MODE OF INHERITANCE AND GENE ACTION FOR YIELD AND ITS COMPONENTS IN PHASEOLUS AUREUS

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A diallel study of yield and its components in F₁, F₂, F₃, and backcross generations was used to estimate components of genetic variation and type of gene action. Graphical and components of variance analyses revealed the importance of non-additive gene action for yield, pods per plant and clusters per plant. Additive gene action was important for 100-seed weight. Partial dominance for yield and seed size and partial- to over-dominance for pods per plant, clusters per plant and pods per cluster was evident from the graphical analysis. Dominant genes seem to govern inheritance of high yield and fewer pods per plant. The study indicated the appropriateness of studying one additional generation, either F₅ or backcross, to confirm the F₁ results. Implication of this study on breeding methodology is discussed.

Introduction

Phaseolus aureus Roxb., a self-pollinated diploid species, is an important grain legume in India. Significant heterosis for yield and other agronomic traits in this crop have been observed (Singh, 1970; Singh and Jain 1970), but its exploitation for breeding superior pure lines would depend upon the magnitude of additive genetic variance. Moreover, the choice of an appropriate breeding system will be guided by the relative contribution of genetic and environmental variances for yield and associated characters. Diallel cross analysis has been useful in obtaining information on these aspects.

Very little information has been published on the mode of inheritance and gene action on this crop. From an F₁ diallel set, Singh and Jain (1971a) reported partial dominance for yield and partial- to over-dominance for pods per plant. The importance of both additive and non-additive gene effects has been reported for yield and pods per plant and of additive gene effects for seed size (Singh and Jain, 1971b). The present investigation was, therefore, designed to gather detailed information on the genetic architecture for yield and its components from diallel study of F₁, F₂, F₃ and backcross generations. The other objective was to see whether complete information on gene action can be obtained from F₁ diallel alone or whether additional generations would be needed.

Materials and Methods

Seven promising true breeding lines namely, Hyb.4, Hyb.45, L 24-2 No.54, P 23-67, No.305 and Jalgaon 781 were chosen for this study. A diallel cross of 7 × 7 in F₁ and F₃, and 5 × 5 in F₅ and backcross generations were made which have been designated as set I, II, III and IV, respectively. Material comprising 79 entries including seven parents, 21 F₁'s, 21 F₃'s, 10 F₅'s and 10 lines of each backcross generation were grown in a randomized block design with four replications at Ludhiana during July-October, 1969. Each parent, F₁, B₁ and B₂ was sown in a single row, while each F₅ and F₆ family was grown in four and six rows, respectively. Each row was 3 m long, accommodating 10 plants, dibbled 30 cm
apart. The rows were spaced 60 cm apart. Non-experimental rows were pro-
vided all along the plot to avoid border effects. Observations were recorded on
all competitive plants in each entry for grain yield (g), pods and clusters per plant,
pods per cluster and 100-seed weight (g).

Mean values from each entry were used for statistical analysis. Graphical
and components of variance analyses were done according to the methods given
by Hayman (1954, 1958) and Jinks (1956), respectively. The estimates of the
frequency of positive (u) and negative (v) acting genes, degree of dominance and
order of dominance of the parents were obtained by the following formulae:

\[
\begin{align*}
\text{Gene frequency } u \cdot v &= \frac{H_2}{4} H_1 \\
\sqrt{1-4u \cdot v} &= (u-v) \\
u &= \frac{1+(u-v)}{2} \quad \text{Since } u + v = 1 \\
\text{and } v &= 1-u \\
\text{Degree of dominance } &= \left(\frac{H_2}{D}\right)^{1/2} \\
\text{Order of dominance of the parents } &= (W_r + V_r)
\end{align*}
\]

Results

Graphical Analysis

Vr-Wr graphs for different characters in different generations are given in
Figs. 1 to 5. The parents Hyb.4, Hyb.45, L 24-2, No. 54, P 23-67 No. 305 and
Jalgaon 781 are designated by numbers 1 through 7 respectively.

The slopes of regression lines in the Vr-Wr graphs for yield in different
generations differed significantly from unity suggesting that some of the basic
assumptions underlying the diallel analysis were not met (Fig. 1a,b,c,d). The
regression line intersected the Wr-axis above the point of origin in all sets thus
indicating partial dominance for yield. In sets I and II, array point 7 for Jalgaon
781, lying nearest to the point of origin, suggested a concentration of dominant
genes in this parent. The parents Hyb.45 and P 23-67 (arrays 2 and 5) showed
the largest concentrations of recessive genes in sets I, II, and III but in set IV, No.
54 and L 24-2 (arrays 4 and 3) exhibited concentrations of recessive genes. The
wide scatter of the array points around the regression lines confirmed that some
of the assumptions of diallel analysis were not fulfilled.

