Theor. Appl. Genet. 53, 169-179 (1978)

# A 9 x 9 Diallel Analysis in Peanuts (*A. hypogaea* L.): Flowering Time, Tops' Weight, Pod Yield per Plant and Pod Weight

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**Summary.** Four quantitative traits were studied by analysing $F_2$ data derived from a 9 x 9 diallel cross utilizing widely divergent, inbred, erect cultivars of peanuts, *A. hypogaea.* Bidirectional dominance was found in the traits total pod yield per plant and number of days from planting to first flower; in pod size, the alleles giving small pods were consistently dominant and for high tops' weight, dominance and overdominance were found. The high heritability of pod yield/plant (0.79) indicates that breeding for higher yield/plant can succeed if large $F_2$ populations are grown and rigorous visual selection combined with progeny testing are employed. The genetic correlations of pod yield/plant with other traits were low. Breeding for plants with large (jumbo) pods can be aided by the fact that they are homozygous recessive, or nearly so. Simultaneous breeding for high yields and large pods is possible: there was a positive (but low) genetic correlation between the two (0.16). A modification by which less biased estimates of the number of effective factors can be obtained and a possible relationship between bidirectional dominance and genic interaction were proposed.

**Key words:** Diallel analysis – *A. hypogaea* L. – Quantitative traits

## Introduction

The peanut, *Arachis hypogaea* L., is an important oil and food crop. It is an allotetraploid (2n = 40), indeterminate and cleistogamous (Gregory et al. 1973). The cultivated species is divided into four botanical types according to the pattern and sequence of vegetative vs. reproductive branches, but only three are widely important in agriculture, viz. Virginia, Spanish and Valencia (Gregory et al. 1973).

The breeding of improved, high yielding peanut cultivars has been hampered by the lack of information on the genetics of yield and yield components (Hammons 1973; Norden 1973). Pod size was found to be controlled by polygenes (Badami 1923; Hassan and Srivastava 1966; Ilief 1942) and large pods were dominant (Badami 1923; Hassan and Srivastava 1966). Wynne, Emery and Rice (1970) concluded from studies of the $F_1$ plants in a series of diallel crosses that usually the alleles which increased pod size were dominant, but exceptions, including overdominance, were noted. In a later study with $F_2$ plants in a 6 x 6 diallel, Wynne et al. (1975) found that small pods were dominant. Overdominance in tops' weight was noted by Shakudo and Kawabata (1963). Several investigators (Hammons 1973; Hassan and Srivastava 1966; Higgins 1941; Wynne et al. 1970; Wynne, Emery and Rawlings 1975) reported that $F_1$ hybrids between cultivars belonging to certain types showed hybrid vigour which was manitested by bigger plants and higher yields.

The genetic control of the length of the period from planting to first flower was studied by Wynne et al. (1970): the $F_1$ hybrids were earlier than the early parent, or intermediate, or later than the late parent, depending on the botanical types of the parents in each combination. Shakudo and Kawabata (1963) found that the $F_1$ hybrids flowered after a period which equaled the means of their parents.

Correlation studies in peanuts were reviewed by Bernard (1960), Hammons (1973) and Coffelt and Hammons (1974). As the latter point out, some of these studies used limited and fairly uniform populations, often without the segregating generations. Correlations between the characters studied in this investigation have not been reported before.

Heritability estimates for various traits in peanuts have been derived using different methods; they were reviewed by Bernard (1960), Hammons (1973) and Coffelt and Hammons (1974). Heritability values for the characters included in the present study have not been published before.

The diallel method of analysis was developed in order to give information on the genetic structure of the populations under study and the genetic mechanisms controlling various traits (Hayman 1954; Hayman 1958; Jinks 1954; Jinks 1956; Jinks and Hayman 1953; Mather and Jinks 1971; Yates 1947). Since then, many diallel studies have been published, some of them have actually attempted to use the detailed genetic information of the diallel method of Hayman (1954) and Jinks (1954) in actual breeding programs, e.g. Hayward and Breese (1966), Innes et al. (1974), Johnson (1963), Johnson and Aksel (1959), Lupton (1961), Riggs and Hayter (1972) and Wilson and Cooper (1969). The present study was undertaken in order to develop and enhance the genetic knowledge based on the Hayman (1954) and Jinks (1954) method and to evaluate its application in peanut breeding programs.

## Materials and methods

### *Parent Cultivars*

The cultivars used as parents are cleistogamous, were grown in progeny rows for several generations (three to ten) and were shown to be homozygous inbred lines. The nine bunch accessions used in the diallel crosses, selected so as to sample the wide range of variability in the crop, represent the three main botanical types and contribute maximum variance. The parents were:

A. Virginia type:

1. 'Shulamit' – Bred by E. Goldin (1969) from the cross 'Florispan' × 'Florigiant'. It is early (135 days) and has large, two-seeded pods.
2. 'Line 203' (= 203) – Bred by A. Ashri from the cross 'Dixie Anak' × 'Virginia Beit Dagan No. 4'. Its plants are compact and early (135 days). The pods are large, two-seeded.
3. 'Dixie Anak' (= DA) – Selected by E. Goldin about 20 years ago from an accession labeled 'Dixie' introduced from the U.S.A. The plants are open bunch, early (120 days) and productive. The pods are two-seeded and fairly small.
4. 'Virginia Sihit Meshubahat' (= VSM) – Selected by E. Goldin about 30 years ago from introduced U.S. material labelled 'Virginia Bunch'. The plants are later (145 days) and have large, two-seeded pods.

