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# Detection of Genic Interactions by Analyzing the $F_2$ Generation of Diallel Crosses

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**Summary.** The ability of the Hayman and Jinks method of analysis of diallel crosses to detect genic interactions was studied in peanuts. Six traits, measured in the $F_2$ generation of a diallel cross of four cultivars, were analyzed. In $F_2$ analyses of the diallel, least squares estimates of variance components D, $H_1$, $H_2$, F, E, were used as an additional criteria for the adequacy of the diallel model. They were found to be in substantial agreement with the tests based on $W_r$ and $V_r$ values, and probably more reliable. The regression of $W_r$ on $V_r$ was shown to be unsuitable to detect 'duplicate gene' type of interactions; it was detected, however, by the ratio of the mean within-$F_2$-family variance and the variance among the parents. Using the different criteria, 'duplicate genes' type of interactions was detected for two traits, 'complementary genes' type was detected for one trait and three traits were found to fit the additive-dominance model without any genic interactions.

**Key words:** Peanuts – *Arachis hypogaea* L.

## Introduction

Genic interactions affecting quantitative traits are very important in breeding. Such effects, when present, are expressed in the means and variances of inbred lines and their hybrids. The available experimental and statistical methodology of detecting the various modes of genic interaction are less comprehensive than one should expect.

Although detection of genic interactions is not the main objective of the Hayman and Jinks method of diallel analysis (Hayman 1954, 1958; Jinks 1954, 1956), it can do it indirectly. This method is based on an additive-dominance model and assumes inbred, homozygous parents, two alleles at each locus, diploid segregation, no linkage or association between genes, no reciprocal differences and no genic interactions. Two statistical tests of the adequancy of the model are the first steps of the diallel analysis (Mather and Jinks 1971). Both tests are based on the covariances between parent means and the means of their hybrids ('$W_r$') and the variances between hybrids within parents ('$V_r$'). When the model was rejected by both tests while some of the assumptions were known to be valid, it was concluded that genic interactions must be involved (Allard 1956; Halloran 1975; Jana 1976; Khaleque and Eunus 1975; Lupton 1961; Whitehouse et al. 1958). On the other hand, statistical acceptance of the model by one or both tests was interpreted as absence of genic interactions. But this interpretation does not hold generally. Mather (1967) showed that one of the tests ('$W_r$ $V_r$ regression') can detect 'complementary genes' type of interactions but not 'duplicate genes' type. Mather's theoretical finding was demonstrated by Jana and Seyffert (1972). In their study, 'duplicate genes' interaction was known to exist (Jana and Seyffert 1971) but it was not detected by the $W_r$ $V_r$ regression.

In the course of a study on the quantitative traits of peanuts, using Hayman's and Jinks' diallel method, an attempt was made to improve the ability of this method to detect genic interactions. This was done by analyzing the $F_2$ generation of diallel crosses and using two additional tests which utilize the variance among $F_2$ individuals within crosses.

## Materials and Methods

### *Experimental Procedures*

The peanut (*Arachis hypogaea L.*) is cleistogamous, thus a self-fertilizer (Gregory et al. 1973). The species is allotetraploid (2n = 40) and seems to have regular disomic inheritance (Hammons 1973; Krapovickas 1973). Four erect peanut cultivars were chosen as parents for the diallel cross:

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(a) Shulamit': The main commercial cultivar in Israel; a Virginia-type (Gregory et al. 1973), medium-early (130-140 days from planting to harvest) with large plants and large two-seeded pods.
(b) 'Line 203': A Virginia type, medium-early cultivar, with compact plants and large, two-seeded pods.
(c) 'Congo': A Spanish type (Gregory et al. 1973), early (110-120 days) cultivar with large plants and 2-, 3- and 4-seeded pods, all of medium size.
(d) 'Chico': A Valencia type (Gregory et al. 1973) and extremely early (80-90 days) cultivar with small plants and small 2-seeded pods (Bailey and Hammons 1975).

The large divergence of the considered traits in these four cultivars compensated for the weakness of analyzing a diallel cross resulting from only four parents. Furthermore, it enabled us to collect data from a reasonable number of plants per family.

