Inheritance of Seed Yield and its Components in a Six-Parent Diallel Cross in Peas[1]

Aage Krarup and David W. Davis[2]
University of Minnesota, St. Paul

Abstract. Pea seed yield (W) and its components—pods per plant (X), seeds per pod (Y), and average seed weight (Z)—and also seeds per plant were found to be controlled by an additive genetic system, on the average. The existence of some departure from additivity was indicated by deviation of the F_1 from the midparent, especially for X, W, and seeds per plant. This deviation was more likely due to epistasis or linkage than to dominance. Specific Heterosis (specific combining ability) was important for all components, while Variety Heterosis (general combining) was important only for Y and Z. Estimates of heritability were high, ranging from .38 for seeds per plant to .65 for Z. Yield was found to be closely related to X, Y, and Z in descending order. Pods per plant (X) probably is a good selection index for dry seed yield in the pea.

In various leguminous crops the number of pods per plant (X), the number of seeds per pod (Y) and the average seed weight (Z) have been defined as the components of seed yield (W). Examples are seen in field beans, *Phaseolus vulgaris* L. (5, 12, 1), in soybeans, *Glycine max* (L.) (2), and in peas (10). Component relationships have shown number of pods per plant to be the most important component (3, 5, 10, 12). These same characters were studied as the components of seed yield in peas *(Pisum sativum* L.) in this investigation.

In F_2 progeny from 3 crosses in peas Johnson (10) studied 13 quantitative characters and found that genes for low yield, small number of seeds, fewer pods and low average seed weight were partially dominant on the average. Yield component relationships showed that variation in yield was due primarily to variation in pod number and seed number per plant. He suggested that yield and its components were probably a pleiotropic manifestation of the same set of genes.

Duarte (5) indicated that relative progress under independent selection for X, Y, and Z and also for dry seed yield (W) was nearly the same when starting at either high or low levels in field beans. Progress in one component could be made only at the expense of another or others leading to comparable seed yields. Phenotypic correlations among components of yield in legumes frequently are negative (1, 5, 12), occasionally positive (3, 5), and sometimes lacking (4). This may arise from differences in plant material used, and in the cycle of selection, as suggested by Duarte (5). The correlations may be developmental rather than genetic *per se,* and have been postulated to be caused by genetically independent components which develop sequentially (1, 5). The components can vary in response "to either a limited constant input of metabolites, or an oscillatory input of these substances such that input is limiting at critical stages of developmental sequence" (1).

After finding a positive relationship among components in beans, Coyne (3) was not able to improve seed yield in the F_3 by selecting the top yielding 5% of the F_2, or by selecting separately for each of the 3 components. The estimates of heritability were very low for seed yield and for each of its 3 components. Dickson (4) reported that additive genetic variance predominated for pods per plant, seeds per pod, seeds per plant and pod length in snap beans.

The present study was initiated to investigate the genetic behavior of seed yield and yield components in peas, from populations derived from a diallel cross of 6 lines.

Materials and Methods

Six inbred lines were selected initially for wide differences in ovule number in a related study. However, with regard to seed yield and its components these lines constituted a random sample of unknown material. They were:

P.I. 236493 (Lamprecht #375), short compact habit, 3 flowers per node and high ovule number.

B 667-1104-0[3], short compact habit, 2 flowers per node, and high ovule number.

67MF 459, an S_4 selection from Early Perfection, short compact habit, 2 flowers per node and intermediate ovule number.

X1-2-1-7[4], short compact habit, 2 flowers per node and intermediate ovule number.

P.I. 269811[3], tall viney habit, 2 flowers per node, and low ovule number.

B 264-1060-26[1], tall viney habit, single flowers per node, and low ovule number.

All possible F_1's, (including reciprocals), F_2's, and first backcross populations were generated in the greenhouse and together with the 6 parental lines were sown in the field on May 1, 1969 at St. Paul in 3 replications (6 for F_2's) of a randomized block design. Trellised plants were grown at 3-inch spacing in rows spaced 6 feet apart.

