could select for the specific combination or "nick" that has the highest performance, regardless of the relative importance of the kind of gene effect involved. This procedure may be applicable to any multiflowered crop species. Its usefulness depends on the ease in which self- and cross-pollinated seed can be obtained from one plant and whether sufficient heterosis is obtained to warrant a hybridization program.

The only empirical result applying this procedure on some prolific corn populations has been obtained by Hallauer (1967a, 1967b) and the summary of the data is presented in Table 1. Note the sharply improved yield of the crosses relative to the mean of the checks.

During the selection process the two-eared property was maintained in order to use the method. However, one could use one-eared unrelated populations of maize and produce self- and cross-pollinated seeds on the same ear as was done by Sprague (1939) and Williams et al (1965).

Table 1. Relative comparisons for 4 generations of selection for two prolific populations of corn using the Hallauer method.

Generations	No. of Crosses	Crosses above $\bar{X}$ of checks*		Crosses 2_s above $\bar{X}$ of checks*		Original Parents remaining	
		No.	%	No.	%	No.	%
$A^{S}{}_{o}x_{B}S_{o}$	144	2	1.4	0	0.0	144	100.0
$A^{S}{}_{1}x_{B}S_{1}$	160	37	23.1	7	4.4	54	37.5
$A^{S}{}_{2}x_{B}S_{2}$	173	131	75.7	47	27.2	31	21.5
$A^{S}{}_{3}x_{B}S_{3}$ +	77	59	76.6	20	26.0	12	8.3
$A^{S}{}_{4}x_{B}S_{4}$ +	67	59	88.0	47	70.1	7	4.9

* Check hybrids included 3 single-crosses (B14xB45, B37xOh43, and B45xC131A) and 3 double-crosses (A.E.S.704, Ia.515, and Ia.5116).

\+ Personal communication.

The advantage of the Hallauer procedure is contingent on being able to select for non-additive gene effects. How much non-additive variance was present in the two populations used in the Hallauer experiment is not known at the present time. However, a series of experiments were planned for obtaining estimates of the relative proportions of the total genetic variance that was additive and non-additive.

Further evidence has been obtained which indicates the presence of non-additive gene action in corn. Eberhart and Hallauer (1968) detected epistatic effects of genes in the maize populations studied. Stuber and Moll (1969) used interpopulation single-crosses (F_1's) and the selfed progenies (S_1's) arising from unselected lines of Jarvis Golden Prolific and Indian Chief varieties in an experiment to further determine the relative importance of epistatic gene effects. Significant epistatic effects were detected in some specific sets of crosses. However, the amount of the total variability that could be attributed to epistasis was, on the average, less than 10%. They concluded that epistasis might be important in unique genetic combinations but these combinations occurred either too infrequently or with such limited effect that they were not detectable in random mating equilibrium populations of maize.

III. MEAN OF A SELFED POPULATION

The genotypic mean of a selfed population will be derived, allowing for epistasis between pairs of loci. Then, the specific genotypic values associated with the different genetic models used in this study will be fitted into this genotypic mean to obtain a set of prediction equations for calculating the expected inbred and hybrid means in the absence of selection. This will allow the judgment of a change in the mean due to selection in some cases to evaluate the reciprocal selection effects of the Hallauer method.

Consider a population with an arbitrary number of pairs of independent loci with two alleles per locus and having an arbitrary degree of inbreeding, F. Selection pressure is not operating on this population and there is no linkage between the loci. The genotypic mean of such a population can be derived with respect to one pair of segregating loci as follows;

	Second locus	BB	Bb	bb	
First Locus	Frequency	$q_1^2+q_1q_2F$	$2q_1q_2(1-F)$	$q_2^2+q_1q_2F$	Partial Mean
AA	$p_1^2+p_1p_2F$	Y_{22}	Y_{21}	Y_{20}	$Y_{2.}$
Aa	$2p_1p_2(1-F)$	Y_{12}	Y_{11}	Y_{10}	$Y_{1.}$
aa	$p_2^2+p_1p_2F$	Y_{02}	Y_{01}	Y_{00}	$Y_{0.}$

By definition

$$p_1 + p_2 = 1.0,$$

$$q_1 + q_2 = 1.0,$$

$$[p_1^2 + p_1p_2F + 2p_1p_2(1-F) + p_2^2 + p_1p_2F] = 1.0,$$

$$[q_1^2 + q_1q_2F + 2q_1q_2(1-F) + q_2^2 + q_1q_2F] = 1.0, \text{ and}$$

$$0.0 \leq F \leq 1.0.$$

When $F = 0$, the population is in the state of random mating and the genotypic mean of the population is denoted by μ_R. When $F = 1$, the population is composed of many inbred lines and is referred to as an inbred population with genotypic mean μ_I. When $0 < F < 1$, the population is partially inbred and its genotypic mean is shown by μ_F.

If there are k independent sets of segregating loci in the population, the genotypic mean is obtained by summing over the k sets. The frequency of + alleles at the first and second loci are shown by p_1 and q_1, respectively. The frequency of - alleles at the first and second locus are denoted by p_2 and q_2, respectively. A genotypic value is shown by Y subscripted by two numbers. The first number shows the number of + alleles at the first locus and the second number indicates the number of + alleles at the second locus for that genotype.

Now, consider the partial means

$$\bar{Y}_{2.} = (q_1^2+q_1q_2F)Y_{22} + (2q_1q_2-2q_1q_2F)Y_{21} + (q_2^2+q_1q_2F)Y_{20},$$

$$\bar{Y}_{1.} = (q_1^2+q_1q_2F)Y_{12} + (2q_1q_2-2q_1q_2F)Y_{11} + (q_2^2+q_1q_2F)Y_{10}, \text{ and}$$

$$\bar{Y}_{0.} = (q_1^2+q_1q_2F)Y_{02} + (2q_1q_2-2q_1q_2F)Y_{01} + (q_2^2+q_1q_2F)Y_{00}, \text{ where}$$

., dot, in the subscripts of $\bar{Y}$'s represent the summation over

the corresponding locus (second locus).

The genotypic mean of this selfed population is obtained by summing the partial means each weighted with the appropriate coefficient as follows

$$\mu_F = (p_1^2+p_1p_2F)\bar{Y}_{2.} + (2p_1p_2-2p_1p_2F)\bar{Y}_{1.} + (p_2^2+p_1p_2F)\bar{Y}_{0.},$$

which in terms of genotypic values extends to

$$\begin{aligned}
\mu_F = {} & p_1^2q_1^2Y_{22} + p_1^2q_1q_2FY_{22} + p_1p_2q_1^2FY_{22} + p_1p_2q_1q_2F^2Y_{22} + \\
& 2p_1^2q_1q_2Y_{21} - 2p_1^2q_1q_2FY_{21} + 2p_1p_2q_1q_2FY_{21} - 2p_1p_2q_1q_2F^2Y_{21} + \\
& p_1^2q_1^2Y_{20} + p_1^2q_1q_2FY_{20} + p_1p_2q_2^2FY_{20} + p_1p_2q_1q_2F^2Y_{20} + \\
& 2p_1p_2q_1^2Y_{12} + 2p_1p_2q_1q_2FY_{12} - 2p_1p_2q_1^2FY_{12} - 2p_1p_2q_1q_2F^2Y_{12} + \\
& 4p_1p_2q_1q_2Y_{11} - 4p_1p_2q_1q_2FY_{11} - 4p_1p_2q_1q_2FY_{11} + 4p_1p_2q_1q_2F^2Y_{11} + \\
& 2p_1p_2q_2^2Y_{10} + 2p_1p_2q_1q_2FY_{10} - 2p_1p_2q_2^2FY_{10} - 2p_1p_2q_1q_2F^2Y_{10} + \\
& p_2^2q_1^2Y_{02} + p_2^2q_1q_2FY_{02} + p_1p_2q_1^2FY_{02} + p_1p_2q_1q_2F^2Y_{02} + \\
& 2p_2^2q_1q_2Y_{01} - 2p_2^2q_1q_2FY_{01} + 2p_1p_2q_1q_2FY_{01} - 2p_1p_2q_1q_2F^2Y_{01} + \\
& p_2^2q_2^2Y_{00} + p_2^2q_1q_2FY_{00} + p_1p_2q_2^2FY_{00} + p_1p_2q_1q_2F^2Y_{00} \\
= {} & \mu_R + [p_1^2q_1q_2(Y_{22}-2Y_{21}+Y_{20})+2p_1p_2q_1q_2(Y_{12}-2Y_{11}+Y_{10})+p_2^2q_1q_2(Y_{02}- \\
& 2Y_{01}+Y_{00})+p_1p_2q_1^2(Y_{22}-2Y_{12}+Y_{02})+2p_1p_2q_1q_2(Y_{21}-2Y_{11}+Y_{01})+p_1p_2q_2^2(Y_{20}- \\
& 2Y_{10}+Y_{00})]F+[p_1p_2q_1q_2(Y_{22}-2Y_{21}+Y_{20}-2Y_{12}+4Y_{11}-2Y_{10}+Y_{02} \\
& -2Y_{01}+Y_{00}]F^2. \qquad [3]
\end{aligned}$$

Kempthorne (1957) derived the genotypic mean of an inbred population for arbitrary epistasis, multiple alleles and no selection. He found

$$\mu_F = \mu_R + F D_1 + F^2 D_2, \qquad [4]$$

where, for two locus epistasis and two alleles per locus

$$D_1 = \prod_{i=1}^{2} \sum_{m_i=1}^{2} p^i_{m_i} d^i_{m_i m_i}, \text{ and}$$

$$D_2 = \prod_{i=1}^{2} \sum_{m_i=1}^{2} \sum_{m_i'=1}^{2} p^i_{m_i} p^{i'}_{m_i'} (d^i d^{i'})_{m_i m_i m_i' m_i'}.$$

See Kempthorne (1957) pages 442-444 and Kempthorne (1955) for notation.

Note that the D's are defined in terms of the dominance and dominance by dominance effects of genes in the original random mating population. In the absence of dominance by dominance and dominance gene effects, the genotypic mean of a population with arbitrary epistasis does not change under inbreeding. A linear relationship exists between μ_F and F if there is no dominance by dominance effect of genes even if other types of epistatic gene effects exist. In order to demonstrate the equality between [3] and [4], I will show that D_1 and D_2 are equal to the coefficients of F and F^2 in [3], respectively. The genetic parameters required to show that D_1 is equal to the coefficient of F in [3] are four dominant deviations defined in a random mating population in terms of gene frequencies and genotypic values, Y_{ij} $(i = j = 0,1,2)$. The four dominant effects can be shown as follows

$$\begin{aligned} d'_{11} = {} & q_1^2 Y_{22} + 2q_1 q_2 Y_{21} + q_2^2 Y_{20} + p_1 p_2 q_1^2 Y_{12} + 2p_1 p_2 q_1 q_2 Y_{11} + p_1 p_2 q_2^2 Y_{10} + \\ & p_2^2 q_1^2 Y_{02} + 2p_2^2 q_1 q_2 Y_{01} + p_2^2 q_2^2 Y_{00} - p_1^2 q_1^2 Y_{22} - 2p_1^2 q_1 q_2 Y_{21} - p_1^2 q_2^2 Y_{20} - \\ & p_1 p_2 q_1^2 Y_{12} - 2p_1 p_2 q_1 q_2 Y_{11} - p_1 p_2 q_2^2 Y_{10} - 2p_1 p_2 q_1^2 Y_{22} - 4p_1 p_2 q_1 q_2 Y_{21} - \\ & 2p_1 p_2 q_2^2 Y_{20} - 2p_2^2 q_1^2 Y_{12} - 4p_2^2 q_1 q_2 Y_{11} - 2p_2^2 q_2^2 Y_{10}, \end{aligned}$$

$$d_{22}^{1} = q_1^2Y_{02}+2q_1q_2Y_{01}+q_2^2Y_{00}+p_1^2q_1^2Y_{22}+2p_1^2q_1q_2Y_{21}+p_1^2q_2^2Y_{20}+p_1p_2q_1^2Y_{12}+$$
$$2p_1p_2q_1q_2Y_{11}+p_1p_2q_2^2Y_{10}-p_1p_2q_1^2Y_{12}-2p_1p_2q_1q_2Y_{11}-p_1p_2q_2^2Y_{10}-p_2^2q_1^2Y_{02}-$$
$$2p_2^2q_1q_2Y_{01}-p_2^2q_2^2Y_{00}-2p_1^2q_1^2Y_{12}-4p_1^2q_1q_2Y_{11}-2p_1^2q_2^2Y_{10}-2p_1p_2q_1^2Y_{02}-$$
$$4p_1p_2q_1q_2Y_{01}-2p_1p_2q_2^2Y_{00},$$

$$d_{11}^{2} = p_1^2Y_{22}+2p_1p_2Y_{12}+p_2^2Y_{02}+p_1^2q_2^2Y_{20}+p_1p_2q_2^2Y_{10}+p_1p_2q_2^2Y_{10}+p_2^2q_2^2Y_{00}-$$
$$p_1^2q_1^2Y_{22}-p_1p_2q_1^2Y_{12}-p_1p_2q_1^2Y_{12}-p_2^2q_1^2Y_{02}-2p_1^2q_1q_2Y_{22}-4p_1p_2q_1q_2Y_{12}-$$
$$2p_2^2q_1q_2Y_{02}-2p_1^2q_2^2Y_{21}-4p_1p_2q_2^2Y_{11}-2p_2^2q_2^2Y_{01}, \text{ and}$$

$$d_{22}^{2} = p_1^2Y_{20}+2p_1p_2Y_{10}+p_2^2Y_{00}+p_1^2q_1^2Y_{22}+2p_1p_2q_1^2Y_{12}+p_2^2q_1Y_{02}-$$
$$p_1^2q_1^2Y_{20}-2p_1p_2q_2^2Y_{10}-4p_1p_2q_1^2Y_{11}-2p_2^2q_1q_1Y_{00}-p_2^2q_2^2Y_{00}-2p_1^2q_1^2Y_{21}-$$
$$2p_2^2q_1^2Y_{01}-2p_1^2q_1q_2Y_{20}-4p_1p_2q_1q_2Y_{10}.$$

The superscripts of the d's should not be confused with powers. These superscripts refer to the first and second loci.

By definition

$$D_1 = p^1_{m_i} d^1_{m_i m_i} + p^1_{m_i'} d^1_{m_i' m_i'} + p^2_{m_i} d^2_{m_i m_i} + p^2_{m_i'} D^2_{m_i' m_i'}.$$

Substituting p_1 for $p^1_{m_i}$, p_2 for $p^1_{m_i'}$, q_1 for $p^2_{m_i}$, and q_2 for $p^2_{m_i'}$ and expressing the d's in terms of p's, q's and Y's, the equation for D_1 becomes

$$D_1 = p_1q_1^2Y_{22}+2p_1q_1q_2Y_{21}+p_1q_2^2Y_{20}+p_1^2p_2q_1^2Y_{12}+2p_1^2p_2q_1q_2Y_{11}+p_1^2p_2q_2^2Y_{10}+$$
$$p_1p_2^2q_1^2Y_{02}+2p_1p_2^2q_1q_2Y_{01}+p_1p_2^2q_2^2Y_{00}-p_1^3q_1^2Y_{22}-2p_1^3q_1q_2Y_{21}-p_1^3q_2^2Y_{20}-$$
$$p_1^2p_2q_1^2Y_{12}-2p_1^2p_2q_1q_2Y_{11}-p_1^2p_2q_2^2Y_{10}-2p_1^2p_2q_1^2Y_{22}-4p_1^2p_2q_1q_2Y_{21}-$$
$$2p_1^2p_2q_2^2Y_{20}-2p_1p_2^2q_1^2Y_{12}-4p_1p_2^2q_1q_2Y_{11}-2p_1p_2^2q_2^2Y_{10}+p_2q_1^2Y_{02}+$$

$$2p_2q_1q_2Y_{01}+p_2q_2^2Y_{00}+p_1^2p_2q_1^2Y_{22}+2p_1^2p_2q_1q_2Y_{21}+p_1^2p_2q_2^2Y_{20}+$$
$$p_1p_2^2q_1^2Y_{12}+2p_1p_2^2q_1q_2Y_{11}+p_1p_2^2q_2^2Y_{10}-p_1p_2^2q_1^2Y_{12}-2p_1p_2^2q_1q_2Y_{11}-$$
$$p_1p_2^2q_2^2Y_{10}-p_2^3q_1^2Y_{02}-2p_2^3q_1q_2Y_{01}-p_2^3q_2^2Y_{00}-2p_1^2p_2q_1^2Y_{12}-4p_1^2p_2q_1q_2Y_{11}-$$
$$2p_1^2p_2q_2^2Y_{10}-2p_1p_2^2q_1^2Y_{02}-4p_1p_2q_1q_2Y_{01}-2p_1p_2^2q_2^2Y_{00}+p_1^2q_1Y_{22}+2p_1p_2q_1Y_{12}+$$
$$p_2^2q_1Y_{02}-p_1^2q_1^3Y_{22}-p_1p_2q_1^3Y_{12}-p_1p_2q_1^3Y_{12}-p_2^2q_1^3Y_{02}-2p_1^2q_1^2q_2Y_{22}-4p_1p_2q_1^2q_2Y_{12}-$$
$$2p_2^2q_1^2q_2Y_{02}-2p_1^2q_1q_2^2Y_{21}-4p_1p_2q_1q_2^2Y_{11}-2p_2^2q_1q_2^2Y_{01}+p_1^2q_2Y_{20}+2p_1p_2q_2Y_{10}+$$
$$p_2^2q_2Y_{00}+p_1^2q_1^2q_2Y_{22}+2p_1p_2q_1^2q_2Y_{12}+p_2^2q_1q_2Y_{02}-p_1^2q_2^3Y_{20}-p_1p_2q_2^3Y_{10}-$$
$$p_1p_2q_2^3Y_{10}-2p_2^2q_1q_2^2Y_{00}-p_2^2q_2^3Y_{00}-2p_1^2q_1q_2Y_{21}-4p_1p_2q_1^2q_2Y_{11}-$$
$$2p_2^2q_1^2q_2Y_{01}-2p_1^2q_1q_2^2Y_{20}-4p_1p_2q_1q_2^2Y_{10}.$$

Collecting terms

$$D_1 = p_1p_2q_1^2Y_{22}+p_1^2q_1q_2Y_{22}+2p_1p_2q_1q_2Y_{21}-2p_1^2q_1q_2Y_{21}+p_1p_2q_2^2Y_{20}+$$
$$p_1^2q_1q_2Y_{20}-2p_1p_2q_1^2Y_{12}+2p_1p_2q_1q_2Y_{12}-8p_1p_2q_1q_2Y_{11}-2p_1p_2q_2^2Y_{10}+$$
$$2p_1p_2q_1q_2Y_{10}+p_1p_2q_1^2Y_{02}+p_2^2q_1q_2Y_{02}+2p_1p_2q_1q_2Y_{01}-2p_2^2q_1q_2Y_{01}+$$
$$p_1p_2q_2^2Y_{00}+p_2^2q_1q_2Y_{00}.$$

Thus, D_1 is equal to the coefficient of F in [3]. To show that D_2 is equal to the coefficient of F^2 in [3] the (dd) parameters are required. The equality of D_2 and the coefficient of F^2 in [3] is not shown, however, the calculations are similar to those for D_1. Therefore, [3] is a special case of [4].

