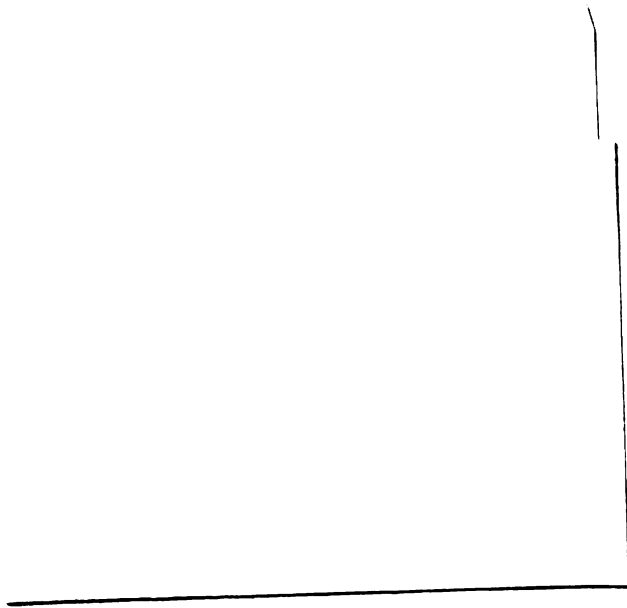




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COMPONENT INTERACTION IN RELATION TO
MEAN EXPRESSION OF COMPLEX TRAITS
IN A FIELD BEAN CROSS

Thesis for the Degree of M. S.
MICHIGAN STATE UNIVERSITY
Rodrigo A. Duarte
1961



COMPONENT INTERACTION IN RELATION TO MEAN EXPRESSION
OF COMPLEX TRAITS IN A FIELD BEAN CROSS

By

Rodrigo A. Duarte

AN ABSTRACT

Submitted to the College of Agriculture
of Michigan State University of Agriculture and
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requirements for the degree of

MASTER OF SCIENCE

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W. H. Adams

ABSTRACT

The complex characters Total Leaf Area (T), Seed Yield (W), and Seed Size (V) in field beans (*Phaseolus vulgaris*) were analyzed by partitioning them into simpler components. For the purpose of the discussion, a complex trait was defined as one that has a physiological and/or morphological component structure.

The population studied consisted of progeny obtained from intra-specific crosses of *Phaseolus vulgaris*, variety Algarrobo, a kidney bean from Colombia, South America, by Michelite, a navy bean variety from Michigan. During 1960, parental, F_1 , F_2 and F_3 generations were grown in the field as well as in the greenhouse.

The product of Number of leaflets per plant (N), and the average Size of the leaflet (S) was Total Leaf Area (T); Seed yield (W) was partitioned into Number of pods per plant (X), Number of seeds per pod (Y), and Weight of the seed (Z); Length (L), Width (Wi), and Depth (D) of the seed were proposed as components of the Size of the seed (V).

Independent genetic systems for N and S, components of Total leaf area (T), were postulated when a non-significant correlation between them was found. A similar situation prevailed for the yield components, X, Y, and Z. Contrary to these findings, highly significant correlations (positive) were obtained

Rodrigo A. Duarte

between the seed size components, L, Wi, and D, suggesting that seed size is an allometric trait with a single genetic basis rather than a complex trait depending on interactions of independent gene systems.

Number of leaflets per plant (N), and Size of the leaflet (S) were found to be influenced by dominance and additive genetic systems respectively, i.e. complete dominance for high number of leaflets, and lack of dominance for the size of the leaflet. This conclusion was reached after testing the F_1 against the parents and mid-parent; it was later supported by the estimates of the average degree of dominance $\bar{a}$, calculated from the partition of the variances of F_2 and means of F_3 into genetic variance and its components.

Complete dominance for high number of pods, X, and no dominance for Y and Z was obtained in regard to the yield components. These findings implied that X was governed by a nonadditive genetic system, and Y and Z by additive ones.

A high degree of heterosis was observed in the complex traits, total leaf area (T), and seed yield (W). Since none of the components of these characters exhibited heterosis (or overdominant gene action), the heterosis observed was ascribed to the multiplicative effect of the gene systems of the components, interacting at the level of morphological

Rodrigo A. Duarte

integration, rather than at the nuclear or cytoplasmic level, i.e. a case of "component epistasis," in which the effect of one component on the complex trait, is conditioned by the value of the other component (or components), and vice versa.

Theoretically additive and nonadditive genetic systems could be fixed in true breeding forms; therefore heterosis due to epistatic effects could be fixable also, by fixing separately the genetic systems of the components.