B. Spanish type:

5. 'Sepharadi No. 9' (= S9) – Selected by E. Goldin from introduced material. It is early (90-100 days) with very small, 2-seeded pods.
6. 'Congo' – Selected by E. Goldin from introduced material. It is early (90-100 days), with many 3- and 4-seeded pods; the seeds are small. Except for its branching pattern it fits the Valencia type description.

C. Valencia type:

7. 'Chico' – A U.S. selection from USDA P.I. No. 268,661, introduced to the U.S. from Rhodesia where it was brought from Krasnodar, USSR. It is an extremely early line (80 days) with small plants and very small 2-seeded pods (Bailey and Hammons 1975).
8. '1125' – USDA P.I. No. 241,632 from Ecuador. It is more tolerant to some insects (Langford and Sowell 1974). It is late, has very large plants and multi-seeded pods; the seeds are small. The testas were purple – while Langford and Sowell (1974) listed it as having flesh testas.
9. 'Avir' – USDA P.I. No. 314,980. Developed in Krasnodar, USSR (known there as 'VNIIMK 433'). It is early (100 days) with multiseeded pods, some of which develop above ground; the seeds are small.

### *Hybridization and Evaluation*

In order to rule out possible variation between plants within cultivars, plants of each were grown in the summer of 1974 in the greenhouse and ten cuttings were rooted from one typical plant per cultivar. These plants were used as parents in the diallel crosses. The $F_1$ hybrids (7-9 per combination) were grown in the winter of 1974-75 in the greenhouse. For that reason they were not studied or evaluated. Their $F_2$ seeds were sown in the field at the optimal time (May 15, 1975) at the Beit-Dagan Experimental Farm. The plot was divided into three blocks. For each hybrid or parent, twelve hills were sown completely at random in each block with one to three seeds, depending on availability. Chlorotic, brachytic or otherwise deviating seedlings were removed and of the remaining normal seedlings one was retained, at random. The hills were widely spaced (116 × 140 cm). All culturing practices were as customary in commercial fields.

The traits were scored or measured as follows:

Days from planting to first flower-flowering was recorded individually for each plant.

Pod yield – the plants were harvested in a period of three days, starting 140 days after planting; all pods (including immature ones) were air-dried for two weeks and weighed.

Tops' weight – the fresh weight of all the above-ground parts was determined immediately after the plants were dug and the pods removed. The fresh weight per plant was converted to oven dry weight using two regression formulae (derived from samples in this study), one calculated for small plants (up to 500 g fresh weight) and one for larger plants. The correlation of fresh weight with dry weight was very high, $r = 0.98$.

Mature pod mean weight – all the mature pods, if up to 50/plant, were counted and weighed to obtain the mean weight. Where plants had higher yields, a random sample of 30 pods/plant was weighed and the mean weight was calculated.

### *Statistical Variance Components* (symbols as in Mather and Jinks 1971)

$V_r$, $\bar{V}_r$, $V_{F_2}$: The above variance components were estimated by nested and cross classified analysis of variance. See for details the expected mean squares in Table 1. This analysis was carried out by Harvey's LSMLMM program (Least Square, Maximum Likelihood Mixed Model) based on the principles of analysis of data with unequal subclass numbers presented by Harvey (1960). In this analysis, the individual observations were used and, therefore, the effects of blocks, and interactions between blocks and arrays and $F_2$ family means were taken into account. The $F_2$ families were unequal in size with a mean of 23.46 plants/family; they ranged widely from 3 to 34 plants/family, but only five families out of 36 had fewer than 10 plants. Consequently, in Table 1, the coefficients $K_{4,1}$ and $K_{4,2}$ are different and the $K_{i,j}$ coefficients differ from each other.

$V_{\bar{p}}, \bar{V}_p$: The variance components between and within parents' families were obtained from two-way analysis of variance (parents and blocks) for unequal subclasses. On the average there were 27.7 plants/family and they ranged from 17 to 33. It should be noted that the variance component $V_{\bar{p}}$ does not include environmental variance, therefore $V_{\bar{p}} = D$.

$W_r$: The mean covariance between the $F_2$ family means and the non-common parental family means was calculated as follows: first, a 9 X 9 table of the weighted means of the three replications of each cell was calculated, then $W_{ri}$ for each array was computed. $\bar{W}_r$ is the mean of the 9 $W_{ri}$ values which equals: $\bar{W}_r = \frac{1}{2}D - \frac{1}{8}F + \frac{1}{9 \times 23.46}E$

*Genetic Variance Components* (symbols as in Mather and Jinks 1971)

The six statistics described above ($V_{\bar{p}}$, $\bar{V}_p$, $\bar{V}_r$, $V_{\bar{r}}$, $VF_2$, $\bar{W}_r$) were used to estimate the environmental variance E and the four genetic variance components D, $H_1$, $H_2$ and F. These estimates were obtained by a stepwise multiple regression analysis, therefore the regression equation included only significant estimates

Imposing zero intercept in the analysis facilitated derivation of the above estimates with their standard errors, and thus tests of significance were performed for each variance component.

