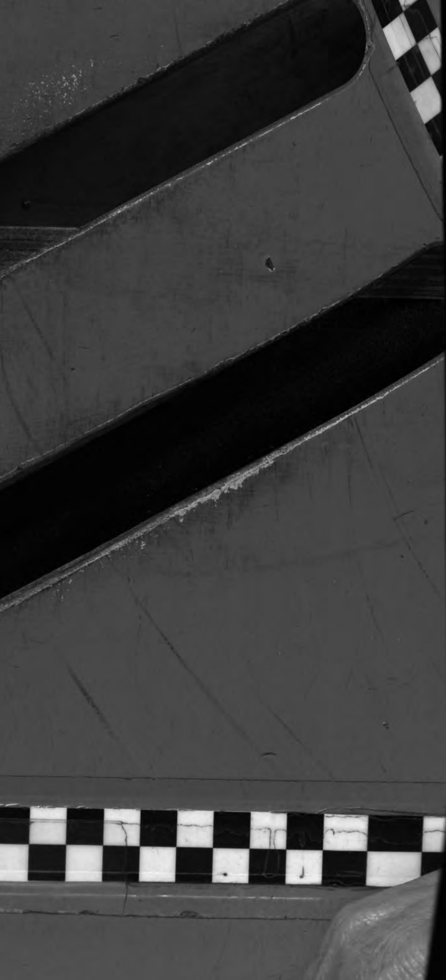

AN ATTEMPT TO OVERCOME THE YIELD-DAMPENING EFFECT OF NEGATIVE CORRELATIONS AMONG YIELD COMPONENTS IN BEANS (Phaseolus vulgaris L.)

Thesis for the Degree of Ph. D.
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OSWALDO VOYSEST VOYSEST
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This is to certify that the

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An attempt to overcome the yield-dampening
effect of negative correlations among yield
components in beans (*Phaseolus vulgaris* L.)

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Oswaldo Voysest Voysest

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ABSTRACT

AN ATTEMPT TO OVERCOME THE YIELD-DAMPENING EFFECT OF NEGATIVE CORRELATIONS AMONG YIELD COMPONENTS IN BEANS (*Phaseolus vulgaris* L.)

By

Oswaldo Voysest Voysest

Negative correlations among the several components of yield in field beans (*Phaseolus vulgaris* L.) impede progress for higher yield when individual components become the direct object of selection. A plan in which the seed number components are held constant, in the genetic context, while selection pressure is placed on the seed size component, is proposed as one practical method of overcoming the effects of the negative correlations.

The rationale of this approach implies the following premises:

a. Additive behavior of genes for number of pods per plant (X), number of seeds per pod (Y) and seed weight (Z).

b. Low heritability for X and Y; high heritability for Z.

c. The identification of high seed number types (XY) by selecting from among small Z lines, thus taking advantage of the negative relationship between seed number and seed size to offset, to some extent, the low heritability of XY.

Crosses were made between lines showing low Z (high XY) and large Z (low XY). Two successive generations of backcrosses to the small Z parents were produced but selection was practiced for large Z.

Studies on the nature of the gene action and estimates of heritability for yield and its components confirmed satisfactorily the validity of the assumptions on which this work was based.

Negative correlations among some of the components of yield were shown to exist. These negative associations persisted through the BC_1 and BC_{11} generations. Through path coefficient analysis X was found to be the most important component influencing yield in a direct as well as in an indirect way.

When the effects of correlation of X on Y and X and Y jointly on Z were removed, based on the premise that the characters first in the sequence of development influence the expression of those following them in the sequence, variations in the degree of influence of the different sources of variation (genotypic, environmental and their interaction) on the expression of the traits were found as compared with the reported influence of these sources of variation when correlations were present. Variation in the heritable value of Z was also noticed. It is postulated

that the genetic variance of X is reflected in the genetic variance of Z. The genetic variance of Z then would be composed of a part that is common to X and another which is independent of X, both of which are available for selection. Through backcrossing the variance of X would have been made to vanish and selection would have been based rather on the portion of the genetic variance of Z which is independent from X.

As expected, the genetic complex for seed number represented by the recurrent parent was recovered through recurrent backcrossing. When individual components for the seed number trait were considered, however, significant variations were noted with respect to the expected values. These deviations were attributed mainly to component compensation.

Selection for seed size in the BC_1 was effective in about half of the populations studied. A regression toward the Z-values of the recurrent parent was evident in the populations where selection for large Z was not effective. A narrow genetic base in the parent population was singled out as the most probable cause of lack of success in selection for large Z. In the populations where selection for Z was effective, the regression towards the recurrent parent values was successfully overcome. Increases over the progenitor ranged from 10 to 31%.

Selection in certain crosses of the BC_1 might have successfully isolated a genetic portion more associated with the mid-parental performance than with that of the recurrent parent. This was confirmed by the similar percent increase in seed size of the BC_1 and BC_{11} with respect to the recurrent parent.

With respect to yield most lines showed a numerical increase over the recurrent parent although only 6 lines showed significance. A summary of the changes in the populations studied with respect to their components and yield presents the following picture: of the 20 populations studied in 12 of them there was no significant gain in seed size; stability of the seed number component was maintained but no gain in yield was evident over the recurrent parent with the exception of 2 populations where significant increase in X and Y, respectively, accounted for most of the increase in yield. This performance was attributed to complementary gene action. In the other 8 populations where selection for Z was effective in 4 of them there was significant gain in yield and in 4 of them increases in Z were unable to compensate for variations in the X or Y components. Lack of genetic gain in yield in these crosses was attributed to the narrow genetic base among the parent populations and to the lack of an outstanding recurrent parent.

Average yields of BC_1 and BC_{11} exceeded the recurrent parent by 28% and 32%, respectively. It appeared from data derived from BC_1S_1 and BC_1S_2 that yield performance of the BC_1 was influenced favorably by heterozygosity.

Our data support the idea that new levels of yield can be attained by increasing the level of expression of the component most highly heritable through selection, while holding constant the levels of expression of the less heritable characters through recurrent backcrossing. Ample genetic diversity for the character under selection, and high levels of expression for the traits to be stabilized are *sine qua non* requirements for the success of this approach.

AN ATTEMPT TO OVERCOME THE YIELD-DAMPENING EFFECT OF NEGATIVE CORRELATIONS AMONG YIELD COMPONENTS IN BEANS

(*Phaseolus vulgaris* L.)

By

Oswaldo Voysest Voysest

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INTRODUCTION

In beans, as in many other crops, efforts directed at raising grain-yield potential, based on selection of this character *per se*, have often been in vain.

A widely-used approach to understanding the inheritance of yielding ability in grain crops has been the analysis of the components of yield. In the case of common beans the primary components of yield are number of pods per plant, number of seeds per pod, and seed weight. Since yield is the multiplicative product of these components, all three assume importance in efforts to understand the basis of yield and in efforts to attain new levels of productivity.

If the object of a breeding program is to increase the level of yield, then a positive correlation among the components may be considered an asset while negative correlations would be detrimental. Progress by selection for components of yield rather than yield *per se* has been limited by moderate to strong negative correlations among the components. Gains in a single yield component offset by decreases in one or both of the other components have impeded progress for higher yields. The net result in selection programs where individual components have become the direct object of selection have not differed substantially from those based on selection for yield alone.

A compensatory mechanism has been postulated to control the relationships among components. Evidence seems to suggest that negative correlations arising from this system of compensation are primarily developmental in nature, i.e., components compete for a common limited pool of resources produced by or available to the plant, and in order to attain a typical yield a compromise is established among the components with respect to their levels of expression.

The gradual attainment, however, of new higher levels of yield is clear indication that these negative correlations among yield components may be at least partially surmounted. The aim of this thesis is to test whether yield limitations imposed by negative associations can be overcome by shifting only one of the traits composing the complex character from its typical value while holding constant the genetic basis of the other yield-comprising traits. A concurrent objective is to explore the idea that the penetrance of the genes which regulate the development of the yield components is not affected by the persistence of the negative relationships since it is not encumbent on this procedure that negative associations be made to vanish, only that the yield be improved within a framework where negative correlations have been shown to exist.

REVIEW OF LITERATURE

Efforts to improve grain yield in crop plants involve two general kinds of approaches. Some workers have emphasized the study of the physiological characters underlying differences in yield capacity; some papers in beans (19, 32, 33) and in small grains (6, 30, 34) may be cited as examples. Others have preferred to deal with characters more amenable to observation, that is, end points of phenotypic expression that could be evaluated in terms of size, morphology or number and that either comprise yield or can be associated with it.

A more subtle kind of controversy has arisen involving the yield structure and ways to define it. The view that hereditary control of yield may be studied best at its component level (16) was challenged on the grounds of a dubious cause and effect relationship between yield and the components closer than that of genes for yield *per se* (23). The argument that yield is indeed the product of a set of yield components and that there can be no genes for yield which by-pass the components (14) has remained unchallenged.

The use of yield components as an approach to varietal improvement has been criticized (22) on the grounds that components are nothing else than manifestations of yield, with value only as indicators of the general trends taking place during plant growth, or valuable only in providing a model when selecting for particular ecological conditions. On the other hand, the importance of breeding for yield utilizing knowledge of yield components and their genetic relationships, has long been emphasized for self-pollinated crops (37).

Selection programs for yield based on component analysis are no more widespread than those using the strictly statistical-genetic approach, primarily because of the nature of the interdependence of the components and their sometimes nonsignificant effect on the levels of expression of the complex trait itself, as indicated by numerous studies on phenotypic (correlations) and genotypic (heritabilities and genetic correlations) parameters of yield and its components.

Total seed yield has been reported unanimously as a character of low heritability of soybeans. Estimates of heritability for pods per plant and seeds per pod have varied from intermediate to low, but seed weight has been reported in most cases as highly heritable (4, 18, 20, 35). A similar pattern has been observed in common beans. Heritability estimates in the broad sense showing values such as 51.1% for number of pods per plant, 82.9% for number of seeds per pod, 84.8% for seed size, and 15.1% for yield have been reported (9). Other reports present very low heritability estimates for total yield and each yield component (8).

Interdependence among the components of yield in common beans is clearly indicated by almost all the numerous studies where the correlation coefficients have been calculated (5, 7, 9, 10, 11, 17, 26, 27). The values of the correlation coefficients between yield and the components, number of seeds per pod and seed weight are, in general, small or negligible. Number of pods per plant is the only component whose correlation with yield has been consistently reported as high. Correlations among components themselves are reported mostly as negative. When positive, the values are of small magnitude.

Duarte (11) used a path coefficient analysis to separate the correlation coefficient into components of direct and indirect effect. Number of pods per plant was the component which showed the greatest direct effect on yield. Seed weight, on the other hand, had the least influence upon seed yield.

Coyne (8) calculated partial correlation coefficients between total seed yield and yield components. Based on the high values of the partial correlation coefficients between total yield and each yield component, he concluded that each component was about equal in importance in determining total seed yield. The fact that the majority of the partial correlation coefficients were low and positive was interpreted as an indication that it would be possible to select for an increased value of one yield component without producing a reduction in value of the other components.

There are only a few studies on the genetics of the components of yield. Dickson (10) reported that number of pods per plant, number of seeds per pod, and number of seeds per plant were determined by a simple additive gene system. In the case of pod number some incomplete degree of dominance was reported with high pod number being mostly determined by recessive genes. Coyne (8) reported complete dominance for higher number of pods per plant and lack of dominance for mean seed weight.

The nature of gene action and the complex structure of yield bears a close relationship to the presence or absence of heterotic behavior. Evans (13) has reported significant positive heterosis for seed yield per plant and number of pods per plant in beans. She noticed that some crosses involving determinate and indeterminate types of plants did not maintain their heterotic behavior through the second generation whereas others involving only determinate types showed a considerable amount of heterosis in the F_2 generation. She concluded that morphological differences between the two types of plants are associated with differences which produce superior F_1 combinations but not well-balanced segregates in advanced generations.

Adams and Duarte (2) explained heterosis for a complex trait as a result of component interaction. Their studies with total leaf area as a complex character confirmed other reports (15, 36) that the multiplicative interaction between components can successfully explain heterosis in a complex trait. The component traits, leaf area and leaflet number, were influenced by an additive and a dominant gene system, respectively.

Selection studies based on components of yield have not succeeded in raising the level of productivity in beans. Duarte (11) applied recurrent selection methods for yield and each of the components of yield for three levels of expression in a bean population. No progress was attained for yield itself during two cycles of selection. Progress in each of the components of yield was offset by an opposite response in the other components.

Coyne (8) selected the top 5% of the F_2 of a cross between two bean varieties on the basis of total yield and separately for each of the three yield components. No yield improvement was realized for any of these traits. These results were attributed to the large environmental effect on the expression of these traits, which made it difficult to identify genetically superior individuals, or to low additive genetic variance.

In barley, Nickell and Grafius (25) failed to realize the expected genetic gain after one generation of selection based on yield and the seed size component. Different environmental conditions requiring different optima in the gene pool for yield components and their interrelationships for attaining maximum yield was suggested as an explanation for this negative response to selection.

Increases in yield by selecting for morphological components have been reported in other crop species. Torregroza and Harpstead (31) obtained an increase of 28% in the number of ears per plant and 14% more yield than the original population in the fifth cycle of selection for multiple ears in corn. In single-eared selections yields were reduced by 5% while the number of ears decreased by 7%. Rasmusson and Cannell (29) carried on selection experiments on the basis of yield and its components in two populations of barley. The results were not consistent for the four selection criteria for the two populations. Selection for number of heads per plant was effective in one of the two populations studied; the positive correlation with yield was high. Selection for kernel weight was effective for both populations but its positive correlations with yield was high in only one population. Selection for kernels per head was successful in one population and failed in the other. Yield was reduced when selection for kernels per head was effective.

All these studies of grain yield in terms of the components showed that the varieties achieve their yield in different ways, i.e., either through an increase in the seed number components or through an increase in seed size. However, because components of yield are interdependent, increases in one are often accompanied by decreases in one or more of the others. The nature of these responses are both genetic and environmental as suggested by Adams (1) in beans and Rasmusson and Cannell (29) in barley. The associations between components are described by Adams as deriving from developmentally-induced relationships between these attributes of yield whereas Rasmusson and Cannell ascribed these relationships to genetic linkage.

MATERIALS AND METHODS

Plant Materials

Plant material for this study consisted of eleven lines of navy-type beans (*Phaseolus vulgaris* L.) selected from among 227 lines grown in 1967 and previously classified by seed size. The lines were divided into two sets: the first, on the basis of small seed size and high seed number, the second, on the basis of large seed size. In addition, two large-seeded varieties, Great Northern (selection #27) and Perry Marrow, were included in the second set.

Because of the negative associations between seed size and seed number in navy beans, and the lower heritability of seed number, it was deemed advantageous to select the high seed number lines partially on the basis of their small seed size. For this reason, the recurrent parents, which contribute genes for high pod number and/or high number of seeds per pod to the crosses, are often referred to as the small-seeded parents.

The characteristics of the original parent population are shown in Table 1. Parents will be referred hereinafter as P-01, P-02...P-12 and P-13.

Table 1. Mean plant performance of the original parent population evaluated at East Lansing, Michigan in 1967

Lines	Weight/100 Seeds (in gms)	Seed Number per Plot[a]	Yield per Plot[a] (in gms)
Small Seed Set			
P-01	16.8	1434	240.9
P-02	15.6	1327	207.0
P-03	14.9	1396	208.0
P-04	14.0	1471	205.9
P-05	14.0	1328	205.9
Mean	15.1	1391	209.5
Large Seed Set			
P-06	19.5	953	185.9
P-07	19.6	969	189.9
P-08	19.5	1112	216.8
P-09	18.2	1111	184.0
P-10	17.8	1253	223.0
P-11	16.6	1337	222.0
Mean	18.5	1122	203.4
P-12 (G. Northern)	28.9	...	...
P-13 (P. Marrow)	35.9	...	...