When the inbreeding coefficient, F, is unity [3] becomes

$$\mu_I = \mu_R + p_1^2q_1q_2(Y_{22}-2Y_{21}+Y_{20})+p_2^2q_1q_2(Y_{02}-2Y_{01}+Y_{00}) +$$
$$p_1p_2q_1^2(Y_{22}-2Y_{12}+Y_{02}) + p_1p_2q_2^2(Y_{20}-2Y_{10}+Y_{00}) +$$

$$p_1p_2q_1q_2(Y_{22} + Y_{20} - 4Y_{11} + Y_{02} + Y_{00})$$

$$= p_1q_1Y_{22} + p_1q_2Y_{20} + p_2q_1Y_{02} + p_2q_2Y_{00} \quad [5]$$

Thus, the genotypic mean of an inbred population, F = 1, is equal to the summation of genotypic values of homozygous individuals, weighted with appropriate gene frequencies in that population.

When the genetic model is known, the genotypic values can be used in equation [5], to obtain an equation for μ_I only in terms of gene frequencies.

The following equations were obtained for the genetic models used in this study:

$$\mu_{IA} = 2(p_1 + q_1) + 1, \quad [6]$$

$$\mu_{ICD} = 2(p_1 + q_1) + 1, \quad [7]$$

$$\mu_{IOD} = 1 , \quad [8]$$

$$\mu_{ION} = 4(p_1 + q_1 - 2p_1q_1) + 1, \quad [9]$$

$$\mu_{IAA} = 4(2p_1q_1 - p_1 - q_1) + 5, \text{ and} \quad [10]$$

$$\mu_{IAD} = 2(p_1 + q_1) + 1, \quad [11]$$

where the second and third subscripts of μ_I's stand for the genetic model used in deriving that equation.

The initial frequencies of + alleles were the same at all loci in the populations simulated. Self-fertilization, without selection, does not change the initial gene frequencies. Self-fertilization pushes the population toward a homozygous condition with initial gene frequencies unchanged. Having considered these

facts, [6] to [11] become;

$$\mu_{IA} = 4p_1 + 1, \quad [12]$$

$$\mu_{ICD} = 4p_1 + 1, \quad [13]$$

$$\mu_{IOD} = 1, \quad [14]$$

$$\mu_{ION} = -8p_1^2 + 8p_1 + 1, \quad [15]$$

$$\mu_{IAA} = 8p_1^2 - 8p_1 + 5, \text{ and} \quad [16]$$

$$\mu_{IAD} = 4p_1 + 1. \quad [17]$$

It is recalled that [12] to [17] were obtained in the absence of selection pressure. Selection pressure, if effective, changes the genotypic mean of a population through the changes in gene frequencies.

Under condition of self-fertilization and selection pressure, the resulting inbred population, F = 1, can be obtained whose observed genotypic mean, μ_I', can be substituted in the appropriate equation, [12] to [17], to predict the gene frequency, p_1', actually obtained in that inbred population. Then, with the initial gene frequencies in the random mating population and the gene frequencies in the inbred population, F = 1, one would be able to calculate the efficiency of the selection pressure in terms of changes made in the gene frequencies. With the predicted gene frequency p_1' and with the assumption that q_1' is equal p_1' on the average, one should be able to calculate a predicted genotypic mean, μ_I''. The difference between μ_I', the observed genotypic mean, and μ_I'', the predicted genotypic mean, can be associated with the reciprocal

effects of selection. Equations [12] to [17] will be used to separate the effects of the average gene frequencies changes due to selection and the reciprocal effects due to selection on the genotypic means of the hybrid populations as well as the inbred populations.

IV. THE MECHANISM AND LOGIC OF POPULATION SIMULATION

The feasibility of setting automatic digital computers to simulate a reproductive population with its properties was first realized by Fraser (1957a). He saw the similarities of the stochastic processes, i.e. Monte Carlo techniques, that can be generated by the high speed computers and processes such as random or nonrandom segregation of alleles, gamete formation, random combination of gametes and selection which prevail in Mendilian populations.

The storage module of any digital computer consists of many "words" each of which is made up of numbers of "bits", depending upon the computer system. Each word can be visulized as a chromosome and its bits as the sites of the genes. Therefore, a pair of words can represent a diploid individual having a pair of homologous chromosome. The computer system used in the present study had 60 bits in each word labeled from one to sixty; thus each bit can be referred to if desired.

Three basic subprograms were used in the simulation of populations.

A - Subprogram 1: Generating the Initial Population

This subprogram generates a word consisting of 60 bits. Each bit on the word is given a value, either one or zero, based

on the magnitude of a random number and a preassigned probability. A bit is assigned one if the random number is greater than the preassigned probability, the gene frequency; otherwise the bit receives a zero.

The plus or dominant allele was represented by a one in a bit and the minus or recessive allele by a zero.

An even number, 2N, of words, containing either one or zero, was generated and paired to produce a diploid population with N individuals. The diploid individuals were labeled precisely so that each could be referred to whenever desired.

B - Subprogram 2: Generating Gametes

A pair of words generated by the first subprogram (a parent) was used in this subprogram. The member of the word pair chosen to contribute the first bit to a third word (a gamete) was determined at random. The value (0 or 1) in the first bit of the first word chosen was placed in the first bit of the third word. A random number was then generated and compared to a preassigned probability, the recombination value. If the number generated was larger than or equal to the recombination value, the same parent word would contribute its second bit to the second bit of the gamete. If the number generated was smaller than the recombination value, the alternate parent word would contribute its second bit to the gamete. This random walk procedure was continued until all bits of the gamete was determined. The recombination value in all the populations simulated was 0.50, i.e. free recombination (no linkage).

By varying the recombination value it is possible to study the effect of linkage on selection progress.

C - Subprogram 3: Evaluating Individuals

An individual, represented here by two words, was used in this subprogram. The adjacent pairs of bits on both words are considered simultaneously and based on the combination of ones and zeros, a numerical value is given to each pair of bits. There are nine possible genotypes possible for each pair of bits, if no distinction is made between the coupling and repulsion phases. Genetic models were determined by the numerical value assigned to these nine genotypes.

The values given to the 30 independent pairs of bits are summed up to represent the genotypic value for that individual.

Pair-wise consideration of bits or loci, which was required in the epistatic models, did not affect the genetic parameters in the non-epistatic models, which behaved as if there were 60 independent bits or loci.

A random error with a normal distribution was added to the genotypic value of each individual to obtain the phenotypic value.

Many different problems of population genetics have recently been attacked by means of Monte Carlo techniques. Further work by Fraser (1957b, 1960a, 1960b, 1962), Barker (1958a, 1958b), Crosby (1961), Gill (1965a, 1965b, 1965c), Young (1966, 1967), Cress (1967), Pfaffenberger and Gates (1967), and Qureshi (1968a, 1968b, 1968c) could be cited as some examples to demonstrate the various population genetic problems that can be

approached by simulation.

D - Distribution of Random Error

The random errors followed a normal distribution with zero mean and a specific variance.

The error variance was fixed in a manner to obtain an estimate of heritability in the broad sense, H_B, in the neighborhood of 25 percent. To have such an error variance, maximum genotypic variances, $\sigma^2_{G,max}$, which are a function of gene frequencies and the genotypic values, were calculated. Given $H_B = .25$, the error variance, σ^2_E, was calculated from the following equation for each of the genetic models simulated by Gill (1963).

$$H_B = \sigma^2_{G,max} \div (\sigma^2_{G,max} + \sigma^2_E)$$

The magnitude of error variance for a maximum $H_B = .25$ for additive (A), complete dominance (CD), pure overdominance (OD), optimum number (ON), duplicate factors (DF), complementary factors (CF), additive by additive (AA), additive by dominance (AD), and dominance by dominance (DD) models were 90, 180, 180, 212, 348, 120, 89, 184, and 90, respectively. The median error variance which was 180, was selected to represent a constant error variance for the six genetic models used in this study, (A), (CD), (OD), (ON), (AA), and (AD).

A computer tape was available which contained 10,000 standardized normal deviates. One of these normal deviates was picked up randomly and multiplied by the square root of error variance, 13.416, and then added to each genotypic value to obtain the corresponding phenotypic value.

E - Number of Runs

Variations between independent runs of a specific simulation experiment were due to chance fixation of loci and random error. The genotypic means of two independent runs of a specific experiment was expected to be different due only to chance fixation of loci or random drift. The phenotypic means for any cycle were also expected to be different not only due to chance fixation of loci but also due to error variation.

Since the magnitude of the variation contributed by chance fixation of loci to the between run differences was not known, it was decided to examine the empirical variance of the differences between the phenotypic means of the hybrid populations in two independent runs resulting from Hallauer selection. All genetic models, each with three combinations of initial gene frequencies, were run twice with separate random starting points.

The variances of individuals within cycles within runs were pooled over cycles and the two runs. The harmonic mean of the number of indidivduals per cycle was used in calculating an approximate standard error of the difference between runs for any cycle, Table 2 (Appendix A). A few differences between runs were declared significant ($\alpha = 0.05$) for one or more cycles. In no case was the difference between runs large in magnitude (i.e. no larger than $\pm$ 6.8 units). Thus it was decided to broaden the scope of the study at the expense of duplicate runs.

F - Genetic Models Simulated and Initial Gene Frequencies

The values chosen for the genetic models were such that the maximum genotypic value was the same for each of the six models (Table 3, Appendix A). The 7 combinations of initial gene frequencies used in the base populations A and B are as follows:

		Population A			
	Gene Frequencies	0.1	0.3	0.5	0.7
	0.1	+		+	+
Population B	0.3		+	+	+
	0.5			+	

The seven gene frequency combinations and six models were simulated for

1. the reference experiment,
2. the Hallauer method,
3. top-cross selection, and
4. reciprocal recurrent selection.

G - The Essential Features of Simulated Experiments

1 - Reference experiment

This experiment was simulated to serve as a reference method. Selection was not practiced throughout the experiment and the population size was reduced arbitrarily. In each generation of selfing only one selfed progeny was produced. Random production of single-cross hybrids between populations A and B were practiced for each generation.

a - Two base populations were generated with specific gene frequencies, each having 960 individuals.

b - Both populations were selfed for 4 generations.

c - Selfing was continued for 3 more generations while reducing the population size by half in each generation.

d - Three more generations of selfing were followed.

2 - Top-cross experiment

A completely recessive inbred line was generated to serve as the top-cross tester. Only S_1 individuals were crossed with the tester and on the basis of top-crossed progeny performance, half of the populations were selected for a further test. The number of top-crossed progenies and selfed progeny was five and one, respectively. In each generation of selfing a number of single-cross hybrids were produced randomly between the two populations A and B.

a - Two base populations were generated with specific gene frequencies, each having 960 individuals.

b - Based on the top-cross progeny performance fifty percent of the base populations were discarded.

c - Selection, then, was practiced on the basis of phenotypic expression of S_1's, S_2's, and S_3's in each population while reducing the population size by half in each generation of selfing.

d - Seven more generations of self-fertilization were followed without selection to produce 60 inbred lines in each of the inbred populations A and B.

3 - Experiments with the Hallauer method

Two classes of experiments were simulated in which different fractions of populations were saved, 0.50 and 0.10, to study the effect of selection intensity on selection progress. Enough selfed progenies were produced to keep the population size constant when necessary.

Selection was on the basis of full-sib progeny performance. Five full-sib progeny were generated for each parental pair.

a - Two base populations were simulated with particular initial gene frequencies, each having 960 individuals.

b - S_o individuals of both populations were paired randomly to produce 960 pairs of individuals which were kept separately thereafter throughout the experiments.

c - These 960 pairs were selfed, crossed and selection between pairs practiced for 3 generations, holding the population size constant.

d - Four generations of selfing, crossing, and selection were followed while reducing the population size by half in each generation.

e - Selfing and crossing continued for 3 more generations without selection to obtain 60 pairs of $_{A}S_{10} \times {}_{B}S_{10}$ single-cross hybrids.

The experiments simulated by the Hallauer method in this study will hereafter be denoted by "Hallauer" experiments for sake of simplicity.

4 - Reciprocal Recurrent Selection (RRS) experiments

Two classes of experiments were generated in which different fractions of populations were saved, 0.50 and 0.10, to study the effect of selection intensity on selection progress. The essential features of these experiments were simulated according to those given by Cress (1965).

V. RESULTS AND DISCUSSION

A - Reference Experiment

As the name indicates, these experiments were conducted to serve as reference points. Selection was not practiced at any point in the selfing process. Reduction in population size was at random. A hybrid population was made for each generation of self-fertilization using random individuals from populations A and B.

The expected and observed genotypic means of the random mating populations, F = 0, and the inbred populations, F = 1, with different genetic models and gene frequencies for 30 independent pairs of loci are presented in Table 4 (Appendix A). There existed a very close agreement between the observed and expected genotypic mean for different populations simulated.

The genotypic means of additive (A), and additive by additive (AA) populations, as expected, did not change under self-fertilization. For most of the remaining genetic models, a reduction in the genotypic means was expected because of self-fertilization.

However, under the additive by dominance (AD) genetic model the genotypic mean decreased, stayed the same, and increased as the inbreeding coefficient, F, approached unity depending on the starting gene frequencies. The genotypic means decreased when $p_1 = q_1 = 0.1$ and $p_1 = q_1 = 0.3$, unchanged when $p_1 = q_1 = 0.5$, and increased

when $p_1 = q_1 = 0.7$.

Considering all gene frequency combinations, maximum reduction in the genotypic mean of the populations due to selfing occurred under the (OD) model. The relationship between the genotypic mean of a population, average degree of dominance (a), and the inbreeding coefficient (F) for non-epistatic models is shown by Fig. 1 (i), (ii), and (iii), (Appendix B), when $p_1 = q_1 = 0.1$, $p_1 = q_1 = 0.3$, and $p_1 = q_1 = 0.7$, respectively. The genotypic mean has a linear relationship with both (a) and (F) under non-epistatic models. The concept of average degree of dominance is not defined for the epistatic models.

The relationship between the genotypic mean of a population, frequencies of plus alleles, and the inbreeding coefficient, F, are illustrated in Fig. 2 and 3 (Appendix B) for (ON) and (AD) genetic models, respectively. The genotypic mean has a linear relationship with the inbreeding coefficient, F, but a quadratic one with the gene frequencies under (ON) and (AD) models. The observed genotypic means of the inbred populations A and B and the corresponding genotypic mean of the hybrid populations (A x B) are presented, following 10 generations of inbreeding, in Table 5 (Appendix A).

The inbreeding coefficient, F, is zero in the hybrid populations. Therefore, their genotypic means should be equal to the genotypic means of populations A and B when $F = 0.0$. These can be checked by comparing the genotypic means of the hybrid populations of column three, six, and nine in Table 5 (Appendix A) with columns four, six, and 8, respectively, in Table 4 (Appendix A)

for F = 0.0. The other observed genotypic means were in agreement with the expected ones. Since selection was not practiced in the Reference experiment, gene frequencies did not change in either population A or B.

B - Top-cross Experiment

A completely recessive inbred line was used as the top-cross tester in testing the S_1 progeny, F = 0.5. The observed genotypic means of the parental populations A, B, and the hybrid after 0, 2, and 10 generations of self-fertilization accompanied with selection are presented in Table 6 (Appendix A). Recall that phenotypic selection was practiced after discarding 50% of the 960 individuals in the base population based on the top-cross progeny performance. Phenotypic selection was continued until the population size was reduced to 60, with a reduction in population size of 50% in each generation. Self-fertilization was continued without further selection.

The genotypic means of populations A, B, and (A x B) were increased throughout the generations due to selection for all the initial gene frequency combinations under the (A) model, Table 6 (Appendix A). The increase in the genotypic means from the S_o generation to the S_2 generation was due to top-cross progeny selection and was about 4-7 units, depending upon the initial gene frequencies. An increase in the genotypic means from S_2 to S_{10} was due to phenotypic selection. Over all cycles, the genotypic means of population A, B, and (A x B) increased about

10-12 units under the (A) model. Similar trends were seen in the (AA) model.