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TABLE OF CONTENTS

	Page
INTRODUCTION	1
REVIEW OF LITERATURE	3
MATERIALS AND METHODS	8
EXPERIMENTAL RESULTS AND DISCUSSION.	10
SUMMARY AND CONCLUSIONS	29
LITERATURE CITED	32

LIST OF TABLES

Table	Page
1. Correlation coefficients (r) measuring the inter-relationship of number of leaflets per plant (N), size of the leaflet (S), and total leaf area (T) in the F_2 generation	11
2. t-tests, variances, and mean values of leaflet number (N) of parents, mid-parent, and F_1	13
3. Variances in F_2 and variances of the means of F_3 progeny, and the average degree of dominance $\bar{a}$, for number of leaflets (N)	13
4. t-tests, variances, and mean values of leaflet size (S) of parents, mid-parent, and F_1	16
5. Variances in F_2 and variances of the means of F_3 progeny, and the degree of dominance $\bar{a}$, for size of the leaflets (S)	17
6. t-tests, variances, and mean values of total leaf area (T) for parents, sum of the parents, and F_1	19
7. Variances in F_2 , and variances of the means of F_3 progeny, and the degree of dominance $\bar{a}$, for total leaf area (T)	19
8. Correlation coefficients (r) measuring the inter-relationships of number of pods per plant (X), number of seeds per pod (Y), weight of the seed (Z), and total yield per plant (W), in the F_2 generation	21
9. t-test, variances, and mean values of number of pods per plant (X) of the parents and F_1	23
10. t-test, variances and mean values of number of seeds per pod (Y) for parents, mid-parent and F_1	24
11. t-test, variances, and mean values of weight of the seed (Z) for parents, mid-parent, and F_1	24
12. t-test, variances, and mean values of seed yield per plant (W) for parents and F_1	25

Table

Page

13. Correlation coefficients (r) measuring the inter-relationships between length (L), width (W_i), and depth (D), of the seed in the F_2 generation . . . 27

INTRODUCTION

Most phenotypic characters in plants are joint results of the actions and interactions of genes, together with environmental forces, that act upon the developing individual as it successively directs its transformation from the onset of germination to senescence. Certain traits are themselves nothing more than abstractions or artifacts compounded of two or more subsidiary or component traits. Yield of grain, forage, and fiber in various plant species can be so categorized, that is, these are complex traits with a component structure. When the components are uncorrelated it is postulated that real genetic systems exist only for the components, and that the complex "trait" is only an interaction product of the components.

To gain a fuller knowledge of the genetic behavior of major complex traits, plant breeders have found it expedient to partition the traits into simpler components for individual study. In this thesis the complex traits total leaf area, seed yield, and seed size in a field bean cross are subdivided into appropriate components for independent analysis. Total leaf area (T) is a complex trait independently of its relationship to other characters and is the product of number of leaves per plant (N) by mean leaf size (S). Components of

yield (W) are number of pods per plant (X), average number of seeds per pod (Y), and average weight per seed (Z). The product of mean length of a seed (L), mean width (W_i), and mean depth (D) results in seed size (V), which in turn is one of the yield components.

The main object of the study was to learn whether certain important traits in field beans have a component structure and whether independent analysis of the components would lead to any better understanding of the genetic basis of variation of the complex traits themselves.

REVIEW OF LITERATURE

Since the early years of the present century, when the first theories on the nature of heterosis were devised, the concept of heterosis due to interaction of the components of complex traits, which is essentially a developmental concept, has been over-shadowed by the more strictly genetic hypotheses of dominance and overdominance. More recently there has been a renewal of interest in the developmental concept in relation to heterosis for complex traits.

Waddington (13) has proposed that genetic studies of phenotypic characters such as body weight or milk yield, should be done on bases of analysis of independent factors, that is, to try to partition the physiological system into less complex parts. He suggested that some genes might affect the milk yield by increasing the quantity of secreting tissue, others by affecting the efficiency of secretion, and perhaps some genes in still other ways. He also pointed out a case of variation in the quantity of vein formed in a region of Drosophila wing, in which the genetic systems fell into distinct physiological groups in this way.

Working with intra-specific crosses in Phaseolus vulgaris Sax (11) found a very close association between size and pigmentation of the seeds. It was reported that size differences even in the case of no dominance where several

factors are involved, may be affected by the independent action of the size factors, which when combined have cumulative effects.

Genotypic-environmental interactions influencing seed size in lima beans have been studied by Parsons and Allard (9). Seed size in lima beans was described as a complex trait made up of complicated interactions between genotype and micro-environment, and it was emphasized that seed size is one of the components of fitness in lima beans.