[a] Five-foot plots.

General Scheme of the Experiment

To fulfill the objectives of this thesis, the breeding plan selected to be effective involved combining the high seed number characteristic of one set of lines with the high seed weight characteristic of a second set of lines. Because of the divergent levels of heritabilities of the components it was planned to place major selection pressure on the component of highest heritability, seed weight, so as to regulate the frequency of genes for seed weight, since the heritability of this trait is high enough that selection should be effective. To recover the frequency of genes for high seed number, of lower heritability, recurrent backcrossing to the high-seed-number lines was intended.

Inclusion of the Great Northern and Perry Marrow lines--clearly too large to be classified as Navy beans--represents deliberate overshooting so that a large amount of genetic variance for seed size would be generated and a continual regression in seed size could be tolerated during backcrossing to small-seeded lines.

Greenhouse, 1967

Crosses were made in 1967 between small-seeded (high seed number) and large-seeded lines. A total of twenty combinations were obtained. Plants of the F_1 generation were backcrossed to the small-seeded parent to give the BC_1 generation. The notation used for identification of the backcross material is as follows: two two-digit numbers corresponding to the original parents are shown after the conventional notation for identification of the generations (BC_1, F_1, F_2, etc.). The first two-digit number indicates the progenitor used as female, the second one, the male. The smallest number is always the recurrent parent. For example, BC_1-0106 indicates the first backcross generation of the cross P-01 (used as female) with P-06 (used as male), the F_1 being backcrossed to P-01. As far as the identification of the particular backcross generation is concerned, the subscript 1 is used to indicate backcrossing to the small-seeded parent. Two backcrosses made to the same recurrent parent is indicated by the corresponding subscript written twice.

Each small-seeded parent was crosses with at least three large-seeded lines. The 20 combinations obtained are shown in Table 2.

F_2 seed from 17 of the 20 combinations was obtained by selfing the F_1 plants used for the backcrosses.

Field Trials, 1968

An experiment including 19 BC_1 lines, 17 F_2 lines, and 13 parental varieties was grown in 1968 at Saginaw, Michigan. The experimental design was a randomized block with 4 replications. Each plot consisted of one 15-plant row with a 70 cm (28 inches) distance between rows and a

Table 2. Backcross combinations obtained from crossing small-seeded lines x large-seeded lines, small-seeded lines being the recurrent parents

Large-Seeded Lines	Small-Seeded Lines				
	P-01	P-02	P-03	P-04	P-05
P-06	BC_1-0106	BC_1-0206	BC_1-0306	BC_1-0406	BC_1-0506
P-07	BC_1-0107	..	..	..	BC_1-0507
P-08	..	..	..	BC_1-0408	..
P-09	BC_1-0109	BC_1-0209	BC_1-0309	BC_1-0409	BC_1-0509
P-10	..	..	BC_1-0310	..	BC_1-0510
P-11	..	..	..	BC_1-0411	BC_1-0511
P-12	BC_1-0112	..	..	..	..
P-13	..	BC_1-0213	BC_1-0313	..	..

plant spacing of 20 cm (8 inches) in the row. Moisture conditions were above normal at the beginning of the growing season but two sprinkler irrigations were necessary at the blooming period and during pod and seed development.

Twenty-five competitive plants were harvested from each backcross line and twenty from each F_2 line. Four competitive plants were chosen from each plot for each parental line.

Data were collected for yield (W), number of pods per plant (X), number of seeds per pod (Y), and average seed weight (Z), recorded as grams per 100 seeds. Total grain yield per plant was determined by weighing all the grain produced on each plant. The X component was determined by counting on each plant all the pods with at least one viable seed. The total number of seeds produced by each plant was counted and the number of seeds per pod was estimated by dividing the total number of seeds by the number of pods ($Y = (XY)/X$). The average seed weight was computed using the total yield per plant and the seed number ($Z = W/(XY) \times 100$).

Statistical analyses were made on the basis of plot means.

Selection was practiced for seed weight in each BC_1 population. Two plants with the largest seed size out of 25 were selected. F_2 seed from each line was bulked.

Greenhouse, 1968

Seed from each BC_1 selection was stored as BC_1S_1 seed and a part was planted in the greenhouse and backcrossed to the respective small-seeded parent to produce the BC_{11} generation. Selfed plants from each BC_1 selection used in the greenhouse produced BC_1S_2 seed. Some crosses were repeated to obtain F_1 seed.

For the field trials the materials available were: 42 lines of the BC_1S_1 and BC_1S_2 generations, 37 BC_{11}, 17 F_3 and 6 F_1 lines plus the 13 parental lines, and the non-selected BC_1S_1 generation.

Field Trials, 1969

Five field experiments were conducted at Saginaw, Michigan in 1969. The 37 BC_{11} lines and the five small-seeded parents were tested in one experiment using a 6 x 7 rectangular lattice design. The rest of the study involved four additional experiments in which the following material was tested, respectively: (1) BC_1S_1 lines, (2) BC_1S_2 lines, (3) F_1, F_3 and parental lines, and (4) the non-selected BC_1S_1 generation. The experimental layout in all cases except the last experiment was a 6 x 7 rectangular lattice with 4 replications. Samples from individual BC_1 plants from the 1968 experiment were tested in a systematic design without replications.

Plot characteristics for all five experiments were the same. Each plot was formed by one 20-plant row. Spacing between rows was 70 cm (28 inches) and plant spacing in rows was 15 cm (6 inches). Five competitive plants were harvested from each plot and data on yield of grain and yield components were collected in the same way as in the 1968 experiments. For the BC_1S_1 unselected plants a sample of pods was taken from 17 different plots for each of the 21 backcross combinations. Only data on seed size was collected in this particular experiment.

Statistical analyses were made on plot means. Separate analyses of variance were computed for each experiment, for each trait measured. Further, the 1968 and 1969 data for the parental material were analyzed according to the form of variance analysis presented by Johnson, Robinson and Comstock (20, 21). The form of variance analysis and mean square expectations for data collected in two years and one location are presented in Table 3.

Table 3. Variance analysis and mean square expectations for data from two years at one location

Source	d.f.[a]	Mean Square Expectations[b]
Years	y-1	$\sigma_e^2 + g\sigma_{r(y)}^2 + rg\sigma_y^2$
Replications in years	y(r-1)	$\sigma_e^2 + g\sigma_{r(y)}^2$
Lines	n-1	$\sigma_e^2 + r\sigma_{gy}^2 + ry\sigma_g^2$
Lines x years	(n-1)(y-1)	$\sigma_e^2 + r\sigma_{gy}^2$
Rep. x lines in years	y(n-1)(r-1)	σ_e^2

[a] r = number of replications; n = number of genotypes; and y = number of years.

[b] The variance components estimated were:

σ_g^2 = Line component due to genetic differences among lines.

σ_{gy}^2 = Genotype x year component.

σ_e^2 = Plot error variance.

The model used to estimate these components assumes fixed genotypic and random environmental effects.

Heritability estimates for yield and the components of yield were calculated on a per plot basis by the formula $H = \hat{\sigma}_g^2/\hat{\sigma}_{ph}^2$ where $\hat{\sigma}_g^2$ is the estimated variance attributable to genotypic effects and $\hat{\sigma}_{ph}^2$ the phenotypic variance of lines ($\hat{\sigma}_{ph}^2 = \sigma_g^2 + \sigma_{gy}^2 + \sigma_e^2$). Heritability values were calculated also by other methods. Parent-offspring regression was used with the F_1 data and the F_2 data were used for the regression of the offspring on the mid-parent. Realized heritability for seed weight was also obtained using the following formula:

$$\text{Heritability} = \frac{\bar{X}_{BC_1S_1s} - \bar{X}_{BC_1S_1}}{\bar{X}_{BC_1s} - \bar{X}_{BC_1}} \times 100,$$

where the numerator is the selection differential in the BC_1S_1 generation and the denominator is the difference in performance between the mean of the selected BC_1 lines and the BC_1 population mean.

Selection was considered effective when the mean values of the progenies of the selected BC_1 plants differed significantly from the BC_1S_1 population mean. Realized heritability estimates were used as one means of evaluating the effectiveness of selection.

Estimates of expected genetic gain from the selection practiced for seed size in the BC_1 generation were computed for each backcross line as the product of the heritability estimate based on variance component analysis, the standardized selection differential and the estimated phenotypic standard deviation ($GA = K\hat{\sigma}_{ph}H$). For the purpose of this work K was given the value of 1.76 which is the expectation in the case of 8% selection (2 in 25) from a normally distributed population. The phenotypic standard deviation was calculated on a per plot basis from the BC_1 population. Since the expected genetic gain was calculated assuming a normally distributed population and using heritability estimates in the broad sense, the resulting values were considered only as maximum expectations.

The expected means for the backcross generations were calculated on the assumption of additive gene action with the midparent value representing the F_1. The expected progress towards the recurrent parent value was one-half of the remainder for each succeeding generation. For the character under selection, seed size, deviations from the additive scheme were considered significant when they fell outside the ranges of the confidence interval for the observed BC_{11} means. Also, a maximum value for the expected BC_{11} mean due to selection was derived by adding half of the value of the maximum genetic advance to the expected BC_{11} mean calculated under the assumption of additive gene action.

The effect of heterozygosis on the grain yield and its components was studied using the genetic material shown in Table 4.

The sums-of-squares due to heterozygosis levels were partitioned into single degrees of freedom using

Table 4. Genetic material representing four levels of heterozygosis

Percent Heterozygosis	Genetic Material
0	Inbred lines P_1 and P_2
25	$F_3 = F_2$ selfed
50	$F_2 = F_1$ selfed
	$BC_1 = F_1 \times P_1$
100	$F_1 = P_1 \times P_2$

polynomial regression to test for the significance of the linear, quadratic and cubic effects.

Polynomial coefficients applicable to the unequally spaced levels were derived previously (3).

Since the BC_{11} and BC_1 generations were grown in a different year from the rest of the material, adjustments were made on X, Y, and Z based on the change experienced by the common sets of parents grown in both years. Only BC_1 values were used for the 50% level of heterozygosity in the partitioning of the sums of squares. The percentage of adjustments made are shown in Table 5.

Table 5. Percent increase (+) or decrease (-) of BC_1 values based on performance of parents on 1968 and 1969

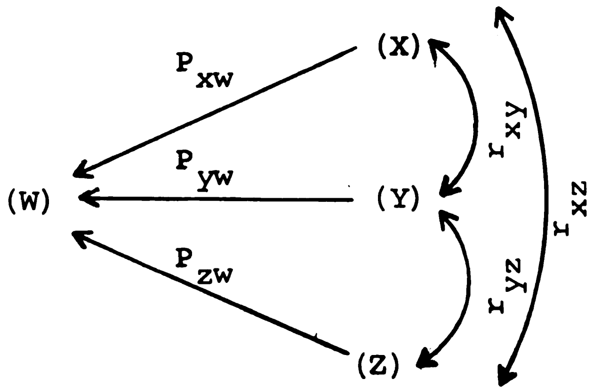
	X		Y		Z	
	Avg.[a]	Specific[b]	Avg.	Specific	Avg.	Specific
0106	-28.2	-27.1	9.0	11.5	3.0	4.5
0209	-17.1	-17.3	12.9	13.5	5.9	2.1
0408	-20.0	-17.8	10.8	11.5	4.9	3.0
0506	-20.2	-19.6	6.2	6.2	4.9	6.0
0510	-20.2	-22.6	6.2	2.6	4.9	3.4
0511	-20.2	-21.5	6.2	7.6	4.9	5.4

[a] Average change of all populations with the same genetic background.

[b] Change for the specific population studied.

The interrelationships among plant characters were studied by computing simple correlation coefficients among yield and the components of yield in all possible combinations on a plot basis. A further analysis of the correlation coefficient was undertaken by the path coefficient method and by multivariate analysis.

For the path coefficient analysis four variables were included. The nature of the causal system is represented diagramatically as follows:



(W) Total grain yield
(X) Number of pods per plant
(Y) Number of seeds per pod
(Z) Seed weight

In the path coefficient diagram the double-arrowed lines indicate the correlation between two variables as measured by the correlation coefficient. Direct effects are represented by single-arrowed lines and measured by path coefficients.

The basic relationship between correlation and path coefficients are expressed as follows:

$$r_{xw} = P_{xw} + r_{xw}P_{yw} + r_{xz}P_{zw}$$

$$r_{yw} = P_{yw} + r_{xy}P_{xw} + r_{yz}P_{zw}$$

$$r_{zw} = P_{zw} + r_{yz}P_{yw} + r_{xz}P_{xw}$$

The path coefficients were computed from the above set of equations by solving for the P's.

Since yield (W) is a multiplicative product of X, Y, and Z, for the correct application of the path coefficient method, a logarithmic transformation of the data was undertaken.

A multivariate technique described by Rao (28) was used to remove the correlation effect of number of pods per plant (X) on number of seeds per pod (Y), and the effect of these two components on the seed size component (Z). A program intended to compute the Mahalanobis distance value (24) was adapted in its pertinent parts for our purposes.

A 3 x 3 phenotypic variance-covariance matrix was calculated and a matrix of multipliers obtained by a pivotal condensation of the variance-covariance matrix such that the original character means (X, Y and Z) could be transformed to an uncorrelated set ($\tilde{X}$, $\tilde{Y}$ and $\tilde{Z}$); the uncorrelated set being defined by the equations:

$$X = X$$

$$\tilde{Y} = Y - a_{yx}X$$

$$\tilde{Z} = Z - a_{zy}Y - a_{zx}X$$

where

$$a_{yz} = \frac{\text{covariance YX}}{\text{variance X}}$$

$$a_{zx} = \frac{\text{covariance ZX}}{\text{variance X}}$$

$$a_{zy} = \frac{\text{covariance ZY} - a_{y} \cdot \text{covariance ZX}}{\text{variance X}}$$

RESULTS

Analysis of the Parent Population

Grain yield (W) and the yield components, number of pods per plant (X), number of seeds per pod (Y), and seed weight (Z) are summarized for parental lines in Tables 6 and 7. The small-seeded lines were on the average more productive than the large-seeded ones. Yields ranging from 22.4 to 30.9 grams per plant are shown for the small-seeded lines. Large-seeded parents recorded yields ranging from 15.8 to 29.8 grams per plant.

Number of pods per plant was a highly variable trait, ranging from 39.3 to 46.8 for P-05, from 31.5 to 39.3 for P-02 among the small Z lines and from 12.2 to 22.0 for P-12 and 37.0 to 44.8 for P-08 among the large Z lines. On the average, lines with small seeds produced a greater number of pods per plant than those with large seeds.

Although lines with small seeds showed on the average more seeds per pod, the individual examination of the lines did not give evidence of any consistent pattern of variation that could be related to seed size as confirmed by the ranges 3.9 to 5.2 and 3.9 to 4.9 shown by the small and large Z parents, respectively.