*Adequacy of the Diallel Model*

The two tests which were recommended by Mather and Jinks (1971), both of which must be satisfied in order to ascertain goodness of fit of the data to the model, were conducted: First, the consistency of the $(W_r - V_r)$ differences over arrays was tested by a two-way analysis of variance of arrays X blocks. Second, a joint regression analysis of $W_r$ on $V_r$ was performed in order to test the significance of the deviation of the joint linear regression coefficient from unity, as well as the heterogeneity of the regression coefficients over blocks.

Since both tests are only approximate, only when both indicated a significant disagreement with the model ($P \ll 0.05$) was it concluded that the data did not confirm to one or more of the basic assumptions of the model (Jinks – personal communication). The critical level of significance adopted for these two tests was 0.025.

*Dominance Ratio*

When both D and $H_1$ were significantly different from zero, the dominance ratio was calculated by $\sqrt{H_1/D}$. However, in cases where $H_1$ was not significant, the dominance ratio was calculated from the intercept of the $W_r$, $V_r$ graph and D (from the least squares analysis) as suggested by Jinks (1956) and adapted to $F_2$ data as follows:

**Table 1.** Expected mean squares degrees of freedom (d.f.) and variance ratio (F) values in the nested and cross classified analysis of variance for the four traits

| Item | Expected mean squares | d.f. | F values | | | |
|---|---|---|---|---|---|---|
| | | | Wt/plant | | $\bar{X}$ wt mature pods | Days to 1ste flower |
| | | | Pod yield | Tops | | |
| Between arrays | $\sigma^2_{F_2} + K_{4,1}\sigma^2_{\bar{F}_2(A)} + K_5\sigma^2_A$ | 8 | 7.2*** | 6.4*** | 5.9*** | 6.1*** |
| Between $F_2$ families within arrays | $\sigma^2_{F_2} + K_{4,2}\sigma^2_{\bar{F}_2(A)}$ | 72 | 18.6*** | 6.8*** | 29.3*** | 9.5*** |
| Between plants within $F_2$ families within blocks | $\sigma^2_{F_2}$ | 835 | | | | |
| Between blocks | $\sigma^2_{F_2} + K_{1,1}\sigma^2_{\bar{F}_2(A) \times B} + K_3\sigma^2_B$ | 2 | 0.7N.S. | 5.7** | 11.0*** | 1.4N.S. |
| Arrays x blocks | $\sigma^2_{F_2} + K_{1,2}\sigma^2_{\bar{F}_2(A) \times B} + K_2\sigma^2{}_{A \times B}$ | 16 | 1.0N.S. | 0.8N.S. | 0.9N.S. | 0.9N.S. |
| $F_2$ families within arrays x blocks | $\sigma^2_{F_2} + K_{1,3}\sigma^2_{\bar{F}_2(A) \times B}$ | 144 | 0.9N.S. | 0.9N.S. | 1.0N.S. | 1.4N.S. |

$$\sigma^2_A = V_{\bar{r}} = \frac{1}{4}D + \frac{1}{16}H_1 - \frac{1}{16}H_2 - \frac{1}{8}F + \frac{1}{9 \times 23.46}E$$

$$\sigma^2_{F_2(A)} = \bar{V}_r = \frac{1}{4}D + \frac{1}{16}H_1 - \frac{1}{8}F + \frac{1}{9 \times 23.46}E$$

$$\sigma^2_{F_2} = V_{F_2} = \frac{1}{4}D + \frac{1}{8}H_1 + E$$

**$K_i$ and $K_{ij}$ are the coefficients of the variance components which where calculated by the least square method – see Harvey (1960)**

$$\sqrt{H_1/D} = \sqrt{4\left(\frac{\frac{1}{4}D - a}{\frac{1}{4}D}\right)}$$

where a is the intercept of the Wr, Vr graph and equals in $F_2$ data $\frac{1}{4}D - 1/16\ H_1$

*Heritability Estimates*

Estimates for narrow and broad sense heritability, $h^2{}_n$ and $h^2{}_b$, respectively, were obtained following the procedure presented by Mather and Jinks (1971);

$$h^2{}_n = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{2}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E} = \frac{V_A}{V_p}$$

$$h^2{}_b = \frac{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F}{\frac{1}{2}D + \frac{1}{2}H_1 - \frac{1}{4}H_2 - \frac{1}{2}F + E} = \frac{V_A + V_D}{V_p}$$

Where E was not significant, heritability coefficients were not estimated. When only D and E were significant, the heritability was estimated as follows:

$$h^2 = \frac{\frac{1}{2}D}{\frac{1}{2}D + E}$$

In such cases distinction between $h^2{}_b$ and $h^2{}_n$ is meaningless, therefore it was denoted as $h^2$ in Table 2.

*Correlations*

The phenotypic correlations for all possible pairs of characters were calculated from the phenotypic variances and covariances of the $F_2$ hybrid populations. The mean within cultivar variances and covariances served as estimates for the environmental variances and covariances. The environmental correlations were calculated from these estimates. Genetic variances and covariances were obtained by subtracting the environmental variances and covariances from the respective phenotypic ones. These estimates were used to calculate the genetic correlations between the traits in the $F_2$ generation.