According to Williams and Gilbert (16) yield heterosis in tomato hybrids could be explained by means of component interactions. Instances were described of yield heterosis in crosses when the components of yield were not heterotic. It was suggested as erroneous to speak of heterotic genes for complex traits such as crop yield. It was also mentioned that near maximal levels have been fixed in pure breeding varieties which fell in the upper ranges of variation and these were not exceeded by heterotic hybrids between poorer parents.

Powers (10) reported a case of heterosis in yield of ripe fruit in tomato hybrids, due to intra- and inter-allelic interactions between components of the main trait, namely number of fruits that ripen, and weight per fruit. In turn number of fruits that ripen was found to be dependent on earliness of maturity, i.e. number of days from seeding to the

first ripe fruit. Weight per fruit was partitioned into weight per locule and number of locules per fruit. Different degrees of dominance and heterosis were reported in the components as well as in the main characters. It was suggested that the study of genetics of heterosis could be simplified and improved by breaking the main traits down into their component characters.

Working with cotton, Hutchinson (6) was able to analyze its yield components. They were: bolls per plant, seed cotton per boll, seeds per boll, lint per seed etc. Environmental variations seemed to affect more greatly some characters than others, and selection also was found to be more effective in certain characters. Perhaps the main idea of this work was shown in the compensatory variation of the components; that is, the intensification of one character can only be obtained at the expense of the others because of physiological incompatibilities.

In a study of the breeding of self-pollinating cereals Whitehouse et al. (15) reported yield components of wheat, using as the components: weight per grain, grains per spikelet, spikelets per ear, and ears per plant. Correlation analysis between components were made, and it was found they were completely independent of each other. Yield predictions by means of diallel crosses, in which the best varieties for yield components were chosen, was also mentioned.

Grafius (3) has interpreted yield in oats as the volume of a rectangular parallelepiped, whose edges are the yield components: the number of panicles per unit area X , the average number of kernels per panicle Y , and the average kernel weight Z . It was pointed out that the edge most subject to change would be the longest and that changes in the components or edges would tend to counterbalance. In a study of heterosis in grain yield of barley, the same author (4) has clearly demonstrated the efficacy of the 3-dimensional component model. Components of yield in barley were the same as in oats except for X which in the case of barley was number of heads per plant. It was pointed out that yield is an artifact composed of "epistatic" interactions between components. Since X showed non-additive variability, further studies of this component were made, and it was found that earliness, or time, was the factor contributing to the dominance variability of heads per plant.

In recent months, Grafius (5) has proposed ear number per plant (R), kernels per row (S), rows per ear (T), and kernel weight (U) as yield components in corn, assuming uniform stand.

Frey (2) attributed yield in oats to the multiplicative interaction of components; because of this, the variety $\times$ location interaction variance was smaller for yield components

than for grain yield. A new term "geometric epistasis," was also proposed to denote the combination of components to produce grain yield.

Yield of oat parents and progeny of crosses was discussed by Luedders (7), using the yield components method. The results were quite similar to those Grafius (4) obtained in barley.

MATERIALS AND METHODS

Intra-specific crosses of Phaseolus vulgaris variety Algarrobo by variety Michelite were produced. Algarrobo is a mottled kidney bean variety from Colombia, South America, which possesses the determinate type of growth (bush type). Michelite is a navy bean variety, produced by the Michigan Agricultural Experiment Station. It has the indeterminate type of growth (vine type).

Crosses were made under greenhouse conditions in 1959-60, and F_1 and F_2 progenies were grown in that environment, in order to give rise to F_2 and F_3 generations for planting in the field. During the summer of 1960, 25 F_1 plants, 90 F_2 plants, 100 F_3 families with 10 plants per each family, along with 20 plants for each one of the parents, were planted on land of the Michigan Agricultural Experiment Station, at East Lansing. Unfortunately bacterial and virus diseases decimated the population. Field data were obtained from individuals free of diseases, which consisted of 10 F_1 plants, 24 F_2 plants, 65 F_3 families ranging from 2 to 5 plants in each family, and 10 plants for each of the parents.

During the fall of 1960, from crosses made in the field during the summer, and F_2 and F_3 seeds harvested in the same field, a new population was grown in the greenhouse. Fifteen F_1 plants, 200 F_2 plants, 24 F_3 families with 20

plants per family, in addition to 20 plants of each of the parents, were grown. Because of the appearance of virus symptoms on some plants, affected ones were eliminated. Data were taken from the following population: 6 F_1 plants, 165 F_2 plants, 23 families ranging from 2 to 17 plants in each family. Nineteen plants of Algarrobo, and 18 of Michelite were retained.