Failure to meet some of the basic assumptions of the diallel analysis for pods
per plant was indicated by the slopes of regression lines in sets I, II and III, but
set IV seems to indicate the absence of gene interaction (Fig. 2a, b, c, d). Partial-
to over-dominance was deduced from the position of regression lines. The graphs
showed that P 23-67 possessed more recessive genes than the other arrays in sets I,
II and III, while No. 54 had most of the recessive genes in set IV. The parents
L 24-2 and Hyb. 4 appeared to possess most of the dominant genes in sets I, II,
III and IV, respectively.

In the Vr-Wr graphs for 100-seed weight, the slopes of the regression lines
did not differ significantly from unity, suggesting the absence of non-allelic inter-
actions (Fig. 3a,b,c,d). The regression lines intersected the Wr-axis above the
origin, indicating partial dominance in all the sets. The array of parent Hyb. 4
appeared to possess the most of the recessive genes and also had high 100-seed
weight, while the array of L 24-2 had the most of dominant genes and low seed
weight. Narrow spread of array points around the regression lines c...
that the basic assumptions of diallel analysis were satisfied and also that genetic interactions were absent.

Deviation from unity of the slopes of the regression lines for clusters per plant suggests that some of the basic assumptions underlying diallel analysis were not met within sets II and IV but were met in set III (Fig. 4a,b,c). Partial- to over-
Fig. 3. a) Vr-Wr graph for 100-seed weight in F	extsubscript{1}; b) Vr-Wr graph for 100-seed weight in F	extsubscript{2}; c) Vr-Wr graph for 100-seed weight in F	extsubscript{3}; d) Vr-Wr graph for 100-seed weight in 1/2(B	extsubscript{1} + B	extsubscript{2}). Fig. 4. a) Vr-Wr graph for clusters per plant in F	extsubscript{1}; b) Vr-Wr graph for clusters per plant in F	extsubscript{2}; c) Vr-Wr graph for clusters per plant in 1/2(B	extsubscript{1} + B	extsubscript{2}). Fig. 5. a) Vr-Wr graph for pods per cluster in F	extsubscript{1}; b) Vr-Wr graph for pods per cluster in F	extsubscript{2}; c) Vr-Wr graph for pods per cluster in F	extsubscript{3}; d) Vr-Wr graph for pods per cluster in 1/2(B	extsubscript{1} + B	extsubscript{2}).
dominance was observed for this character. No. 54 was noted to be the recessive most, while No. 305, in set II and Hyb.4 in set III and IV showed the largest concentrations of dominant genes. Some of the assumptions of diallel analysis were not met in set I but were satisfied in the remaining sets for pods per cluster (Fig. 5a,b,c,d). Partial- to over-dominance was noted from the intersection of regression line and Wr axis above the origin. The L 24-2 showed maximum concentration of recessive genes in sets I, II and III, but in set IV No. 54 appears to possess most of the recessive genes. The arrays descended from Jalgaon 781 in sets I and II and from Hyb. 45 in sets III and IV had the most dominant genes.

Components of Variance

Components of variance and degree of dominance and gene frequency for different characters is given in Tables I and II respectively.

For yield, the non-additive component of variance, \( H_1 \) and \( H_2 \), was significantly high in all generations, while the additive component \( D \) was not significant in any generation. Values of \( F \) were significant only in \( F_1 \) and being negative suggested a preponderance of negative acting genes among parents while for other generations balanced contribution by positive and negative genes is suggested. Estimates of \( u \) and \( v \) indicated greater frequency of genes that tend to reduce grain yield. Overdominance for this character was indicated by \( (H_1D)^{1/2} \).

### Table I

Components of genetic variance in various generations for yield and its components