Plants of the four parent cultivars were crossed in the winter of 1973, in a 4 × 4 complete diallel. The resulting $F_1$ plants and the selfed progenies of the parents were grown in the field in the 1973 season. Due to the difficulties in crossing peanuts and some pod-rot damage, the numbers of $F_1$ plants were not sufficient for diallel analysis. Therefore, the $F_1$ and parent plants were harvested and their yield supplied the $F_2$ and parent seeds which were grown in the 1974 season, under optimal conditions, including irrigation. The experimental field was divided into three blocks. In each of them, 30 $F_2$ seeds of each cross and 18 seeds of each parent-cultivar were planted at random. The plants were widely spaced (120 × 140 cm.) to avoid effects of neighbors or missing plants; 669 plants were harvested 120 days after planting.

The six traits included in this report are:
(1) Weight of pods per plant (PWP). All pods were weighed after two weeks of air drying.
(2) Total number of pods per plant (PNP).
(3) Mean pod weight (MPW). The mature pods of each plant were counted and weighed to calculate mean weight.
(4) Oven-dry weight of tops per plant (TWP).
(5) Number of flowers per plant (NFP). Flowers were counted daily during the first 45 days after planting.
(6) R/R + V ratio on the main ('n') branch (RVN). R stands for reproductive secondary branches and V stands for vegetative ones. The R/R + V ratio (Perry 1968; Wynne 1975) described the branching pattern of each plant.

These six traits are not completely independent of each other. Among the fifteen possible combinations, however, only in two cases were the phenotypic correlations found to be higher than 0.5.

### *Statistical Analysis*

The diallel was analyzed according to Hayman's and Jinks' method (Hayman 1954, 1958; Jinks 1954, 1956), using the procedure and notations as summarized by Mather and Jinks (1971).

For each array (i, i = 1,4) within each block (j, j = 1,3), the variance ($V_{rij}$) between its four families (one parent and its hybrids with the three other parents) and the parent-hybrid covariance ($W_{rij}$) were calculated from the family means. Each parent-family contained about 15 plants and each hybrid family contained about 27 $F_2$ plants. Since no significant reciprocal differences were found, the analysis was performed on pooled reciprocals within hybrid combinations (Hayman 1954).

The existence of dominance was tested by two-way analysis of variance (arrays × blocks) of the ($W_{rij} + V_{rij}$) values (Mather and Jinks 1971). Similarly, an analysis of variance of the ($W_{rij} - V_{rij}$) values and the joint regression analysis of $W_{rij}$ on $V_{rij}$ over blocks were performed. They are the standard tests of the model's adequacy, as suggested by Mather and Jinks (1971). Since all three analyses showed no significant difference between blocks for all traits, the data were pooled over blocks for the rest of the analysis and the $W_{ri}\,V_{ri}$ graphs. These graphs served as an additional tool to study the existence and nature of genic-interactions (Hayman 1954; Jinks 1954; Mather 1967).

Six variances were calculated from the pooled diallel data:

$\bar{W}_r$ = the mean $W_{ri}$ value over arrays.
$\bar{V}_r$ = the mean $V_{ri}$ value over arrays.
$V_{\bar{r}}$ = the variance of array means.
$\bar{V}_{F_2}$ = the mean within-family variance, calculated from all $F_2$ and parent families.
$V_{\bar{p}}$ = the component of variance between parent families.
$\bar{V}_p$ = the mean within-parent-family variance. Since parents are known to be pure inbred, homozygous lines, $\bar{V}_p$ is the estimate of environmental variance designated as E.