Data on total leaf area and its components come from the field as well as from the greenhouse experiments. Yield and seed size components data come from the field experiment only. Leaf area measurements and leaf counts were made two weeks after the onset of flowering. At maturity, number of pods per plant, and number of seeds per pod were recorded. In order to obtain the average weight of a seed, a sample of 100 seeds was taken. The 3-dimensional measurements of the seed to obtain seed size components were made on a random sample of 10 seeds per plant.

EXPERIMENTAL RESULTS AND DISCUSSION

The results are presented according to the following outline:

I. Leaf Area

A. Field results. B. Greenhouse results. 1960

- (a) Correlation coefficients
- (b) Number of leaflets per plant (N)
- (c) Size of the leaflet (S)
- (d) Total leaf area per plant (T)

II. Yield

A. Field results

- (a) Correlation coefficients
- (b) Number of pods per plant (X)
- (c) Number of seeds per pod (Y)
- (d) Weight of the seed (Z)
- (e) Total yield per plant (W)

III. Seed Size

- (a) Correlation coefficients

I. Leaf Area

A--Field Results. B--Greenhouse Results

(a) Correlation Coefficients

The correlation coefficients of the number of leaflets per plant (N), size of the leaflet (S), and total leaf area (T) are presented in Table 1.

TABLE 1. Correlation coefficients (r) measuring the inter-relationship of number of leaflets per plant (N), size of the leaflet (S), and total leaf area (T) in the F_2 generation

A--Field		
Comparison	df	r
N vs S	22	-.3230
N vs T	22	+.7931**
S vs T	22	+.7692**
B--Greenhouse		
N vs S	160	-.1872
N vs T	160	+.8820**
S vs T	160	+.8261**

**p < .01

Negative but non-significant correlations were found for N vs S in the field as well as in the greenhouse experiments. The relationship is not so strong but that each one of the components (N and S) can be supposed to be conditioned largely by its own genetic system; changes in one of the

components only slightly affect changes in the other. As was expected, N and T and S and T are highly significantly correlated (positive). Changes in N, S, or both should affect total leaf area.

(b) Number of Leaflets (N)

From the t-tests given in Table 2 it may be seen that the F_1 differs significantly from the mid-parent (m), but not from Michelite (P_2) for average number of leaflets (N); this suggests complete dominance of genes for the high leaflet number of Michelite, although interactions of non-alleles could not be excluded as a conditional possibility.

In Table 3 an estimate of the average degree of dominance $\bar{a}$, of number of leaflets (N) from F_2 and means of F_3 progeny is presented, along with total observed variances and estimates of genetic and environmental variances and their components.

The total variation measured in a population can be partitioned into components, using suitable models which have been developed. According to Mather (8), among others, total variance of segregating populations can be divided into three components: first, non-heritable variation due to environmental agencies (E); second, additive genetic variance (D); third, nonadditive or dominance genetic variance (H). The two

TABLE 2. t-tests, variances and mean values of leaflet number (N) of parents, mid-parent, and F_1

Generations	$\bar{N}$	Observed variance	----- Comparison -----	t-test df	----- t-value -----
A--Field					
P_1 (+)	83.0	245.60			
P_2	320.0	1272.35	F_1 vs. P_2	18	.83
m	201.5	215.60			
F_1	334.3	1682.81	F_1 vs. m	18	9.63**
B--Greenhouse					
P_1	26.7	22.15			
P_2	63.7	83.27	F_1 vs. P_2	22	1.07
m	45.2	76.59			
F_1	68.2	84.77	F_1 vs. m	22	8.76**

(+) For this and for the following tables P_1 = Algarrobo, P_2 = Michelite, m = Mid-parent.

** $P < .01$

TABLE 3. Variances in F_2 and variances of the means of F_3 progeny, and the average degree of dominance $\bar{a}$, for number of leaflets (N)

Generations	Observed variance	Genetic variance	Components of Variance			$\bar{a} =$
			H	D	E	$\sqrt{H/D}$
A--Field						
F ₂	7347.17	6588.19	9680.75	8306.01	758.98	1.08
$\bar{F}_3$	5012.00	4743.05			268.95	
B--Greenhouse						
F ₂	226.27	173.56	135.73	279.25	52.71	.697
$\bar{F}_3$	153.29	148.11			5.18	

latter are heritable components of the variance. The variance of an F_2 is $VF_2 = 1/2 D + 1/4 H + E_1$, and the variance of means of F_3 families, $V\bar{F}_3 = 1/2 D + 1/16 H + E_2$.