<table>
<thead>
<tr>
<th>Character</th>
<th>Component</th>
<th>( F_1 )</th>
<th>( F_2 )</th>
<th>( F_3 )</th>
<th>( 1/2(B_1+B_2) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yield</td>
<td>D</td>
<td>0.000</td>
<td>3.930</td>
<td>2.100</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>( H_1 )</td>
<td>92.948**</td>
<td>45.266**</td>
<td>175.418**</td>
<td>224.472**</td>
</tr>
<tr>
<td></td>
<td>( H_2 )</td>
<td>82.753*</td>
<td>33.766**</td>
<td>179.981**</td>
<td>196.498**</td>
</tr>
<tr>
<td></td>
<td>( F )</td>
<td>-19.159</td>
<td>-11.376</td>
<td>-13.738*</td>
<td>-28.530</td>
</tr>
<tr>
<td>Pods per plant</td>
<td>D</td>
<td>82.02</td>
<td>207.62</td>
<td>310.80**</td>
<td>283.35</td>
</tr>
<tr>
<td></td>
<td>( H_1 )</td>
<td>1814.00*</td>
<td>1427.68**</td>
<td>581.76**</td>
<td>3911.68**</td>
</tr>
<tr>
<td></td>
<td>( H_2 )</td>
<td>1579.72</td>
<td>9390.20**</td>
<td>645.12**</td>
<td>2810.24**</td>
</tr>
<tr>
<td></td>
<td>( F )</td>
<td>-529.04</td>
<td>-256.96</td>
<td>271.68**</td>
<td>-1069.84</td>
</tr>
<tr>
<td>Seed weight</td>
<td>D</td>
<td>0.447**</td>
<td>0.455*</td>
<td>0.604**</td>
<td>0.587**</td>
</tr>
<tr>
<td></td>
<td>( H_1 )</td>
<td>0.167*</td>
<td>2.016**</td>
<td>3.098**</td>
<td>0.598*</td>
</tr>
<tr>
<td></td>
<td>( H_2 )</td>
<td>0.146*</td>
<td>1.786**</td>
<td>2.694**</td>
<td>0.507*</td>
</tr>
<tr>
<td></td>
<td>( F )</td>
<td>0.062</td>
<td>0.075</td>
<td>0.421**</td>
<td>0.067</td>
</tr>
<tr>
<td>Clusters per plant</td>
<td>D</td>
<td>N.S.</td>
<td>14.01</td>
<td>30.73*</td>
<td>26.85</td>
</tr>
<tr>
<td></td>
<td>( H_1 )</td>
<td>N.S.</td>
<td>117.92**</td>
<td>1466.24**</td>
<td>482.86</td>
</tr>
<tr>
<td></td>
<td>( H_2 )</td>
<td>N.S.</td>
<td>105.44**</td>
<td>1523.20**</td>
<td>339.49**</td>
</tr>
<tr>
<td></td>
<td>( F )</td>
<td>N.S.</td>
<td>-26.88</td>
<td>-26.88</td>
<td>-26.47</td>
</tr>
<tr>
<td>Pods per cluster</td>
<td>D</td>
<td>0.105</td>
<td>0.160**</td>
<td>0.204*</td>
<td>0.204**</td>
</tr>
<tr>
<td></td>
<td>( H_1 )</td>
<td>0.456</td>
<td>0.054</td>
<td>9.747**</td>
<td>0.075</td>
</tr>
<tr>
<td></td>
<td>( H_2 )</td>
<td>0.472*</td>
<td>0.170*</td>
<td>8.966**</td>
<td>0.165*</td>
</tr>
<tr>
<td></td>
<td>( F )</td>
<td>-0.171</td>
<td>-0.202*</td>
<td>0.395**</td>
<td>-0.083</td>
</tr>
</tbody>
</table>

N.S. = Not significant.
*Significant at 5% level.
**Significant at 1% level.
### Table II
Gene frequency, degree of dominance and order of dominance of the parents

<table>
<thead>
<tr>
<th>Character</th>
<th>Gene frequency u(v)</th>
<th>Degree of dominance</th>
<th>Order of dominance dom—rec.</th>
<th>Order of performance high—low</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F₁</td>
<td>F₂</td>
<td>F₃</td>
<td>1/2(B₁+B₂)</td>
</tr>
<tr>
<td>Yield</td>
<td>0.34 (0.66)</td>
<td>0.25 (0.58)</td>
<td>0.42 (0.58)</td>
<td>0.33 (0.67)</td>
</tr>
<tr>
<td>Pods per plant</td>
<td>0.32 (0.68)</td>
<td>0.21 (0.54)</td>
<td>0.66 (0.54)</td>
<td>0.23 (0.77)</td>
</tr>
<tr>
<td>100-seed weight</td>
<td>0.68 (0.32)</td>
<td>0.57 (0.33)</td>
<td>0.68 (0.33)</td>
<td>0.69 (0.31)</td>
</tr>
<tr>
<td>Clusters per plant</td>
<td>–</td>
<td>0.34 (0.56)</td>
<td>0.40 (0.60)</td>
<td>0.23 (0.77)</td>
</tr>
<tr>
<td>Pods per cluster</td>
<td>0.41 (0.59)</td>
<td>–</td>
<td>0.64 (0.36)</td>
<td>–</td>
</tr>
</tbody>
</table>

u = frequency of positive acting genes.
ν = frequency of negative acting genes (in parentheses).
For pods and clusters per plant the non-additive (H1 and H2) component was significantly high but the additive component was relatively low in both the cases. F value was significant for pods per plant in F2 generation only. In other generations, the values of F for pods and clusters per plant were negative but non-significant, thus showing gene symmetry. Actual estimates of u and v indicated the greater frequency of negative acting genes.