Under the (CD) model both inbreeding depression and selection pressure were operating. These two forces were in the opposite direction with respect to increase or decrease in the genotypic means of the A and B populations. While inbreeding depression was decreasing the genotypic means, the selection pressure was increasing the genotypic means. With $_{A}p_{1} = {}_{B}p_{1} = 0.1$, the genotypic means of populations A and B were expected to be 42.0 after 10 generations of selfing without selection pressure. As it can be seen from Table 6 (Appendix A), the genotypic means of populations A and B for this combination of initial gene frequencies after 10 generations of selfing are 51.8 and 51.5.

Selection force was not as strong as the inbreeding depression in the early generations of self-fertilization; thus a reduction was observed in the genotypic means of populations A and B from the S_o to the S_2 generations. For the other combinations of initial gene frequencies, selection pressure overcame part of the effects of inbreeding as can be checked by comparing the genotypic means of populations A and B after 10 generations of selfing with the expected genotypic mean of these populations when $F = 1.0$, Table 4 (Appendix A). In the hybrid populations (A x B) since selection pressure was present, an increase in their genotypic means was expected throughout the experiment as it can be observed from Table 6 (Appendix A). Similar trends were observed under (ON) genetic model.

With the (OD) model the average degree of dominance was the maximum; therefore, the inbreeding depression was the most intense. In this case, no selection pressure can be effective in overcoming the effects of inbreeding in A or B. Therefore, the genotypic means of populations A and B were reduced to the minimum genotypic value possible, 30 for this model, for all gene frequency combinations. With this model, the phenotypic selection, which followed the top-cross progeny selection, seemed to be incapable of increasing the hybrid population means significantly for any combination of initial gene frequency. This is indicated by the very small progress seen in the hybrid population genotypic means after 0 and 10 generations of self-fertilization and selection, Table 6 (Appendix A).

The trends in the (AD) model are interesting. As indicated in the Reference experiment, under (AD) model inbreeding may decrease, remain unchanged, or increase the genotypic mean of a population, depending upon the frequencies of + alleles present in that population. Therefore, because of self-fertilization, progress was seen in the genotypic means of population A and B from S_o to S_2 and from S_2 to S_{10} generations whenever $_AP_1$ or $_BP_1$ were greater than or equal to 0.5. A reduction in the genotypic means of population A and B was observed when $_AP_1$ or $_BP_1$ were below 0.5. The genotypic mean of the hybrid population (A x B) was increased significantly only when the initial gene frequencies in both populations A and B were very low, 0.1. When the initial gene frequencies in both populations A and B were 0.3, the genotypic mean of the hybrid population increased only

by 4 units from S_o to the S_{10} generations. For the rest of the gene frequency combinations no substantial change occurred in the genotypic means of the hybrid populations for the (AD) model. For this peculiar model, (AD), the progress in the hybrid population mean was made only when the frequencies of + genes were very low in the parental populations.

Over all the genetic models, maximum progress in the hybrid population mean took place when the initial frequencies of the desirable alleles in the base populations A and B were very low, 0.1. Generally speaking, the progress in the hybrid population mean was lowest when the initial gene frequencies of populations A and B were at different sides of 0.5, Table 6 (Appendix A). The maximum progress in the hybrid population mean was achieved with the (CD) model. The hybrid population mean was also increased significantly under the (A) model, the (ON) model, and the (AA) model but generally not under the (OD) and (AD) models.

Some discussion about the top-cross tester is in order.

The completely recessive tester was chosen in the present study as ideal for discrimination in non-epistatic models. Such a tester is unlikely in a practical situation. The optimum choice of tester for the general case of epistasis is not known and is probably not unique. When the tester is an unrelated inbred line, selection for the dominant favorable allele would, of course, be effective at loci recessive in the top-cross tester. However, such loci would not necessarily be the ones at low frequency in population under selection. Lonnquist (1968) stated that progress in population improvement from selection based on top-cross progeny

performance has not been as great as would seem possible or desirable from the standpoint of the effort involved.

Rawlings and Thompson (1962) showed, equation [2], that genes exhibiting a high degree of dominance contribute much more to top-cross variance than those with low dominance, provided that gene frequency of a dominant allele in the tester is low (below 0.5). Horner et al (1969) concluded, on the basis of the Rawlings and Thompson argument, that selection based on testcross performance when the parental population itself was the tester, was expected to be most effective at loci when the frequency of the cominant favorable allele is appreciably below 0.5 and which exhibits both large differences between homozygotes and a high level of dominance. However, the Rawlings and Thompson theory was developed for situations where epistatic gene effects were absent. Allison and Curnow (1966) pointed out that the parental population was an effective tester because it was more likely than any other tester to be recessive at loci where improvement is most needed, and, if overdominance is important, gene frequency will be stablized at optimum frequencies.

Cockerham (1963) partitioned the total genotypic variance among selfed progeny means for a single locus with two alleles. Horner et al (1969) compared equation [1] which was developed by Rawlings and Thompson (1962) with the additive component of the genotypic variance among selfed progeny means which was developed by Cockerham (1963) and concluded that selection based on selfed progeny performance per se was much more effective than parental top-cross performance as well as inbred top-cross performance for

population improvement. Theoretical comparisons have not been considered when epistatic gene effects are present. This is, probably, due to the complication involved in mathematical development and, furthermore, the concept of the average degree of dominance is not defined when epistasis exists.

C - "Hallauer" Experiments

1 - Mild selection intensity

The observed genotypic means of the inbred populations A and B with the corresponding hybrid populations (A x B) for different initial gene frequencies and genetic models are presented in Table 7 (Appendix A).

The observed genotypic means of the inbred populations, $_i\mu'_{Ij}$ (i = A, B and j = A, CD, OD, ON, AA, AD), were used to predict the gene frequencies, $_ip'_1$, in the inbred populations after 10 generations of self-fertilization and selection. Since the observed genotypic mean of the inbred populations, $_i\mu'_{Ij}$, were obtained for 30 independent pairs of loci, the right hand side of equations [12] to [17] must be multiplied by 30 when $_i\mu'_{Ij}$ are used in these prediction equations.

Hence, equations [12] to [17] become:

$$_i\mu'_{IA} = 120\ _ip'_1 + 30, \qquad [18]$$

$$_i\mu'_{ICD} = 120\ _ip'_1 + 30, \qquad [19]$$

$$_i\mu'_{IOD} = 30, \qquad [20]$$

$$_i\mu'_{ION} = -240\ _ip'^2_1 + 240\ _ip'_1 + 30, \qquad [21]$$

$$_i\mu'_{IAA} = 240\ {}_ip_1'^2 - 240\ {}_ip_1' + 150, \text{ and} \qquad [22]$$

$$_i\mu'_{IAD} = 120\ {}_ip_1' + 30. \qquad [23]$$

Equation [20], for this particular overdominant, (OD), model, is independent of $_ip_1'$ and therefore can not be used in predicting the gene frequency in the inbred populations. The average gene frequencies in the inbred populations under this model were calculated from the proportion of the fixed + alleles and were designated by $_ip_1''$ to distinguish them from $_ip_1'$, gene frequencies predicted from the prediction equations.

The independence of equation [20] from $_ip_1'$ is because the same genotypic value was given to the four homozygotes, AB/AB, Ab/Ab, aB/aB, and ab/ab. Some overdominant model other than pure overdominance could have been used to overcome this problem. For instance, we could have used the following genetic model which is overdominant and at the same time the four homozygotes do not possess the same genotypic values:

		A-a locus		
		3	4	2
B-b	locus	4	5	3
		2	3	1

In this example the dominant and recessive homozygotes, AB/AB and ab/ab, are distinguished from the two other homozygotes by their genotypic values of 3 and 1, respectively. The prediction equation for this example is:

$$_i\mu'_{IOD} = 60\ {}_ip'_1 + 30$$

which is dependent on ${}_ip'_1$.

The prediction equations [21] and [22] are second degree equations with respect to ${}_ip'_1$. These equations are associated with the optimum number and additive by additive models, where selection pressure accompanied with self-fertilization could, potentially, push the inbred populations in two directions. With the additive by additive model, selection pressure pushes each 2-locus pair in the inbred populations toward both dominant or both recessive homozygotes, whereas, with the optimum number model the 2-locus pairs are directed toward the two other homozygotes. Because of the reciprocal selection effects between the interacting pairs of loci, inbred means were obtained that would be impossible if ${}_ip_1 = {}_iq_1$. The consequences of this ambidirectional selection were that equations [21] and [22] gave impossible or no solutions for ${}_ip'_1$. We were unable to devise a method by which the direction of the selection pressure on the A-a and B-b loci could be determined for each of the 30 independent pairs directly from the inbred population means. For these reasons, the proportion of fixed loci was used to obtain ${}_ip''_1$ for the (ON) and (AA) models.

The initial gene frequencies $({}_ip_1)$, predicted gene frequencies $({}_ip'_1)$, and the average gene frequencies calculated from the proportion of + alleles $({}_ip''_1)$ are presented in Table 8 (Appendix A) for various genetic models. This table shows that gene frequencies in a population can be increased, stay the same, or

decreased, depending upon the initial gene frequencies, $_{i}p_{1}$, and the genetic models. The observed genotypic mean of an inbred population is a function of the final average gene frequency and the epistatic effects of the genes. We will show that the inbred performance was enhanced by epistasis for certain models when the reciprocal selection method of Hallauer was used. The selective value of an individual in population A or B is determined entirely by the performance of the full-sib progenies of one population with an individual of the other population. Each population is considered as a tester for the other. Depending upon the initial and subsequent gene frequencies in population A and B and the genotypic value of the homozygous individuals, selection pressure may decrease or increase the gametic frequencies of the population and thus its structure. When heritability in the narrow sense is relatively low for a trait, the progeny test is used to evaluate the superiority of the parents. If only the additive component of the genotypic variance in the progeny is used, i.e. half-sibs, no response to selection is observed when gene frequencies are at equilibrium unless they are changed by some forces. In contrast, when both additive and non-additive components of the genotypic variance are used, i.e. full-sibs, an immediate response to selection is observed even though the gene frequencies are at equilibrium. The genotypic means of the inbreds, developed by the Hallauer method, were the indirect result of selection among full-sibs. For the epistatic models with ambidirectional selection pressure, (ON) and (AA), inbred means were higher than would be expected based on the average change in gene frequency, Table 9

(Appendix A). The reciprocal effects of selection was reflected in the inbred population A and B and their corresponding hybrid populations (A x B) and can be measured by comparing the observed genotypic means with the predicted means calculated based on the average gene frequency, ${}_ip_1'$ or ${}_ip_1''$, where ${}_ip_1' = {}_iq_1'$ and ${}_ip_1'' = {}_iq_1''$.

The predicted genotypic means of the inbred populations A and B and their corresponding hybrid populations (A x B) are presented in Table 9 (Appendix A). The differences between the observed and the predicted genotypic means of the inbred populations A and B and the hybrid populations (A x B), which contributed to the reciprocal effects of genes, are presented in Table 10 (Appendix A) for different initial gene frequencies and genetic models. If the differences in Table 10 are interpreted as the reciprocal effects of selection, then the inbred reciprocal effects result entirely from interlocus effects between pairs of interacting loci. The differences for the hybrids were composed of both an intralocus and an interlocus compatibility between the inbreds. For the additive genetic model all differences were expected to be zero. The non-zero differences are due to rounding error. The differences between the observed and the predicted means of the inbred populations for the (CD) and (OD), which are non-epistatic models, were expected to be all zero. The reciprocal effects of selection were reflected in the genotypic means of both the inbred populations and hybrid population for the epistatic models (ON) and (AA).

However, for the (AD) epistatic model, zero differences were obtained between the observed and predicted genotypic means for the inbred populations. One may ask why positive reciprocal effects of genes have been reflected in the genotypic means of the inbred populations for the (ON) and (AA) models but not for (AD) model. The obvious answer is that in the (AD) model selection pressure was one-sided whereas it was two-sided for (ON) and (AA) models. For the same reason second degree prediction equations were obtained for (ON) and (AA) models whereas a first degree prediction equation was obtained for (AD). One expects to obtain zero differences between the observed and predicted genotypic means for the inbred populations when the observed genotypic means are used in the prediction equation to get $_{i}p_{1}'$.

The reciprocal effects of selection were all non-zero for the genotypic means of hybrid populations (A x B) except for the additive model as was expected. The maximum difference occurred under the overdominant, (OD), model when the initial gene frequencies, $_{i}p_{1}$, were 0.5 for population A and B, respectively. The maximum reciprocal effects, averaged over all gene frequencies, the inbred populations, and the hybrid populations were obtained under (ON) and (AA) models, respectively. Averaging over the genetic models, the maximum reciprocal effects were obtained for the inbred populations A, B, and the hybrid population (A x B) when the initial gene frequencies were 0.5 and 0.5, 0.5 and 0.3, and 0.7 and 0.3, respectively.

2 - Strong selection intensity

Using the Hallauer method, a breeder is restricted by the number of pairs of crosses produced at the beginning of the first cycle. As soon as the number of $_{A}S_{0} \times {}_{B}S_{0}$ crosses is set, the breeder has to work within and among that number of entries. New recombination take place within a line only in the early generations. The within line variation vanishes very quickly as self-fertilization is continued. There is no possibility of gene exchange within and between the lines making a pair; hence no chance of obtaining new genotypic combinations and genotypic variation. These, although they impose some problems, provide grounds to match the lines pairwise and select for the specific combinations of lines which perform the highest from the early cycles of inbreeding. Self-fertilization leaves little chance for selection to change gene frequency within a pair. Thus, it would seem desirable to start with two genetically diverse base populations to increase the chance of obtaining desirable combinations when the S_0 plants are randomly paired and crossed. But the selection of genetically diverse populations does not, necessarily, bring out the favorable specific combinations that we are looking for, particularily if a different set of alleles are presented in the base populations (Cress 1966). To overcome these restrictions, one should start with a large number of $_{A}S_{0} \times {}_{B}S_{0}$ crosses and practice relatively high selection intensity for the first few cycles of inbreeding. Enough selfed progeny should be produced within a pair during the early cycles of self-fertilization to raise the opportunity of obtaining desirable

specific combinations when these selfed progenies are crossed. After a few generations of self-fertilization the within line selection is fruitless and the selfed progeny may be bulk to represent a line.

The magnitude of the selection intensity practiced within and between ${}_{A}S_{0} \times {}_{B}S_{0}$, ${}_{A}S_{1} \times {}_{B}S_{1}$, ${}_{A}S_{2} \times {}_{B}S_{2}$, and ${}_{A}S_{3} \times {}_{B}S_{3}$ crosses by Hallauer (1967b) were 37.5%, 35.0%, 10.4%, and 8.3%, respectively. Hallauer (1967a) suggested and practiced mild selection intensities to produce sufficient seed for evaluating the pairs of crosses extensively.

In this study two selection intensities were practiced and kept constant for different ${}_{A}S_{i} \times {}_{B}S_{i}$ $(i = 0,1,2,3,...)$ by using the Hallauer techniques to compare the effect of selection intensity on the progress made.

The observed genotypic means of the inbred populations A and B and their hybrid populations (A x B) after 10 cycles are presented in Table 11 (Appendix A) when selection intensity was strong.

The same set of prediction equations was used in predicting ${}_{i}p'_{1}$. The proportion of fixed + alleles was used to obtain ${}_{i}p''_{1}$. The gene frequencies ${}_{i}p_{1}$, ${}_{i}p'_{1}$, and ${}_{i}p''_{1}$ are given in Table 12 (Appendix A) for different inbred populations and genetic models. Having obtained these gene frequencies, ${}_{i}p'_{1}$ and ${}_{i}p''_{1}$, and the assumption that ${}_{i}p'_{1} = {}_{i}q'_{1}$ and ${}_{i}p''_{1} = {}_{i}q''_{1}$, the predicted genotypic means for the inbred population A and B and their hybrid populations (A x B) were computed and presented in Table 13 (Appendix A) for various initial gene frequencies and genetic models.

Table 14 (Appendix A) contains the differences between the observed and the predicted genotypic means for different populations. These differences reflect the reciprocal effects of selection. Similar trends for mild and strong selection may be observed. But the non-zero values for strong selection are much greater than those observed for mild selection.

However, none of the observed genotypic means reached the limit value of a 150 set for all the genetic models. To observe the effect of selection intensity on the genetic progress several figures out of 84 possible (6 genetic models, 7 combinations of initial gene frequencies, and 2 selection intensities) combinations are presented. These figures numbered from 4 to 11 (Appendix B) contain the phenotypic mean of selected individuals in population A, B, and the phenotypic mean of the hybrid populations for 10 cycles of self-fertilization. Selection ceased at seventh generation of inbreeding but self-fertilization was continued for three more generations.

The S.I. in the figures stands for selection intensity and S_{PSC}, the standard error of the phenotypic mean of the single crosses, calculated as follows:

$$S^2_{PSC} = \left[\sum_{i=1}^{11} (N_i - 1) S^2_{iPSC} \Big/ \sum_{i=1}^{11} (N_i - 1) \right] / N_H,$$

where N_H is the harmonic mean of the number of single-cross hybrids made for the hybrid populations (A x B) over eleven generations, S^2_{iPSC} and N_i are the phenotypic variance between the single crosses and the number of single-crosses for ith generation, respectively.

In Fig. 4-11 (Appendix B) there are curves for reciprocal recurrent selection (RRS). Discussion of these curves will be given when comparisons between the "Hallauer" and (RRS) experiments are made.