Table 6. Comparative mean plant performance of the small-seeded pure lines evaluated at Saginaw, Michigan in 1967, 1968, and 1969

		Small-Seeded Lines						Relative
Trait	Year	P-01	P-02	P-03	P-04	P-05	Avg.	Change (1968=100)
Yield of grain (grams)	1968	30.010	24.650	22.447	23.895	27.525	25.709	100.0
	1969	28.500	27.669	27.091	27.729	26.735	27.545	107.1
	1969	28.801	25.568	30.944	23.982	27.124	27.284	106.1
	Avg.	29.104	25.962	26.827	25.202	27.128	26.846	
No. of pods per plant	1968	39.950	39.300	40.421	46.000	46.750	42.484	100.0
	1969	32.450	34.050	39.050	40.050	39.300	37.080	87.3
	1969	31.368	31.500	43.584	36.371	40.062	36.577	86.1
	Avg.	34.589	34.950	41.018	40.807	42.037	38.714	
No. of seeds per pod	1968	4.685	3.920	3.805	3.370	4.325	4.101	100.0
	1969	5.250	5.000	4.600	4.675	4.575	4.820	117.5
	1969	5.169	4.677	4.506	4.322	4.730	4.681	114.1
	Avg.	5.013	4.532	4.304	4.223	4.543	4.534	
Total number of seeds	1968	187.166	154.056	153.802	173.420	202.194	174.128	100.0
	1969	170.362	170.250	179.630	187.234	179.798	177.455	101.9
	1969	162.518	146.686	194.483	150.306	190.738	168.946	96.6
	Avg.	173.349	156.997	175.972	170.320	190.910	173.510	
Weight of 100 seeds (grams)	1967	16.800	15.600	14.900	14.000	14.000	15.100	98.2
	1968	16.730	16.470	15.640	14.000	14.040	15.367	100.0
	1969	17.080	16.420	14.850	14.500	14.850	15.540	101.1
	1969	17.648	17.022	15.586	15.449	14.284	15.998	104.0
	Avg.	17.064	16.378	15.244	14.487	14.294	15.504	

Table 7. Comparative mean plant performance of the large-seeded pure lines evaluated at Saginaw, Michigan in 1967, 1968, and 1969

Trait	Year	Large-Seeded Lines P-06	P-07	P-08	P-09	P-10	P-11	P-12	P-13	Avg.	Relative Change (1968=100)
Yield of grain (gms)	1968	29.020	19.235	29.805	27.120	28.585	25.584	20.143	24.729	25.528	100.0
	1969	28.556	18.988	26.268	25.599	23.878	22.654	15.839	19.788	22.696	88.3
	Avg.	28.788	19.112	28.036	26.360	26.231	24.119	17.991	22.258	24.112	
No. of pods per plant	1968	40.550	23.250	44.800	37.400	38.900	32.421	22.143	18.571	32.254	100.0
	1969	30.900	20.100	37.000	31.350	30.450	25.850	12.200	18.000	25.731	79.8
	Avg.	35.725	21.675	40.900	34.375	34.675	29.136	17.172	18.186	28.992	
No of seeds per pod	1968	4.270	4.220	3.915	4.580	4.390	4.805	3.987	3.329	4.187	100.0
	1969	4.875	4.575	3.925	4.825	4.375	4.625	4.450	3.625	4.409	105.3
	Avg.	4.572	4.398	3.920	4.702	4.382	4.715	4.218	3.472	4.298	
Total number of seeds	1968	173.148	98.115	175.392	171.292	170.771	155.783	88.262	61.823	118.232	100.0
	1969	150.638	91.958	145.225	151.264	133.219	119.556	54.290	65.250	113.925	94.4
	Avg.	161.893	95.036	160.308	161.278	151.995	137.670	71.276	63.536	116.078	
Weight of 100 seeds (gms)	1967	19.500	19.600	19.500	18.200	17.800	16.600	28.900	35.900	22.000	100.2
	1968	17.740	20.440	17.780	16.820	17.480	17.860	28.500	39.700	22.040	100.0
	1969	19.020	21.800	18.280	16.850	17.780	18.880	29.150	32.150	21.739	98.6
	Avg.	18.753	20.613	18.533	17.290	17.687	17.780	28.850	35.917	21.926	

A negative association of total number of seeds with seed size was observed. The average difference in 100-seed weight between small- and large-seeded parents was 6.4 grams.

Consistency of performance of the traits over two years is illustrated by the analysis of variance shown in Table 8, the measurements being expressed as percentage values to those of 1968, taken as reference, and presented in Figure 1. There were no significant differences from year to year in yield of grain, total number of seeds, and seed size. Significant differences were found for number of pods per plant and number of seeds per pod. Seed size behaved as the more stable character, showing only slight changes due to seasons. Components X and Y, on the other hand, showed marked changes from year to year. Values of these two components varied in opposite directions consistently for the two sets of lines tested. This compensatory action of X and Y resulted in an almost stable seed number component. Whereas in the small Z population the components X and Y varied by the same amount, percentage-wise, though in opposite directions, in the large Z lines some limitation impeded the upward change in the Y component necessary to compensate for the rather large decrease in the X component. The final outcome is a reduced total number of seeds in large seeded populations as compared with its counterpart.

Table 8. Analyses of variance of grain yield and the components of yield measured for eleven parental lines grown at one location for two years

		Mean Square				
Source	dF	Yield	No. of Pods per Plant	No.Grains per Pod	Total Seed Number	Weight of 100 Seeds
Reps. within a year	6	40.78049	55.76201	0.09702	1350.65502	0.49490
Year	1	4.29006	951.07375**	3.73313**	3549.01503	2.85480**
Genotypes	10	55.99604	328.26564**	0.68905**	5698.81993**	34.09590**
Years x genotypes	10	22.32717	12.70019	0.36163**	993.34015	0.71310
Error	60	25.95913	46.62720	0.07247	1059.29041	0.43660

**Significant at the 1% level.

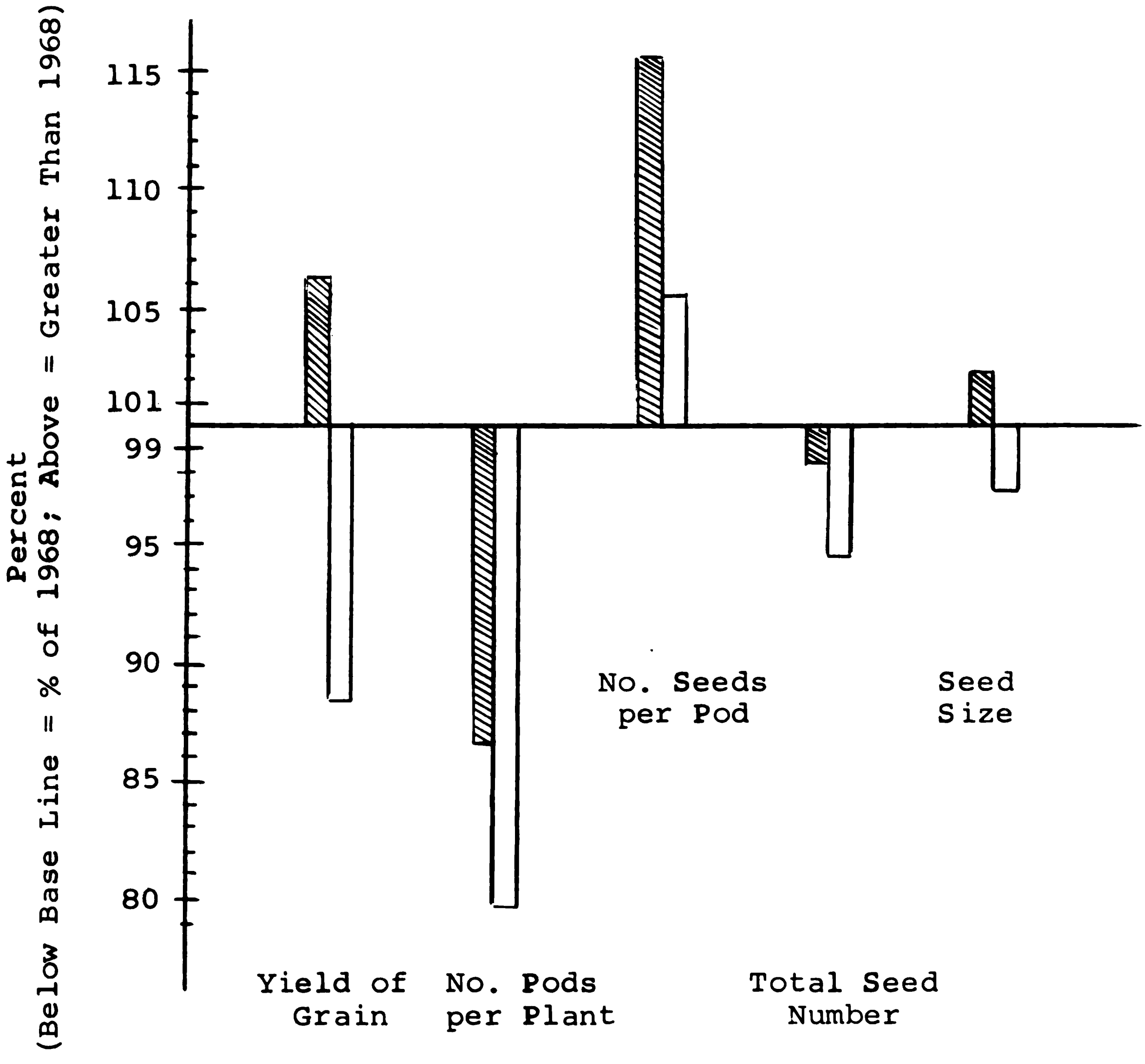


Figure 1. Graphical representation of the values for grain yield and the components of yield in the 1969 experiments expressed in percent of the values from 1968 trials. Hachured blocks refer to small-seeded lines, white blocks represent large-seeded parents.

Study of Correlations

Phenotypic correlation among the yield components, and grain yield for the parent population and the backcross generations are given in Table 9.

Number of pods per plant was more closely associated with high seed yield than any other component. The values of the correlations were similar for the parent and backcross populations. Number of seeds per pod was significantly associated with yield in the small-seeded parents. No correlation was found between these two variables in the large Z population. The degree of correlation between Y and W appears to be related to seed size. When the whole BC_{11} population was compared with BC_{11} populations where selection for high seed size was effective, the results were the same as when small and large seeded populations were compared. This was expected inasmuch as the comparison between the BC_{11} populations was in reality a small versus a large seed comparison.

In general, the values of the correlation coefficients among components of yield were negative and they ranged in size from negligible to moderate. Ten out of twelve of the coefficients were negative in the four populations studied. Although only four were statistically significant the trend for negative relationships among the components was evident and in accordance with previous findings.

Table 9. Simple correlation coefficients among three yield components and grain yield in common beans[a]

Characters Correlated	1968			1969	
	(1) Large Z Parents	(2) Small Z Parents	(3) BC_1	(4) BC_{11}[b]	(5) BC_{11}[c]
Yield vs no. pods/plant	0.856**	0.849**	0.746**	0.860**	0.911**
Yield vs no. grains/pod	0.038	0.473**	0.164**	0.238**	0.006
Yield vs seed size	-0.144	0.064	0.274**	0.115	0.085
No. pods/plant vs no. grains/pod	-0.040	0.052	-0.069	-0.042	-0.030
No. pods/plant vs seed size	-0.484**	-0.190	-0.009	-0.252**	-0.244*
No. grains/pod vs seed size	-0.493**	0.024	-0.156*	-0.045	-0.501**

[a] (1) With 108 degrees of freedom "r" at 5% = 0.195; "r" at 1% = 0.254.
(2) With 78 degrees of freedom "r" at 5% = 0.217; "r" at 1% = 0.283.
(3) With 498 degrees of freedom "r" at 5% = 0.088; "r" at 1% = 0.115.
(4) With 149 degrees of freedom "r" at 5% = 0.159; "r" at 1% = 0.208.
(5) With 62 degrees of freedom "r" at 5% = 0.246; "r" at 1% = 0.321.

[b] Whole BC_{11} population.

[c] BC_{11} populations where selection for Z was effective.

In Tables 10, 11, and 12, path coefficient analyses of the relationships among yield and its component characters are shown for the small- and large-seeded parents and the BC_{11} populations, respectively.

The simple correlation between X and W was high and positive. The direct path effect of X and W was likewise high and positive. The indirect effects via Y and Z were very small. This same pattern was the same for both sets of parents and was not altered by the process of backcrossing.

The simple correlation between W and Y was positive and intermediate in level for small Z parents. This value was determined mainly by the direct effect (r_{yw} = 0.473 vs P_{yw} = 0.423). The indirect effects via X and Z were positive but small. In the large-seeded parents the direct effect and the indirect effect via X were near the same magnitude as in the small seeded parents. In spite of this, however, the correlation coefficient of W and Y was very small and nonsignificant due to the decisive influence of a negative indirect effect of Y via seed size.

The BC_{11} population showed a significant positive correlation between W and Y (r_{wy} = 0.238). Most of this relationship was ascribed to the direct effect of Y (P_{yw} = 0.297). The indirect effect via the other two components X and Z were negative but unimportant. When only the crosses where selection for seed size was effective

Table 10. The path-coefficient analyses showing direct and indirect effects of the components of grain yield for the small-seeded parent populations

Pathways of Association	Direct Effect	Indirect Effect	r
Yield vs No. of Pods/Plant			0.8494**
Direct effect	0.8695		
Indirect effect via no. grains/pod		0.0221	
Indirect effect via seed size		-0.0416	
Yield vs No. of Seeds/Pod			0.4732**
Direct effect	0.4226		
Indirect effect via no. pods/plant		0.0454	
Indirect effect via seed size		0.0052	
Yield vs Seed Size			0.0641
Direct effect	0.2192		
Indirect effect via no. pods/plant		-0.1651	
Indirect effect via no. grains/pod		0.0100	

Table 11. The path-coefficient analyses showing direct and indirect effects of the components of grain yield for the large-seeded parent population

Pathways of Association	Direct Effect	Indirect Effect	r
Yield vs No. of Pods/Plant			0.8560**
Direct effect	1.1684		
Indirect effect via no. grains/pod		-0.0156	
Indirect effect via seed size		-0.2969	
Yield vs No. of Seeds/Pod			0.0381
Direct effect	0.3874		
Indirect effect via no. pods/plant		-0.0470	
Indirect effect via seed weight		-0.3026	
Yield vs Seed Size			-0.1440
Direct effect	0.6131		
Indirect effect via no. pods/plant		-0.5657	
Indirect effect via no. grains/pod		-0.1914	

Table 12. The path-coefficient analyses showing direct and indirect effects of the components of grain yield for the second backcross generation[a]

Pathways of Association	Direct Effect	Indirect Effect	r
<u>Yield vs No. of Pods/Plant</u>			0.9114** (0.8604**)
Direct effect	1.0548 (0.9670)		
Indirect effect via no. grains/pod		-0.0082 (-0.0127)	
Indirect effect via seed size		-0.1175 (-0.0938)	
<u>Yield vs No. of Seeds/Pod</u>			0.0060 (0.2582**)
Direct effect	0.2731 (0.2966)		
Indirect effect via no. pods/plant		-0.0318 (-0.0414)	
Indirect effect via seed size		-0.2409 (-0.0170)	
<u>Yield vs Seed Size</u>			0.0846 (0.1147)
Direct effect	0.4805 (0.3721)		
Indirect effect via no. pods/plant		-0.2579 (-0.2439)	
Indirect effect via no. seeds/pod		-0.1369 (-0.0135)	

[a] Numbers in parentheses indicate values for the whole BC_{11} population. The others are values for the BC_{11} where selection for seed size was effective.

were analyzed, the results were almost the same, with the exception of the relationship between yield and number of seeds per pod. No correlation was found for W and Y in these crosses. The direct effect was almost of the same magnitude as that of the whole BC_{11} population ($P_{yw} = 0.297$ vs $P_{yw} = 0.273$), however, the indirect effect via seed weight, was negative and almost of the same value as the direct effect ($P_{yw} = 0.273$ vs $P_{yw}r_{zw} = -0.241$).