The six calculated variances were used to estimate the environmental variance (E) and four hypothetical genetic variances: D, $H_1$, $H_2$ and F. They were obtained by the least-squares' solution of the following six equations:

$$\begin{array}{llllll}
\bar{W}_r & = 1/2\,D & & & -1/8\,F + 1/116\,E \\
\bar{V}_r & = 1/4\,D + 1/16\,H_1 & & & -1/8\,F + 1/290\,E \\
V_{\bar{r}} & = 1/4\,D + 1/16\,H_1 & -1/16\,H_2 & & -1/8\,F + 1/290\,E \\
\bar{V}_{F_2} & = 1/4\,D + 1/8\,H_1 & & & +\quad E \\
V_{\bar{p}} & = \quad D & & & \\
\bar{V}_p & = & & & \quad E
\end{array}$$

The coefficients of D, $H_1$, $H_2$ and F in the above expectations are those of the $F_2$ generation, based on the diallel's additive-dominance model (Hayman 1958; Jinks 1956). The coefficients of E resulted from the number of plants in families and arrays. The genetic information which derived from D, $H_1$, $H_2$ and F are not presented in this report, but attention was given to their significance as an additional indication of the adequacy of the diallel's model.

## Results and Discussion

The results of the tests of adequacy of the diallel's genetic model and existence of dominance, as well as the significance of the estimates of D, $H_1$, $H_2$, F and E variance components, are presented in Table 1 and Figure 1.

The joint regression of $W_{ri}$ on $V_{ri}$ (Table 1,c) was significantly different from zero for all six traits. indicating non-additive genetic variance. This conclusion is supported by the significant difference between the arrays' ($W_{ri} + V_{ri}$) values, found for five traits (Table 1,a). The ($W_{ri} - V_{ri}$) values were found to be significantly inconsistent only for MPW (Table 1,b) while the $W_{ri}\,V_{ri}$ regression slope was significantly different from unity only for NFP (Table 1,d). It has been suggested that only when both tests indicate significant disagreement with the model can it be concluded that the data do not conform to one or more of the model's basic assumptions (Jinks – personal communication; Gibori et al. 1978). Therefore, one can conclude that all the six traits agree with the additive-dominance model. Nevertheless, the non-significant estimates of $H_1$, $H_2$, F and E obtained for the traits PWP, MPW and NFP (Table 1,e), indicate that such a conclusion may be incorrect. The non-significance cannot be taken as an evidence for absence of environmental variance (E) or dominance variance ($H_1$ and $H_2$), which was found to exist in these traits (Table 1,a and c). Although sampling error could be the reason for non-significant estimates, it seems to be more likely the result of disagreement between those traits' variances and the expectations which were used. These expectations were based on the additive-dominance model, but for two of the three traits (MPW and NFP) disagreements with this model have been indi-