The phenotypic means of A, B, and (A x B) populations increased for both selection intensities in Fig. 4 (Appendix B). This was expected since any change in gene frequency is reflected in the inbreds and single crosses with additive gene effects. The phenotypic mean of the (A x B) population increased from 66 to 80 under mild selection intensity, while it increased from 66 to 83 under strong selection intensity after 10 generations of self-fertilization and 7 generations of selection. With strong selection intensity the phenotypic mean of (A x B) reached 80 at the fifth generation while with mild selection intensity the same value was not obtained until the tenth generation. Selection was practiced within lines and between pairs of crosses at the early generations of selfing while selection was entirely between pairs of crosses after the fifth generation. This is one reason a steeper response was obtained during the early generations.

The effect of selection intensity on the mean of (A x B) and the inbred populations is illustrated for one case for the (CD) model in Fig. 5 (Appendix B). The interesting phenomena in Fig. 5 are associated with means of populations A and B. Since the initial gene frequencies for + alleles were 0.7 and 0.1 in populations A and B, respectively, the mean of A population was expected to be greater than the mean of population B over all cycles of inbreeding and selection. The mean of population A decreased

due to inbreeding for the first few generations then increased as selection reversed this downward trend. The mean of the population B decreased without a substantial increase at later generations. Selection pressure increased the frequencies of + alleles in population A considerably from the initial gene frequencies of 0.7. Selection caused the dominant homozygotes, AB/AB, to be accumulated in population A and little increase in the dominant alleles in population B.

When the initial gene frequencies were the same in both population A and B, Fig. 6 (Appendix B), the means of both populations decreased without any increase in the later generations. Again a rapid increase was observed in the hybrid population mean in the early generations for the stronger selection intensity.

The trends in Fig. 7 (Appendix B) are typical for the overdominant, (OD), model no matter what combination of initial gene frequencies were present in the base populations. In Fig. 7 the initial gene frequencies were at equilibrium in both populations A and B. Therefore, the additive component of genetic variance was zero and no response would be expected for selection methods using only the additive component of genetic variance such as the half-sib progeny test (Cress 1967).

Here an immediate response was seen, not only because full-sib performance was used to select individuals contributing to the hybrid population, but also the self-fertilization in the Hallauer method was a factor (Li 1967). As mentioned by Cress (1967), forces such as chance fluctuations could alter the equilibrium gene frequencies in populations A and B and cause a response in selection

even when half-sibs were used as a test criterion.

The effect of selection intensity on the mean progress for an optimum number, (ON), model with initial gene frequencies 0.1 in both populations A and B is seen in Fig. 8 (Appendix B). Even though the initial gene frequencies were very low in the populations, a high response to selection was observed for the hybrid population. If selection increases the frequency of the first + alleles and decreases the frequency of the second + allele at a locus pair in one population and the reverse situation happens in another population, such an increase in the hybrid mean is expected. This was observed previously as an interlocus reciprocal effect. The phenotypic means of the inbred populations were decreased for one or two generations of self-fertilization. Later selection between pairs of lines within a population caused the means of populations A and B to increase only slightly. As in all models, strong selection resulted in an increased response in the hybrid during the early generations of inbreeding.

In Fig. 9 (Appendix B), both inbred population means were greater than the hybrid population. This is not surprising for the additive by additive, (AA), model if one notes that the initial frequencies of the + alleles were 0.7 and 0.3 for population A and B, respectively. In this model, both the dominant and recessive homozygotes had the highest genotypic value relative to the other genotypes.

In Fig. 10 (Appendix B) the hybrid population was between the two inbred populations. By a glance at the model, (AD), it is seen that the dominant homozygotes have the highest genotypic

values, recessive homozygotes have the lowest genotypic values, and the double heterozygotes intermediate genotypic values. It may be noted that little average change in gene frequency occurred (Tables 8 and 12) in either population. Thus, the increase in the hybrid mean is the result of selection for specific combinations. Essentially all of the increase in population A is the result of inbreeding and not a change in gene frequency (see Table 4, (AD) model, $p_1 = 0.7$).

Figure 11 (Appendix B) illustrates a case when equilibrium gene frequencies existed in the base populations A and B. That is, the additive component of genetic variance was zero when gene frequencies were 0.5. With mild selection intensity the inbred population means basically did not change over ten cycles of self-fertilization and selection. With strong selection intensity the phenotypic mean of population B increased slightly due to a little increase in the average gene frequency. The hybrid population means increased under both mild and strong selection intensities. Since no substantial changes in the average gene frequencies were observed in either population A or B for either mild or strong selection intensity, this progress in the phenotypic mean of the hybrid populations was related to selection for specific combinations.

D - Comparison Between the Breeding Methods

1 - Top-cross method vs. the Hallauer and (RRS) methods

Absolute comparisons between the top-cross method and the Hallauer and (RRS) methods are improper because the goal of breeding,

type of selection practiced, and the cycle time were different for these breeding procedures. Therefore, the trends observed in the phenotypic means of hybrid populations for various breeding methods will be compared for different initial gene frequencies, genetic models, and only for mild selection intensity as it was the only selection intensity practiced in the top-cross experiment.

The total progress made in the phenotypic mean of the hybrid populations after 8 cycles of mild selection using the Hallauer, (RRS), and top-cross method are presented in Table 15 (Appendix A) for different initial gene frequencies and genetic models. Selection was practiced for four cycles in top-cross experiment and then self-fertilization was followed. In the "Hallauer" and (RRS) experiments selection was practiced for 8 cycles. The data in Table 15 (Appendix A) is the differences between the phenotypic means of the hybrid populations at cycle zero and cycle eight.

Over the initial gene frequencies, greater progress was seen in the hybrid population mean using top-cross method than (RRS) method under the (A) model. For the same genetic model, similar progress was observed for the top-cross and the Hallauer methods. Very similar trends were seen for all the breeding methods under the (CD) model. With the (OD) model, total progress made in the phenotypic mean of the hybrid population was much smaller for top-cross method compared to the (RRS) and the Hallauer methods. Under the (ON) and (AA) models, the total progress seen for the top-cross method was similar to that of the (RRS) method but

smaller than the progress made by the Hallauer method. Both (RRS) and the top-cross methods were ineffective for the (AD) model except when the frequency of the dominant allele was low in both populations. Except for the (OD) model, the top-cross method resulted in greater progress in the hybrid population mean than (RRS) but generally smaller progress as compared with the Hallauer method. This is rather surprising because the low heritability and epistatic models would seem to favor recurrent progeny testing over the top-cross and phenotypic selection for 3 cycles.

When the average degree of dominance was zero, additive gene effects, and one, complete dominant gene effects, the top-cross method seemed to be the most preferred method in improving the hybrid population mean. Its advantage in simplicity is obvious. With the epistatic gene effects present in a population, the top-cross method of breeding was found to be superior to (RRS) method but inferior to the Hallauer method in the rate of progress of the hybrid population mean. Only when the average degree of dominance was the highest, overdominant, the (RRS) method as well as the Hallauer method were superior to the top-cross method. These are not totally satisfying results in light of the modest performance reported for the top-cross in corn breeding.

It should be recalled that in this study an inbred top-cross tester, completely recessive, was used that is very unlikely in a practical situation.

2 - The Hallauer method vs. (RRS) method

In the comparison of (RRS) with the Hallauer selection method we must be confined to a comparison of trends. Absolute comparison is inadvisable for several reasons. First, the immediate goal and the end products of the two methods are not the same. Second, the cycle time is three generations for (RRS) and two generations for Hallauer's method. Third, the nature of the breeding systems dictated population sizes that were not comparable except in a general sense. Fourth, progress by the Hallauer method terminates in relatively few cycles, where progress by (RRS) should be possible over a much longer period of time. In spite of the lack of precise comparisons, it is felt that qaulitative contrasts, such as presence or absence of response to selection, are meaningful.

Under an additive model and with initial frequencies of the desirable alleles 0.3 in both populations A and B, similar progress was observed in the phenotypic means of the hybrid population (A x B) for both types of experiments in early cycles of breeding, Fig. 4 (Appendix B). Similar advances were observed for the completely dominant, (CD), model with initial frequencies of favorable alleles 0.7 and 0.1 in populations A and B, respectively, Fig. 5 (Appendix B). The "Hallauer" and (RRS) experiments responded the same throughout the experiments under the completely dominant, (CD), model and initial frequencies of + alleles 0.3 in both populations A and B, Fig. 6 (Appendix B). These figures are typical of the comparison of (RRS) and the "Hallauer" methods for the (A) and (CD) models.

The initial gene frequencies in the base populations presented in Fig. 7 (Appendix B) were at equilibrium, 0.5. Therefore, in the absence of chance fluctuation, which alters the gene frequencies, no early response to selection was expected for the hybrid population in the (RRS) experiments. Genetic progress or advance is a function of selection intensity, heritability in the narrow sense, and the phenotypic variance of the character under consideration. No progress is expected if any one of these components is zero. When gene frequencies are at equilibrium, the additive component of genetic variance is zero which makes heritability in the narrow sense zero when half-sibs are used as the test criterion.

However, response to selection was observed in the (RRS) experiments after the eighth generation of breeding when selection intensity was mild. This can be attributed to the accumulation of the additive component of genetic variance established in the populations through random drift of the gene frequencies from 0.5.

When selection intensity was stronger, it took fewer generations for response to be observed in the (RRS) hybrid mean. Under these same conditions of the (OD) model, larger response to selection was observed for the Hallauer method, Tables 15 and 16 (Appendix A).

The progress in the phenotypic means of the hybrid populations (A x B) were similar for both the "Hallauer" and (RRS) experiments for the particular (ON) gene frequencies presented in Fig. 8 (Appendix B). This was typical response for (RRS) with the (ON) model only when the gene frequencies of both populations

were low or when both populations were high (see Tables 15 and 16, Appendix A). Progress by (RRS) was at best very modest when both populations had gene frequencies near 0.5 or when the population gene frequencies were on opposite sides of 0.5. The smallest response of about 11 units for the Hallauer method was obtained when ${}_{A}p_{1} = 0.7$ and ${}_{B}p_{1} = 0.3$ with mild selection. The average response was much greater (see Tables 15 and 16, Appendix A).

No progress was observed in the mean of the hybrid populations for the (RRS) experiments under the additive by additive model, Fig. 9 (Appendix B), with the initial frequencies of + alleles 0.7 and 0.3 in populations A and B, respectively, and a mild selection intensity.

Griffing (1962) showed that progress due to selection from a single cycle of (RRS) with 2-locus epistasis is

$$\mu_1 = \tfrac{1}{2}(i/{}_{ab}\sigma^2_{h.s.})\{[({}_{ab}\sigma^2_{Aa}) + ({}_{ab}\sigma^2_{Ab})] + \tfrac{1}{2}(1 + d_y)$$

$$[({}_{ab}\sigma^2_{AaAa}) + ({}_{ab}\sigma^2_{AbAb})]\},$$

where i is selection differential measured in terms of general combining ability effects, ${}_{ab}\sigma^2_{h.s}$ is the variance of the general combining ability estimates in the hybrid populations, ${}_{ab}\sigma^2_{Aa}$, ${}_{ab}\sigma^2_{AaAa}$, ${}_{ab}\sigma^2_{Ab}$, and ${}_{ab}\sigma^2_{AbAb}$ are the additive and additive by additive component of genetic variance in the hybrid population contributed from population A and B, respectively. The effects of linkage is measured by d_y.

In the absence of linkage, $d_y = 0$, the formula becomes

$$\mu_1 = \tfrac{1}{2}(i/{}_{ab}\sigma^2_{h.s.})\{[({}_{ab}\sigma^2_{Aa}) + ({}_{ab}\sigma^2_{Ab}) + \tfrac{1}{2}[({}_{ab}\sigma^2_{AaAa}) + ({}_{ab}\sigma^2_{AbAb})]\}.$$

Of the four classes of additive by additive epistatic effects which occur in the hybrid population, only those involving two alleles coming from the same population contribute to genetic advance. Some progress is expected in the hybrid population even when the additive component of genetic variance is zero, provided that at least one of the additive by additive components of variance associated with the genetic advance or gain not be zero. Thus, it was surprising to find in four of the seven gene frequency combinations, the total progress after 8 cycles of (RRS) with mild selection was less than 4 units (see Table 15, Appendix A). Even with strong selection the performance of (RRS) was less than satisfactory (see Table 16, Appendix A).

There are two adaptive peaks associated with the (AA) model. Population A and B could be driven by selection to one of the adaptive peaks or to different adaptive peaks or to none, depending upon the initial gene frequencies in the populations. If population A goes to one of the adaptive peaks and population B to another, no progress is expected in the hybrid population (A x B). In contrast if both populations A and B go to one of the adaptive peaks, progress is expected in the hybrid population (A x B).

With the (AA) model, when the initial frequencies of the desirable alleles are 0.7 and 0.3 in population A and B, respectively, each population is close to one of the adaptive peaks. When population B is used as the tester I suggest that upward pressure is put on the (ab) gamete in population A. This decreases the frequency of the (AB) gamete in population A and increases the frequency of the (ab) gamete. After a few cycles of selection, depending upon

the selection intensity, the (ab) gamete is as frequent as the (AB) gamete in population A. However, when population A is used as the tester, the frequency of the (AB) gamete increases in population B and as a consequence the frequency of the (AB) gamete is as frequent as (ab) in population B. When selection intensity is mild changes in the gametic frequencies take place slowly in both populations A and B. However, it takes fewer cycles of selection to make the (ab) gametes as frequent as the (AB) gamete in population A and the (AB) gamete as frequent as the (ab) gamete in population B when selection intensity is strong.

At this stage average gene frequencies are close to 0.5 for both populations. If by chance fluctuation, the gene frequencies of some of the independent pairs of loci in population A drifts upward or downward from 0.5 and similar procedure happen for the corresponding pairs of loci in population B some progress is expected in the hybrid population because both populations A and B are moving toward the same adaptive peak with respect to these pairs of loci. These loci have, relatively, a greater selection advantage with respect to other loci. As the proportion of these independent pairs of loci become larger, the response to selection become greater.

With the additive by dominance, (AD), model and frequencies of desirable alleles in a range of 0.3-0.7 in both populations A and B, no progress in the hybrid population was made in the (RRS) experiments when selection intensity was mild (see Table 15, Appendix A). Very little response was observed when selection intensity became stronger, Fig. 10 and Fig. 11 (Appendix B) and Table

16 (Appendix A). Under this model, (AD), the (RRS) method of breeding seemed to be incapable of improving the hybrid population mean unless the frequencies of the favorable alleles were very low or very high in both populations A and B. In contrast, when the Hallauer method of breeding was employed, the phenotypic means of the hybrid populations were improved considerably.

VI. SUMMARY AND GENERAL CONCLUSIONS

A set of prediction equations was developed to separate the reciprocal effects of selection from the effects of an average change in gene frequency on the mean of parental populations A and B and their hybrid populations (A x B) for the "Hallauer" experiments. The direct application of these prediction equations was not possible for some genetic models following selection. Some extreme genetic models such as pure overdominance and other epistatic models were included in the study which may be only rarely found in natural populations. It was thought that these models would reflect differences that are present but not as obvious for less extreme models.

Reciprocal recurrent selection (RRS) was found to be as effective as the Hallauer method in advancing the hybrid population means when most of the genetic variance was additive. However, it was less effective than both the Hallauer and the top-cross methods when epistatic gene effects were present. The top-cross method was inferior to both (RRS) and the Hallauer methods under the (OD) model.

The genetic variance within pairs of individuals was exhausted rapidly under the Hallauer method of breeding due to its mating system. All the genetic variance present in the later generations of selection was due to variation between pairs of inbred

lines in population A and B. In contrast, genetic variance was expected in population A and B and their hybrids (A x B) when the (RRS) method of breeding is employed. This provides a basis for improving these populations for a long period selection. However, the Hallauer method produced a set of superior single-cross hybrids in a shorter period of time when compared with the (RRS) method.

In the "Hallauer" experiments, population A and B consisted of 960 S_0 individuals which were then reduced by selection to 60 S_{10} individuals, each representing an inbred line. In the (RRS) experiments, starting population size was 90 in both populations and it kept constant throughout the experiments.

The effect of two different selection intensities was studied. In the "Hallauer" experiments a sharp increase in the hybrid population means resulted from stronger selection intensity. Strong selection exploited variation in the early generations of selection, and thus, an improved rate of progress was made. For this reason as many pairs of individuals as practical should be used in the first cycle and the amount of selfed seed produced should be enough to maintain this population size for three cycles. Subsequent selection is largely between pairs. Therefore, it would seem more efficient to defer testing until the lines are essentially inbred. In the last two or three generations of inbreeding, a thorough evaluation of the single crosses may be made over a range of environments. In the Hallauer method, emphasis is on specific combining ability and the so-called "nicking" effects both within and between loci. Individuals from A and B which contribute to a superior hybrid are selected immediately and maintained as separate

pairs. The nicking effects of the alleles contributed by these selected individuals are not lost in the Hallauer method since selection is not followed by random mating but by self-fertilization which preserves some of the genetic constitution of selected pairs.

There is no rigorous basis to compare the Hallauer method with the (RRS) method from the viewpoint of time and expenses involved. If the purpose of breeding is to produce and maintain a good germplasm or to generate population hybrids, some form of recurrent selection may be indicated. But, if the goal is production of superior single-cross or even double-cross hybrids over a short period of time, the Hallauer method seems to be an effective one for a wide range of situations.

Hallauer, 1967b, has suggested modifications for situations where multiple matings are not possible on a single genotype. As a general view of the three selection systems simulated:

1. The rate of progress of the hybrid population by the top-cross and subsequent phenotypic selection was competitive with (RRS) and the Hallauer methods for the (A), (CD), and certain conditions of epistasis. Because of the simplicity of the method and the good progress under certain conditions, one should not discount some form of the top-cross as a breeding tool.
2. For several reasons, reciprocal recurrent selection is not directly comparable to the other systems simulated. The merits of (RRS) have been established both in theory and in practice, but the total benefits are very long range. The poor performance of (RRS) for some conditions

with epitasis places some limits on its utility.