As an example using the field results presented in Table 3, the total variance was partitioned as follows:

$$VF_2 = 1/2 D + 1/4 H + E_1 = 7,347.17$$

where environmental variation (E_1) is measured by the mean variance of the parents (Table 2),

$$E_1 = \frac{VP_1 + VP_2}{2} = 758.98.$$

Genetic variance, GVF_2 , is obtained by subtracting E_1 from VF_2 :

$$(1) \quad GVF_2 = 1/2 D + 1/4 H = 6,588.19.$$

E_2 for the variance of means of F_3 families, $V\bar{F}_3$, is equal to

$$\frac{E_1}{k_o},$$

k_o being the adjusted mean of the number of individuals in each F_3 family. The formula for finding k_o , as given by Snedecor (12), is

$$k_o = \frac{1}{q-1} \left(\sum n - \frac{\sum n^2}{\sum n} \right)$$

in which q represents the number of families in F_3 , and n the number of individuals per family.

For the present example $k_o = 2.822$. Therefore

$$E_2 = \frac{758.98}{2.822} = 268.95. \quad \text{Genetic variance of the means of } F_3, GVF_3$$

is obtained by subtracting E_2 from $V\bar{F}_3$. Therefore

$$(2) \quad \text{GV}\bar{\text{F}}_3 = 1/2 D + 1/16 H = 4,743.05.$$

Setting up the simultaneous equations (1) and (2), the values of H and D are found.

$$(1) \quad \text{GV}\bar{\text{F}}_2 = 1/2 D + 1/4 H = 6,588.19$$

$$(2) \quad \text{GV}\bar{\text{F}}_3 = 1/2 D + 1/16 H = 4,743.05$$

Subtracting equation (2) from equation (1):

$$3/16 H = 1,845.14 \text{ and } H = 9,680.75.$$

Adding up equations (1) and (2):

$$D + 5/16 H = 11,331.24 \text{ and } D = 8,306.01$$

From the values of H and D it is possible to obtain, according to Mather (8), an estimate of the average level of dominance of the genes for a given character by means of the formula $\bar{a} = \sqrt{H/D}$, assuming no epistasis. Values of $\bar{a}$ near zero mean no dominance for either one of the parents, that is, additivity for the genes concerned. Values close to unity suggest complete dominance for genes of one of the parents, really, nonadditivity of the genes. Values exceeding unity suggest overdominance.

The value of $\bar{a} = 1.08$ from the field results presented in Table 3, suggests complete dominance of the genes conditioning high number of leaflets and agrees completely with the results of the t-test between F_1 and P_2 (Table 2). Although the value of $\bar{a} = .697$ from the greenhouse experiment is less than 1, it indicates a high degree of dominance, though not complete dominance.

(c) Leaflet Size (S)

Table 4 shows comparisons of the F_1 with the mid-parent (m) and with Algarrobo (P_1) for average size of the leaflets. The t-tests on field data imply no dominance for either one of the parents, that is, additivity of the genes that govern this trait, inasmuch as the F_1 is not significantly different from the mid-parent (m). From the greenhouse results it appears that the F_1 is significantly superior to the mid-parent (m) at the 5 percent level.

TABLE 4. t-tests, variances and mean values of leaflet size (S) of parents, mid-parent, and F_1

Generations	$\bar{S}$ cms. ²	Observed variance	----- t-test ----- Comparison	df	t-value
A--Field					
P_1	84.032	2.817			
P_2	33.161	1.864			
m	58.596	1.664	F_1 vs. m	18	1.38
F_1	57.580	3.784			
B--Greenhouse					
P_1	147.16	593.47	F_1 vs. P_1	22	4.46**
P_2	63.94	134.88			
m	105.55	280.10	F_1 vs. m	22	2.47*
F_1	118.37	62.27			

* $P < .05$.

** $P < .01$.

When the F_1 is tested against Algarrobo (P_1), the parent with greater leaflet size, the test indicates significance at the 1 percent level for P_1 over the F_1 , suggesting no more than partial dominance for the greater leaflet size, even under artificial growing conditions.

Estimates of the average degree of dominance $\bar{a}$ for the size of the leaflets (S) are presented in Table 5. Analysis of the field and greenhouse data results in values of $\bar{a} = .485$ and $\bar{a} = .344$ respectively, suggesting partial dominance for this particular component. However as the values of the additive genetic variance (D) are compared with the nonadditive or dominant genetic variation (H), it is found that the former exceeds greatly the amount of the latter, indicating that the greatest portion of the genetic variance is due to additivity of the genes responsible for size of the leaflets.

TABLE 5. Variances in F_2 , and variances of the means of F_3 progeny, and the degree of dominance $\bar{a}$, for size of the leaflets (S).