## Results and Discussion

Reciprocals were obtained in 25 of the 36 hybrid combinations possible in a 9 × 9 diallel cross. The differences between the means of these reciprocals for each of the four traits studied were examined by the t test and all of

**Table 2.** Components of variance and various genetic estimates for four trais in peanuts[a]

| Statistic[b] | Pod yield per plant | Tops per plant | Mean wt mature pods | Days to 1ste flower |
|---|---|---|---|---|
| Estimates of observational components of variances: | | | | |
| $V_{\bar{p}}$ | 19339 | 26092 | 0.4414 | 20.97 |
| $V_{\bar{r}}$ | 4313 | 6611 | 0.0846 | 3.60 |
| $\bar{V}_r$ | 5988 | 11747 | 0.1385 | 6.67 |
| $V_{F_2}$ | 7303 | 32512 | 0.1027 | 12.81 |
| $\bar{W}_r$ | 7182 | 10855 | 0.2073 | 8.33 |
| $\bar{V}_p$ | 2490 | 9175 | 0.0495 | 7.41 |
| Estimates of genetic components of variances and their standard errors: | | | | |
| D | 18557*** | 26233*** | 0.436*** | 20.03*** |
| $H_1$ | N.S. | 131222*** | N.S. | N.S. |
| $H_2$ | N.S. | 104111*** | N.S. | N.S. |
| F | N.S. | 21456*** | N.S. | N.S. |
| E | 2541** | 9362*** | N.S. | 6.15** |
| Other statistics | | | | |
| $\sqrt{H_1/D}$ | 0.94 | 2.20 | 0.92 | 1.02 |
| K | – | 2.71 | – | – |
| C | – | 0.33 | – | – |
| $\bar{u}$ | – | 0.80 | – | – |
| $K_d/K_r$ | – | 1.48 | – | – |
| $h^2$ | 0.79 | – | – | 0.62 |
| $h^2_n$ | – | 0.31 | – | – |
| $h^2_b$ | – | 0.82 | – | – |
| $\overline{u \cdot v}$ | – | 0.16 | – | – |

[a] K, C, $\bar{u}$, $K_d/K_r$ and $\overline{u \cdot v}$ were calculated only when all their relevant components were significant

[b] For definitions of these statistics and their derivations see Mather and Jinks 1971. C is the symbol for the ratio $(F/2)/\sqrt{D(H_1 - H_2)}$ which expresses the consistency of the degree of dominance and its direction inall loci controlling the trait: when C = 1 the degree and the direction of dominance are uniform; C decreases towards 0 as uniformity is disturbed

**Table 3.** Tests of goodness of fit of the data to the diallel model: degrees of freedom, F values, regression coefficients and their standard errors

| Item | d.f. | wt/plant | | | $\bar{X}$ wt. | Days to |
|---|---|---|---|---|---|---|
| | | Pod | Tops | | mature | 1st |
| | | yield | before correction | after correction | pods | flower |
| A. ($W_r - V_r$) differences consistency (d.f. and F. values): | | | | | | |
| Between arrays | 8 | 4.5** | (3.6* ) | 2.2 | 2.6 | 1.4 |
| Between blocks | 2 | 0.5 | (2.0 ) | 2.0 | 6.6 | 3.2 |
| Error | 16 | – | ( – ) | – | – | – |
| B. Joint regression of $W_r$ on $V_r$ from three blocks (d.f. and F values): | | | | | | |
| Joint regression | 1 | 73.3*** | (7.5* ) | 4.9* | 415.4*** | 23.4*** |
| Heterogeneity of regression | 2 | 1.1 | (3.3 ) | 1.7 | 0.4 | 5.6 |
| Remainder | 21 | – | ( – ) | – | – | – |
| C. Joint linear regression coefficients (b) and their standard errors [$S_{(b)}$]: | | | | | | |
| b | – | 0.73 | (0.36[a]) | 0.54 | 0.89 | 0.46[a] |
| $S_{(b)}$ | 21 | 0.15 | (0.14 ) | 0.24 | 0.05 | 0.10 |