3. The response to selection by the Hallauer method was both rapid and immediate. The increase in the single cross performance was without regard to choice of model. For no model or gene frequency simulated did the Hallauer method fail to respond. The terminal nature of the method leaves very small possibility that the maximum genotypic value will be attained when a large number of loci are involved in determining the trait.

Hallauer (1967a) recommended a selection intensity of 30 to 50%. However, it would seem advisable to select much more intensely during the early generations when segregation within lines is occurring.

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APPENDIX A

Table 2. Standard Errors of the Differences Between Runs for the Phenotypic Means of the Hybrid Populations (A x B) in any Generation Obtained from the Hallauer Method.

Initial Gene Frequencies	Genetic Models					
	(A)	(CD)	(OD)	(ON)	(AA)	(AD)
$_{A}p_{1} = 0.1$, $_{B}p = 0.1$	0.834	0.949	0.967	1.072	0.907	1.038
$_{A}p_{1} = 0.5$, $_{B}p = 0.5$	0.916	0.960	1.018	0.928	0.912	0.924
$_{A}p_{1} = 0.7$, $_{B}p = 0.1$	0.859	0.947	0.957	0.874	0.875	0.872

Table 3. Genetic Models Simulated and the Expected Genotypic Means for 30 Independent Pairs of Loci for Different Combinations of Gene Frequencies.

Genetic Models		Genotypic Values			Gene Frequencies A^{p_1}	0.1	0.3	0.5	0.7
					B^{p_1}	0.1	0.3	0.5	0.7
		AA	Aa	aa		Exp. Gen. Means			
	BB	5	4	3					
Additive (A)	Bb	4	3	2		42.0	66.0	90.0	114.0
	bb	3	2	1					
Complete	BB	5	5	3					
Dominance (CD)	Bb	5	5	3		52.8	91.2	120.0	139.2
	bb	3	3	1					
Over-	BB	1	3	1					
dominance (OD)	Bb	3	5	3		51.6	80.4	90.0	80.4
	bb	1	3	1					
Optimum	BB	1	4	5					
Number (ON)	Bb	4	5	4		62.4	105.6	120.0	105.6
	bb	5	4	1					
Additive by	BB	5	3	1					
Additive (AA)	Bb	3	3	3		128.4	99.6	90.0	99.6
	bb	1	3	5					
Additive by	BB	5	2	3					
Dominance (AD)	Bb	2	3	4		59.3	86.2	90.0	93.8
	bb	3	4	1					

Table 4. The Expected (E) and Observed (O) Genotypic Mean of a Random Mating Population, F = 0.0, and an Inbred Population, F = 1.0, in the Absence of Selection for Different Gene Frequencies and Genetic Models.

Genetic		Gene Frequencies							
Models	F	$p_1=q_1=0.1$		$p_1=q_1=0.3$		$p_1=q_1=0.5$		$p_1=q_1=0.7$	
		E	O	E	O	E	O	E	O
	0	42.0	42.0	66.0	66.1	90.0	89.9	114.0	114.2
(A)	1	42.0	42.3	66.0	65.8	90.0	89.3	114.0	113.6
(CD)	0	52.8	52.9	91.2	91.0	120.0	119.8	139.2	139.1
	1	42.0	41.9	66.0	65.9	90.0	89.9	114.0	113.3
(OD)	0	5.16	51.8	80.4	80.5	90.0	89.9	80.4	80.1
	1	30.0	30.0	30.0	30.0	30.0	30.0	30.0	30.0
(ON)	0	62.4	62.2	105.6	105.7	120.0	120.2	105.6	105.6
	1	51.6	50.6	80.4	81.5	90.0	90.7	80.4	80.4
(AA)	0	128.4	128.4	99.6	99.8	90.0	90.1	99.6	99.6
	1	128.4	128.5	99.6	99.5	90.0	89.9	99.6	98.9
(AD)	0	59.3	59.3	86.2	86.1	90.0	90.1	93.8	93.7
	1	42.0	42.8	66.0	65.3	90.0	90.4	114.0	114.8

Table 5. The Observed Genotypic Means of the Inbred Populations A and B after 10 Generations of Selfing with the Hybrid Populations (A x B) for the Reference Experiment.

Genetic Models	Populations	Initial Gene Frequencies						
		$_AP_1$ 0.1	0.5	0.7	0.3	0.5	0.7	0.5
		$_BP_1$ 0.1	0.1	0.1	0.3	0.3	0.3	0.5
	A	42.1	89.3	112.8	66.8	90.0	114.3	88.4
(A)	B	42.0	42.7	42.3	66.1	64.1	66.1	89.6
	(AxB)	41.5	65.8	77.9	66.0	76.1	90.3	89.2
	A	41.7	88.9	113.1	65.2	90.7	113.5	90.7
(CD)	B	41.3	42.2	42.3	67.8	64.7	65.8	89.2
	(AxB)	51.6	95.6	117.8	93.0	108.7	123.7	120.5
	A	30.0	30.0	30.0	30.0	30.0	30.0	30.0
(OD)	B	30.0	30.0	30.0	30.0	30.0	30.0	30.0
	(AxB)	51.1	91.3	107.3	81.4	89.5	98.2	89.1
	A	50.6	90.6	81.1	81.6	88.6	79.8	90.7
(ON)	B	50.9	50.6	50.5	81.7	82.7	81.2	93.0
	(AxB)	62.6	109.3	127.0	105.9	117.8	124.9	121.1
	A	128.6	88.4	99.0	99.4	90.4	98.7	90.9
(AA)	B	128.4	128.9	128.9	101.6	97.7	99.2	90.5
	(AxB)	129.0	98.4	91.6	99.6	91.8	89.8	91.1
	A	42.9	89.9	114.5	66.1	90.3	115.1	90.9
(AD)	B	42.4	42.4	43.4	65.2	64.2	65.5	90.5
	(AxB)	61.4	89.7	95.2	84.7	91.3	90.4	90.0

Table 6. The Observed Genotypic Means of Populations A, B, and (A x B) after 0, 2, and 10 Generations of Self-fertilization and Selection using the top-cross Method with Mild Selection Intensity.

Genetic Models	Initial Gene Frequencies																					
	$_AP_1$	0.1			0.5			0.7			0.3			0.5			0.7			0.5		
	$_BP_1$	0.1			0.1			0.1			0.3			0.3			0.3			0.5		
	Generations	0	2	10	0	2	10	0	2	10	0	2	10	0	2	10	0	2	10	0	2	10
	Populations																					
	A	42.0	46.9	51.0	89.8	97.7	103.5	114.1	120.6	125.6	66.0	73.0	80.0	90.2	97.7	104.8	114.1	120.9	126.7	90.1	99.1	105.6
(A)	B	42.0	46.2	50.5	42.2	46.8	51.4	42.0	46.5	51.4	65.9	74.3	81.2	66.0	73.4	79.8	66.1	73.9	97.3	90.1	98.1	104.3
	(AxB)*	42.0	46.4	50.8	66.0	72.5	77.6	78.0	83.3	88.8	66.0	73.5	80.8	78.0	85.0	92.4	90.0	97.3	102.9	90.0	98.7	105.2
	A	52.8	48.3	51.8	120.4	101.0	105.0	139.0	123.7	128.4	91.4	76.5	80.6	120.2	100.6	104.5	139.4	124.2	128.1	120.1	100.3	104.9
(CD)	B	52.7	48.1	51.5	52.5	48.1	51.7	52.9	48.1	55.2	91.6	76.2	81.3	91.2	75.9	80.2	91.0	75.6	80.5	120.4	101.1	105.7
	(AxB)*	52.8	62.3	69.4	90.0	106.6	113.0	117.6	126.3	132.4	91.2	102.7	111.9	109.0	116.9	123.7	124.8	132.9	137.3	120.0	128.3	133.0
	A	51.5	32.6	30.0	98.7	35.9	30.0	80.4	34.8	30.0	80.0	35.1	30.0	89.8	36.1	30.0	80.3	35.1	30.0	89.7	35.8	30.0
(OD)	B	51.5	32.9	30.0	51.3	32.7	30.0	51.7	32.9	30.0	80.0	35.2	30.0	80.8	35.4	30.0	80.7	35.3	30.0	90.2	35.8	30.0
	(AxB)*	51.6	55.0	55.2	90.0	82.3	92.3	109.2	109.5	110.9	80.4	82.9	81.0	90.0	91.2	90.8	99.6	99.8	101.0	90.0	90.1	89.7
	A	62.6	62.4	69.5	119.9	100.7	108.0	105.1	88.4	95.5	105.4	93.8	101.3	120.2	102.5	108.7	105.5	88.6	96.1	120.1	101.4	127.8
(ON)	B	61.9	61.2	68.8	62.2	62.1	69.2	62.1	62.0	68.5	105.7	92.6	99.5	105.8	92.4	121.1	105.7	92.9	99.4	120.0	102.1	109.9
	(AxB)*	62.4	74.3	85.6	110.4	116.4	120.1	126.6	128.9	128.5	105.6	115.8	121.0	117.6	122.8	129.0	123.5	127.7	129.7	120.0	124.4	129.9
	A	128.4	136.7	142.5	90.0	99.5	108.3	99.5	107.3	116.7	99.6	110.2	118.6	89.7	99.2	108.7	99.7	108.1	117.3	89.9	99.8	109.9
(AA)	B	128.4	136.7	142.1	128.4	136.6	143.1	128.4	136.3	143.1	99.8	110.1	118.6	99.5	110.6	120.1	99.3	110.1	118.9	90.4	98.2	106.3
	(AxB)*	128.4	136.2	141.2	99.6	104.8	109.6	92.4	94.6	97.5	99.6	107.5	113.1	92.4	97.4	102.0	90.0	93.3	96.7	90.0	94.3	99.8
	A	59.3	49.2	51.9	89.9	96.8	103.6	93.7	118.7	125.3	86.1	74.8	79.3	90.2	96.9	103.0	94.2	118.8	125.8	90.1	97.8	104.1
(AD)	B	59.4	48.9	51.7	59.4	48.6	51.5	59.1	49.0	52.1	86.3	75.2	79.7	86.2	75.8	80.0	86.2	75.8	80.3	89.9	98.1	104.5
	(AxB)*	59.3	68.8	76.6	90.0	92.2	92.7	93.8	91.9	90.5	86.2	88.8	90.0	90.0	90.0	89.8	90.0	88.9	87.3	90.0	89.4	90.4

* Expected values have been used for the hybrid populations in generation 0.

Table 7. The Observed Genotypic Means of the Inbred Populations A and B after 10 Generations of Selfing with the Hybrid Populations (A x B) using the Hallauer Method with Mild Selection Intensity.

Genetic Models	Populations	Initial Gene Frequencies						
		$_AP_1$ 0.1	0.5	0.7	0.3	0.5	0.7	0.5
		$_BP_1$ 0.1	0.1	0.1	0.3	0.3	0.3	0.5
	A	49.6	107.3	127.1	77.8	105.1	124.5	104.3
(A)	B	48.6	48.0	48.4	79.0	78.7	80.7	102.0
	(AxB)	49.1	77.6	87.7	78.4	91.7	102.6	103.1
	A	50.3	106.7	129.6	77.7	103.4	127.0	101.3
(CD)	B	49.5	46.4	43.7	78.0	76.3	71.9	98.6
	(AxB)	67.6	115.0	133.4	111.2	126.3	138.9	135.0
	A	30.0	30.0	30.1	30.1	30.1	30.1	30.0
(OD)	B	30.0	30.0	30.0	30.1	30.0	30.1	30.0
	(AxB)	71.5	109.5	128.4	99.2	110.9	119.8	109.7
	A	69.1	98.1	73.6	92.8	99.3	84.7	97.0
(ON)	B	66.3	54.9	51.8	94.3	88.0	85.1	100.5
	(AxB)	86.6	128.4	138.1	124.8	133.1	135.9	132.7
	A	138.3	104.2	104.0	113.4	101.2	107.9	102.9
(AA)	B	141.3	135.6	133.8	117.8	111.2	108.3	101.1
	(AxB)	140.2	111.6	100.6	115.9	104.7	100.4	102.3
	A	49.7	95.2	111.0	69.3	91.5	112.5	91.5
(AD)	B	50.7	41.0	39.7	69.1	64.0	64.5	89.8
	(AxB)	81.7	104.6	103.6	102.6	102.2	100.8	102.1

Table 8. The Initial Gene Frequencies, $_{i}p_{1}$, the Predicted Gene Frequencies, $_{i}p_{1}'$, and the Gene Frequencies Calculated from the Proportion of + Alleles, $_{i}p_{1}''$, of the Inbred Populations A and B after 10 Generations of Self-fertilization using the Hallauer Method with Mild Selection Intensity.

Genetic Models	Gen. Fre. in Inbred Populations	Initial Gene Frequencies						
	$_{A}p_{1}$	0.1	0.5	0.7	0.3	0.5	0.7	0.5
	$_{B}p_{1}$	0.1	0.1	0.1	0.3	0.3	0.3	0.5
(A)	$_{A}p_{1}'$	0.1633	0.6441	0.8091	0.3983	0.6258	0.7875	0.6191
	$_{B}p_{1}'$	0.1550	0.1500	0.1533	0.4081	0.4058	0.4225	0.6000
(CD)	$_{A}p_{1}'$	0.1690	0.6390	0.8300	0.3970	0.6116	0.8080	0.5940
	$_{B}p_{1}'$	0.1625	0.1366	0.1140	0.4000	0.3858	0.3490	0.5717
(OD)	$_{A}p_{1}''$	0.1836	0.6239	0.8297	0.3483	0.5667	0.7672	0.5122
	$_{B}p_{1}''$	0.1759	0.1070	0.0619	0.3608	0.2883	0.2278	0.4933
(ON)	$_{A}p_{1}''$	0.1883	0.6183	0.7906	0.3661	0.5550	0.7239	0.4917
	$_{B}p_{1}''$	0.1667	0.1133	0.1003	0.3864	0.3161	0.2828	0.5067
(AA)	$_{A}p_{1}''$	0.0511	0.3975	0.6167	0.2253	0.4478	0.6917	0.5072
	$_{B}p_{1}''$	0.0389	0.0722	0.0864	0.2099	0.2711	0.3128	0.5125
(AD)	$_{A}p_{1}'$	0.1642	0.5433	0.6750	0.3275	0.5125	0.6875	0.5125
	$_{B}p_{1}'$	0.1725	0.0917	0.0808	0.3258	0.2833	0.2875	0.4983

Table 9. The Predicted Genotypic Means of the Inbred Populations A and B after 10 Generations Selfing with the Hybrid Populations (A x B) Based on $_{i}p_{1}'$ and $_{i}p_{1}''$ using the Hallauer Method with Mild Selection Intensity.

Genetic Models	Populations	Initial Gene Frequencies						
		$_{A}p_{1}$	0.1	0.5	0.7	0.3	0.5	0.7	0.5
		$_{B}p_{1}$	0.1	0.1	0.1	0.3	0.3	0.3	0.5
	A		49.6	107.3	127.1	77.8	105.1	124.5	104.3
(A)	B		48.6	48.0	48.4	79.0	78.7	80.7	102.0
	(AxB)		49.1	77.7	81.7	78.4	91.9	102.6	103.2
	A		50.3	106.7	129.6	77.7	103.4	127.0	101.3
(CD)	B		49.5	46.4	43.7	78.0	76.2	71.9	98.6
	(AxB)		66.5	112.6	131.9	106.6	121.4	135.0	129.1
	A		30.0	30.0	30.0	30.0	30.0	30.0	30.0
(OD)	B		30.0	30.0	30.0	30.0	30.0	30.0	30.0
	(AxB)		65.4	101.7	124.7	84.9	93.4	107.5	90.0
	A		66.7	86.6	69.7	85.7	89.3	78.0	90.0
(ON)	B		63.3	54.1	51.7	86.9	81.9	79.2	90.0
	(AxB)		82.6	121.2	133.2	114.5	120.2	125.7	120.0
	A		134.4	92.5	93.3	108.1	90.7	98.8	90.0
(AA)	B		141.0	133.9	131.1	110.2	102.6	98.4	90.0
	(AxB)		139.7	106.9	95.3	109.1	94.7	90.0	90.0
	A		49.7	95.2	111.0	69.3	91.5	112.5	91.5
(AD)	B		50.7	41.0	39.7	69.1	64.0	64.5	89.8
	(AxB)		72.5	91.6	94.3	87.5	90.1	90.2	90.0

Table 10. Differences Between the Observed and Predicted Genotypic Means of the Inbred Populations A and B after 10 Generations of Selfing with the Hybrid Populations (A x B) using the Hallauer Method with Mild Selection Intensity.

Genetic Models	Populations	Initial Gene Frequencies						
	$_{A}P_{1}$	0.1	0.5	0.7	0.3	0.5	0.7	0.5
	$_{B}P_{1}$	0.1	0.1	0.1	0.3	0.3	0.3	0.5
	A	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(A)	B	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(AxB)	0.0	-0.1	0.0	0.0	-0.2	0.0	-0.1
	A	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(CD)	B	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(AxB)	1.1	2.4	1.5	4.6	4.9	3.9	5.9
	A	0.0	0.0	0.1	0.1	0.1	0.1	0.0
(OD)	B	0.0	0.0	0.0	0.1	0.0	0.1	0.0
	(AxB)	6.1	7.8	3.7	14.3	17.5	12.3	19.7
	A	2.3	11.5	3.9	7.1	10.0	6.7	7.0
(ON)	B	3.0	0.8	0.1	7.4	6.1	5.9	10.5
	(AxB)	4.6	7.2	4.9	10.3	12.9	10.2	12.7
	A	-0.1	11.7	6.7	5.3	10.5	9.1	12.9
(AA)	B	0.3	1.7	2.7	6.4	8.6	9.9	11.3
	(AxB)	0.5	4.7	5.3	6.8	10.7	10.4	12.3
	A	0.0	0.0	0.0	0.0	0.0	0.0	0.0
(AD)	B	0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(AxB)	9.2	13.0	9.3	15.1	12.1	10.6	12.1

Table 11. The Observed Genotypic Means of the Inbred Populations A and B after 10 Generations of Selfing with the Hybrid Populations (A x B) using the Hallauer Method with Strong Selection Intensity.