Data were recorded at dry seed harvest on 17 equally competitive plants per plot for X, Y, Z and W, and for total seeds per plant. Percentages were transformed by *arc sine* transformation. Means were submitted to the Gardner-Eberhart (7) method of diallel analysis (Analysis I) by computer program[5], and also to Mather's (11)

[1]Received for publication April 23, 1970. Journal Series Paper 7166, Minnesota Agricultural Experiment Station. Supported in part by a scholarship from the Rockefeller Foundation and also representing part of a Ph.D. thesis submitted to the Graduate School of the University of Minnesota by the senior author.

[2]Professor of Vegetable Crops, Facultad de Ciencias Agrarias, Universidad Austral de Chile, Valdivia, Chile, and Professor, Department of Horticultural Science, University of Minnesota, respectively.

[3]Obtained from Dr. G. A. Marx, New York Agricultural Experiment Station, Geneva, New York, Vegetable Crops Department.

[4]Obtained from the Green Giant Company, Le Sueur, Minnesota.

[5]Computer program transformed for IBM Model 30 at the St. Paul Campus Computing Center, Univ. of Minnesota, from program received from J. J. Hammond, Statistical Laboratory, Univ. of Nebraska, Lincoln, Nebraska.

population means approach. Heritability estimates were calculated by Warner's method (13) from the components of variance; the level of dominance was determined according to Mather (11). Heterosis was calculated as $\frac{F_1 - MP}{F_1}$ 100 (Common Method), and inbreeding depression as $\frac{F_1 - F_2}{F_1}$ 100.

Results

Analysis of mean values for X, Y, Z, and W and for seeds per plant indicated significant differences among the 6 parental lines (Table 1). In addition, significant differences were found for all characters when the 36 populations (6 parents and the progenies of their 30 crosses) were compared. No reciprocal differences were noted.

Table 2 gives the relative importance, expressed in percent, of the mean squares from the Gardner-Eberhart analysis of variance (Analysis I). The analysis provides estimates, from the population means, of 3 parameters (Alpha, Delta and Heterosis) for all the characters under study. The analytical method also permits use of the backcrosses (6). Alpha and Delta provide information on the cumulative contribution of the homozygous loci (additivity) and heterozygous loci (dominance), respectively, to line means, if we assume no epistasis or linkage. Heterosis is partitioned into Average Heterosis (mean midparent deviation, or *difference* between mean of lines and mean of crosses) Variety Heterosis (General Combining Ability), and Specific Heterosis (Specific Combining Ability). The Residual, according to Gardner and Eberhart (7) is due to deviations from the model and provides information on epistasis and linkage.

Alpha (additivity) was significantly important for all the characters, while Delta (dominance) was of relatively little importance (Table 2). In addition, relatively high Residual values suggest caution in the interpretation of Alpha and Delta. Heterosis was highly significant for all characters, except pods per plant (X), where only the difference between the line means and the cross means (Average Heterosis) was significant.

Variety Heterosis (General Combining Ability) was significant for seeds per pod (Y) and for seed weight (Z), and Specific Heterosis (Specific Combining Ability) was significant for all characters except number of pods (X). Examination of line cross means revealed that Variety Heterosis for seeds per pod (Y) was significantly higher with B 264-1060-26 than with P.I. 236493, P.I. 269811, or X1-2-1-7; and for seed weight (Z), X1-2-1-7 was higher than P.I. 236493.

Table 2. Relative importance, expressed in percent, of 3 parameters for each of the 5 characters analyzed from the diallel cross by the Gardner-Eberhart method (Analysis I).

Parameters	(X) Pods per plant	(Y) Seeds per pod	(Z) Seed weight	(W) Seed yield per plant	Number of seeds per plant
	No.	No.	g	g	No.
Alpha	39.87**	78.38**	77.88**	34.86**	28.45
Delta	2.89	1.02	0.85	1.97	2.37
Heterosis[1]	26.12	14.37**	13.66**	42.65**	45.32**
Average heterosis	12.18**	1.95**	1.93**	16.86**	17.03**
Variety heterosis	3.53	3.55**	5.91**	4.73	7.26
Specific heterosis	10.41	8.87**	5.82**	21.06**	21.03**
Residual	31.12	6.23	7.61	20.52	23.86

*Significant at the 5% level.
**Significant at the 1% level.
[1]Refers to average midparent deviation.