The simple correlation between W and Z was small in the three populations: positive but unimportant in the small Z lines and the BC_{11} generation and negative but equally small in the large-seeded parents. In all cases, however, the direct path effects were moderately high, 0.219 in the case of small-seeded parents, 0.613 for the large-seeded lines and 0.480 for the backcross generation. In the three populations a comparatively high negative influence of Z upon W via pods per plant ($r_{wz}P_{wx} = -0.165$, -0.566, and -0.258, respectively) offset the direct effects, rendering the correlations small and unimportant.

Since we are dealing with sequential characters, the correlations describing the associations between the traits will reflect the influence of the initial trait or traits upon the subsequent ones in the sequence of development. To remove the effect of correlations would then mean in this case to free a particular trait from the influence of the previous traits in the developmental sequence.

Table 13 shows the mean squares from the analyses of variance for the parent population calculated after the effects of correlations were removed. The mean squares of correlated (actual) minus uncorrelated (transformed) data for yield and two of its components are also shown. The correlation effect of X was removed from Y and the effects of these two components were removed from Z.

A significant effect due to genotype, years, and the interaction of genotype x years was observed for X and Y (Table 8). The genotypic and environmental effects were reported significant for Z and none of the sources of variation is significant for yield. For X and Y the effects due to environment seemed to predominate over the genotypic effects; the opposite was true for the Z component. When the effects of the correlations were removed, significant contributions of genotype, years, and genotype-environment interaction were detected for W, Y, and Z, as shown in Table 13.

The variance components for years, genotypes and the interaction at years by genotypes were calculated for yield and the components of yield making use of the transformed data for the parent population. The values obtained are shown in Table 14. The relative importance of each of the variance components with respect to the total variation represented by their sums is expressed on a percentage basis for each trait for each set of data, in Table 15.

Table 13. Mean squares of analyses of variance for uncorrelated data for grain yield and two components of yield from eleven bean lines evaluated for two years at Saginaw, Michigan

Source	dF	Yield	No. Seeds per Pod	Seed Weight
Reps. within a year	6	44.68600	0.10195	0.60010
Year	1	1164.62599**	10.48628**	206.18280**
Genotype	10	893.19274**	2.29553**	387.75630**
Year x genotype	10	301.94560**	1.41600**	154.76810**
Error	60	43.01006	0.06733	0.63940

**Significant at the 1% level.

Table 14. Estimates of variance components of grain yield and the components of yield for eleven bean lines grown for two years at Saginaw, Michigan and analyzed with respect to two sets of data, (a) actual data, (b) transformed data

Variance Components[a]	Actual				Uncorrelated			
	W	X	Y	Z	W	X	Y	Z
σ_Y^2	0.0000	21.32667	0.07662	0.04868	19.60637	..	0.20614	1.16852
σ_G^2	4.20861	39.44568	0.04093	4.17285	73.90589	..	0.10994	29.12352
σ_{GY}^2	0.0000[b]	0.0000[b]	0.07229	0.06912	64.73388	..	0.33717	38.53218

[a] σ_Y^2 component of variance due to environmental (years) differences, σ_G^2 component of variance due to genetic differences among the lines, σ_{GY}^2 the genotype by environment component.

[b] Negative values for which the most reasonable estimate was assumed to be zero.

Table 15. Estimates of variance components expressed in percent of the total variance for each trait within each set of data (from Table 9)

Variance Component	Actual				Uncorrelated			
	W	X	Y	Z	W	X	Y	Z
Years	....	35.1	40.4	1.2	13.4	....	31.6	1.7
Genotype	100.0	64.9	21.6	97.2	46.7	....	16.8	42.3
Genotype x years	....	....	38.0	1.6	40.9	....	51.6	56.0

With the exception of the seeds-per-pod component, the contribution of the genotype seems to be the most important factor for the expression of the traits, especially for yield and seed weight. For X there is a definite contribution of environment, whereas for Y the environmental effect is as large as that of the interaction. When effects of the correlation of X with Y and of X and Y with Z are removed so that the contribution of each component may be studied freed from relationships with others, there is an increase in the contribution of the year-genotype interaction. The contribution of environment is unaffected in the case of Z but moderately affected in the case of Y, so most of the increase in the genotype by environment portion has been at the expense of a decrease in the genotypic fraction of Z and primarily in the environmental fraction of Y.

The genotype by environmental interaction appears to be the main factor controlling the relationships between components, at least for W and Z. For Y, the interaction effect and the environmental fraction seems to be equally important. The genotypic by environment interaction is more important in controlling the correlation of X and Y with Z than is the environment.

Genetic Advance

Heritability Estimates

Data from the parent population grown for two years in one locality were used to estimate heritability in a *sensus latus*. Estimates of the components of variance are shown in Table 16. The heritability estimates (Table 16) agree in a general way with other reports. Seed weight heritability was high, 89.2%. The estimate for number of pods per plant was intermediate in value, whereas estimates of heritability for number of seeds per pod and grain yield were low.

Table 16. Estimates of variance components and heritability computed for single plots for grain yield and components of yield for the parental bean lines grown for two years at Saginaw, Michigan

Trait	σ^2_G	σ^2_{GY}	σ^2_E	Her.
Yield	4.20861	0.00000[a]	25.95912	14.0
No. pods/plant	35.20481	0.00000[a]	46.62720	43.0
No. seeds/pod	0.04093	0.07229	0.07247	21.2
Weight of 100 seeds	4.17285	0.06910	0.43660	89.2

[a] Negative values for which the most reasonable estimate was assumed to be zero.

Heritability estimates in the narrow sense were obtained from the regression of F_1 means on the small-seeded parents and F_2 means on the mid-parents (Table 20). In general, estimates for seed size were high and seeds per pod were intermediate. Yield and number of pods per plant registered low estimates although some inconsistencies were noted when the estimates from two different years were compared for these two traits; namely, a negative heritability value for X and a large discrepancy in the values for W for 1968 and 1969.

Although heritability estimates cannot be given an unrestrictive use without considering the environmental conditions and the genetic material, our estimates support at least the reported high values of heritability of Z in comparison with values of heritability for yield and the other components of yield.

Table 17 shows the values used to calculate the realized heritability for the character seed weight in each of the crosses where selection for seed size proved to be effective.

The corresponding "t" values for the differences between the selected portions and the population means for the BC_1's and their selfed generations are presented. Whereas the selected BC_1 plants were all significantly different from the mean of the population from which they were extracted, only eight of the twenty sets of crosses studied showed significance when the selfed generations were

Table 17. Means of the seed size trait for a BC_1 population, its selected portion and their respective selfed generation, in twenty sets of crosses of small- and large-seeded lines of beans

	Mean of the BC_1			Mean of BC_1S_1 Lines		
Cross	Population	Selected Lines	t Values[a]	BC_1 Population	Selected BC_1 Lines	t Values[b]
0112	18.125	25.550	12.46**	19.724	24.500	8.18**
0213	22.600	29.200	9.84**	21.453	25.587	6.86**
0313	21.775	31.500	8.32**	21.147	26.900	6.89**
0506	15.575	17.400	8.08**	17.700	18.412	2.66**
0507	15.950	18.950	10.71**	16.765	17.537	3.94**
0509	14.600	17.300	10.34**	16.200	17.338	5.96**
0510	14.875	18.700	12.79**	16.459	17.025	5.30**
0511	15.375	18.500	10.28**	16.235	16.900	3.61**
0206	17.725	21.100	9.64**	18.282	17.987	1.62
0411	15.725	19.450	11.22**	16.482	16.712	1.19
0409	15.075	17.540	12.06**	16.753	16.500	1.41
0406	15.125	17.000	9.24**	16.647	16.813	0.95
0106	17.275	19.750	10.90**	18.724	19.062	1.38
0310	17.100	19.350	8.27**	17.500	17.112	2.06
0309	16.150	18.300	9.03**	17.212	16.750	2.31*
0109	16.700	18.900	10.58**	17.971	17.537	2.67*
0209	17.300	19.200	8.84**	17.865	17.250	2.70*
0306	16.625	20.150	12.11**	17.300	17.800	2.94*
0107	17.525	20.350	12.34**	18.459	18.075	3.28*
0408	16.525	19.600	10.05**	17.347	16.700	4.11*

*Significant at the 5% level. **Significant at the 1% level.

[a] Based on a 25-plant sample. [b] Based on a 17-plant sample.

compared. These crosses were the only ones where selection for high seed size was considered effective. Realized heritability was calculated for these populations (Table 18). These heritability estimates ranged from 14.8 to 64.3.

Table 18. Realized heritability estimates for seed size based on actual response from selection practiced in a first backcross generation in a set of crosses between small- and large-seeded bean lines

Cross	Heritability
0112	64.3
0213	62.6
0313	59.2
0506	43.8
0507	25.7
0509	42.2
0510	14.8
0511	21.3

Heritability estimates were calculated also for W, Y, and Z freed from the variation attributable to correlations. The variance components method was used with the parental data. Table 19 includes the estimates of the variance components and heritability for grain yield and its components. W, X, and Z showed heritability values around 40% while Y values were half this amount.

Estimates derived from the different methods for calculating heritability are compared in Table 20.

Table 19. Estimates of variance components and heritability for single plots for grain yield and components of yield, with effects of correlations removed

Trait	σ^2_G	σ^2_{GY}	σ^2_E	Her.
Yield	73.905892	64.733888	43.010056	40.7
No. pods/plant	35.204806	0.000000	46.627200	43.0
No. grains/pod	0.109940	0.337169	0.067328	21.4
Weight of 100 seeds	29.123500	38.532200	0.639400	42.6

[a] Nontransformed data.

Table 20. Estimates of the heritability of yield and its components in a bean population with operating correlations among components

	Methods of Calculation			
Trait	Variance Components	F_1-Parent Regression	F_2 Mid-Parent Regression	Realized Heritability
W	14.0	31.1	0.7	....
X	43.0	-8.0	9.8	....
Y	21.2	48.2	18.4	....
Z	89.2	82.8	60.6	41.7

Test of Additivity for Seed Size

A test for additive behavior of genes affecting seed size was performed by comparing the observed means of the first backcross generation with the expected values assuming an additive model where the mid-parental values correspond to the performance of F_1's. Results are presented in Table 21. Only 5 out of 20 of the comparisons deviated significantly from the additive scheme.

Crosses involving large-seeded parents, P-06 and P-09, deviated significantly from the additive model when the recurrent parent was the small-seeded parent P-02, however, no significant deviation was observed when the other small-seeded parents were involved except when P-05 and P-06 were used together. Crosses involving P-11 (e.g., 0411 and 0511) showed a differential response, BC_1 progenies derived from the former diverging significantly from the additive model. A particularly large and highly significant value was found for the cross 0408.

Response to Selection

Since the BC_{11} was planted in a different year than the BC_1 the expected values for the second backcross cannot be estimated using the actual BC_1 data. An expected BC_1 mean value was calculated for each cross for seed size making use of the parent population data from the 1969 plantings. An additive model, that proved to be adequate according to the results from 1968, shown in Table 21, was assumed.

Table 21. t-test and mean values for seed size for twenty first-generation backcrossed lines and their expected values under an additive model

	BC_1 Means Under Additive Model		
Cross	Observed[a]	Expected[b]	t Values
0106	17.275	16.980	1.30
0107	17.525	17.760	1.02
0109	16.700	16.760	0.29
0112	18.125	19.180	1.77
0206	17.725	16.788	2.68**
0209	17.300	16.560	3.44**
0213	22.600	22.280	0.45
0306	16.625	16.160	1.60
0309	16.150	15.940	0.88
0310	17.100	16.100	0.37
0313	21.775	21.660	0.10
0406	15.125	14.940	0.81
0408	16.525	14.950	5.15**
0409	15.075	14.700	1.90
0411	15.725	14.960	2.31*
0506	15.575	14.960	2.66**
0507	15.950	15.640	1.11
0509	14.600	14.740	0.52
0510	14.875	14.900	0.08
0511	15.375	15.000	1.24

[a] Twenty-five plants used for each cross.

[b] Calculated using the parent population planted in 1968.

*Significant at the 5% level.

**Significant at the 1% level.

The expected and observed values agreed very closely as indicated in Figure 2. The BC_1 means from the 1968 trials were compared with the values from the parental population grown that year. Parental seed weights from the 1969 trials were compared with the values from the parental population grown in that year. Parental seed weights from the 1969 trials were used to calculate the estimated BC_1 for that year based on an additive scheme. Only 3 out of 20 crosses showed a discrepancy greater than 5% when the observed and expected values were compared.

The expected BC_{11} means assuming an additive model were calculated from the previously estimated BC_1 means for the seed size trait. A maximum expected genetic gain value was set by using broad sense heritability estimates and the standardized selection differential corresponding to a selection intensity of 8%. These values, calculated for the BC_{11} generation, represent the estimates of the minimum and maximum expectations under the additive scheme (Table 22).

The actual BC_{11} means and their comparisons with the small-seeded parents are given in Table 23. Eleven out of 20 backcross lines showed a significant increase in seed size with respect to their particular recurrent parent. Increases ranged from 9 to 31% and were in close agreement with the expected values. In the rest of the lines, positive changes were negligible and even slight decreases from the recurrent parent were noted. Nevertheless, the results

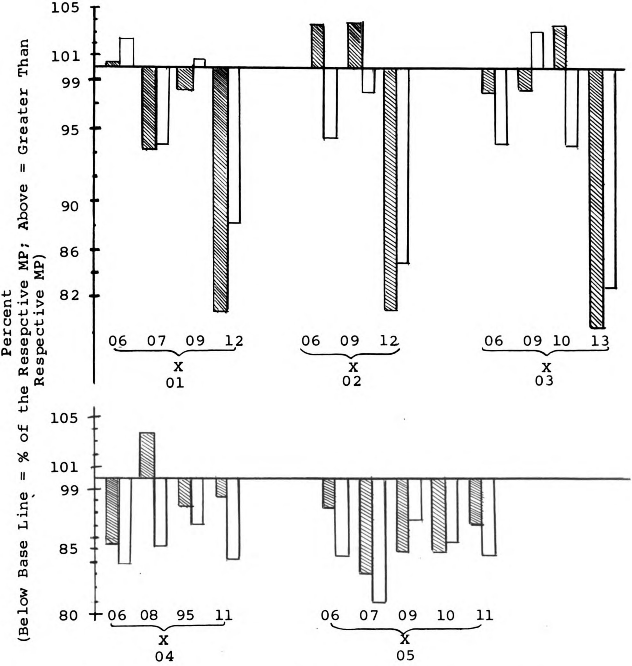


Figure 2. Graphical representation of the deviations of the BC_1 means for seed size expressed in percent of the midparents grown in two years. Hachured blocks refer to observed BC_1 means in the 1968 trials. White blocks represent expected values calculated with the parental 1969 data assuming an additive model.