Genetic Models	Populations	Initial Gene Frequencies						
		$_{A}p_{1}$	0.1	0.5	0.7	0.3	0.5	0.7	0.5
		$_{B}p_{1}$	0.1	0.1	0.1	0.3	0.3	0.3	0.5
	A		49.5	114.4	128.7	83.4	108.2	127.1	102.8
(A)	B		56.7	49.4	52.7	81.7	85.4	81.0	111.4
	(AxB)		53.1	82.1	90.7	82.6	96.8	104.0	107.1
	A		57.2	119.8	139.7	84.0	109.6	134.1	106.4
(CD)	B		52.3	51.2	43.2	84.5	75.5	71.8	102.3
	(AxB)		76.9	128.3	142.5	119.7	134.2	143.8	141.4
	A		30.1	30.1	30.0	30.1	30.0	30.0	30.0
(OD)	B		30.1	30.0	30.0	30.0	30.0	30.0	30.0
	(AxB)		80.5	120.5	133.7	108.4	117.8	129.0	117.3
	A		72.9	97.2	62.1	98.0	96.7	82.8	97.5
(ON)	B		70.7	60.6	45.5	101.0	93.2	80.0	97.2
	(AxB)		93.9	133.7	141.2	130.3	136.6	137.9	137.4
	A		148.1	113.8	110.2	128.4	113.7	111.6	108.5
(AA)	B		146.7	140.0	138.3	116.1	121.7	110.4	112.5
	(AxB)		147.7	119.8	104.4	122.5	112.0	102.3	107.2
	A		51.7	97.1	103.5	69.5	92.4	110.6	89.1
(AD)	B		54.0	39.9	39.7	66.7	72.6	66.6	95.1
	(AxB)		91.8	107.6	109.3	106.0	108.1	105.2	105.9

Table 12. The Initial Gene Frequencies, $_{i}p_{1}$, the Predicted Gene Frequencies, $_{i}p_{1}'$, and the Gene Frequencies Calculated from the Proportion of + Alleles, $_{i}p_{1}''$, of the Inbred Populations A and B after 10 Generations of Self-fertilization using the Hallauer Method with Strong Selection Intensity.

Genetic Models	Gen. Fre. in Inbred Populations	Initial Gene Frequencies						
	$_{A}p_{1}$	0.1	0.5	0.7	0.3	0.5	0.7	0.5
	$_{B}p_{1}$	0.1	0.1	0.1	0.3	0.3	0.3	0.5
(A)	$_{A}p_{1}'$	0.1625	0.7033	0.8225	0.4450	0.6517	0.8091	0.6067
	$_{B}p_{1}'$	0.225	0.1658	0.1892	0.4308	0.4617	0.4250	0.6783
(CD)	$_{A}p_{1}'$	0.2267	0.7483	0.9142	0.4500	0.6633	0.8175	0.6367
	$_{B}p_{1}'$	0.1858	0.1767	0.1100	0.4542	0.3792	0.3483	0.6025
(OD)	$_{A}p_{1}''$	0.1878	0.7375	0.8708	0.3831	0.6292	0.7450	0.4475
	$_{B}p_{1}''$	0.2650	0.0656	0.0303	0.3997	0.2744	0.2714	0.5533
(ON)	$_{A}p_{1}''$	0.2206	0.6406	0.8556	0.4192	0.6050	0.7347	0.5200
	$_{B}p_{1}''$	0.1867	0.1378	0.0644	0.3939	0.3050	0.2369	0.4961
(AA)	$_{A}p_{1}''$	0.0078	0.3286	0.5994	0.1428	0.3853	0.7089	0.5578
	$_{B}p_{1}''$	0.0136	0.0656	0.0778	0.2097	0.1953	0.3461	0.5003
(AD)	$_{A}p_{1}'$	0.1808	0.5592	0.6958	0.3292	0.5200	0.6717	0.4925
	$_{B}p_{1}'$	0.2000	0.0825	0.0808	0.3058	0.3550	0.3050	0.5425

Table 13. The Predicted Genotypic Means of the Inbred Populations A and B after 10 Generations of Selfing with the Hybrid Populations (A x B) Based on $_{i}p'_{1}$ and $_{i}p''_{1}$ using the Hallauer Method with Strong Selection Intensity.

Genetic Models	Populations	Initial Gene Frequencies						
		$_{A}p_{1}$	0.1	0.5	0.7	0.3	0.5	0.7	0.5
		$_{B}p_{1}$	0.1	0.1	0.1	0.3	0.3	0.3	0.5
	A		49.5	114.4	128.7	83.4	108.2	127.1	102.8
(A)	B		56.7	49.4	52.7	81.7	85.4	81.0	111.4
	(AxB)		53.1	82.2	90.7	82.6	96.8	104.1	107.1
	A		57.2	119.8	139.7	84.0	109.6	134.1	106.4
(CD)	B		52.3	51.2	43.2	84.5	75.5	71.8	102.3
	(AxB)		74.5	125.1	140.8	114.0	124.9	139.6	132.7
	A		30.0	30.0	30.0	30.0	30.0	30.0	30.0
(OD)	B		30.0	30.0	30.0	30.0	30.0	30.0	30.0
	(AxB)		72.4	114.8	131.8	87.2	97.0	103.4	90.7
	A		71.3	85.3	59.7	88.4	87.4	76.8	89.9
(ON)	B		66.4	58.5	44.5	87.3	80.9	73.4	90.0
	(AxB)		88.4	123.2	138.2	116.9	122.0	127.4	120.0
	A		148.1	97.1	92.4	120.6	93.2	100.5	90.8
(AA)	B		146.8	135.3	132.8	110.2	112.3	95.7	90.0
	(AxB)		147.5	112.0	96.3	115.3	100.6	90.2	90.2
	A		51.7	97.1	113.5	69.5	92.4	110.6	89.1
(AD)	B		54.0	39.9	39.7	66.7	72.6	66.6	95.1
	(AxB)		75.8	92.1	94.4	87.1	90.1	90.2	90.0

Table 14. Differences Between the Observed and Predicted Genotypic Means of the Inbred Populations A and B after 10 Generations of Selfing with the Hybrid Populations (A x B) Using the Hallauer Method with Strong Selection Intensity.

Genetic Models	Populations	Initial Gene Frequencies						
		$_AP_1$	0.1	0.5	0.7	0.3	0.5	0.7	0.5
		$_BP_1$	0.1	0.1	0.1	0.3	0.3	0.3	0.5
	A		0.0	0.0	0.0	0.0	0.0	0.0	0.0
(A)	B		0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(AxB)		0.0	-0.1	0.0	0.0	0.0	0.1	0.0
	A		0.0	0.0	0.0	0.0	0.0	0.0	0.0
(CD)	B		0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(AxB)		2.4	3.2	1.7	5.7	9.3	4.2	8.7
	A		0.1	0.1	0.0	0.1	0.0	0.0	0.0
(OD)	B		0.1	0.0	0.0	0.0	0.0	0.0	0.0
	(AxB)		8.1	5.7	1.9	21.2	20.8	25.6	26.6
	A		1.6	11.9	2.4	9.6	15.8	6.0	7.6
(ON)	B		4.3	2.1	1.0	13.7	12.3	6.6	7.2
	(AxB)		5.5	10.5	3.0	13.4	14.0	10.5	17.4
	A		0.0	16.7	17.8	7.8	10.5	11.1	17.7
(AA)	B		-0.1	4.7	5.5	5.9	9.4	14.7	22.5
	(AxB)		0.2	7.8	8.1	7.2	11.4	12.1	17.2
	A		0.0	0.0	0.0	0.0	0.0	0.0	0.0
(AD)	B		0.0	0.0	0.0	0.0	0.0	0.0	0.0
	(AxB)		16.0	15.5	14.9	18.9	18.0	15.0	15.9

Table 15. Total Progress made in the Phenotypic Means of Hybrid Populations (A x B) after 8 Cycles of Mild Selection using the Hallauer, (RRS), and top-cross* Methods.

	Initial Gene Frequencies						
$A^{P}1$	0.1	0.5	0.7	0.3	0.5	0.7	0.5
$B^{P}1$	0.1	0.1	0.1	0.3	0.3	0.3	0.5
Gen. Mod.				Hallauer			
(A)	7.2	10.1	9.8	14.3	13.9	13.7	13.4
(CD)	14.6	20.0	15.5	19.3	19.3	14.5	15.6
(OD)	20.2	19.0	17.8	18.9	21.7	30.5	19.4
(ON)	23.1	18.2	13.3	18.5	15.9	11.1	13.9
(AA)	12.5	11.0	9.0	16.1	11.6	10.0	12.9
(AD)	25.0	15.7	10.4	16.9	13.4	11.2	12.4
Gen. Mod.				(RRS)			
(A)	6.5	8.6	6.2	9.4	11.0	10.1	8.8
(CD)	19.1	13.9	12.8	17.3	10.8	8.0	5.1
(OD)	12.0	14.1	14.0	8.3	6.2	6.9	0.9
(ON)	23.8	13.9	7.5	11.0	4.1	3.4	0.8
(AA)	9.0	8.6	3.7	10.6	1.8	-0.4	1.7
(AD)	11.2	3.3	-0.2	2.3	0.0	-0.3	0.1
Gen. Mod.				top-cross			
(A)	12.0	12.7	7.4	12.2	16.3	12.9	16.8
(CD)	18.1	23.2	14.1	17.6	15.5	14.9	13.4
(OD)	2.5	2.1	1.7	0.4	1.2	0.9	-2.2
(ON)	22.8	8.0	2.2	10.1	11.5	4.1	10.7
(AA)	10.5	7.0	4.4	14.8	10.3	6.6	7.6
(AD)	14.5	4.3	-5.5	4.9	2.0	-0.5	0.9

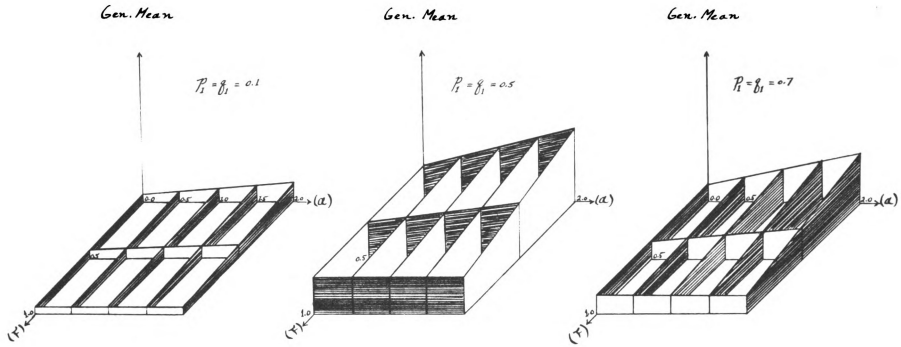
* Four cycles of mild selection was practiced.

Table 16. Total Progress made in the Phenotypic Means of Hybrid Populations (A x B) after 8 Cycles of Strong Selection using the Hallauer and (RRS) Methods.

	Initial Gene Frequencies						
A^{P_1}	0.1	0.5	0.7	0.3	0.5	0.7	0.5
B^{P_1}	0.1	0.1	0.1	0.3	0.3	0.3	0.5
Gen. Mod.			Hallauer				
(A)	10.1	16.8	13.0	16.3	19.0	13.4	15.5
(CD)	24.1	33.4	25.0	28.8	25.6	17.7	20.3
(OD)	28.9	29.8	25.2	26.1	26.6	29.1	29.2
(ON)	31.2	23.6	14.5	23.6	19.7	13.2	16.3
(AA)	18.0	21.6	11.8	24.0	19.2	11.9	18.8
(AD)	33.4	18.1	14.9	22.3	17.9	15.4	16.9
Gen. Mod.			(RRS)				
(A)	7.1	14.9	10.4	15.2	18.1	14.5	22.1
(CD)	26.9	24.1	17.6	26.6	16.7	12.5	9.2
(OD)	22.8	28.7	18.9	11.2	15.5	17.6	11.1
(ON)	34.9	18.1	7.7	22.8	7.3	5.9	3.8
(AA)	12.0	14.0	6.3	17.8	5.1	6.6	6.2
(AD)	23.8	8.5	3.0	4.7	1.5	3.1	1.8

APPENDIX B

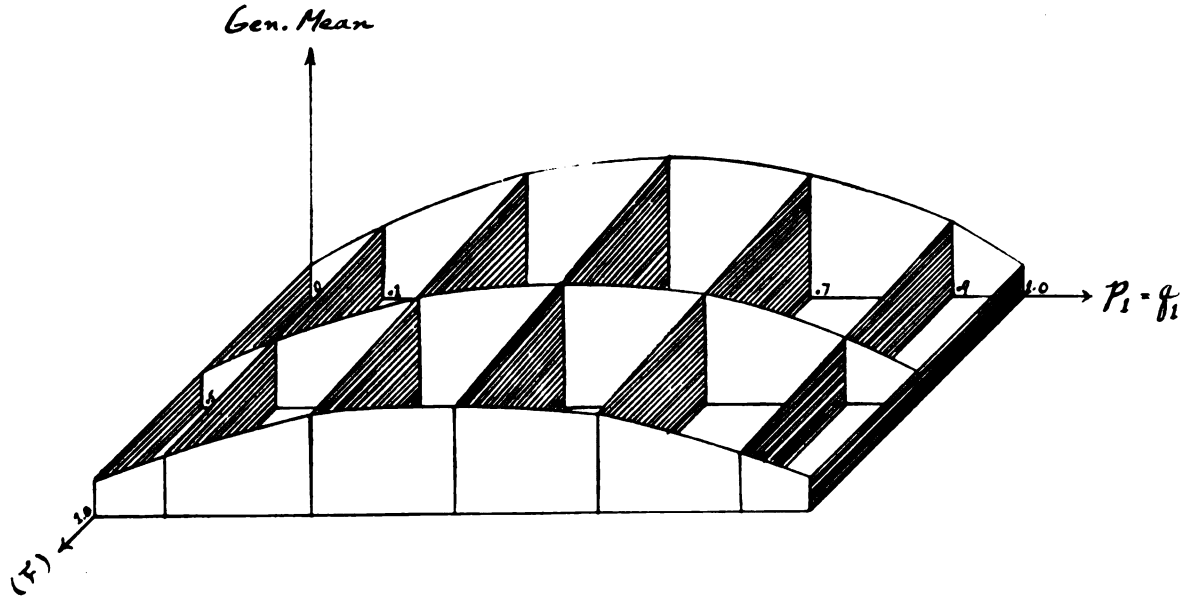
Fig. 1 - Relationship among the genotypic mean of a non-epistatic population, the average degree of dominance (a) and the inbreeding coefficient (F) for dominant allele frequency equal to (i) 0.1, (ii) 0.5, and (iii) 0.7.


Gen. Mean
$P_1 = q_{11} = 0.1$
0.0
0.5
1.0
1.5
2.0 → (α)
0.5
1.0
(T)
Gen. Mean
$P_1 = q_{11} = 0.5$
2.0 → (α)
0.5
1.0
(T)
Gen. Mean
$P_1 = q_{11} = 0.7$
0.0
0.5
2.0 → (α)
0.5
1.0
(T)

(i) (ii) (iii)

Fig. 2 - Relationship among the genotypic mean, gene frequency, and inbreeding coefficient (F) with the optimum number model.

Fig. 3 - Relationship among the genotypic mean, gene frequency, and inbreeding coefficient (F) with the additive by dominance model.


Gen. Mean
0
.3
.7
.9
1.0
$p_1 = q_1$
.5
(F)
1.0

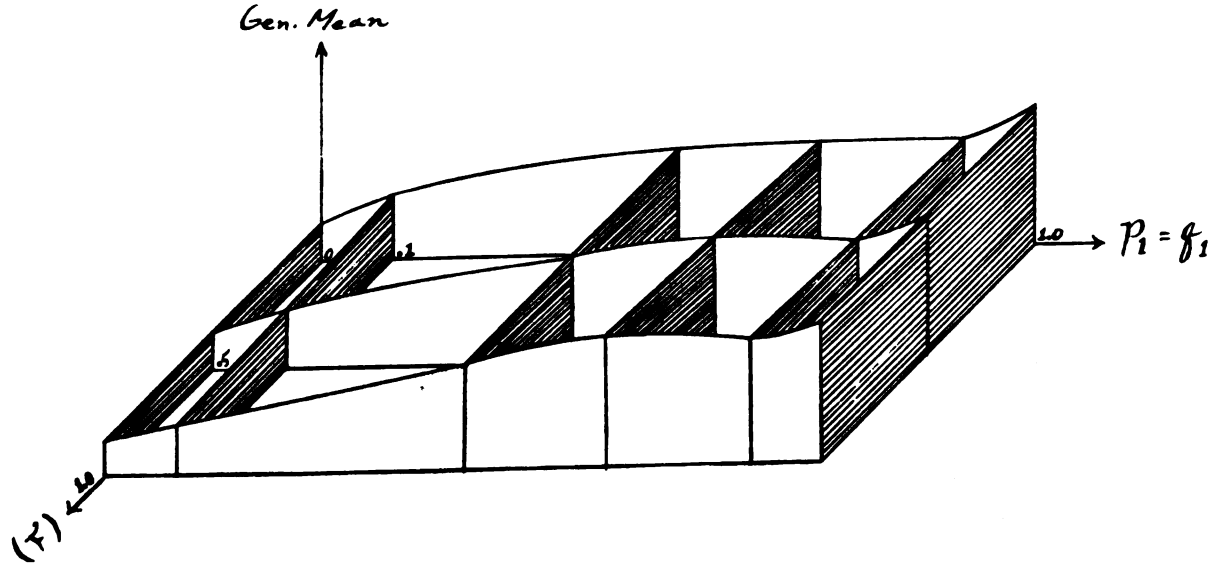

Gen. Mean
0
.2
1.0
$p_1 = q_1$
.5
(F)
1.0

Fig. 4 - Mean progress for population A, B, and (A x B) for the Hallauer method, and the hybrid population for the (RRS) method with initial gene frequencies $_{A}p_{1} = 0.3$ and $_{B}p_{1} = 0.3$ for the additive model and two selection intensities.