Gener- ations	Observed variance	Genetic variance	Components of Variance			$\bar{a} = \sqrt{H/D}$
			H	D	E	
A--Field						
F_2	274.237	271.998	114.73	486.602	2.239	.485
$\bar{F}_3$	251.265	250.470			.795	
B--Greenhouse						
F_2	852.98	488.80	109.81	922.69	364.18	.344
$\bar{F}_3$	503.98	468.21			35.77	

(d) Total Leaf Area (T)

Total leaf area (T), variances, mean values, and t-test results are presented in Table 6. The F_1 exceeds at the 1 percent level the better parent (P_2) for total leaf area, and in fact exceeds numerically the sum of both parents, in the field as well as in the greenhouse, though not significantly.

Heterosis for total leaf area (T) is postulated as a result of the multiplicative effect of the two components, one of them (N) under the control of genes with mostly dominant effects, and the other (S) under the control of genes largely additive in their action.

Table 7 shows the average degree of dominance $\bar{a} = 3.066$ and $\bar{a} = 2.850$ for total leaf area (T) in the field and in the greenhouse, respectively. These values coincide completely with those presented in Table 6, which makes it appear that heterosis for this complex trait is due to overdominant loci in the F_1 . But since total leaf area is compounded of size (S) times number of leaflets (N), and these components do not exhibit heterosis (or overdominant gene action) in themselves, it is patently clear that the heterosis (and high level of overdominance) exhibited in the compounded trait, total leaf area, is due to the multiplicative effects inherent in the process of combining size and number of leaflets to get total leaf area.

TABLE 6. t-tests, variances, and mean values of total leaf area (T) for parents, sum of the parents, and F_1

Gener- ations	$\bar{T}$ cms. ²	Observed variance	----- t-test ----- Comparison	df	t-value
A--Field					
P_1	6,964.63	17,342,860			
P_2	10,611.59	870.422	F_1 vs. P_2	18	10.73**
P_1+P_2	17,586.22	1,265.107	F_1 vs. P_1+P_2	18	2.005
F_1	19,249.19	5,604,327			
B--Greenhouse					
P_1	3,936.70	1,191,643			
P_2	4,109.17	1,146,336	F_1 vs. P_2	22	7.81**
P_1+P_2	8,045.87	1,110,916	F_1 vs. P_1+P_2	22	.012
F_1	8,052.33	1,144.611			

**P < .01

TABLE 7. Variances in F_2 , and variances of the means of F_3 progeny, and the degree of dominance $\bar{a}$, for total leaf area (T)

Gener- ations	Observed variance	Genetic variance	Components of Variance			$\bar{a} = \sqrt{H/D}$
			H	D	E	
A--Field						
F_2	22,603,239	13,496,598			9,106,641	
			44,516,674	4,734,338		3.066
$\bar{F}_3$	8,376,217	5,149,200			3,227.016	
B--Greenhouse						
F_2	3,870,248	2,701,258			1,168,989	
			8,661,197	1,070,903		2.850
$\bar{F}_3$	1,191,100	1,076,268			114,832	

Multiplicative interaction between leaflet number (N) and leaflet size (S) may be interpreted to mean that a condition of epistasis exists for the complex trait.

Epistasis in statistical-genetic language has been defined (Grafius, 4) as an interaction term containing variances due to interactions of additive x additive, additive x non-additive, nonadditive x nonadditive effects, and so on.

According to Cockerham (1) epistasis in the simplest cases results from the joint action of two genes, one acting additively and the other dominantly, symbolized as $V A \cdot D$. Since part of the variance due to dominant genes behaves in an additive manner, some variance of this kind also exists, symbolized by $V A \cdot A$. The case of heterosis of total leaf area (T) fits the Cockerham model except that the interaction between components in this case, is at the morphological level rather than at the intracellular level or, in other words, is a kind of somatic interaction. In Frey's (2) terminology, this is a case of "geometric epistasis" which denotes combination of components to produce total leaf area.

II. Yield

A--1960 Field Results

(a) Correlation Coefficients

Correlation coefficients are given in Table 8 showing the relationships between number of pods per plant (X), number of seeds per pod (Y), weight of the seed (Z), and total seed yield per plant (W), in the F_2 generation.

TABLE 8. Correlation coefficients (r) measuring the inter-relationships of number of pods per plant (X), number of seeds per pod (Y), weight of the seed (Z), and total yield per plant (W), in the F_2 generation.

Comparison	df	r
X vs. Y	22	+.0729
X vs. Z	22	-.0189
Y vs. Z	22	-.3954
X vs. W	22	+.8630**
Y vs. W	22	+.8910**
Z vs. W	22	+.8321**

**P < .01

Non-significant correlations are found for X vs. Y, X vs. Z, and Y vs. Z, indicating that changes in one or two of the components do not greatly affect the remainder, that is, that variation in each component is largely independent of variation in the others. The negative association between Y and Z, however, is probably a real one, and not unexpected since development would tend to impose a condition of

complementarity between number of seeds per pod (Y) and size of the seed (Z). The genetic relationship between Y and Z, however, is not revealed by this association.