Table 22. Expected means for two backcross generations under no selection and under 8% selection intensity on the BC_1 for the character seed weight

	Expected Means for Z		
Cross	BC_1	BC_{11} From Unselected Population[a]	BC_{11} From Selected Population[b]
0106	17.565	17.322	18.958
0107	18.260	17.670	19.306
0109	17.020	17.050	18.686
0112	20.098	18.589	20.224
0206	17.070	16.745	18.381
0209	16.530	16.475	18.111
0213	20.352	18.386	20.022
0306	15.900	15.375	17.011
0309	15.350	15.100	16.736
0310	15.280	15.065	16.701
0313	19.175	17.012	18.648
0406	15.630	15.065	16.701
0408	15.445	14.972	16.608
0409	15.090	14.795	16.431
0411	15.595	15.048	16.684
0506	15.900	15.375	17.011
0507	16.580	15.715	17.351
0509	15.350	15.100	16.736
0510	15.580	15.215	16.851
0511	15.860	15.355	16.991

$$^{a}BC_{11} = \frac{BC_1 + F_1}{2}$$

$$^{b}BC_{11} = \frac{(BC_1 + \Delta G) + F_1}{2}$$

Table 23. Actual seed size means of the BC_{11} lines as weight of 100 seeds, under an additive model when selection is based on seed size

		Percent Increase of BC_{11} Over Small Z Parent		
Cross	Observed BC_{11} Mean, grams	Expected Under No Selection	Expected Under Selection	Observed
0313	20.400 ± 2.168	14.6	25.6	30.8**
0112	21.250 ± 1.166	8.8	18.4	20.4**
0506	16.875 ± 0.558	3.5	14.5	18.1**
0511	16.750 ± 0.223	3.4	14.4	17.3**
0509	16.400 ± 0.643	5.8	16.8	14.8**
0510	16.363 ± 0.346	1.7	12.7	14.5**
0507	16.075 ± 0.302	5.8	16.8	12.6**
0213	20.175 ± 1.249	12.0	21.9	11.8**
0309	17.200 ± 0.577	1.7	12.7	10.3**
0306	17.025 ± 0.423	3.5	14.5	9.2**
0310	17.037 ± 0.424	1.4	12.4	9.2**
0406	16.075 ± 0.583	3.9	15.1	4.1
0411	15.975 ± 0.860	3.8	15.0	3.5
0408	15.937 ± 0.613	3.3	14.5	3.1
0206	17.188 ± 0.563	2.0	11.9	1.0
0409	15.600 ± 0.519	2.0	8.9	1.0
0106	17.750 ± 0.691	1.4	11.0	0.6
0107	17.625 ± 0.456	3.4	13.0	-0.1
0109	17.125 ± 0.678	-0.2	9.4	-2.9
0209	16.137 ± 0.843	0.3	10.3	-5.2

**Significant at 1% level using Dunnett test.

confirmed the validity of the additive model since deviations from expected values under no selection were in all cases unimportant. Some exceptions were registered, as, for example, in the crosses 0306, 0309, and 0310 which showed increased seed size in the BC_{11} according to an expectation of effective selection, but actually no response to selection had been detected in the selfed BC_1 generation. The cross 0406 worked in the opposite direction: selection for seed size in the BC_1 generation was effective, but this population failed to show a significant increase in BC_{11}.

When the BC_1 and BC_{11} generations were compared with respect to variations in seed size as a result of the selection practiced in the BC_1, no significant change was observed for the population where selection for large Z was effective. This observation is a valid one when the mean of all the populations was considered since large differences between BC_1 and BC_{11} may be noticed when the individual populations are compared. Where selection was not successful, however, the BC_{11} average seed size was, as expected, significantly lower than that of the BC_1 (Table 24).

The response of the seed number components selection had been practiced for seed size are shown in Table 25. The increases in seed number in relation to the recurrent parent ranged from 3 to 60%. Some lines showed a decrease that in one instance was on the order of 14%. Only two of these changes, however, were significant.

Table 24. Differences in seed size of the BC_1 and BC_{11} generations of twenty bean populations, expressed as percent change over the recurrent parents

Population	% Change Over the Recurrent Parent		t Values[a]
	BC_1	BC_{11}	
Populations Where Selection for Large Z Was Effective			
0112	8.3	20.4	
0213	37.2	11.8	
0313	39.3	30.8	
0506	11.0	18.1	
0507	13.6	12.6	
0509	4.0	14.8	
0510	6.0	14.5	
0511	9.5	17.3	
Mean	16.1	17.5	0.768 ns
Populations Where Selection for Large Z Was Not Effective			
0106	3.3	0.6	
0107	1.4	-0.1	
0109	-0.2	-2.9	
0206	5.9	1.0	
0209	5.0	-5.2	
0306	6.3	9.2	
0309	3.3	10.3	
0310	9.3	9.2	
0406	8.0	4.1	
0408	18.0	3.1	
0409	7.7	1.0	
0411	12.3	3.5	
Mean	6.7	2.8	2.452*

[a] Calculated after arc-sine transformation was performed on data.

*Significant at 5% level.

Table 25. Observed and expected changes on seed number and seed number components in the BC_{11} generation under two successive backcrosses to the small-seed parent and selection in the BC_1 for large-seed

	% Change With Reference to Recurrent Parent				
		Seed Number Components			
		No. Pods/Plant		No. Seeds/Pod	
Cross	Seed Number	Obs.	Exp.	Obs.	Exp.
0209	60.2**	60.8**	-1.0	-1.6	-0.4
0408	38.8	22.5	-1.0	8.3*	-2.0
0406	27.9	11.3	-2.9	9.3*	0.5
0411	20.6	9.4	-4.4	5.7	-0.2
0306	20.4*	16.2	-2.6	11.0*	0.7
0510	17.9	18.4	-2.8	0.5	-0.6
0206	17.3	10.9	-1.2	4.7	-0.3
0506	12.8	10.5	-2.7	2.2	0.8
0309	12.3	-2.9	-2.5	14.6**	0.6
0107	10.4	14.3	-4.8	-2.4	-1.6
0313	7.1	4.5	-6.7	1.1	-2.6
0109	7.6	8.7	-0.4	-0.7	-1.0
0213	7.1	12.2	-5.9	-5.2	-3.4
0511	6.4	-1.6	-4.3	8.4*	0.2
0106	3.4	6.6	-0.8	-2.8	-0.9
0507	-1.0	-5.7	-6.1	5.5	0.0
0310	-5.6	-10.7	-2.8	15.9**	-0.6
0509	-6.4	-8.7	-2.5	3.7	0.7
0409	-6.7	-5.9	-2.7	-5.8	0.9
0112	-14.2	-1.2	-7.8	-12.8**	-1.9

*Significant at 5% level using Dunnet test.

**Significant at 1% level using Dunnet test.

Some characteristic patterns of variation may be distinguished by examining the seed number trait and its components. Seed number increased due to a simultaneous rise of the components X and Y. Increases were also noted when a positive response in one of the components was of sufficient magnitude to offset a decrease in the other component. On the other hand, a decrease in seed number occurred due to lack of compensatory effect in the changes of the seed number components. Either X and Y decreased simultaneously or the increase of Y was unable to compensate for the negative change of the X component. It is worth pointing out, however, that although in no case was the variation of both seed number components simultaneously significant, deviations from expected values under an additive scheme were substantial.

The final outcome of the component relationship is yield. The whole picture of the variation of yield and its components with respect to the five recurrent parents is presented in Table 26 for each of the BC_{11} lines. Most lines showed a numerical increase in yield over the recurrent parent but only six lines showed as significant increase in yield compared with the small-seeded progenitor. Four of the six lines that did raise their grain productivity appear to have reached this level through an increase in seed size. One of these lines, 0511, showed a simultaneous positive change in the Z and Y components. The

Table 26. Grain yield and percent change in yield and its components with reference to the recurrent parent for twenty BC_{11} populations

Cross	Grain Yield (gms)	% Change Over Recurrent Parent			
		Yield	No. Pods Per Plant	No. Grains Per Pod	Seed Size in Wt./100 Seeds
0107	31.6101	9.8	14.3	-2.4	-0.1
0109	29.7830	3.4	8.7	-0.7	-2.9
0112	29.7623	3.3	-1.2	-12.8**	20.4**
0106	29.7424	3.3	6.6	-2.8	0.6
P-01	28.8014	0.0	0.0	0.0	0.0
0209	37.6581	47.3**	60.8**	-1.6	-5.2
0213	31.3544	22.6	12.2	-5.2	11.8**
0206	29.5002	15.4	10.9	4.7	1.0
P-02	25.5677	0.0	0.0	0.0	0.0
0313	42.7626	38.2*	4.5	1.1	30.8**
0309	37.8330	22.3	-2.9	14.6**	10.3**
0306	37.1758	20.1	16.2	11.0**	9.2**
0310	34.7442	12.3	-10.7	15.9**	9.2**
P-03	30.9436	0.0	0.0	0.0	0.0
0408	32.8387	36.9*	22.5	8.3*	3.1
0406	30.4884	27.1	11.3	9.3*	4.1
0411	29.2338	21.9	9.4	5.7	3.5
0409	20.8906	-12.9	-5.9	-5.8	1.0
P-04	23.9817	0.0	0.0	0.0	0.0
0511	38.9811	43.7*	-1.6	14.6**	17.3
0510	36.5474	34.7*	18.4	0.5	14.5**
0506	36.5474	32.8*	10.5	2.2	18.1**
0507	30.4110	12.1	-5.7	5.5	12.6**
0509	29.6646	9.4	-8.7	3.7	14.8**
P-05	27.1241	0.0	0.0	0.0	0.0

*Significantly different at 5% level using Dunnet test.

**Significantly different at 1% level using Dunnet test.

remaining two lines which showed significant increases in yield attained it either through higher X level, as was the case of the cross 0209, or through significant rise in the Y component coupled with a noticeable though not a significant increase in X, as shown by cross 0408. Some significant increases in seed size were offset by significant changes in the opposite direction in the Y component as in the lines 0112, 0306, 0309, 0310. In other cases, we did not overcome the compensatory forces by recurrent backcrossing; the high Z values, although significant, were not large enough to compensate for slight negative responses in Y (as 0213) or in X (as 0507 and 0509).

In order to compare the grain productivity of the different populations in the BC_1 and BC_{11} generations, the BC_{11} values were transformed relative to those of the BC_1 grown in the previous year. The adjustment was made by comparing the variation of the parental population grown in 1969 with respect to that grown in 1968. Variations on each component were expressed on a percent basis and the respective change was either added to or substracted from the component values of the 1969 populations according to whether there was a decrease or an increase in the values of the same parent population grown in both years. Each of the components of the parents grown in 1969 was adjusted at the 1968 parental values in this way. BC_{11} values were then calculated using their adjusted values according to an additive model.

Table 27 shows the expected and observed grain yields for the BC_1 and BC_{11} generations. Populations were divided according to whether selection for seed size was effective or not, and progress of the BC_1 and BC_{11} with respect to the recurrent parent values were estimated for each set. Where selection for Z was not effective no significant change in yield was observed between the BC_1 and BC_{11} generations with respect to the recurrent parent. Where selection was effective for Z there was a large increase in yield in the BC_1 with respect to the recurrent parent and a further, though much smaller, increase in the BC_{11}.

When selected plants in the BC_1 were selfed for two generations the reduction in yield as compared with the BC_{11} generation was noticeable only in the first generation of selfing as shown in Table 28.

Heterozygosis-Performance Relationship

In order to elucidate any relationship between the level of heterozygosity and the performance of the BC_{11} lines, the average values for yield and the components of yield were calculated for different levels of heterozygosity in six bean populations (Table 29).

These values were plotted in Figures 3, 4, 5, and 6. In general, the average heterozygosis-performance for all the populations studied was similar, when each individual trait was taken into consideration.

Table 27. Observed grain yield for the first and second backcross generation of twenty bean populations

	Grain Yield/Plant (gms)					
Population	Recurrent Parent	BC_1	% Change Over R.P.	BC_{11}	% Change Over R.P.	t Value
Populations Where Selection for Large Z Was Effective						
0112	30.010	37.872	26.2	36.078	22.2	
0213	24.650	41.073	66.6	32.369	31.3	
0313	22.447	34.727	54.7	35.007	56.0	
0506	27.525	30.031	9.1	37.015	34.5	
0507	27.525	34.516	25.4	31.326	13.8	
0509	27.525	31.019	12.7	32.296	17.3	
0510	27.525	33.020	20.0	42.678	55.0	
0511	27.525	30.644	11.3	36.003	30.8	
Mean	26.158	34.112	28.2	35.346	32.6	
Difference $BC_{11} - BC_1$				1.234 gm/plt	4.4%	.875 ns
Populations Where Selection for Large Z Was Not Effective						
0106	30.010	28.412	-5.3	32.190	7.3	
0107	30.010	36.720	22.4	33.426	11.4	
0109	30.010	33.066	10.2	34.562	15.2	
0206	24.650	29.439	19.4	32.126	30.3	
0406	23.895	29.857	25.0	31.606	32.3	
0409	23.895	26.663	11.6	23.497	-1.7	
0411	23.895	28.298	18.4	29.407	23.1	
Mean	26.185	30.351	14.5	30.975	16.8	
Difference $BC_{11} - BC_1$				0.624	2.3%	.431 ns

Table 28. Comparison of grain yield among the BC_1S_1 and BC_1S_2 vs BC_{11} generations derived from selected BC_1 populations

	Grain Yield (gms)					
Population	BC_{11}	%	BC_1S_1	%	BC_1S_2	%
0112	29.760	100	31.612	106.2	30.882	103.8
0213	31.790	100	29.528	92.9	37.968	119.4
0313	42.490	100	31.612	74.4	32.232	75.9
0506	36.320	100	30.178	83.1	23.770	65.4
0507	30.310	100	31.442	103.7	28.305	93.4
0509	29.095	100	33.975	116.8	27.208	93.5
0510	36.815	100	30.715	83.4	28.168	76.5
0511	34.045	100	27.158	79.8	26.920	79.1
Mean	34.487	100	30.270	89.1	29.516	86.7

Generations	Differences	t Values
BC_{11} - BC_1S_1	4.217 gms/plant	4.253**
BC_{11} - BC_1S_2	4.971 gms/plant	4.050**
BC_1S_1 - BC_1S_2	0.754 gms/plant	0.830

**Significant at the 1% level.

Table 29. Means of yield and the components of yield at four levels of heterozygosity in six bean populations

		Type of Combination and Percent Heterozygosity			
Character	Population	Inbred Lines 0	F_3 25	BC_1 50	F_1 100
Grain yield (grams)	0106	28.500	27.967	28.412	51.896
	0209	27.669	29.663	29.606	42.536
	0408	27.729	29.031	31.578	52.913
	0506	26.735	31.407	30.031	32.193
	0510	23.878	24.750	33.020	35.893
	0511	22.654	26.867	30.644	35.744
No. pods per plant	0106	32.450	31.450	25.971	54.750
	0209	34.050	34.900	37.587	45.450
	0408	40.050	29.150	35.081	57.500
	0506	39.300	41.950	37.573	38.950
	0510	30.450	31.650	38.989	47.400
	0511	25.850	34.600	43.250	43.250
No. seeds per pod	0106	5.250	5.175	5.185	4.800
	0209	5.000	4.700	4.504	5.275
	0408	4.675	4.475	4.604	4.900
	0506	4.575	4.650	4.774	4.775
	0510	4.375	4.675	4.742	4.650
	0511	4.625	4.475	5.071	4.975
Weight of 100 seeds (grams)	0106	17.075	17.600	18.052	19.425
	0209	16.425	16.950	17.663	17.375
	0408	14.500	17.225	17.021	19.175
	0506	14.850	16.000	16.541	17.625
	0510	17.775	16.250	15.381	16.125
	0511	18.875	16.825	17.330	16.500