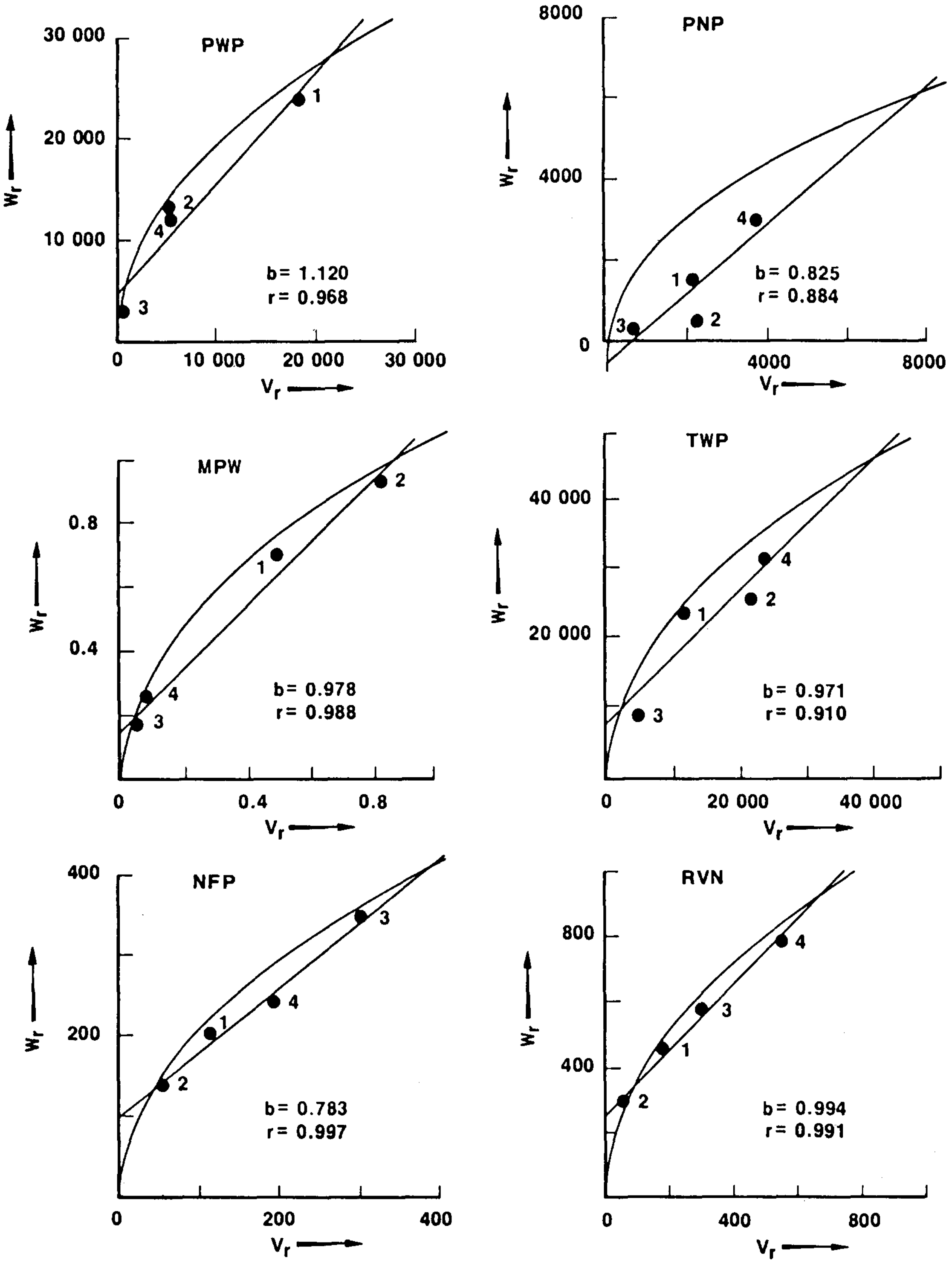

Fig. 1. $W_rV_r$ graphs for the six traits

Table 1. Tests of the adequacy of the diallel's model (b, c and d) and dominance (a) and the estimates of variance components (e), from $F_2$ generation of 4 × 4 diallel cross

| Item | df | PWP | PNP | MPW | TWP | NFP | RVN |
|---|---|---|---|---|---|---|---|
| (a) $(W_{r_i} + V_{r_i})$ values (df ratio and F values) | | | | | | | |
| Arrays | 3/6 | 16.1$^b$ | 6.39$^a$ | 145$^c$ | 2.38 | 6.38$^a$ | 5.74$^a$ |
| Blocks | 2/6 | 0.1 | 0.39 | 0.7 | 0.10 | 0.65 | 0.71 |
| (b) $(W_{r_i} - V_{r_i})$ values (df ratio and F values) | | | | | | | |
| Arrays | 3/6 | 4.1 | 0.44 | 19.2$^b$ | 2.99 | 2.23 | 1.86 |
| Blocks | 2/6 | 1.9 | 0.27 | 4.16 | 2.71 | 3.88 | 1.03 |
| (c) Joint regression of $W_{r_i}$ on $V_{r_i}$ (df ratio and F values) | | | | | | | |
| Regression | 1/6 | 73.5$^c$ | 8.88$^a$ | 210$^c$ | 13.9$^b$ | 100$^c$ | 179$^c$ |
| Blocks | 2/6 | 0.07 | 2.92 | 0.02 | 0.01 | 0.29 | 0.06 |
| (d) Joint regression coefficients (b) and their standard errors ($^s$b) | | | | | | | |
| b | – | 1.12 | 0.82 | 0.98 | 0.94 | 0.78$^d$ | 0.99 |
| $^s$b | 6 | 0.13 | 0.20 | 0.07 | 0.25 | 0.07 | 0.07 |
| (e) Significance of variance components | | | | | | | |
| $D_1$ | | c | c | c | c | c | c |
| $H_1$ | | N.S. | c | N.S. | c | N.S. | c |
| $H_2$ | | N.S. | c | N.S. | c | N.S. | c |
| F | | N.S. | c | N.S. | c | N.S. | a |
| E | | N.S. | c | N.S. | c | N.S. | c |