*, **, *** – Significant at the 0.05, 0.01 and 0.001 levels, respectively

[a] Values which differ significantly (0.025) from unity

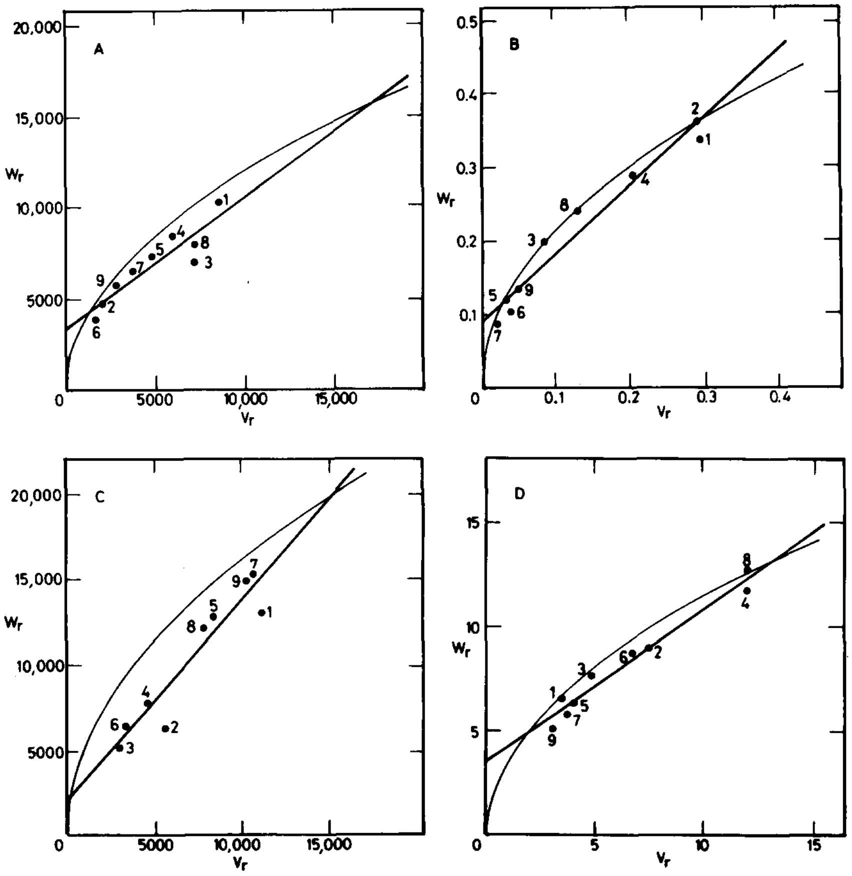

Fig. 1. The regressions of $W_r$ on $V_r$ for: A. Pod yield per plant; B. Mature pod weight; C. Tops' dry weight; D. Days to first flower

**Table 4.** Total pod yield (gm) per plant, 140 days after planting: $F_2$ means and deviations of $F_2$ means from midparent (upper and lower values in each cell, respectively); parents' means and arrays' means (in left column upper and lower values, respectively, in each cell)

| Parents | Parents' & arrays' means | $F_2$ mean and deviation from midparent in hybrids of | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 |
| 1. Shulamit | 432.6 | 188.9 | 307.2 | 207.3 | 228.1 | 227.2 | 407.3 | 336.2 | 209.1 |
| | 285.6 | –72.0 | 43.0 | –27.0 | –86.3 | –42.2 | 25.1 | –33.6 | –97.3 |
| 2. 203 | 180.3 | 127.6 | 160.6 | 139.7 | 184.2 | 148.9 | 258.3 | 225.1 | |
| | 181.5 | – 7.2 | 22.5 | 30.6 | – 4.0 | 5.8 | 2.6 | –18.6 | |
| 3. DA | 307.1 | 180.7 | 340.0 | 176.2 | 154.9 | 222.8 | 382.7 | | |
| | 258.4 | –17.5 | 138.5 | 3.7 | –96.7 | 16.1 | 63.6 | | |
| 4. VSM | 331.1 | 239.5 | 202.4 | 218.6 | 205.9 | 280.2 | | | |
| | 280.7 | 29.3 | –11.1 | 34.1 | –57.7 | 61.5 | | | |
| 5. S9 | 106.3 | 99.8 | 187.0 | 86.2 | 122.2 | | | | |
| | 164.5 | 2.0 | –85.9 | 14.1 | –29.0 | | | | |
| 6. Congo | 196.2 | 154.7 | 112.9 | 151.7 | | | | | |
| | 167.8 | 12.0 | –33.1 | 34.6 | | | | | |
| 7. Chico | 38.0 | 90.2 | 176.8 | | | | | | |
| | 142.8 | 26.6 | 109.9 | | | | | | |
| 8. 1125 | 95.9 | 127.2 | | | | | | | |
| | 190.0 | 34.6 | | | | | | | |
| 9. Avir | 89.3 | | | | | | | | |
| | 144.2 | | | | | | | | |

**Table 5.** Mean weight of mature pod, gm: $F_2$ means and deviations of $F_2$ means from midparent (upper and lower values in each cell, respectively); parents' means and arrays' means (in left column upper and lower values, respectively, in each cell)

| Parents | Parents' & arrays' means | $F_2$ mean and deviation from midparent in hybrids of | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 |
| 1. Shulamit | 2.34 | 1.61 | 2.13 | 1.07 | 1.22 | 1.25 | 2.44 | 1.65 | 2.40 |
| | 1.72 | –0.29 | 0.18 | –0.43 | –0.64 | –0.33 | 0.15 | –0.17 | –0.11 |
| 2. 203 | 2.69 | 1.54 | 2.01 | 0.98 | 1.50 | 1.33 | 2.17 | 1.89 | |
| | 1.73 | –0.50 | –0.11 | –0.69 | –0.50 | –0.43 | –0.29 | –0.11 | |
| 3. DA | 1.31 | 1.36 | 1.45 | 1.00 | 1.15 | 1.11 | 1.69 | | |
| | 1.41 | –0.02 | 0.01 | 0.01 | –0.19 | 0.04 | –0.08 | | |
| 4. VSM | 2.24 | 1.64 | 1.92 | 1.19 | 1.32 | 1.25 | | | |
| | 1.70 | –0.21 | 0.02 | –0.26 | –0.49 | –0.28 | | | |
| 5. S9 | 0.83 | 1.14 | 1.27 | 0.79 | 0.49 | | | | |
| | 1.14 | 0.00 | 0.07 | 0.05 | –0.11 | | | | |
| 6. Congo | 1.38 | 0.43 | 1.22 | 0.87 | | | | | |
| | 1.21 | 0.01 | –0.25 | –0.15 | | | | | |
| 7. Chico | 0.66 | 0.97 | 1.11 | | | | | | |
| | 1.00 | –0.09 | 0.00 | | | | | | |
| 8. 1125 | 1.56 | 1.52 | | | | | | | |
| | 1.56 | 0.01 | | | | | | | |
| 9. Avir | 1.46 | | | | | | | | |
| | 1.40 | | | | | | | | |