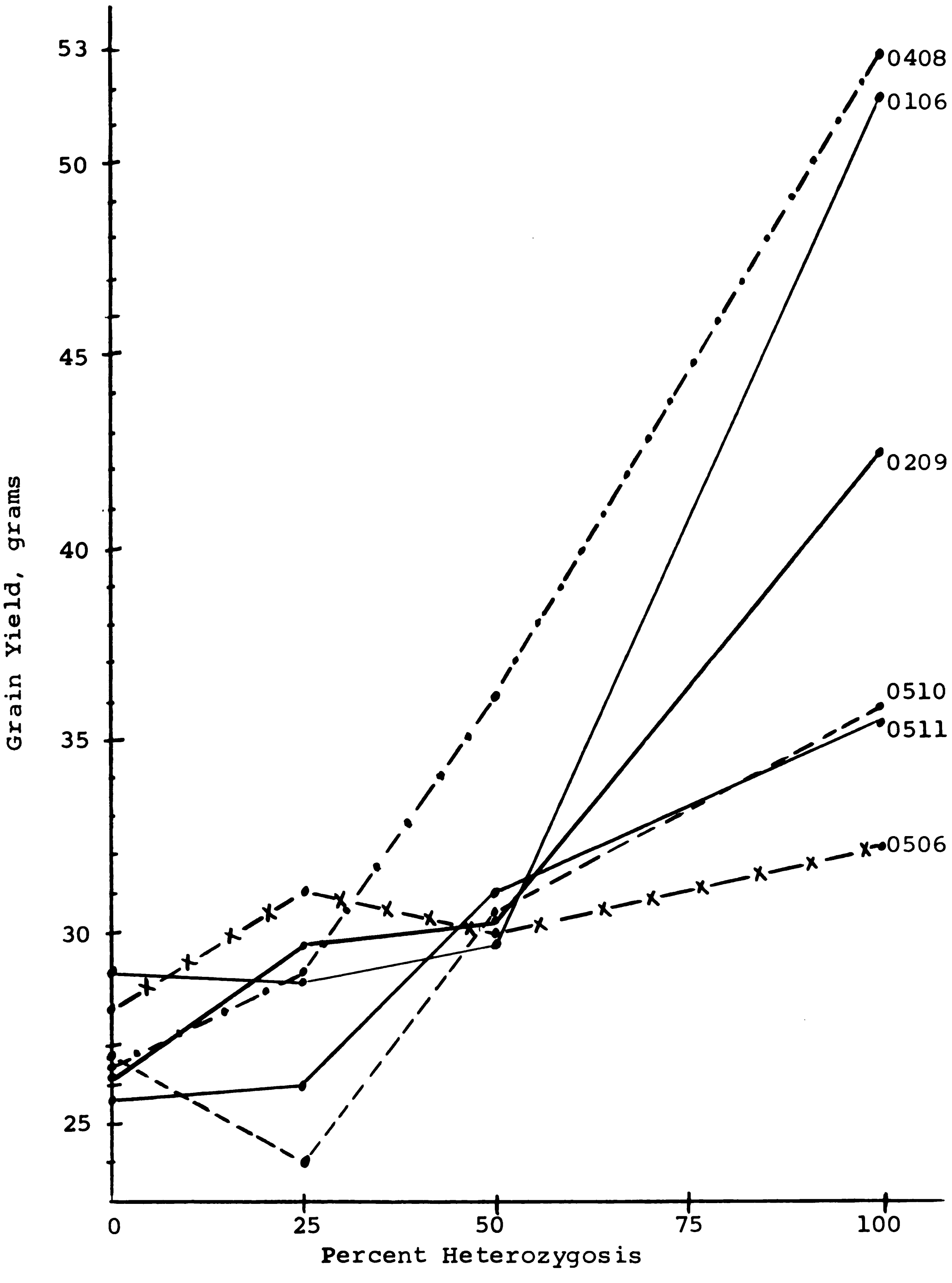


Figure 3. Heterozygosis-performance relationship for yield in six bean populations.

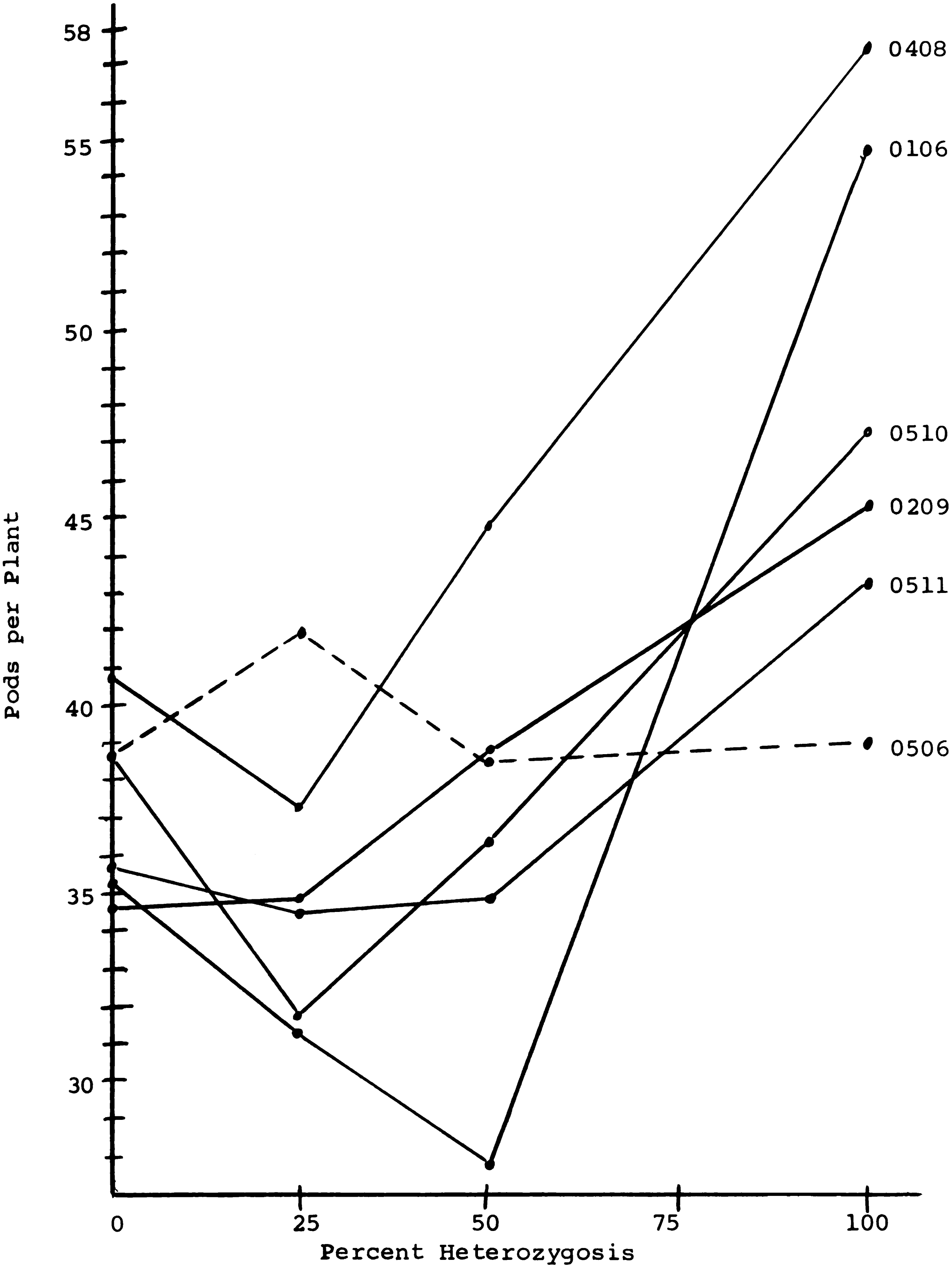


Figure 4. Heterozygosis-performance relationship for number of pods per plant in six bean populations.

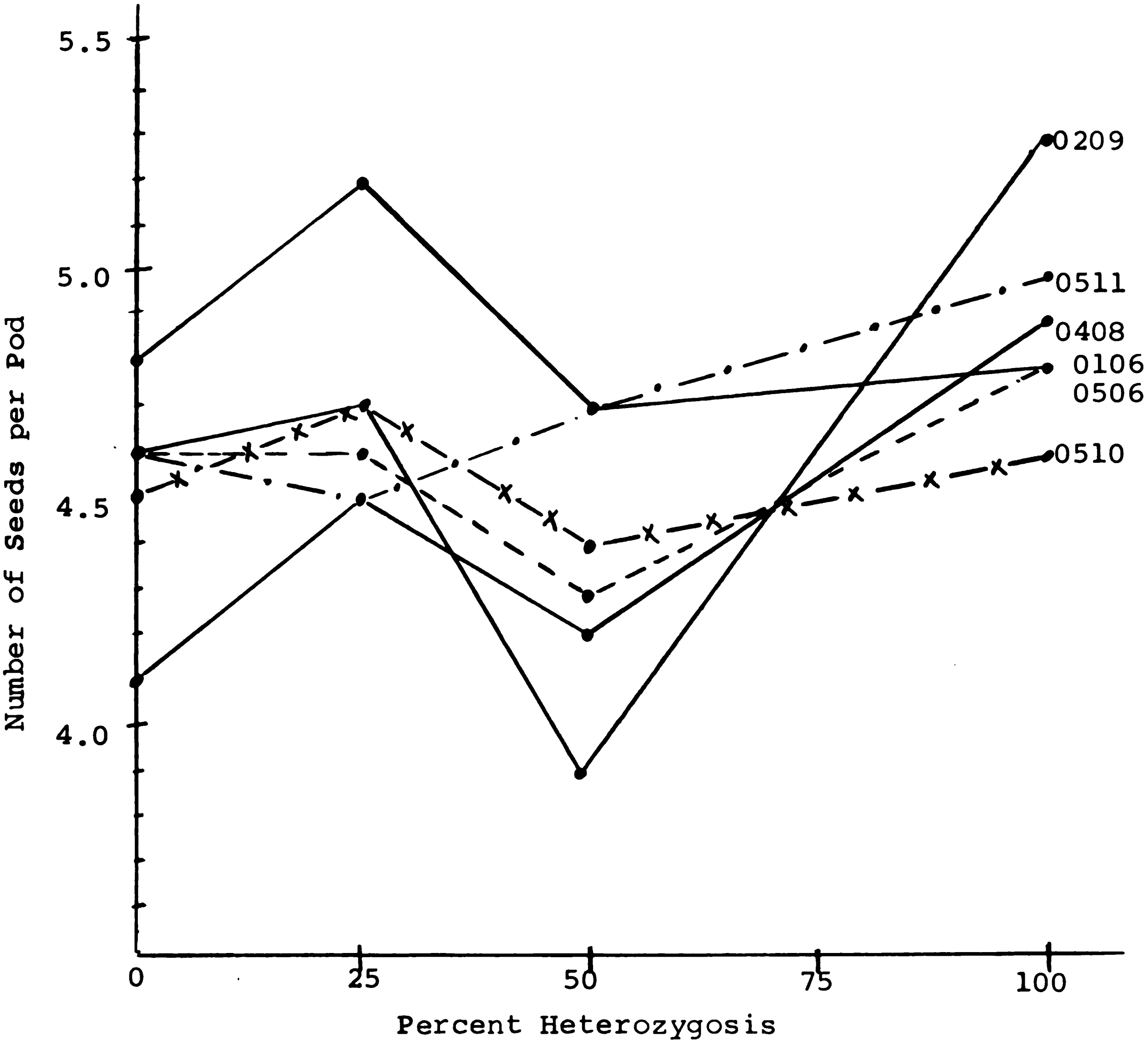


Figure 5. Heterozygosis-performance relationship for number of seeds per pod in six bean populations.

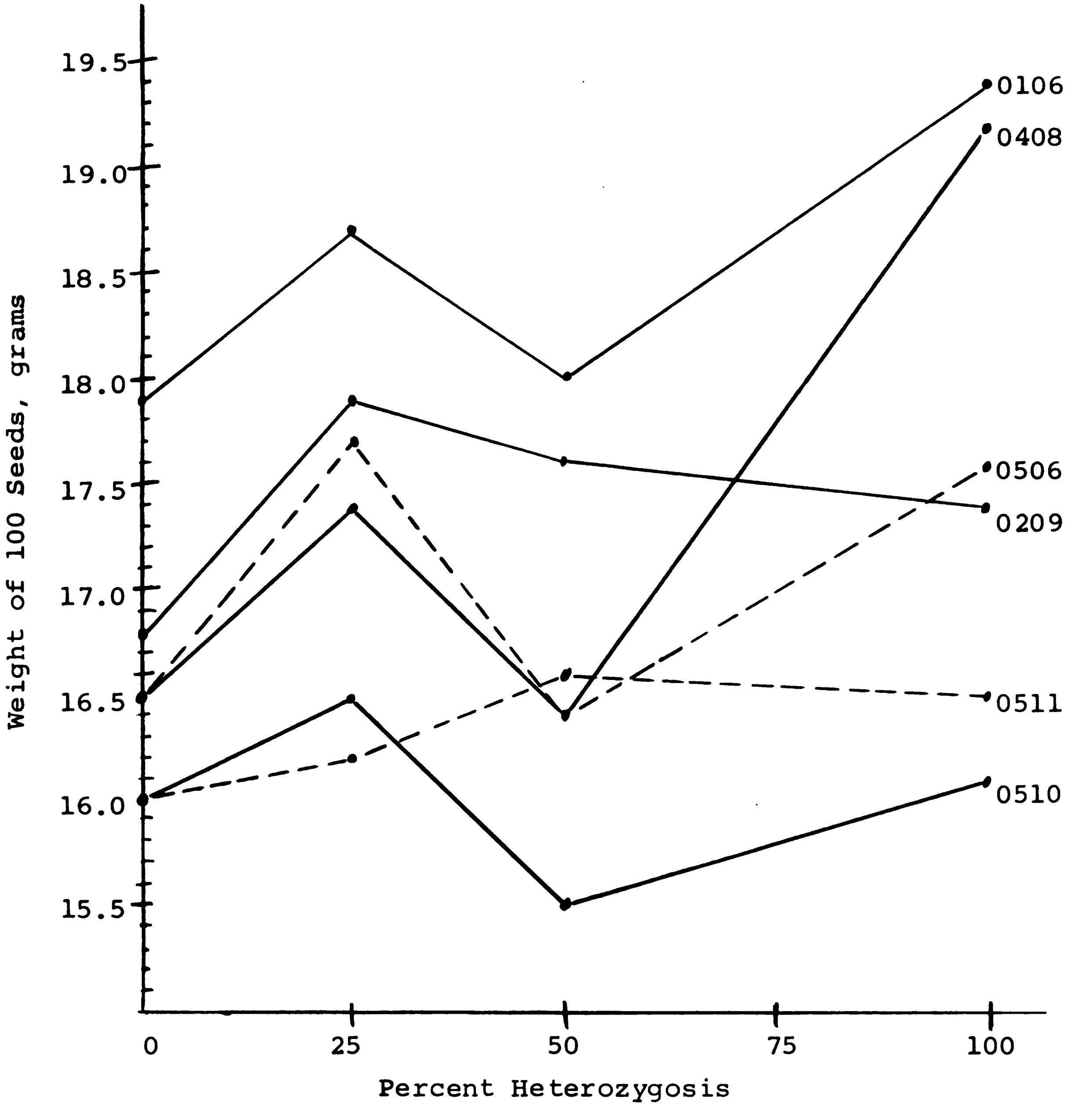


Figure 6. Heterozygosis-performance relationship for seed weight in six bean populations.

The trends for W and its components appeared to be curvilinear. The populations having P-05 as a common genetic background plateaued either at the 20 and 50% level (as 0506) or between 0 and 25% level (as 0510 and 0511) before rising moderately at 100% heterozygosity. The response of Z and Y to levels of heterozygosis showed a decrease in performance from the 25% to the 50% level of heterozygosis whereas the opposite was true for the characteristic X.

With the exception of X, however, the apparent curvilinear trend proved to be unimportant when a test for curvilinear regression was undertaken (Table 30). The non-significance of the curvilinear trends for W, Y, and Z must be taken cautiously, however, since the error as expressed by the interaction lines by levels of heterozygosity was possibly too high. Further partition of the interaction and study of the variation of lines within each level of heterozygosity might change the picture, as indicated by the graphs.