$^{a, b, c}$ Significant at the 0.05, 0.01 and 0.001 levels, respectively
$^d$ Significantly (P = 0.017) different from unity

cated already (Table 1, b and d). Therefore, the significance of the estimates of $H_1$, $H_2$, F and E was taken as an additional indication for discrepancy of the diallel's genetic model; this was suggested by Mather and Jinks (1971), but apparently has not been used to date. When the $F_2$ generation of a diallel is analyzed, this indication is even more reliable since least squares estimates of D, $H_1$, $H_2$, F and E are based, in addition to the variances and covariances between family means, on the within $F_2$ variance, which is ignored in the calculation of $W_{r_i}$ and $V_{r_i}$. Hence, the variance components reflect additional genetic information about the adequacy of the diallel's genetic model's assumptions.

Taking into consideration variance components, as well as $(W_{r_i} - V_{r_i})$ values and the $W_{r_i}$ $V_{r_i}$ regression, it appears that the diallel's genetic model does not fit three of the six traits (Table 1): NFP, with a $W_{r_i}$ $V_{r_i}$ regression slope significantly lower than one and non-significant $H_1$ and $H_2$ estimates, despite other evidence for dominance; MPW, with the same disagreement about dominance and highly significant heterogeneous $(W_{r_i} - V_{r_i})$ values; and PWP, with the disagreement about dominance and almost significant heterogenous $(W_{r_i} - V_{r_i})$ values (P = 0.067).

Some of the six assumptions of the diallel's model are known to hold in this study: the parent cultivars are true-breeding homozygotes; they have a regular disomic inheritance and no association between genes have been found as yet (Gregory et al. 1973; Hammons 1973; Krapovickas 1973). No significant differences between the reciprocal crosses were found for any trait or cross. Although multiple alleles may occur, it seems reasonable to follow previous studies (Allard 1956; Halloran 1975; Jana 1976; Khaleque and Eunus 1975; Lupton 1961; Whitehouse et al. 1958) and conclude that genic interactions are involved in the genetic control of the traits PWP, MPW and NFP.

Two additional approaches were used to confirm the presence or absence of genic interactions and to try to define their nature. Under the additive-dominance model, the expectations of the variance component between parents ($V_{\bar{p}}$) and the mean within-family variance in the $F_2$ generation ($\bar{V}_{F_2}$) are: $V_{\bar{p}} = D$ and $\bar{V}_{F_2} = 1/4\,D + 1/8\,H_1 + E$ (Hayman 1958; Jinks 1956). When dominance and environmental variances exist, the ratio of $4\bar{V}_{F_2}/V_{\bar{p}}$, designated by R, is expected to be greater than one: $R = 4\bar{V}_{F_2}/V_{\bar{p}} = (D + 1/2\,H_1 + 4E)/D\ 1$.

The R values of four traits were indeed bigger than one (Table 2), but not for PWP (R = 1.04) and MPW (R = 0.42). Since dominance was shown to exist for PWP and MPW, as well as environmental variance, such R values indicate that $F_2$ variances were below their expectations.

Table 2. The ratio (R) between four times the mean within $F_2$ families variance ($\bar{V}_{F_2}$) and the variance between parents ($V_{\bar{P}}$)

| Trait | $\bar{V}_{F_2}$ | $V_{\bar{P}}$ | R[a] |
|---|---|---|---|
| PWP | 10050 | 38598 | 1.04 |
| PNP | 8421 | 4745 | 7.10 |
| MPW | 0.122 | 1.173 | 0.42 |
| TWP | 31573 | 53168 | 2.37 |
| NFP | 317 | 439 | 2.89 |
| RVN | 705 | 1284 | 2.20 |

[a] $4\,\bar{V}_{F_2}/V_{\bar{P}}$ with the expectations: $E(4\,\bar{V}_{F_2}) = D + 1/2\,H_1 + 4E$, $E(V_{\bar{P}}) = D$