Occasionally heterosis, as measured by departure of the F_1 beyond the higher parent, was seen for one or more characters in specific crosses (Table 3). Inbreeding depression in the F_2 was about half of the departure of the F_1 from the midparent, except for seed weight, where depression was very low.

Greatest heterosis (55.66%) was obtained for dry seed yield (W); heterosis decreased in the order seeds per plant (which was also high, as expected if W were high), pods per plant (X), seeds per pod (Y), and average seed weight (Z). This agrees, in general, with estimates of heterosis as summarized in Table 2, except that in the Gardner-Eberhart analysis, heterosis and average heterosis for the total number of pods per plant (X) were not significant and significant, respectively. Inbreeding depression was largest in those characters that had highest heterosis,

Table 3. Average percent heterosis, as deviation from midparent, average percent inbreeding depression of the F_2, and heritability (h^2) for 5 characters.

Character	h^2	Heterosis	Inbreeding depression
		%	%
Pods per plant (X)	.41 ± .09	31.92**	14.42**
Seeds per pod (Y)	.45 ± .15	10.46**	5.55**
Seed weight (Z)	.65 ± .13	6.97**	0.91
Seed yield per plant (W)	.45 ± .08	55.66**	18.34**
Seeds per plant	.38 ± .08	46.54**	18.12**

**Significant at the 1% level.

Table 1. Parental habit type and means for seeds per plant, dry seed yield (W) and the components of seed yield.

Parents	Plant habit	(X) Pods per plant	(Y) Seeds per pod	(Z) Seed weight	(W) Seed yield per plant	Seeds per plant
		No.	No.	g	g	No.
P.I. 236493	Short compact	18.48	1.84	.090	3.17	33.95
B 667-1104-0	Short compact	22.06	4.90	.120	13.04	108.64
X1-2-1-7	Short compact	19.35	3.34	.181	11.82	65.37
67 MF-459	Short compact	18.90	4.48	.133	11.31	85.39
P.I. 269811	Tall viney	31.41	2.66	.123	10.12	81.52
B 264-1060-26	Tall viney	18.69	4.72	.122	11.38	89.25
HSD 5%		8.45	1.07	.026	3.04	27.74
HSD 1%		11.07	1.40	.034	3.98	36.34

Note: HSD = Honestly Significant Difference (Tukey's method).

namely, seed yield (W), seeds per plant, and pods per plant (X).

Heritability estimates (h_2) are summarized in Table 3 as averages for the 15 crosses of the diallel. For these calculations the phenotypic variance of the F_1 was used as an estimate of environmental variance. Estimates of h^2 were in general high, especially for average seed weight, and lowest for seeds per plant.

Goodness of Fit tests were made individually for all populations derived from parents that differed at the 1% level for a particular character. This test fits parental, F_1, F_2 and backcross means to the completely additive or completely dominant model. Test results showed that most means fitted both models, but the X^2 values for the additive model were much smaller than for the dominance model for seeds per pod (Y) and average seed weight (Z); for the remaining characters the X^2 values indicated a higher deviation from the additive than the dominance model. This deviation from the additive model increased at the higher levels of heterosis shown for certain characters. Nevertheless, none of the characters fit only the additive or complete dominance model.

Although there usually was no correlation among yield components, the correlations between the components and yield were significant and positive. The value for "r" decreased in the order X *vs* W, Y *vs* W and Z *vs* W. Thus, the order of importance of yield components upon yield was: first X, then Y, and finally Z. Basic ovule number was not found to be consistently correlated with yield components either at the first flowering node or for the plant as a whole. Although ovule number and number of seeds per pod were correlated in 67MF 459 and in B-264-1060-26 this relationship did not consistently appear in the F_1, F_2, or BC_1 derived from these 2 parents.

Discussion

From 1) the Gardner-Eberhart analysis, 2) estimates of heterosis and inbreeding depression, and 3) the Goodness of Fit tests, all five characters—pods per plant (X), seeds per pod (Y), average seed weight (Z), seed yield (W), and seeds per plant—seem to be conditioned by an additive system. For all characters the additive effects were significant while dominance was relatively unimportant. Nevertheless, the presence of heterosis implies some dominance activity, or the presence of other non-additive effects, such as epistasis or linkage. The small values for Delta in Table 2 indicate that epistasis or linkage probably are more important than dominance activity. Such departure from additivity may have been relatively more important for seed yield, seeds per plant, and pods per plant. Speculation as to the nature of epistasis and linkage can not be made from the data.