The results of the regression values showed no significance in the deviations from linearity for W thus suggesting that very little epistatic gene action may be involved in grain yield in beans. Y and Z did not show significance for the differences in the levels of heterozygosis, however, some heterogeneity arising from the pooling of different populations may have caused the lack of significance of the linear trend to account for the heterozygosity-performance relationship for the Z character as suggested by

Table 30. Test for curvilinear regression of the heterozygosis-performance relationship for yield and its components, by orthogonal polynomials

Source	df	Mean Squares			
		Grain Yields (grams)	No. Pods per Plant	No. Seeds per Pod	Weed Weight (grams)
Among levels	3	293.21**	280.55**	0.0460	1.408
Linear	1	829.34**	706.77**	0.1031	4.139
Quadratic	1	48.17	131.85*	0.0081	0.075
Cubic	1	2.12	3.02	0.0268	0.010
Among lines	5	28.08	50.51	0.1992	1.735
Int. lines x levels	15	21.14	23.34	0.0516	1.404

*Significant at the 5% level.

**Significant at the 1% level.

the slight departure from the levels of significance, and also by the results of selection.

For the character, pods-per-plant, a highly significant linear effect was noted accounting for much of the variation; however, a significant nonlinear effect might suggest a curvilinear relationship indicative of a possible interaction between nonallelic genes.

Discrepancies between the F_2 and BC_1 generations, both at the same average level of heterozygosity, are evident. These differences are tabulated in Table 31. The F_2 exceeded the backcross generation in grain yield and number of pods per plant. The opposite was true when the characters seeds per pod and seed size were considered. It must be noticed that the proportion heterozygous-homozygous favorable is different in the BC_1 and F_2 generations. Y and Z seem not to be as affected as W and X by additional increments of heterozygosis.

Since selection in the first backcross generation invalidated the expected degree of heterozygosis, a valid comparison was possibly only among the backcross generations deriving from the selected plants (Table 32). Theoretically, the BC_{11} and the BC_1S_1 should have the same level of heterozygosis, unless, in the selection process, heterozygosis is preferred. BC_{11} outyielded the BC_1S_1 in almost all the populations studied. This higher yield resulted from a superiority in X and Y; in all the crosses the BC_{11} populations produced more pods per plant than their respective

Table 31. Comparison between filial and backcross generations having the same level of heterozygosis. Plus (+) or minus (-) signs used to characterize the group exceeding (or not) the other

	Grain Yield		No. Pods per Plant		No. Seeds per Pod		Seed Size	
Cross	F_2	BC_1	F_2	BC_1	F_2	BC_1	F_2	BC_1
0106	+	-	+	-	-	+	+	+
0209	+	-	+	-	-	+	-	+
0408	+	-	+	-	-	+	-	+
0506	+	-	+	-	-	+	-	+
0510	-	+	-	+	-	+	+	-
0511	+	-	-	+	-	+	+	-

BC_1S_1 generation and, except in two populations (0112 and 0213), the same was true for the Y component. Seed size, on the other hand, was lower in the BC_{11}, with the exception of cross 0309.

No definite pattern was noticed for W, X and Y in comparing the BC_1S_1 and BC_1S_1 generations. About half of the population showed indistinctly lower or higher values for any particular component. Seed weight did show some consistency; excluding populations 0213 and 0507, all the rest of the populations in BC_1S_2 registered higher seed weight values.

When the 100% level of heterozygosity was compared with the zero level, the heterotic response expressed in grain yield and its components could be appraised (Table 33).

Table 32. Comparison between backcross generations derived from a first backcross where selection was practiced for seed size

Population	Grain Yield (gms)			No. Pods/Plant			No. Seeds/Pod			Seed Weight (gms)		
	BC_1S_1	BC_1S_2	BC_{11}	BC_1S_1	BC_1S_2	BC_{11}	BC_1S_1	BC_1S_2	BC_{11}	BC_1S_1	BC_1S_2	BC_{11}
0112	31.612	30.882	29.762	26.600	28.750	31.025	4.762	4.675	4.500	24.500	25.075	21.250
0213	29.528	37.968	31.354	33.775	45.450	35.500	3.475	4.438	4.425	25.587	18.950	20.175
0306	30.782	29.162	37.176	36.300	32.450	50.700	4.938	4.938	5.012	17.300	18.175	17.025
0309	27.295	31.555	37.833	33.525	36.675	42.100	4.862	4.962	5.150	16.740	17.062	17.200
0310	28.670	28.505	34.744	33.150	32.350	38.475	5.050	5.112	5.212	17.112	17.150	17.037
0313	31.612	32.232	42.763	30.625	35.025	45.350	3.888	3.462	4.550	26.900	28.637	20.400
0506	30.178	23.770	36.024	35.150	27.550	44.525	4.662	4.638	4.825	18.412	18.762	16.875
0507	31.442	28.305	30.411	35.700	33.450	37.725	4.988	4.962	4.988	17.537	16.975	16.075
0510	30.715	28.168	36.547	40.500	35.300	47.550	4.488	4.650	4.750	17.025	17.488	16.363
0511	27.158	26.920	38.981	31.550	30.950	39.375	5.088	4.965	5.138	16.900	17.512	16.750

Table 33. Heterotic response for grain yield and the components of yield in six bean populations (percent increase of F_1 as compared with parents)

Hybrid	Criteria	W	X	Y	Z
0106	MP heterosis[a]	81.9**	72.8**	-5.2	7.6
	HP heterosis[b]	81.7**	68.7**	-8.6	2.3
0209	MP heterosis	59.7**	39.0*	7.4*	4.4
	HP heterosis	53.7**	33.5**	5.5	3.1
0408	MP heterosis	96.0**	49.2**	14.0**	17.0**
	HP heterosis	90.8**	43.6**	4.8	4.9
0506	MP heterosis	16.4	11.1	1.1	4.1
	HP heterosis	12.7	-0.9	-2.0	-7.3
0510	MP heterosis	41.8*	35.9*	3.9	-1.0
	HP heterosis	36.6*	20.6	1.6	-9.3
0511	MP heterosis	44.7*	32.8**	8.2*	-2.2
	HP heterosis	33.7*	10.0	7.6	-12.6
Mean	MP heterosis	56.4	40.1	4.9	5.0
	HP heterosis	51.5	29.2	1.5	-3.2

[a] Mid-parental.

[b] High parent.

*Significant at 5% level.

**Significant at 1% level.

Heterosis for seed yield was high, especially for the hybrids 0106 and 0408. Only the cross 0506 registered a relatively low heterotic response. Heterosis, although high also for the X component, was less pronounced than that for yield. Again the hybrid 0506 showed a modest increment and the performance of the F_1 did not quite equal the high parent. The Y and Z components showed only slight heterosis and in most cases none at all.

DISCUSSION

Correlation Among Traits

The extent to which yield and its components and the components *inter se* are correlated has been studied by many workers. Our findings agree in a general way with those reported previously, i.e., the component X seems to be the one most highly correlated with W, and the components of yield are in the majority of the cases negatively correlated in their relationships with each other. Even though the coefficients were relatively small in the case of negative associations, they were statistically significant, indicating a probable association between these characters.

The relationship of X and Y with Z is clearly influenced by the size of Z. Only in large-seeded varieties, in the present data, were these associations negative. The degree and direction of correlation can be affected by the amount of inter-plant competition as has been demonstrated elsewhere (1). Absence of correlations in our studies, then, should be interpreted cautiously since the inter-plant competition was reduced by the 15-cm-spacing within the row in all field-grown material. The correlation between X and Y appeared to be unaffected by seed size.

A more critical examination of associations through the study of path coefficient analysis revealed that the component X is the factor exerting the greatest influence both directly and indirectly upon grain yield. Y and Z did not appear to influence yield as dramatically as X.

Although the total correlation coefficient singled out Y as more closely related with yield in small-seeded populations this difference disappeared in the large-seeded lines. Actually, in large-seeded lines, the direct effect of Z exceeded that of Y. This effect was counteracted, however, because Z was negatively associated with X and Y. Due to these inverse relationships the indirect effects of Z on W and Y were negative and relatively large, the consequence being a null overall effect of Z on W, despite the evidence of a rather strong direct causal relationship between these two traits. In small-seeded parents, the lesser association between components apparently did not have much effect on altering the pattern imposed by the indirect effects of each component on yield.

The varieties tested showed different yield levels but at the same time many of them shared a common pattern of relationships among their component of yield; in a broad sense they also partook similar environmental conditions. Whether a particular configuration may be considered optimum or not for any genotype is a matter that can only be judged if similar genotypes, which disregarding environmental effects must show the same geometric configuration, differ rather on their yielding ability, i.e., show different geometric configuration under the same set of environmental conditions. Differences in the geometric construct, as representation of yield, may be attributed then, to genetic and environmental factors and their interplay.

According to many reports, the environment plays an important role in conditioning the relationship among components and in the eventual form of the geometric configuration. We may assume here that the compensatory relationships derived from physiological, developmental and environmental factors and which eventually will determine the geometric yield construct exert influences on the physical expression of the components only up to the levels that their genetic make-up allows. Theoretically, then, if the potential level of expression of one of the components could be raised without affecting the potential limits of expression of the other components, an increase in yield should result assuming that essentially similar environmental conditions prevailed.

Correlation patterns among the components of yield might be expected to show some changes in response to the genetic changes undergone. Nevertheless, since in our backcrossing series only one of the components has been altered genotypically, the potential levels for compensatory changes have not been greatly disrupted and no drastic changes would be expected. The successive backcrosses to the small-seeded parent while selection was practiced for large seed, did change the correlation pattern of the BC_{11} compared with the recurrent parent for some of the component relationships. The study of more intricate relationships through path coefficient analysis showed slight departures of the BC_{11} generation from the tendencies expressed in the small-seeded population.

We may, however, assume a simpler model as compared with that used for the path coefficient analysis where component influences on yield run parallel to each other. The alternative model considers the traits to function in series; i.e., X, the component first in the sequence, influences both Y and Z which follow in the order of development, and Y influences seed weight Z. When these influences due to sequence were removed, each trait was evaluated according to its own independent contribution.

The comparisons of the components, both under conditions of independence and under the influence of correlations, showed highly significant contributions of the genotypic source of variation to yield. Contribution due to the environment or to interaction of environment by genotype was observed in X and Y when the effects of correlations were operative; Z, however, showed a substantial effect due to environment and a smaller though significant effect due to interaction (year by genotype) when the trait was analyzed free of the influence of X and Y.

The correlations seem to mask the real contribution of the interaction of genotype by environment. The contributions of the genotype in the case of the Z component and that of the environment in the case of Y were artificially exaggerated when the effect of the correlations was present. Since some of the variation in Y and Z is a consequence of variation in X, and the source of variation in X was mainly due to the main effects of the genotype and the environment, the contribution of the genotype by environmental interaction on Y and Z is underestimated. The removal of the effects of the correlations has a substantial effect on the expression of these two components.

The situation with respect to yield is essentially the same. Whereas under the nontransformed situation the variation in yield was explained as based entirely on genotypic effects, when correlations were removed most of the variation is explained as affected by the genotype and genotype-environment interaction.

The actual measure, in terms of variation, of the effect of the correlations between components is given in the analysis of the differences between actual and transformed values. For Y and Z the genotype by environmental interaction and the environment itself are the major factors determining these correlations; the interaction is more important than the environment as such in the case of the Z component. The genotypic influence is more conspicuous in Z than in Y. The rather drastic difference observed when actual and transformed values are compared would indicate a decisive influence of the component X in the expression of the other components. This is in agreement with the findings by path coefficient analysis. The contribution of the environment is substantial, also, in affecting the expression of the different components.

For beans, the above mentioned model has only a limited value for pointing out the masking effects of the correlations and thus clearing up why expected values based on genetic parameters calculated in the conventional way fail to correspond with the observed values. In beans, the developmental pattern is such that different substructures, the nutritional units, coexist in the plant as development proceeds. These units are not wholly independent of each other. Although the seed yield components develop in a sequence and we expect a pattern of influence, one over the other, to move according to the developmental sequence, we cannot disregard a possible influence of any one component in the sequence over any other in different nutritional units. This influence might operate irrespective of the order of development if limitations due to unavailability of nutrients or genetic makeup become apparent.

The first trait in the sequence, X, can be safely regarded as the main determinant character based on the results of the models discussed. This could mean that the influence of the source variation on the transformed Z values may reflect a more real situation as compared with the sources of variation attributable when the effects of correlations were assumed to be operating. It is doubtful, however, that the situation for X and Y might be real since any effect of Z and Y on X and of Z on Y are disregarded.

The use of component analysis in breeding programs requires not only a knowledge of the type of associations among the components of yield, but a knowledge of their heritable nature, as well. In order to estimate the advance to be expected by applying selection pressure for Z in the BC_1 generation, heritability estimates were calculated by different methods and with the different populations used in this study.

Estimates derived by three of the more commonly used methods, variance components, parent-progeny regressions, and realized heritabilities, were compared. The estimates for Z were in close agreement, and whatever the method, seed size was the character showing the highest heritability value.

Estimates based on variance components were relatively high which was not unexpected considering that estimates were made on a plot basis and considering, also, that some nonadditive genetic portion was presumably present. This broad-sense estimate was used in calculating the maximum selection progress predicted for seed weight.

When the effects of correlations were removed there was a substantial change in the heritability estimate of seed size, it being then reduced to less than half its original value. The estimate for yield also changed drastically in a downward direction.

It is difficult to rationalize the kind of genetic control for Z suggested by the results obtained when correlations were removed, with the successful outcome that has generally accompanied selection for Z. Although the results seem to indicate that much of the genetic variance shown by Z is rather a reflection of the hereditary control experted by X, the outcome from the selection process tends to support the view of a more direct genetic control of the Z component.

It is rational on the following hypothesis: some portion, or possibly all, of the genes which make for more pods per plant, make for, through the compensatory system, less weight per seed. And genes that reduce the number of pods cause increased seed weight, again on account of the compensatory process. Thus the genetic variance in X is also reflected in genetic variance in Z, although there may be additional genes affecting the level of Z that have little to do with X. There would, on this assumption, be substantial negative "genetic" covariance between X and Z, which when removed mathematically, would lower the variance in Z. Nevertheless, for selection purposes, all of the genetic variance in Z, both that which is common to X, and that which is independent of X, is available.

If one wishes, this co-response pattern in X and Z, due to genes and the compensatory effects, can be ascribed to pleitropism. But it is pleitropism that is based on a developmental effect, and not pleitropism that flows independently from the primary effects of the genes.

Environmentally-induced shifts in X should also be manifested to some extent in the succeeding components, Y and Z. In addition, there is expected some environmental effect unique to Z. But of course, it is the ratio of genetic to nongenetic variances that is chiefly responsible for differential levels of heritability.

In the final outcome, it is understandable that a given component (Z) should show both a high calculated and a high realized heritability, even as the X component shows a different and generally much lower heritability.

It should be noticed that progress of selection as measured by the estimates of the realized heritability for Z would have been closely predicted by the heritability values obtained for the seed size component when the effects of correlations were removed. It may well be true that in the process of backcrossing we have driven the variance of X closer to zero while "exposing" the actual "unique" variance for Z and thus the results of the selection process reflect more accurately the portion of the genetic variance of Z that is independent of X.

Z Trait Responses to Selection

The effectiveness of selection for Z may be seen by examining the values of the realized heritability (Table 18). The portion selected from the BC_1 generation was highly significant from the mean of the population from which it was extracted, in the 20 populations studied (Table 17). The selfed generations, however, showed only eight populations where the mean of the selected BC_1S_1 plants outnumbered significantly in seed size the mean of the unselected BC_1S_1 population.