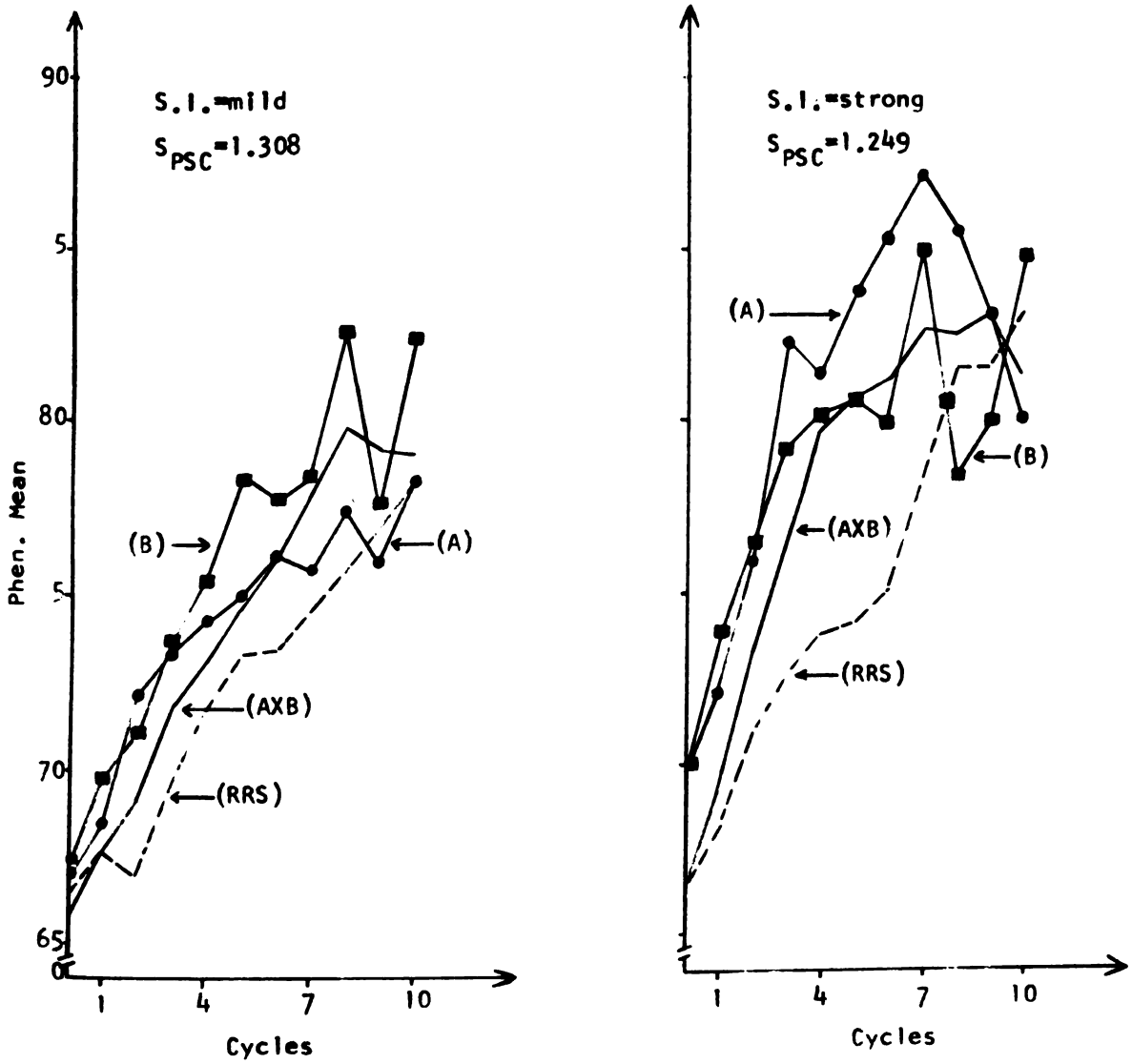

S.I.=mild
S_{PSC}=1.308
90
5
80
Phen. Mean
(B)
(A)
(AXB)
(RRS)
70
65
0
1
4
7
10
Cycles
S.I.=strong
S_{PSC}=1.249
(A)
(B)
(AXB)
(RRS)
1
4
7
10
Cycles

Fig. 5 - Mean progress for population A, B, and (A x B) for the Hallauer method, and the hybrid population for the (RRS) method with initial gene frequencies $_{A}p_{1} = 0.7$ and $_{B}p_{1} = 0.1$ for the completely dominant model and two selection intensity.

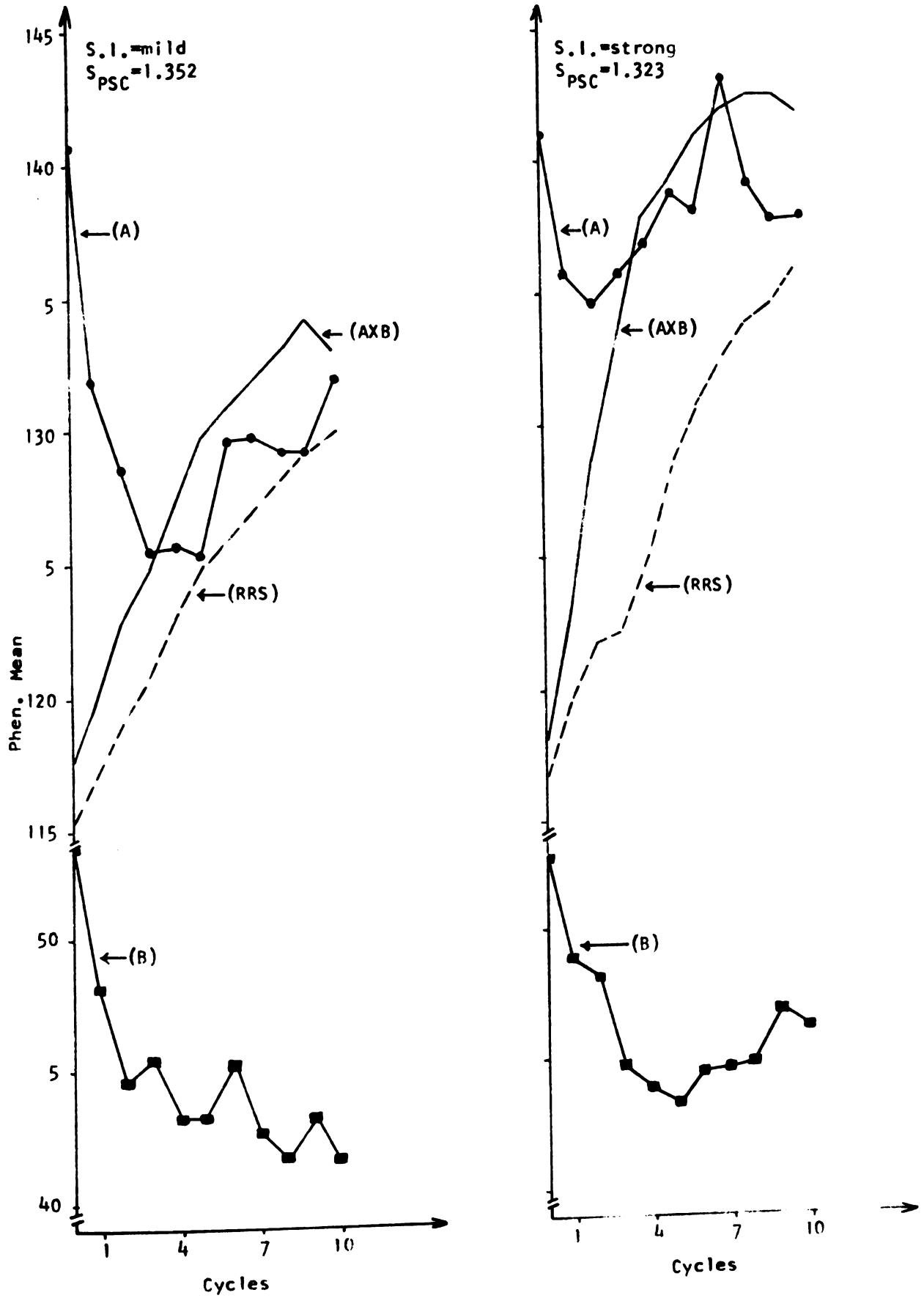

S.I.=mild
S_{PSC}=1.352
S.I.=strong
S_{PSC}=1.323
145
140
5
130
5
120
115
50
5
40
Phen. Mean
(A)
(AXB)
(RRS)
(B)
1
4
7
10
Cycles

Fig. 6 - Mean progress for population A, B, and (A x B) for the Hallauer method, and the hybrid population for the (RRS) method with initial gene frequencies $_{A}P_{1} = 0.3$ and $_{B}P_{1} = 0.3$ for the completely dominant model and two selection intensities.

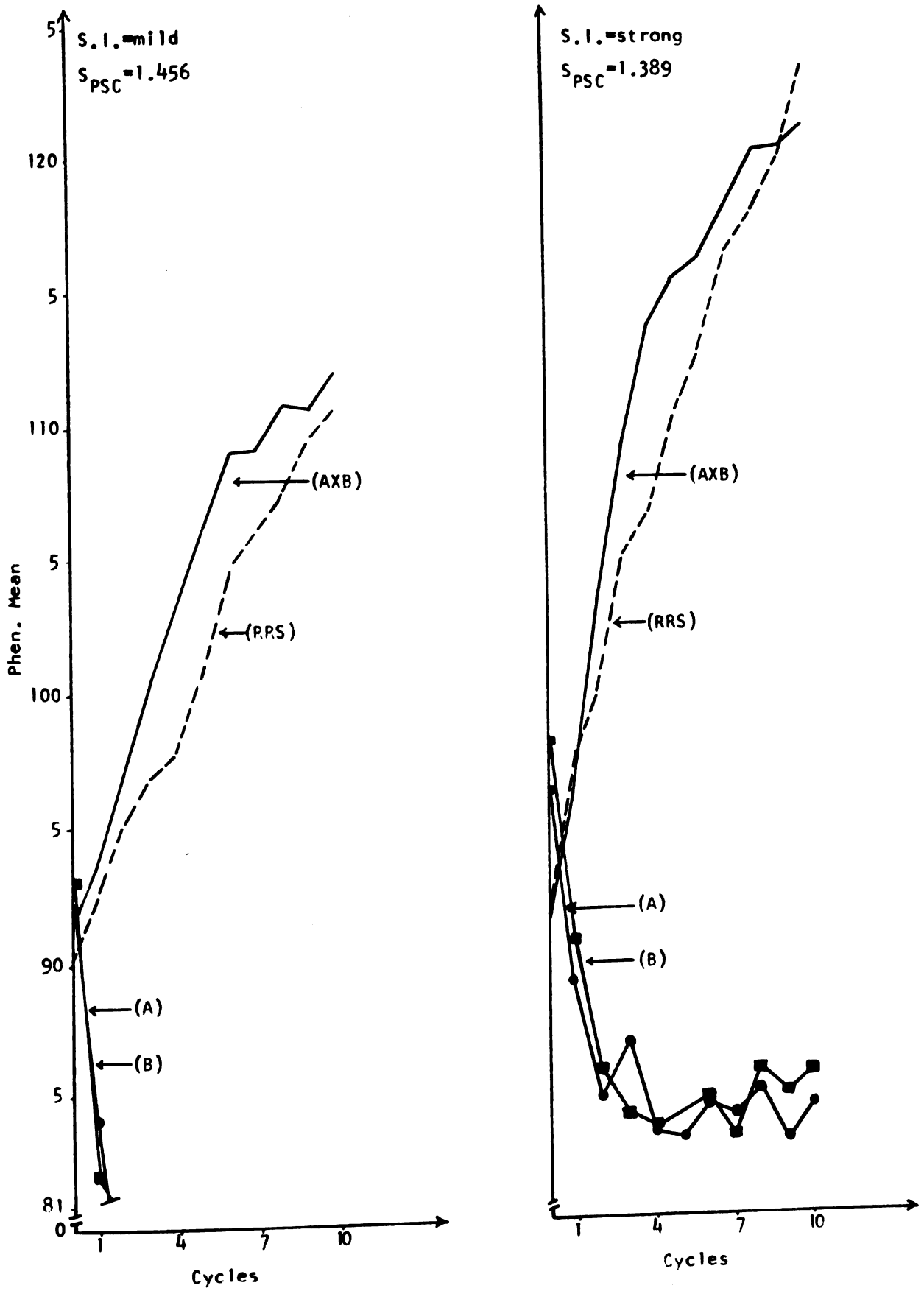

S.I.=mild
S_{PSC}=1.456
S.I.=strong
S_{PSC}=1.389
Phen. Mean
5
120
5
110
5
100
5
90
5
81
0
(AXB)
(RRS)
(A)
(B)
1
4
7
10
Cycles

Fig. 7 - Mean progress for population A, B, and (A x B) for the Hallauer method, and the hybrid population for the (RRS) method with initial gene frequencies $_{A}P_{1} = 0.5$ and $_{B}P_{1} = 0.5$ for the overdominant model and two selection intensities.

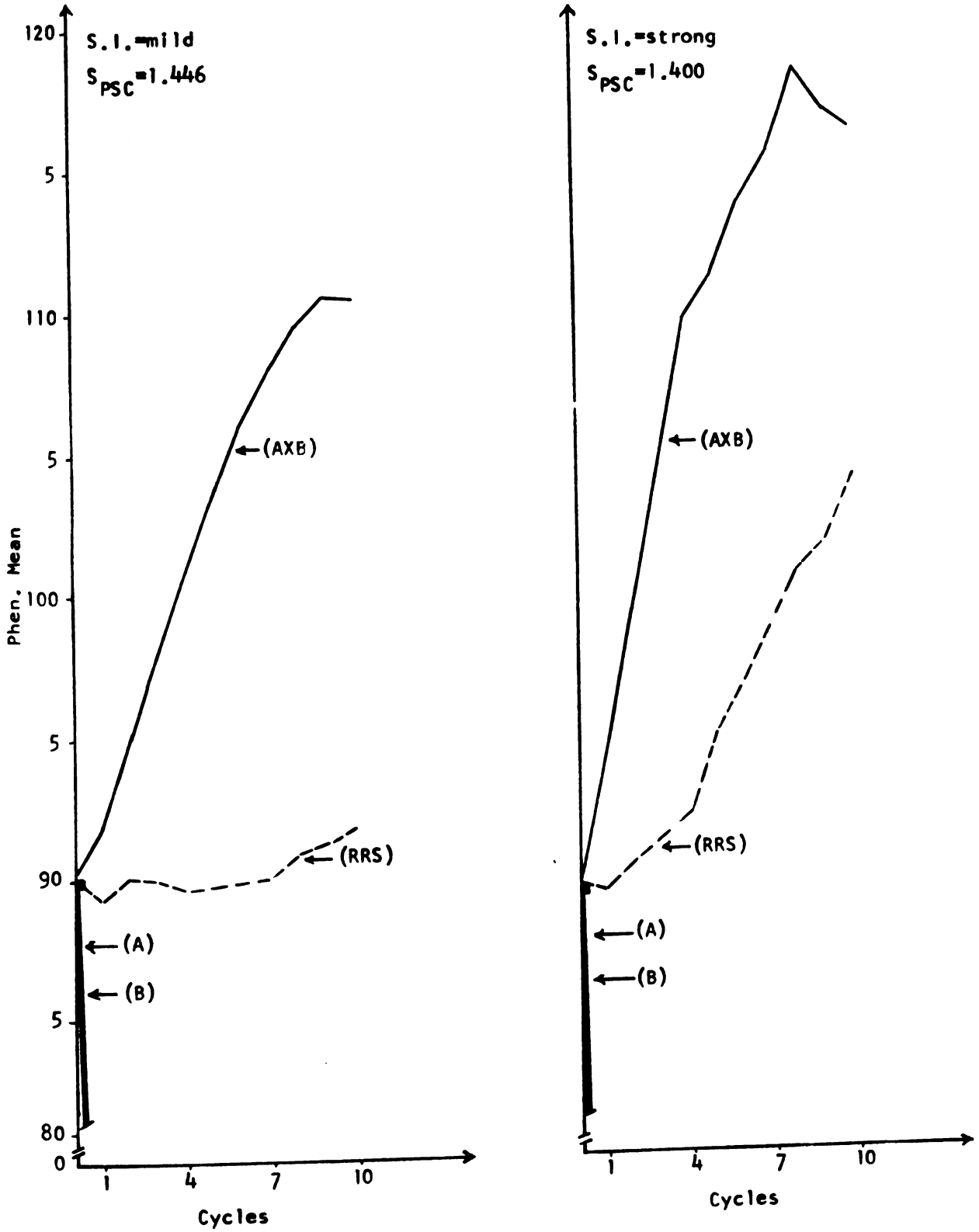

S.I.=mild
S_{PSC}=1.446
120
5
110
5
100
5
90
5
80
0
Phen. Mean
(AXB)
(RRS)
(A)
(B)
1
4
7
10
Cycles
S.I.=strong
S_{PSC}=1.400
(AXB)
(RRS)
(A)
(B)
1
4
7
10
Cycles

Fig. 8 - Mean progress for population A, B, and (A x B) for the Hallauer method, and the hybrid population for the (RRS) method with initial gene frequencies $_{A}p_{1} = 0.1$ and $_{B}p_{1} = 0.1$ for the optimum number model and two selection intensities.