Heterosis for seed yield (55.66%) as calculated from the midparent, agrees with the results of Gritton (9) who found the F_1's out-yielded the midparents by 58% at each of 2 locations in 1967, and by 45% to 50% in 1968.

Most estimates of heritability were high, ranging from .38 for seeds per plant to .65 for average seed weight. Assuming that the h^2 estimates are realistic, selection for these characters should be effective. The order of importance of the correlations agrees well with those of other workers (1, 2, 5) on various leguminous species and leads one to conclude, therefore, that pod number would be a good selection index for dry seed yield in the pea. Nevertheless we must be aware of the results obtained by Coyne (3) in which there was no improvement in the F_3 in *Phaseolus vulgaris* by selecting the top 5% of the F_2 population for each of the 3 yield components.

The general lack of correlation between ovule number and yield or its components, especially number of seeds per pod, seems surprising. Low ovule number parents had a relatively greater number of developed seeds per pod than high ovule parents. However, in any environment it is likely that final seed number will be less than its maximum potential. If ovule number is a relatively minor determinant of yield it follows that lines with low ovule number would achieve a relatively higher final seed yield than would lines with high ovule number.

Caution must be observed in extrapolating our results to peas at the processing stage of maturity. First, 2 of the cultivars used were very viney in plant habit while cultivars grown for processing are much more compact. In the viney types one would expect total dry seed yield and yield at processing maturity to be less closely related than in the more compact cultivars.

Second, plants grown in these studies necessarily were trellised and experienced less competition than would plants grown in the dense, drill-strip culture method used in commercial practice. Work by Gritton (8) has shown that within cultivars yield, pods per plant, and peas per pod are not consistently correlated across methods of culture and time of harvest; and, in addition, that cultivars differ in their degree of response to such changes in practice. The great rapidity with which peas pass through an optimum maturity phase for processing hinders objective study of yield in large populations of single plants or in small plots. Finally, this report summarizes results from only one year and location; the large degree to which yield may vary with environment suggests caution in the extrapolation of the results.

Literature Cited

1. Adams, M. W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean, *Phaseolus vulgaris*. *Crop Sci.* 7:505–510.
2. Anand, S. C. and J. H. Torrie. 1963. Heritability of yield and other traits and interrelationships among traits in the F_3 and F_4 generations of three soybean crosses. *Crop Sci.* 3:508–511.
3. Coyne, D. P. 1968. Correlation, heritability, and selection of yield components in field beans, *Phaseolus vulgaris* L. *Proc. Amer. Soc. Hort. Sci.* 93:388–396.
4. Dickson, M. H. 1967. Diallel analysis of seven economic characters in snap beans. *Crop Sci.* 7:121–124.
5. Duarte, R. A. 1966. Responses in yield and yield components from recurrent selection practiced in a bean hybrid at three locations in North and South America. *Diss. Abstr.* 27:1339–40.
6. Eberhart, S. A. and C. O. Gardner. 1966. A general model for genetic effects. *Biometrics* 22:864–881.
7. Gardner, C. O. and S. A. Eberhart. 1966. Analysis and interpretation of the variety cross diallel and related populations. *Biometrics* 22:439–452.
8. Gritton, E. T. 1969. Comparison of planting arrangements and time of evaluation for peas (*Pisum sativum* L.) *Crop Sci.* 9:276–279.
9. ————. 1969. Estimation of heterosis and genetic and environmental variances in peas. *The Pisum Newsletter.* 1:7.
10. Johnson, K. W. 1957. Inheritance studies in *Pisum sativum* L. *Diss. Abstr.* 17:1862.
11. Mather, K. 1949. Biometrical genetics. Dover Publications, Inc. USA.
12. Pinchinat, A. M. and M. W. Adams. 1966. Yield components in beans, as affected by intercrossing and neutron irradiation. *Turrialba* 16:245–252.
13. Warner, J. N. 1952. A method of estimating heritability. *Agron. J.* 44:427–430.