Either much of the variation in Z was nongenetic, the nonadditive portion of the genetic variance was substantial, or the genetic base was narrow and hence little response could have been expected anyway. We are inclined to think that the latter possibility is more in accordance with the facts at least in some crosses. The very close agreement with expected progress found with lines where selection was successful and the high values of the realized heritability would rule out the suggestion of a disproportionate amount of nonadditive genetic variance.

A test for additive behavior of seed size was made with the 20 BC_1 populations and this showed only five populations deviating significantly from the additive scheme (Table 21).

The lack of consistency between the results from the selected plants and their selfed progenies in certain crosses when compared with the mean of the respective populations from which they were extracted could be due to the narrow genetic base. The variability in these crosses, the statistic that reflects the total response that might be realized from a cross, was small. The starting material covered a wide range of seed sizes, nevertheless many crosses involved lines differing only slightly in this trait. Significantly, the populations derived from the widest crosses were the ones that responded best to selection.

For the BC_{11} generation the lower and upper limits for estimating the degree of advance with respect to the recurrent parent were fixed considering the expected values assuming no selection, i.e., the regression to the recurrent parent based strictly on an additive scheme, and the expectations under selection using the broad sense heritability values and an intensity of selection of 8%.

All the populations where selection for seed size was effective surpassed the respective recurrent parent in seed size in the proportions expected, assuming an additive model and actual genetic advance by selection in the BC_1. Considering that the expected values were calculated using a high heritability value, 89.2%, the observed increases, which ranged from 10 to 31%, provide good evidence of the feasibility of raising the levels of expression of Z through selection and backcrossing without interference due to negative associations with other components. The other populations, those where selection for Z was less effective, agreed remarkably with the expected values set up for these conditions (Table 23).

The results obtained from the progenies of the selected lines in backcrosses suggest that selection may have succeeded in isolating the heterozygous genotypes. Selection of the homozygote would have been likely to result in little more than the recovery of the parental genotype. With the information at hand, however, we cannot determine the number of effective factors in the presumably complex genetic system responsible for the heritable differences in seed size.

Our results indicate that selection in certain crosses of the BC_1 generation successfully isolated a genetic portion more closely associated with mid-parental levels than with those of the recurrent parents, thus raising the mean value of the subsequent BC_{11} generations over the expected values based solely on an increase equivalent to one-half of the remaining difference between the backcross and the recurrent parent means in each succeeding generation.

Further support for this hypothesis may be found in a comparison of the percent increase in seed size of the BC_1 and BC_{11} with respect to the recurrent parent (Table 24). Both values were very similar, thus indicating that through the process of selection we accumulated some plus genes for large seed size even as heterozygosity was declining. Where selection was not effective we expected the percent increase of the BC_{11} over the recurrent parent to be less than that of the BC_1 over the same parent, and that actually did happen.

Stability of the Seed Number Components

The successive backcrosses to the small-seeded parent were intended to maintain stability, in the genetic context, of the seed number components. To a considerable degree this aim was accomplished since only two of the 20 populations tested departed significantly from the expected values in total seed number. The situation changed slightly when the seed number components were examined. One-third of the tested populations showed significant changes in seeds per pod with respect to the recurrent parent; only one outnumbered significantly the recurrent parent in pods per plant (Table 25).

The possibility that genes for high Z were linked with genes for high X and Y and that therefore selection for the first character dragged along seed-number genes, seems unlikely, at least as the only or main explanation, in view of the fact that only two cases of significant changes in X and Y occurred in populations where selection for high Z was effective and also since original parents were high Z, low XY or low Z, high XY and therefore we would not expect linkage of high Z with high XY.

With a sufficient number of backcrosses we are virtually assured of recovering the recurrent parent genotype. In the second backcross the average expected percentage of germplasm contributed by the recurrent parent should be 87.5%, so we may expect our results to be influenced to some small extent by this residual heterozygosis. Nevertheless, although heterosis was reported, if we would have to ascribe the deviations in the values for the seed number components, with respect to their expected values, to heterosis we would have to assume it affected one component but not the other in some cases, or it affected the components in opposite directions in other cases--a rather unlikely situation.

Other causes may be invoked as more plausible to account for the deviations of the seed number component from its expected value. Assuming additivity, we may expect the means to regress by one-half of the difference per generation. It is unlikely, however, that the additive scheme would be the only genetic system operating, nor that all the assumptions on which the backcross theory is based would prevail. For example, the study of the relationship of performance with heterozygosity showed that as increments of plus genes were added to a genotype the expression of hybrid vigor for X, one of the seed number components, did not follow a linear trend. This curvilinear relationship, then, could suggest the presence of dominance, overdominance, or interaction among nonallelic genes. Of course, a conclusive assertion based only on the study of heterozygosity is not possible in our data.

Lastly, the fact that total number of seeds remained almost unchanged but the components for seed number did vary could suggest an operative mechanism such as the one described by Adams (1) to explain the basis of yield component compensation in beans, i.e., these changes are only consequence of compensatory relationships derived from developmental process in the plant.

A further look at the components of yield through study of the F_1 and F_2 would lead one to conclude that the gene action involved in the expression of the components Y and Z is mostly additive. This is indicated by the infrequent manifestations of heterosis for these components. The X component, on the other hand, showed a most conspicuous heterotic effect. Even transgressive segregation was observed for this character. This may indicate that there are epistatic genetic factors conditioning the number of pods per plant or other conditions that can produce heterosis. Since maximum heterozygosity is achieved in the F_1 the transgressive segregation in the F_2 may result from complementary effects brought together by recombination.

Genetic Advance in Yield

The components of yield interact in the expression of a yield phenotype. As a result of a plan based strictly on the components-of-yield approach, alterations in grain yield ranging from a decrease of 12% to an increase of 47% with respect to the recurrent parent, were obtained.

Increase in seed size as a result of selection did not necessarily result in an increase in yield and in two cases an increase in the mean value of a component other than Z resulted in a significant increment in yield (Table 26).

Populations formed by crosses 0107, 0109, 0106, 0206, 0406, 0411, and 0409, where no increases in yield were obtained, represent the populations where no responses for selection for high Z were obtained. Presumably this outcome resulted from the failure to isolate genetically distinct genotypes due to insufficient genetic variability. Neither were the seed number components altered. For each particular population there are plus or minus variations of the components with reference to their respective counterparts in the recurrent parent. This variation we interpret more as random fluctuations of the developmental process in the plant rather than as evidence of component compensation. Granted, the components compete for the same total amount of metabolic substrate produced by the plant and the values shown may very well be a reflection of the compromise that the level of the components have to reach to attain the maximum grain yield under such circumstances. In the absence, however, of significance in the differences, relatively low fluctuation values, and absence of a characteristic pattern, no inferences from these populations can be made.

Populations derived from the crosses, 0112, 0213, 0306, 0309, 0310, 0406, 0507, and 0509 showed significant increases either in X, in Y, and some also in Z, but no significant increase in yield was noticed. Insufficient genetic variability may not explain the whole situation because of populations such as 0213 and 0112 which showed a wide range of variability.

Genetic advance for character Z was attained in these populations; decreases in the Y component, however, may have offset the gains in Z, the final result being no change in yield. Since in the selection and backcross program planned, the theoretical expectations called for no change in the components X and Y, the fact that component Y was altered by the selection pressure placed on Z suggests that physiological controls over the components still operate in spite of genetic control. Other crosses, however, showed a positive association in Y and Z, which, if explained on the basis of competitional alternatives of plant development alone, would imply biological significance to an otherwise nonsignificant statistical variation in X.

Population 0209 showed a significant increase in grain yield due exclusively to a substantial rise in X. Both original parents have equal numbers of pods per plant; it may have happened that as a result of selection for Z, different plus genes for X could have been brought together thus producing a new genotype capable of giving expression to high X.

A similar case may have occurred with population 0408 where only the Y component was significantly above the values of the recurrent parent, nevertheless, increased yield resulted. This outcome, however, should not be attributed solely to the higher Y. An increase in yield on the order of 37% is hardly explained by increasing Y only 8%. Similar increases of Y in populations with the same genetic background, as in 0409, did not result in a significant increase in yield. Undoubtedly, the parallel rise in the X component made this increment possible.

With the information at hand it is not possible categorically to assign to indirect selection the cause of variation in components X and Y. Since backcrossing and selfing lead rapidly to homozygosis it could be possible that the detected variation may have resulted from the recombination of entire or large segments of chromosomes. New gene combinations for X and Y, some favorable and others unfavorable, could have been brought about as a consequence of these processes.

Of course, there is also some residual heterozygosis which could explain part of the discrepancies from the expected values. A comparison of the BC_1 and the F_2 generations may throw some light on the effect of heterozygosity. Both generations have identical distributions of heterozygous and homozygous phases. Although the distribution of homoqygous alleles is different, the distribution of heterozygous pairs is identical. Since we observed differences between the BC_1 and the F_2 (Table 26) heterozygosis cannot be the cause of the difference between these two generations; it may therefore be due to the differences in the homozygous portion AA versus 1/2 AA + 1/2 aa or aa versus 1/2 AA + 1/2 aa. With less heterozygosis present it is doubtful that it may account for the differences. On the other hand, this unexpected response of X and Y was observed only in a few of the 20 populations examined whereas all have the same amount of residual heterozygosis present.

We cannot discard the possibility of random variation. Expectations under the backcross theory are based on infinite populations; the possibility that our sample could have been divergent from the infinite population cannot be ruled out.

One final explanation of the joint variation of selected and nonselected components may be the competition taking place at the level of the metabolic developmental processes in the plant. The different components of yield follow a succession of development during the course of which a competition for environmental resources occurs. Although the components are subject to genetic control, the final outcome, yield, depends upon a complex interaction of genetic and environmental processes as a result of which a particular geometric construct is obtained. A high level of genetic control was exerted over Z, the component subject to selection, as indicated by the genetic gains in seed weight. Unexpected changes in the other components, however, might be an indication that physiologic adjustments within the plant maintain their preeminence in adjusting the geometric configuration whenever limitations of any order threaten the potential efficiency of the plant. This point of view is not incompatible with that which contemplates the possibility that the components not subject to selection might have been modified in their genetic make-up since the above mentioned developmental or physiological adjustments might take place also in response to a new broader genetic potential for the expression of the components.

A good measure of the rate of progress in yield as a result of the selection pressure put on Z is the comparison of the different backcross generations since the BC_1 populations were not derived from selected material. The populations are grouped in Table 27 according to whether selection for Z was effective or not. An increase in yield over the recurrent parent well above that expected assuming an additive model were noted for both groups in the BC_1 generation. Since selection had not been practiced at this stage in either of the populations, the difference in magnitude between the two groups (28.2% vs 14.5%) is a mere consequence of the genetic diversity in the parental material in the sets. On the other hand, the difference of either set with respect to their expected values could be explained on the basis of some heterotic effect.

The heterosis observed for seed yield when the F_1 was studied (Table 29) suggests that other kinds of gene action other than additive may also be operative. The fact that the F_2 populations yielded less than their corresponding mid-parents and F_1 hybrids may indicate the presence of epistatic gene action or of adverse component interaction.

The marked difference in progress for yield in the BC_1 generation between populations where selection for seed size was effective may indicate that the success in selection for high seed size was indeed linked to the wider genetic base of certain crosses. In the BC_{11} generation there was a gain in yield over the recurrent parent as compared with the BC_1 generation. Whereas the BC_1 generation exceeded the recurrent parent by 14.5% in yield the BC_{11} did it only by 16.8% in populations where selection for Z was not effective. Where selection for seed size was effective, however, yield increased from 28.2% over the recurrent parent in the BC_1 to 32.6% in the BC_{11}.

The increase in yield from one backcross generation to the other was not spectacular in many crosses, but neither was the reduction experienced when the selected BC_1 populations were selfed.

The idea behind this thesis proved to be effective since improvement in yield was achieved through effective manipulation of the components of yield based on their differential heritable value and taking advantage of the negative correlations among them. The yield-dampening effect of these negative associations was overcome by holding constant the genetic complex for seed number while increasing the seed size component. Penetrance of the large-seed-size genes was not affected by either introducing them into an alien background or because of environmental conditions as evidenced by the recovery of the expected genotypes in spite of the persistence of negative correlations among the components of yield.

Where increased yield was not achieved, the causes could be traced to either a narrow genetic base among the parent population or the inability to isolate the truly large-seeded genotypes in the process of selection. These limitations, however, might be surmounted by choosing parents such as to give a wider genetic base, growing large populations in which selection is to be practiced and selecting on basis of a progeny test.

SUMMARY AND CONCLUSIONS

This study confirms the findings of previous works with respect to gene action and heritability of the components of yield. The relationships between each of the components of yield as well as the type of association among the components themselves, conform to results of a majority of previously reported studies.

The component Z appeared to have the highest heritability. Pods-per-plant, however, was found to be of overriding importance in determining yield levels either in a direct or indirect way. Negative correlations among components were evident through the fact that none of the high yielding lines showed a high mean value for all three components in the parent population. Yield seemed to be related more to an harmonious balance of the levels of the different components.

The possibility that the effect of the correlations might bias the estimation of the true genetic contribution of the components involved was examined by removing the effects of correlation in a unidirectional and sequential model.

The study of the character when isolated from the one preceding it in the sequence revealed differences in the degree with which genotypic and environmental sources of variation affect the expression of the character as compared with those acting when correlations were present. Differences in the heritable contributions of the components late in the sequence were also detected. Based on the results of selection as denoted by the realized heritability estimates, it was suggested that the heritability values for seed size obtained after correlations were removed may have been closer to the true genetic situation. The unidirectional model of influence based on the sequential origin of correlated characters was considered to explain only partially the developmental sequence of events in beans, being accurate inasmuch as it explains the processes taking place at the level of the nutritional unit. Considering the whole integrated biological system, however, interpretations derived from this model should be taken cautiously, especially for the components X and Y.

Through recurrent backcrossing it was possible to exercise genetic control over the most heritable component and to raise its mean value to a desired level by exerting selection pressure. Seed size values for the BC_1 and BC_{11} generations were similar. It is postulated that through selection we succeeded in accumulating plus genes for large seed size while retaining some heterozygosis.

The expected regression toward the mean values of the recurrent parents for the seed number components was not attained uniformly. In some cases, the value of only one of the components corresponded with the expected rate of regression; in none of the cases did this happen with the two components simultaneously. The total seed number, however, did remain stable, according well with expectations.

Aside from explanations derived from nonfulfillment of some basic assumptions underlying the backcross theory, the lack of a consistent approach towards their expected values by the seed number components examined separately, may indicate that despite the genetic control exerted the environmental or physiological influences prevail when stress develops. The fact that negative correlations persisted and that departures from the expected values in the seed number components were observed even in the populations where selection for Z was not effective, may be an indication that an explanation based on component compensation would be very plausible.

A significant increase in yield was obtained in six of the twenty populations studied. Five other populations outyielded the recurrent parent although the differences were not significant. It is postulated that new levels of yield can be attained by increasing the level of expression of one of the components of yield while maintaining the others constant. Component compensation, though present, would not necessarily be incompatible with higher levels of productivity under this approach.

One of the basic requirements for a successful backcross breeding program is to have a satisfactory recurrent parent. Among all the small-seeded parents studied, P-03 and P-05 were the only ones meeting these requirements on a seed number basis. Significantly, the populations where significant genetic gain in yield was reported as a result of changes in Z, were populations involving these particular parents. Much of the lack of response for increase in yield despite gains in seed size could be explained by the lack of outstanding recurrent parents.

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