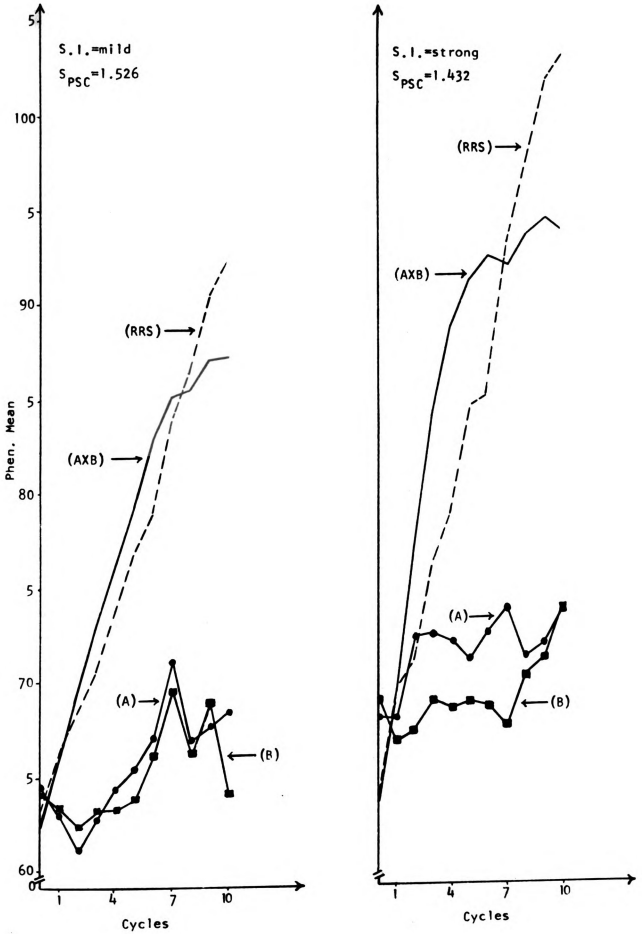
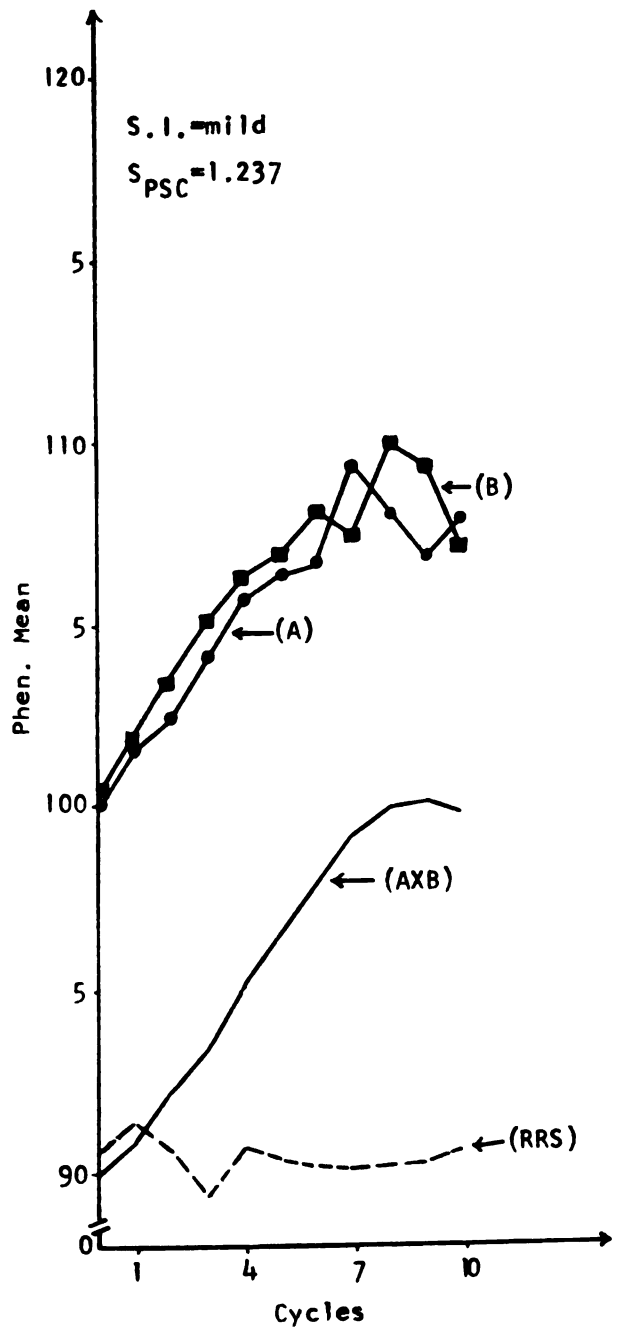

S.I.=mild
S_{PSC}=1.526
(RRS)
(AXB)
(A)
(B)
Phen. Mean
Cycles
S.I.=strong
S_{PSC}=1.432
(RRS)
(AXB)
(A)
(B)
Cycles

Fig. 9 - Mean progress for population A, B, and (A x B) for the Hallauer method, and the hybrid population for the (RRS) method with initial gene frequencies ${}_{A}p_{1} = 0.7$ and ${}_{B}p_{1} = 0.3$ for the additive by additive model and two selection intensities.


S.I.=mild
S_{PSC}=1.237
120
5
110
5
100
5
90
0
Phen. Mean
(A)
(B)
(AXB)
(RRS)
1
4
7
10
Cycles

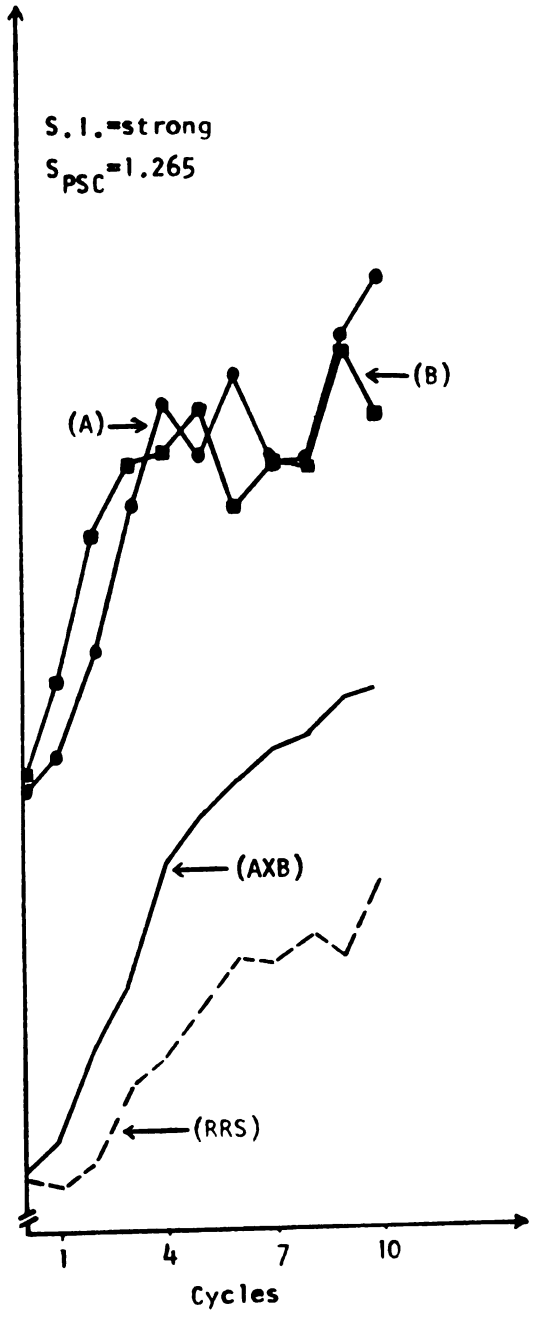

S.I.=strong
S_{PSC}=1.265
(A)
(B)
(AXB)
(RRS)
1
4
7
10
Cycles

Fig. 10 - Mean progress for population A, B, and (A x B) for the Hallauer method, and the hybrid population for the (RRS) method with initial gene frequencies $_{A}p_{1} = 0.7$ and $_{B}p_{1} = 0.3$ for the additive by dominant model and two selection intensities.

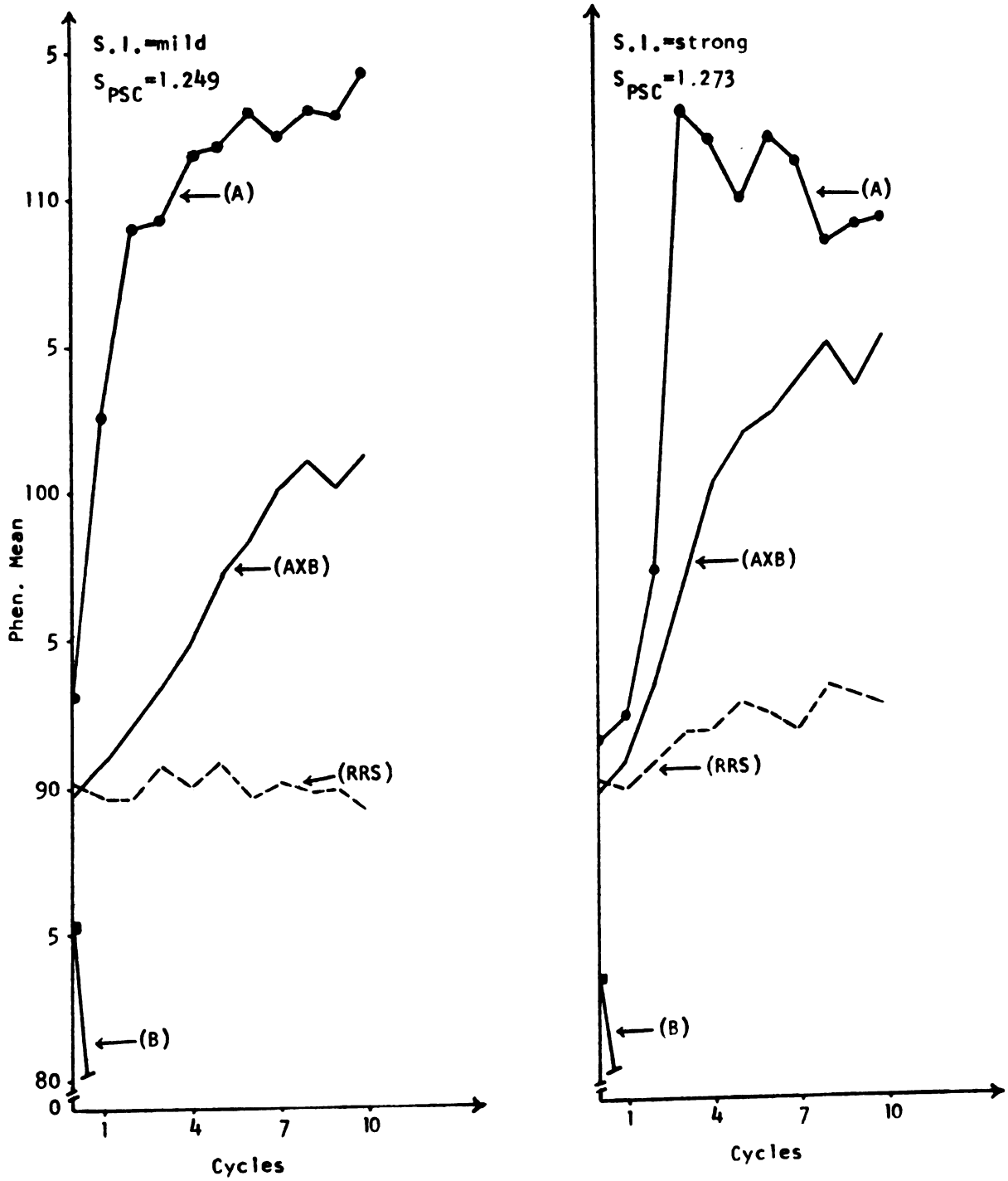
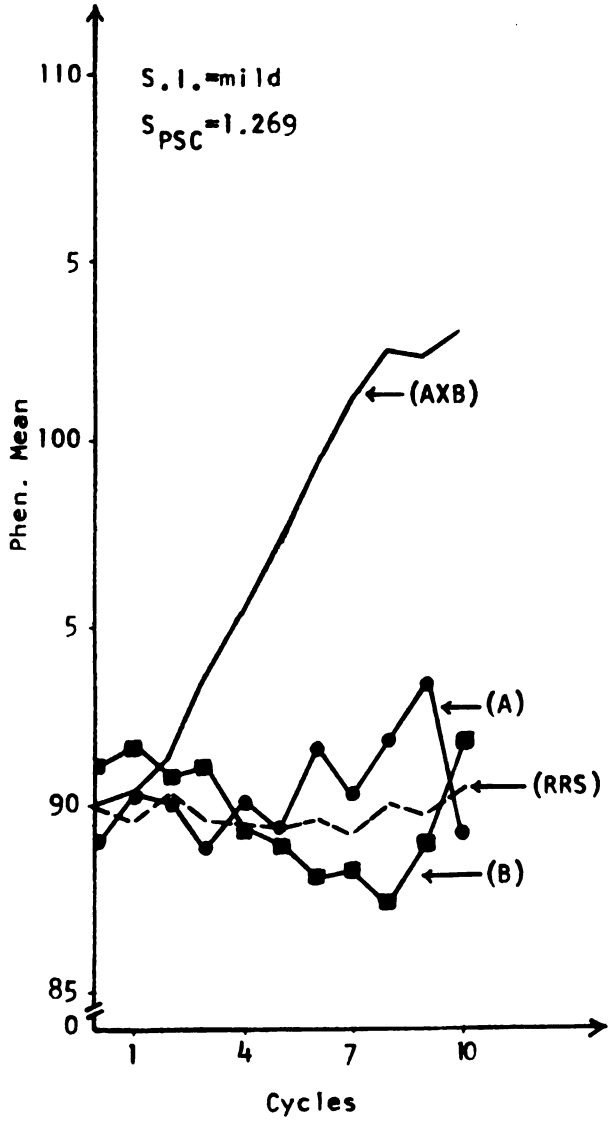
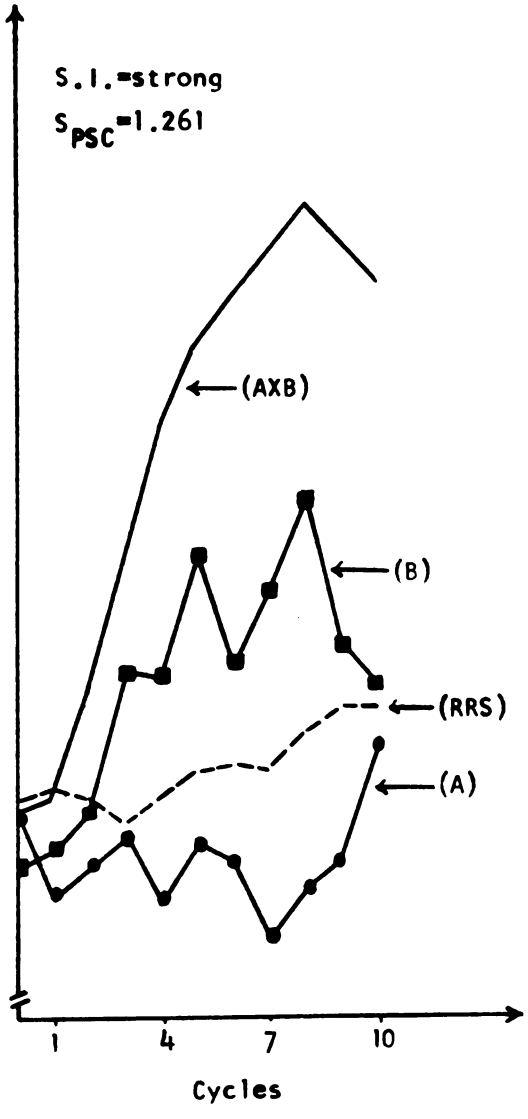

S.I.=mild
S_{PSC}=1.249
(A)
(AXB)
(RRS)
(B)
Phen. Mean
5
110
5
100
5
90
5
80
0
1
4
7
10
Cycles
S.I.=strong
S_{PSC}=1.273
(A)
(AXB)
(RRS)
(B)
1
4
7
10
Cycles

Fig. 11 - Mean progress for population A, B, and (A x B) for the Hallauer method, and the hybrid population for the (RRS) method with initial gene frequencies ${}_{A}p_{1} = 0.5$ and ${}_{B}p_{1} = 0.5$ for the additive by dominant model and two selection intensities.


S.I.=mild
S_{PSC}=1.269
110
5
100
5
90
85
0
Phen. Mean
(AXB)
(A)
(RRS)
(B)
1
4
7
10
Cycles


S.I.=strong
S_{PSC}=1.261
(AXB)
(B)
(RRS)
(A)
1
4
7
10
Cycles