This is a typical effect of 'duplicate genes' interactions, which reduce $F_2$ segregation and variation. In our study, R values of PWP and MPW are in agreement with the ($W_{r_i} - V_{r_i}$) heterogeneity test (Table 1,b) which showed slight departures from the model for PWP and a substantial one for MPW. The 'duplicate genes' nature of interaction for PWP and MPW could also explain why their $W_{r_i}\,V_{r_i}$ regression slope (Table 1,d; Fig. 1) did not differ significantly from one. It was shown theoretically (Mather 1967) that this slope is hardly affected by 'duplicate genes' interaction, and experimentally, as far as we know, there is no report on a $W_r\,V_r$ slope significantly greater than one. The $W_r\,V_r$ graph for PWP (Fig. 1) shows the two middle points of arrays 2 and 4 to be above the $W_r\,V_r$ line. Although the four-point graph cannot be taken as proof, it is identical to the theoretical one plotted by Mather (1967) for interaction between two duplicate genes. The $W_r\,V_r$ graph for MPW does not show such similarity with the expected one, but we did get an additional indication for 'duplicate genes' inheritance of this trait. Among 850 second generation plants of double crosses between the four parents of the diallel cross, only two reached the mean pod weight (MPW) of the parents with large pods ('Shulamit' and 'line 203'). Such restricted segregation can be explained only by 'duplicate genes'-interaction. Considering the allotetraploidy of peanuts and the fact that several qualitative traits were found to be controlled by duplicate genes (Hammons 1971, 1973; Wynne 1975), our finding of such interactions is not surprising.

The $W_r\,V_r$ regression line (Fig. 1) of the trait NFP has a slope significantly smaller than unity, indicating, according to Jinks, 'complementary genes' interaction. The ratio $4\bar{V}_{F_2}/V_{\bar{P}}$ (Table 2) for this trait (R = 2.80) indicates that it is possible. The extremely high ratio for PNP (R = 7.10) may also indicate 'complementary genes' but such a conclusion cannot be supported by the other results shown in Table 1. The traits TWP and RVN seem to fit the diallel's additive-dominance model.

An additional approach to detect genic interactions is to measure $F_1$ and $F_2$ deviations from mid-parent values

Table 3. The means of $F_1$ and $F_2$ (F) and mid-parents (P), and the differences (D) between the deviation of $F_1$ mean from mid-parents and twice the deviation of $F_2$ mean from mid-parents, for each cross combination and the entire diallel for two traits

| | | MPW (gr.) | | | PWP (gr.) | | |
|---|---|---|---|---|---|---|---|
| Cross combination | | 1973($F_1$) | 1974($F_2$) | D[a] | 1973($F_1$) | 1974($F_2$) | D |
| Shulamit X 203 | F | 2.62 | 2.72 | −0.08 | 382 | 371 | 183[c] |
| | P | 2.74 | 2.74 | | 279 | 411 | |
| Shulamit X Congo | F | 1.55 | 1.51 | 0.42[c] | 313 | 253 | 364[c] |
| | P | 2.05 | 1.97 | | 215 | 386 | |
| Shulamit X Chico | F | 1.21 | 1.29 | 0.29[b] | 343 | 259 | 272[c] |
| | P | 1.55 | 1.56 | | 177 | 312 | |
| 203 X Congo | F | 1.68 | 1.47 | 1.05[c] | 260 | 214 | 141[c] |
| | P | 2.25 | 2.28 | | 211 | 260 | |
| 203 X Chico | F | 1.32 | 1.19 | 0.83[c] | 170 | 212 | −54[c] |
| | P | 1.85 | 1.87 | | 170 | 185 | |
| Congo X Chico | F | 1.07 | 1.14 | −0.11 | 179 | 220 | −116[c] |
| | P | 1.10 | 1.10 | | 175 | 160 | |
| All the diallel | F | 1.57 | 1.56 | 0.36[c] | 274 | 255 | 142[c] |
| | P | 1.95 | 1.93 | | 194 | 286 | |