This case is similar to that involving the components of leaf area as discussed above; in general, the values of the correlation coefficients imply that each component has for the most part an independent genetic system.

Highly significant correlation coefficients are observed between each one of the yield components, X, Y, and Z, and the total seed yield per plant (W), as was expected. From these results, coupled with the fact that the components show independence each to the other, it is evident that the total seed yield per plant is due to the product of the three components, namely: number of pods per plant (X); number of seeds per pod (Y); and average weight of the seed (Z).

(b) Number of Pods per Plant (X)

Table 9 shows the t-test, variances, and mean values of number of pods per plant (X) of the parents and F_1 . Comparison between F_1 and Michelite (P_2), the parent with higher number of pods per plant, indicates non-significant difference between them, suggesting complete dominance of the genes, that is, that a nonadditive genetic system is governing this character. Values of the degree of dominance $\bar{a}$, and the components of variance in F_2 and means of F_3 families, are not

given for yield and its components, because the low number of individuals in each family of the F_3 was considered insufficient to represent adequately the population, especially for traits as variable as yield and its components.

TABLE 9. t-test, variances, and mean values of number of pods per plant (X) of the parents and F_1

Generations	$\bar{X}$	Observed variance	----- t-test -----		
			Comparison	df	t-value
P_1	27.70	63.90			
P_2	71.00	266.75	F_1 vs. P_2	16	.81
F_1	65.22	189.70			

(c) Number of Seeds per Pod (Y)

The t-test, variances, and mean values of number of seeds per pod (Y) for parents, mid-parent (m) and F_1 are presented in Table 10. It was unnecessary to test the F_1 against the mid-parent because the means were exactly equal. This fact implies no dominance for either parent, which indicates additivity of the genes responsible for the number of seeds per pod (Y).

(d) Seed Weight (Z)

As far as seed weight (Z) is concerned, results of the t-test, variances, and mean values for parents, mid-parent and

F_1 are given in Table 11. A non-significant difference is found when the F_1 is compared with the mid-parent (m), indicating absence of dominance in both parents. As has been mentioned, lack of dominance in the parents suggests an additive genetic system for the trait observed, in this case, seed weight (Z).

TABLE 10. t-test, variances, and mean values of number of seeds per pod (Y) for parents, mid-parent and F_1

Generations	$\bar{Y}$	Observed variance	----- t-test ----- Comparison	df	t-value
P_1	3.02	.1288			
P_2	4.70	.0512			
m	3.86	.0510	F_1 vs. m	16	0
F_1	3.86	.0175			

TABLE 11. t-test, variances, and mean values of weight of the seed (Z) for parents, mid-parent, and F_1

Generations	$\bar{Z}$ grms.	Observed variances	----- t-test ----- Comparison	df	t-value
P_1	.6580	.000766			
P_2	.1850	.000025			
m	.4215	.000187	F_1 vs. m	16	1.96
F_1	.3450	.013458			

(e) Total Seed Yield per Plant (W)

Table 12 shows results of total yield per plant (W). As in the total leaf area (T), yield per plant exhibits heterosis. This is concluded after observing a statistically significant superiority of the F_1 over the better parent for total grain yield.

TABLE 12. t-test, variances and mean values of seed yield per plant (W) for parents and F_1

Generations	$\bar{W}$ grms.	Observed variance	----- t-test ----- Comparison	df	t-value
P_1	55.026	285.77			
P_2	62.307	256.46	F_1 vs. P_2	16	3.053**
F_1	86.646	314.95			

**p < .01

Evidence that this is a case of heterosis due to component epistatic effects, was implied when independence of each one of the components of yield was demonstrated. Therefore, yield is the result of interactions of three different genetic systems, one acting in a nonadditive or dominant way (number of pods per plant, X), and the other two showing additivity of the genes (number of seeds per pod, Y, and seed weight, Z).

The dominance gene action apparently associated with number of pods per plant (X), might be the result of a major

dominant gene affecting development, for example, early versus late maturity. In the case of barley, Grafius (4) was able to determine that earliness of maturity, conditioned by a single gene, was influencing the number of heads per plant.

Since yield is the multiplicative construct of its components, any alteration of one, two or all of them, must affect the yield.

III. Seed Size (V)

A--1960 Field Results

(a) Correlation Coefficients

In Table 13 are presented correlation coefficients between length (L), width (Wi), and depth (D) of the seed, assumed to be seed size components. It was thought that size of the seed could be a complex character made up of the three components already mentioned. However, the high significant positive values of r for the comparisons made, show a very close relationship of the "components." It indicates that changes of any one of the factors is highly associated with changes in the other two.