**Table 6.** Oven dry weigth of tops, gm: $F_2$ means and deviations of $F_2$ means from midparent (upper and lower values in each cell respectively); parents' means and arrays's means (in left column upper and lower values, respectively, in each cell)

| Parents | Parents' & arrays' means | $F_2$ mean and deviation from midparent in hybrids of | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 |
| 1. Shulamit | 469.3 | 422.9 | 592.9 | 301.2 | 477.8 | 400.1 | 541.3 | 396.6 | 252.2 |
| | 428.3 | 77.0 | 77.0 | 40.7 | 4.4 | 50.6 | 106.0 | −32.6 | −112.7 |
| 2. 203 | 260.6 | 357.0 | 547.4 | 204.1 | 458.3 | 361.8 | 357.5 | 315.1 | |
| | 346.0 | 115.4 | 135.9 | 48.0 | 89.3 | 116.7 | 26.5 | − 9.7 | |
| 3. DA | 389.1 | 390.0 | 642.2 | 300.9 | 336.8 | 381.5 | 469.4 | | |
| | 402.4 | 84.2 | 166.4 | 80.5 | −96.5 | 72.1 | 74.2 | | |
| 4. VSM | 401.4 | 429.6 | 556.2 | 368.7 | 438.4 | 445.4 | | | |
| | 445.3 | 117.6 | 74.3 | 142.2 | − 1.0 | 129.9 | | | |
| 5. S9 | 229.7 | 299.7 | 418.5 | 150.7 | 387.3 | | | | |
| | 343.3 | 73.6 | 22.4 | 13.6 | 33.7 | | | | |
| 6. Congo | 447.5 | 422.3 | 302.5 | 323.6 | | | | | |
| | 402.7 | 72.3 | −217.5 | 59.0 | | | | | |
| 7. Chico | 51.7 | 165.7 | 326.4 | | | | | | |
| | 243.7 | 25.0 | 19.3 | | | | | | |
| 8. 1125 | 562.5 | 446.0 | | | | | | | |
| | 488.3 | 53.5 | | | | | | | |
| 9. Avir | 222.6 | | | | | | | | |
| | 349.0 | | | | | | | | |

**Table 7.** Days to first flower: $F_2$ means and deviations of $F_2$ means from midparent (upper and lower values in each cell, respectively); parents' means and arrays' means (in left column upper and lower values, respectively, in each cell)

| Parents | Parents' & arrays' means | $F_2$ mean and deviation from midparent in hybrids of | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | 9 | 8 | 7 | 6 | 5 | 4 | 3 | 2 |
| 1. Shulamit | 37.0 | 35.0 | 37.0 | 35.0 | 38.0 | 36.0 | 39.0 | 38.0 | 41.0 |
| | 37.4 | 1.5 | 1.5 | 1.0 | 2.5 | − 0.5 | − 0.5 | 1.0 | 2.0 |
| 2. 203 | 41.0 | 35.0 | 42.0 | 37.0 | 39.0 | 38.0 | 44.0 | 41.0 | |
| | 39.7 | − 0.5 | 4.5 | 1.0 | 1.5 | − 0.5 | 2.5 | 2.0 | |
| 3. DA | 37.0 | 34.0 | 35.0 | 34.0 | 37.0 | 37.0 | 38.0 | | |
| | 36.7 | 0.5 | − 0.5 | 0.0 | 1.5 | 0.5 | − 1.5 | | |
| 4. VSM | 42.0 | 33.0 | 40.0 | 35.0 | 39.0 | 35.0 | | | |
| | 37.2 | − 3.0 | 2.0 | − 1.5 | 1.0 | − 4.0 | | | |
| 5. S9 | 36.0 | 32.0 | 33.0 | 33.0 | 34.0 | | | | |
| | 34.8 | − 1.0 | − 2.0 | − 0.5 | − 1.0 | | | | |
| 6. Congo | 34.0 | 31.0 | 36.0 | 36.0 | | | | | |
| | 36.0 | − 1.0 | 2.0 | 3.5 | | | | | |
| 7. Chico | 31.0 | 32.0 | 33.0 | | | | | | |
| | 34.0 | 1.5 | 0.5 | | | | | | |
| 8. 1125 | 34.0 | 31.0 | | | | | | | |
| | 35.7 | − 1.0 | | | | | | | |
| 9. Avir | 30.0 | | | | | | | | |
| | 32.6 | | | | | | | | |