[a] $(\bar{F}_1 - \bar{P}_{73}) - 2(\bar{F}_2 - \bar{P}_{74})$

[b], [c] D differs significantly from zero, at the 0.01 and 0.001 levels, respectively

(Hayman and Mather 1955). Under the additive-dominance model, $F_2$ mean performance is mid-way between $F_1$ mean and mid-parent value for any single cross-combination and for the entire diallel. Unfortunately, only two traits (MPW and PWP) were measured in the $F_1$ generation of our study, and for them mid-parent values and cross means are presented in Table 3. Since the two generations were grown in two different years, the yield (PWP) of some of the parents and hybrids changed, but not the mean pod weight (MPW). To eliminate year effects we compared the deviation of the $F_1$ means and the $F_2$ means from the mid-parents within years. The difference between $(\bar{F}_1\text{-}\bar{P}_{73})$ and $2(\bar{F}_2\text{-}\bar{P}_{74})$, which is expected to be zero in the additive-dominance model, was tested by t-test using the variances of the four populations involved, and the results are presented in Table 3. The significant differences from the expectation for almost all crosses in both traits, MPW and PWP, are in agreement with previous indications for genic interactions in these traits.

Table 3 supplies additional information about the inheritance of these two traits. The crosses between parents with similar mean pod weight (MPW), i.e. 'Shulamit' × 'line 203' and 'Congo' × 'Chico', did not deviate from mid-parents in either $F_1$ or $F_2$ generations. In four other crosses, the negative deviation of the cross means from mid-parents are almost the same in $F_1$ and $F_2$ generations. Thus, these deviations were not only a reflection of heterozygosity (which decreased by half from $F_1$ to $F_2$) but were probably caused by genic interactions. In the second trait, PWP, the situation is more complicated. Four hybrids had means greater than the respective mid-parent in $F_1$, but smaller in $F_2$. It is clear that such deviations cannot be a result of dominance alone. Similar results for pods weight per plant (PWP) in peanuts had been obtained by Wynne et al. (1970, 1975). They concluded that genic interactions are involved in the control of this trait.

## Conclusions

To detect genic interactions, it is advisable to analyse the $F_2$ generation of a diallel cross rather than the $F_1$ generation only. In the $F_1$ generation, genic interactions can be reflected only by the crosses means, while in the $F_2$ they can be detected also from the variance among individuals within crosses. In the analysis of the $F_2$ generation of a diallel cross, the least squares estimate of D, $H_1$, $H_2$, F and E seem to be a reliable indication of the fitness of the diallel's genetic model. They reflect the $F_2$ segregation and variation while $W_r$ and $V_r$ values do not.

The present study demonstrates once more that the $W_r$ $V_r$ regression slope can detect 'complementary genes' type of genic interactions but not that of 'duplicate genes.' On the other hand, we suggest that the ratio between four times the mean within-family variance in the diallel's $F_2$ generation and the variance between the parents $(4\bar{V}_{F_2}/V_{\bar{P}})$ is an indication of 'duplicate genes' type of genic-interaction, when equal or less than one.

Using all the criteria mentioned above, we concluded that out of six traits under study, 'duplicate genes' type of interactions were involved in the inheritance of two traits, PWP and MPW, and 'complementary genes' were involved with the inheritance of the trait NFP. The traits PNP, TWP and RNV seem to be controlled by additive-dominant genes.

Hayman's and Jinks' method is efficient enough in detecting genic interaction and supplying other genetic information when only the $F_2$ generation is recorded and analyzed. However, having the $F_1$ generation's data, one may have some additional indications about genic interactions and their nature by comparing the deviations of the means of $F_1$ and $F_2$ hybrids from their mid-parents.