For 100-seed weight both additive and non-additive (H1 and H2) components were significantly high but the magnitude of H1 was more than D in the F1 and F2 generations. The significant value of F in F1 indicated an excess of positive acting genes, while for other generations gene symmetry is suggested. The actual estimates of positive (u) and negative (v) acting genes also suggested the predominance of the genes that increase 100-seed weight.

For pods per cluster the additive component was relatively greater than the non-additive component in all the generations except F2. Partial- to over-dominance was observed for this character in various generations. The value of F was significant only in F2, indicating a high frequency of the recessive genes. The estimates of u and v gave a high frequency of the genes reducing the number of pods per cluster.

The order of dominance of the parents and their mean performance clearly suggested that recessive genes seem to govern large seed size and more clusters per plant, while concentrations of dominant genes are associated with more pods per cluster. Dominant genes appear to control high yield but recessive genes seem to govern high number of pods per plant.

Discussion

The gene action shown by the Vr-Wr graph suggested the presence of genic interaction for yield, pods per plant and clusters per plant. The importance of non-additive genetic variance for these characters has been confirmed by the significantly high estimates of non-additive components of variance. The combining ability study conducted by Singh (1970) also confirmed the importance of non-additive gene effects for grain yield and pods per plant.

Graphical analysis for seed weight and pods per cluster indicated the absence of genic interactions. The components of variance estimates indicated that for seed weight both additive and dominance components of variance were important, but for pods per cluster the additive component was the most significant. This confirmed the findings of Singh (1970) on the importance of both general and specific combining ability effects for seed size and of general combining ability only for pods per cluster.

Graphical analysis revealed partial dominance for yield and seed weight, but partial- to over-dominance was indicated for pods per plant, clusters per plant and pods per cluster. Partial dominance for yield and partial- to over-dominance for pods per plant was also noted by Singh and Jain (1971a).

The dominance order of the parents revealed by (Wr + Vr), and their per se performance indicated that dominant genes seem to govern the inheritance of high grain yield, but the recessive genes appear to control high number of pods per plant. In both cases the presence of genic interaction probably distorted to some extent the dominance order of the parents. The frequency of u and v was different from the expected frequency of u = v = 0.5. The frequency of negative and positive acting genes showed that negative acting genes for yield,
pods and clusters per plant were more frequent in the parents while positive acting genes were more frequent for seed size. Control by recessive genes of yield, pods per plant and seed size has been reported by Dhaliwal (1969) in *Phaseolus mungo* and by Sen and Murty (1960) in *Phaseolus aureus*. On the contrary, Singh and Jain (1971a) observed that dominant genes govern the inheritance of yield and pods per plant.

**Usefulness of Studying F1 and Subsequent Generations in Diallel Analysis**

One of the objectives of this study was to compare the results obtained from an F1 diallel analysis with those obtained from subsequent generations. In this study we noted that generally the results observed in F1 generations regarding the type of gene action and variance components were in agreement with those of F2 and backcross generations. For example, non-additive gene action with partial dominance was observed for yield in F1 as well as in F2 and backcross generations. There was, however, more similarity in magnitude of variance components between the F1 and backcross generations. The results obtained in F2 were not always the same as those observed in F1. These differences may be largely attributed to the small sample of F2 families. Variable degrees of dominance for various characters has, however, been observed in F1 and later generations, but the estimates of variance in F1 are more reliable because in segregating generations the genic interaction also contributes toward dominance, thus causing inflation of the estimates. Based on this study, it is suggested that it would be more appropriate to study only the additional generation of either F2 or backcross to confirm the findings of an F1 diallel set.

**Implication on Breeding Methodology**

This study revealed the importance of non-additive gene effects for economically important characters such as grain yield and pods per plant. This would mean that the heterosis observed in *Phaseolus aureus* is due to genic interaction and overdominance. Overdominance is non-fixable in advanced generations. Hence the development of hybrid varieties is the best way to exploit the gain observed in the F1 generation. But, in the absence of many prerequisites, it is not possible at present to develop hybrid varieties. Therefore, recurrent selection as suggested by Andrus (1963), although very cumbersome and time consuming, may be the most effective way to handle the breeding material. Despite the disadvantages, this procedure may give high-yielding, pure lines as good as F1 hybrids. It has often been observed that high-yielding offspring occur due to recombination, even though the predominant gene action may be dominance and epistasis. Therefore, to obtain high yielding segregants, it is suggested that both pedigree breeding and recurrent selection be followed simultaneously.

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**References**