**Table 8.** A comparison of the mean deviations of the $F_2$ means from their midparent in each arry: Observed = mean of observational deviations, Absolute = mean of the absolute values of the deviations

| Traits and | Arrays of | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| means | Shulamit | 203 | DA | VSM | S9 | Congo | Chico | 1125 | Avir |
| *Total pod yield/plant* | | | | | | | | | |
| Observed | −36.25 | −8.20 | 6.95 | 18.40 | 14.25 | −32.50 | 28.30 | 48.75 | 1.00 |
| Absolute | 53.35 | 23.55 | 48.55 | 35.65 | 32.05 | 44.15 | 35.05 | 59.80 | 25.15 |
| *Mean weight of mature pod* | | | | | | | | | |
| Observed | − 0.20 | −0.35 | −0.06 | −0.18 | −0.12 | − 0.29 | −0.19 | −0.01 | −0.14 |
| Absolute | 0.29 | 0.35 | 0.08 | 0.22 | 0.16 | 0.29 | 0.21 | 0.08 | 0.14 |
| *Tops' oven dry weight* | | | | | | | | | |
| Observed | 26.30 | 51.15 | 42.35 | 83.65 | 65.50 | − 6.55 | 53.55 | 41.45 | 75.90 |
| Absolute | 62.60 | 81.75 | 77.05 | 83.90 | 65.50 | 71.70 | 53.55 | 95.80 | 75.90 |
| *Days to first flower* | | | | | | | | | |
| Observed | 1.05 | 1.55 | 0.45 | −0.55 | −1.10 | 1.25 | 0.70 | 0.85 | −0.35 |
| Absolute | 1.30 | 1.80 | 0.95 | 1.90 | 1.25 | 1.75 | 1.20 | 1.75 | 1.25 |

them were non-significant. Hence, the data were pooled (Hayman 1954) for the analysis of variance shown in Table 1. It is evident (Table 1) that there were marked genetic differences between the parents in all four traits – the differences between the arrays and between the $F_2$ families within arrays were very highly significant. There were no significant genotype × blocks interactions in all four traits; for two traits (tops' weight and mean weight mature pods) there was a significant difference between blocks.

## *Total Pod Yield per Plant*

The findings are summarized in Tables 2, 3, 4 and 8 and in Figure 1A. Bidirectional dominance was very evident in this trait: Tables 4 and 8 show that in certain hybrid combinations the $F_2$ means exceeded their midparents, i.e., high yield was dominant to low, as in the crosses of '1125' with 'Chico', 'DA', 'Avir' and 'S9'. On the other hand, in certain hybrid combinations the alleles decreasing yield were dominant, viz. 'Congo' with 'VSM', 'DA', 'S9', 'Shulamit' and '1125', and 'Shulamit' with '203'. In view of the bidirectional dominance and the fact that $H_1$ was not significant, the dominance ratio which was derived from the Wr, Vr graph (Table 3) is not meaningful. From Table 3 it can be seen that the ($W_r$-$V_r$) differences between the cultivars were inconsistent; on the other hand, the joint linear regression coefficients did not differ significantly from unity (b = 0.73). Since only one of the two tests indicates disagreement with the model, the additive-dominance model is not rejected.

Allelic frequencies were not estimated from the genetic variance components because they were not significant and not from the $W_r$, $V_r$ graphical analysis (Fig. 1A) because of bidirectional dominance. However, other genetic information can be deduced from Figure 1A. No cultivar was homozygous recessive for all loci. Even 'Shulamit', which contains the highest number of recessive alleles, is homozygous recessive only for about one half of the loci. 'Congo' and '203' were homozygous dominant for most genes. The remaining cultivars contained more dominant alleles than recessives.

Since $H_1$, $H_2$ and F were not significant and only D and E were (Table 2), heritability ($h^2$) was calculated as described above (Materials and Methods). The high heritability value of pod yield per plant (0.79) indicates that breeding for more productive cultivars can be initiated with visual selection of promising plants in large $F_2$ populations followed by careful progeny testing. It should be noted that this conclusion is valid for $F_2$ populations arising from widely different parents.

The low genetic correlations of pod yield/plant with the other characters (Table 9) indicate that selection for yield cannot be assisted by these traits.

## *Mean Weight of Mature Pods*

In most crosses, small pods were dominant to larger pods (Table 5), as evidenced also by Figure 1 B where cultivars 1 and 2, which have the largest pods, are homozygous recessive while cultivars 5 and 7, with the smallest pods, are homozygous dominant for all loci controlling the traits which were tested. The dominance of the small pods is even more evident from the fact that all of the average deviations of $F_2$ family means from their midparent in each array were negative (Table 8). The findings sum-

**Table 9.** Genetic and phenotypic correlation values (r) calculated from the diallel $F_2$ and parents' data

| Traits | Phenotypic | Genetic | Environmental |
|---|---|---|---|
| Degrees of freedom | 793 | 515 | 240 |
| Pod yield/plant and | | | |
| Mean wt/mature pod | 0.216** | 0.160** | 0.307** |
| Tops' weight | 0.388** | 0.401** | 0.361** |
| 1st flower[a] | −0.132** | −0.005 | −0.256** |
| Mean wt/mature pod and | | | |
| Tops' weight | −0.067 | −0.072 | −0.060 |
| 1st flower[a] | −0.091* | 0.041 | −0.179** |
| Tops' weight and | | | |
| 1st flower[a] | 0.036 | 0.235** | −0.122 |

[a] Number of days from germination to first flower

*, ** Significanr at the 5% and 1% level, respectively

marized in Table 3 showed agreement with the model.