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## Literature

Allard, R.W.: Estimation of prepotency from lima bean diallel cross data. Agron. J. **48**, 537-543 (1956)

Bailey, W.K.; Hammons, R.O.: Registration of Chico peanut germplasm. Crop Sci. **15**, 105 (1975)

Gibori, A.; Hillel, J.; Cahaner, A.; Ashri, A.: A 9 × 9 diallel analysis in peanuts (*A. hypogaea* L.): Flowering time, tops' weight, pod yield per plant and pod weight. Theor. Appl. Genet. **53**, 169-179 (1978)

Gregory, W.C.; Gregory, M.P.; Krapovickas, A.; Smith, B.W.; Yarborough, J.A.: Structures and genetic resources of peanuts. In: Peanuts – Culture and Uses. (ed. Wilson, C.T.). Stillwater, OK: Am. Peanut Res. Educ. Assoc. 1973

Halloran, G.M.: Genetic analysis of yield in wheat. Z. Pflanzenzücht. **74**, 298-321 (1975)

Hammons, R.O.: Inheritance of inflorescences in main stem leaf axils in *Arachis hypogaea* L. Crop. Sci. **11**, 570-571 (1971)

Hammons, R.O.: Genetics of *Arachis hypogaea*. In: Peanuts – Culture and Uses. (ed. Wilson, C.T.). Stillwater, OK: Am. Peanut Res. Educ. Assoc. 1973.

Hayman, B.I.: The theory and analysis of diallel crosses. Genetics **39**, 336-355 (1954)

Hayman, B.I.: The theory and analysis of diallel crosses: II. Genetics **43**, 63-85 (1958)

Hayman, B.I.; Mather, K.: The description of gene interaction in continuous variation. Biometrics **10**, 69-82 (1955)

Jana, S.: Graphical analysis of tiller and ear production in a diallel cross of barley. Can. J. Genet. Cytol. **18**, 445-453 (1976)

Jana, S.; Seyffert, W.: Simulation of quantitative characters by genes with biochemical definable action. III. The components of genetic effects in the inheritance of anthocyanins in *Matthida incana* R. Br. Theor. Appl. Genet. **41**, 324-337 (1971)

Jana, S.; Seyffert, W.: Simulation of quantitative characters by genes with biochemically definable action. IV. The analysis of heritable variation by the diallel technique. Theor. Appl. Genet. **42**, 16-24 (1972)

Jinks, J.L.: The analysis of continuous variation in a diallel cross of *Nicotiana rustica* varieties. Genetics **39**, 767-788 (1954)

Jinks, J.L.: The $F_2$ and backcross generations from a set of diallel crosses. Heredity **10**, 1-30 (1956)

Khaleque, M.A.; Eunus, A.M.: Inheritance of some quantitative characters in a diallel experiment of six rice strains. SABRAO J. 7, 217-224 (1975)

Krapovickas, A.: Evolution of the genus *Arachis*. In: Agricultural Genetics, Selected Topics. (ed. Moav, R.). New York: Wiley 1973

Lupton, F.G.H.: Studies in the breeding of the self-polinating cereals: 3. Further studies in cross prediction. Euphytica **10**, 209-224 (1961)

Mather, K.: Complementary and duplicate gene interaction in biometrical genetics. Heredity **22**, 97-103 (1967)

Mather, K.; Jinks, J.L.: Biometrical Genetics (2. ed.) Ithaca, New York: Cornell University Press 1971

Perry, A.: A radiation breeding experiment with peanuts. IV. Effect of the vegetative and reproductive phases of the branching system (NC4-18.5 kR). Radiation Bot. **8**, 109-119 (1968)

Whitehouse, R.N.H.; Thompson, J.B.; Do Valle Ribeiro, M.A.M.: Studies on the breeding of self-pollinating cereals. 2. The use of a diallel cross analysis in yield prediction. Euphytica **7**, 147-169 (1958)

Wynne, J.C.: Inheritance of branching pattern in *Arachis hypogaea* L. Peanut Sci. **2**, 1-5 (1975)

Wynne, J.C.; Emery, D.A.; Rice, P.W.: Combining ability estimates in *Arachis hypogaea* L. II. Field performance of $F_1$ hybrids. Crop Sci. **10**, 713-715 (1970)

Wynne, J.C.; Rawlings, J.O.; Emery, D.A.: Combining ability estimates in *Arachis hypogaea* L. III. $F_2$ generation of intra- and intersubspecific crosses. Peanut Sci. **2**, 50-54 (1975)

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