TABLE 13. Correlation coefficients (r) measuring the inter-relationships between length (L), width (Wi), and depth (D) of the seed in the F_2 generation

Comparison	df	r
L vs. Wi	22	+.870**
L vs. D	22	+.605**
D vs. Wi	22	+.580**

** $p < .01$

These considerations suggest that the size of the seed (V), is not a complex trait in the sense used in this thesis but an allometric trait, with its own genetic system.

The finding that seed size, a trait undeniably geometric in any physical context, fails to behave as a geometric construct in the sense of being a product of independent gene systems, does not invalidate the latter idea. It does underline the point, however, that the idea of a multiplicative construct is basically a conceptual matter--a way of knowing, of gaining insight into the developmental structure of the more complex characters.

Now, returning to the genetic control of seed size, two possibilities may be recognized: one, independent genes or sets exist for each dimension. We should therefore expect no correlation among components, and, concomitantly, a variety of sizes and shapes due to independent combinations of the various dimensions. Neither situation prevails in the material studied here. Two, a gene or genes exist determining relative growth rates throughout development of the seed. From this as a basis, correlated dimensions of shape would follow. Wardlaw (14), summarizing the conclusions of Sinnott, Huxley, Goldschmidt, D'Arcy Thompson, Hammond, and others, points out that such genes determine shape by controlling correlations between the growth rates in different dimensions. How the control is achieved is not understood.

SUMMARY AND CONCLUSIONS

Two complex traits in field beans, total leaf area and total grain yield, have been studied by partitioning them into simpler components. Number of leaflets per plant (N), and mean leaflet size (S) are the components of total leaf area (T), thus $N \cdot S = T$. Components of total grain yield per plant (W) are number of pods per plant (X), number of seeds per pod (Y), and weight of the seed (Z), thus $X \cdot Y \cdot Z = W$.

The occurrence of non-significant correlations for N vs. S in the case of total leaf area, and between X vs. Y, X vs. Z, and Y vs. Z, in the case of yield, indicated that separate genetic systems are governing each one of the components.

Complete dominance for high number of leaflets (N), and size of dominance for lack of the leaflets (S), was found when the F_1 was tested against the parents and mid-parent. These findings were supported completely by the estimates of the degree of dominance $\bar{a}$, calculated from the partition of the variances of F_2 and means of F_3 into genetic variance and its components. Complete dominance for N, and absence of dominance for S indicate that these traits are influenced by a dominant and an additive genetic system respectively.

The F_1 was compared with the parents and mid-parent in regard to the components of yield, X, Y, and Z. Complete dominance for the higher number of pods (X) was found, suggesting a dominant genetic system for this component. Lack of dominance was observed as far as Y and Z are concerned, indicating that these characters are directed by additive genetic systems.

In the complex traits total leaf area (T), and grain yield (W), heterosis was observed. This heterosis was a clear consequence of multiplicative relationship of the components. Estimates of $\bar{a}$ for the complex trait were in the overdominance range. On the basis of the existence of independent genetic systems for components it seems obvious that this overdominance is spurious and does not reflect the behavior of real genes at all.

Since in a two component system ($N \cdot S = T$) the effect of component N on T is dependent upon the value of S, and vice versa, a condition of epistasis exists. As long as variation in N is controlled by a set of genes whose average action approaches complete dominance, and variation in S is governed by one or more genes behaving additively, variation in T can be ascribed to interaction of the dominance x additive kind, i.e. an epistatic variance in the statistical sense set forth by Cockerham (1).

Multiplicative interaction of three components results in yield ($X \cdot Y \cdot Z = W$), and therefore the effect of each one of the components on W depends on the value of the other two remaining factors; this indicates that a kind of epistasis prevails among the components which comprise yield.

Different from heterosis due to heterozygosis, heterosis due to interaction between components, could be potentially fixed in a true breeding form, by fixing separately the genetic systems of the components. Additive and nonadditive systems exclusive of genetic overdominance, theoretically are fixable in true breeding form, although nonadditive systems require more generations of selfing in order to distinguish homozygous and heterozygous individuals. The suggestion is made that it might be more realistic, and more fruitful, to select for high component values, and to attempt to recombine high or optimal values of components in a single line, than to select in a large uncontrolled segregating population for the very infrequent randomly occurring optimal combination.

An attempt was made to partition into components the size of the seed. Length, width, and depth of the seed were proposed as components. However, highly significant correlation (positive) between the "components" demonstrated that seed size is a single, probably allometric character, and not a complex trait in the sense of being comprised of independent components.

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