In breeding for large pod size (ca. 3 g/pod) large populations should be screened in the $F_2$. Breeding for large pods will be aided by the fact that the large-podded plants were homozygous recessive, or nearly so. Breeding for higher yields and large pods can be done simultaneously because of the positive, though low, genetic correlation between them (Table 9). Our findings are in agreement with those of Coffelt and Hammons (1974) on the positive correlation of seed weight with yield, since seed weight and pod weight are closely related.

Even though $H_1$ and $H_2$ did not differ significantly from zero (Table 2), the consistent negative dominance deviations (Table 8) show the weakness of the diallel analysis in the detection of dominance variation (Kearsey 1970).

### *Tops' Oven Dry Weight*

Initially, this trait did not fit the additive-dominance model according to both tests (Table 3). However, it was noted that the deviation was caused mainly by two hybrid combinations out of the 36, namely '1125' x 'DA' and '1125' x '203' (Table 6). After correcting the means of these two hybrid combinations using the missing plot procedure outlined by Hayman (1954) a good fit was obtained (Table 3, Fig. 1C).

In most combinations the alleles which increase tops' weight were dominant and there were indications for overdominance. In 10 combinations (out of the 36), the mean exceeded the higher parent, namely, four combinations with 'Avir', four with 'VSM' and two with others (Table 6). In this trait D, $H_1$, $H_2$, F and E were highly significant ($P < 0.001$), therefore the estimation of the other genetic statistics was possible (Table 2, bottom). The overall dominance ratio was $\sqrt{H_1/D} = 2.2$ (Table 2). Furthermore, in six out of the nine arrays, the arrays' means exceeded their respective common parents' means (Table 6).

The mean within $F_2$ families variance was larger than the variance between the parents' means, probably because of transgressive segregation. Because of the high dominance variation (Table 2, $H_1$ and $H_2$) found in this trait, a large difference between the narrow and broad sense heritabilities was found (Table 2). The relatively low value of the narrow sense heritability and the high dominance level of high tops' weight reduce the efficiency of selection for higher tops weight in the early segregating generations. On the other hand, because plants with lower tops' weight are recessive, selection in this direction would be more successful, despite the low $h^2_n$.

### *Days from Emergence to First Flower*

There was contradictory evidence whether the genetic control of this trait followed the additive-dominant model. The $(W_r\text{-}V_r)$ differences were consistent in the nine arrays (Table 3). On the other hand, the joint regression coefficients of $W_r$ on $V_r$ differed significantly from unity, $b = 0.46$. The low value was due mainly to a very low coefficient in one of three blocks, and in that one it was due to the behaviour of the array of 'Congo'. The linear regression (Fig. 1D) obtained from the pooled data of the three blocks gave a higher value, $b = 0.697$ which still differs significantly from unity ($P < 0.01$; $r = 0.98$).

One reason for the low regression coefficients could be bidirectional dominance, the presence of which was indicated by the parental and $F_2$ means (Table 7) and the deviations shown in Table 8 and Figure 1D. In Figure 1D it is demonstrated that the two cultivars which were homozygous recessive for most loci, one is the latest (No. 4) and one is very early (No. 8). Similarly, of the two cultivars which were homozygous dominant for most loci, one was the earliest (No. 9) while the other was late (No. 1).

### *General Comments*

The estimation of the number of effective factors from diallel crosses has been questioned mainly for two limitations. First, the maximum number estimated is solely a function of the number of parents in the diallel (Hayman 1963). Second, the estimated number of effective factors represents only those in which some degree of dominance is involved. Still, between traits within a given diallel cross it furnishes relative estimates of the number of effective factors controlling the various traits under study.

It has been the common practice to estimate the number of effective factors by $4(h)^2/H_2$. The estimates derived by this method are not considered reliable because they are affected by the above shortcomings as well as from bias due to bidirectional dominance (Hayman 1954). This could be the reason for the estimates of $K < 1$ or just a few genes (Jinks 1954; Park and Davis 1976; Paroda and Hayes 1971; Singh and Chahal 1974).

In order to overcome the bias due to bidirectional dominance we suggest that the number of effective factors could be estimated from the absolute dominant deviations, rather than from the observed ones. The statistic h is usually defined as the difference between the mean of the n parents and the mean of the $n^2$ families in the diallel table. It can be shown that h can also be estimated by first calculating the difference between the mean of the n parents and the mean of the $n(n-1)$ hybrid families, and multiplying this difference by $\frac{n-1}{n}$. It is clear that the above difference is actually the mean of the deviations between each of the $n(n-1)$ hybrids and its respective parents. It is proposed that this difference (h) should be calculated from the mean of the absolute deviations instead of the ordinary arithmetic mean. It should be noted that the values of K obtained by the proposed method are still underestimates because of the inconsistency in the dominance levels of the different loci. Furthermore, where dominance is absent or low and families are small, the K values obtained by the proposed method will have a larger error.

## Acknowledgement

This research is based on the M.Sc. thesis of A.G., submitted to the Hebrew University, Faculty of Agriculture, Rehovot, Israel. It was supported in part by grants from the Harry S. Truman Research Institute to A.A. and by the Philip, David, Daniel, Marc-Eliot and Joel Barach Foundation to A.G. We are grateful to Prof. J.L. Jinks for reviewing a draft of the manuscript and his valuable comments and suggestions.

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Received June 26, 1978
Communicated by R.W. Allard

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