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Diallel Analysis in Groundnut (*Arachis hypogaea* L.)

Part 2. Pod Number and Pod Yield *

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Summary. An 8×8 full diallel experiment based on 4 bunch plus 4 spreading types of groundnut (*Arachis hypogaea* L.) was conducted over three environments. For both number of pods and pod yield, additive, non-additive and reciprocal cross effects were detected and these were also influenced by changes in environments. For number of pods additive genetic variance was predominant whereas it was approximately equal to non-additive genetic variance for pod yield. Graphical analysis revealed the presence of strong non-allelic interaction for number of pods whereas for pod yield absence of dominance and/or presence of non-allelic interaction was evident.

Key words: *Arachis hypogaea* – Groundnut – Combining ability analysis – Non-allelic interactions – Graphical analysis – Pod yield

Introduction

Groundnut (*Arachis hypogaea* L.) is one of the leading oil seed crops and is a rich source of edible oil and protein. In other crops, as a result of selective breeding, substantial increase in yield has been achieved. The most notable advances have been in wheat and corn. The potential for improving pod yield in groundnut seems at least as great considering the wide genetic diversity in the world collection of groundnut. To achieve these objectives, the plant breeder must have a working knowledge of the inheritance of economic traits if he is to efficiently improve them.

With regard to diallel analysis, Griffing (1956a) described a systematic method of evaluating populations, or select groups of inbred lines, for combining ability in hybrid combinations. Because of extensive use of hybrid varieties in many crops, the concept of general and specific combining ability has become more important. Furthermore, with the application of the approaches of Jinks (1954) and Hayman (1954a, b) in the present study, an attempt has been made to partition phenotypic variation into genotypic and environmental components and to ascertain whether the additive-dominance model holds good in the inheritance of number of pods and pod yield.

Materials and Methods

A preliminary trial with 20 varieties (10 bunch + 10 spreading) was conducted. Based on six characters, eight varieties (4 bunch + 4 spreading) were selected using Mahalonobis's D^2 statistics. These varieties are listed below:

Bunch: 1. TG 17 2. Lin-yueh-tsao 3. U4-47-7 and 4. Vniimk K 1657. Spreading: 5. M 145 6. F 334-AB-14 7. M 13 and 8. Pearl.

These varieties were crossed in all possible combinations to produce a full diallel. The 64 progeny were grown during kharif 1979 under three environments; E1 – at Ludhiana under irrigated conditions, E2 – at Ludhiana under rainfed conditions and E3 – at Samrala under irrigated conditions. In the three environments each of the 64 entries were represented by a single row plot in each of three completely randomized blocks. Data were recorded on number of pods per plant (P) and pod yield (PY). For each entry, the mean of five plants was used for statistical analysis. Combining ability analysis was carried out according to Griffing (1956a), the analysis of variance of diallel tables and graphical analysis as suggested by Hayman (1954a, b). In the tables the varieties have been designated by their specific numbers, 1 to 8, and the two characters in abbreviated capital letters.

Results

The general analysis of variance for individual environments (Table 1) for both pod number and pod yield revealed that genotypes, parents as well as hybrids, differed significantly in all three environments. The pooled analysis of variance (Table 2) indicated that

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Table 1. Analysis of variance in individual environments with mean squares

Item	df	Environments					
		P			PY		
		E_1	E_2	E_3	E_1	E_2	E_3
Blocks	2	65.12	12.98	82.78	16.26	3.61	37.89
Genotypes	63	90.41**	29.62**	90.43**	36.42**	16.68**	51.28**
Parents (P)	7	27.02**	14.87*	100.99**	6.06*	11.85**	68.64*
Hybrids (H)	55	98.63**	32.00**	90.66**	39.14**	17.49**	49.86**
P vs H	1	82.31	2.22	4.21	99.17	5.64	8.19
Error	126	17.49	7.39	20.48	12.31	5.41	13.65
Parents × Reps	14	4.82	4.82	21.78	1.84	1.33	23.40
Hybrids × Reps	110	19.09	7.78	20.66	13.76	6.01	12.59
P vs H × Reps	2	18.18	3.78	1.24	5.55	0.69	3.95

* $P \leqq 0.05$ ** $P \leqq 0.01$

environments differed for these 2 characters; also genotypes, parents as well as hybrids, differed among themselves and were also subject to environmental interaction. The significant comparison parents vs hybrids showed the presence of directional dominance for these traits and was subject to environmental fluctuation for pod yield.

Table 2. Pooled analysis of variance with mean squares

Item	df	P	PY
Blocks within environments	6	53.62	19.25
Environments (E)	2	6,082.83**	3,758.17**
Genotypes (G)	63	115.98**	53.16**
Parents (P)	7	59.88**	45.24**
Hybrids (H)	55	124.26**	53.73**
P vs H	1	53.04*	76.97**
G × E	126	47.25**	25.61**
Parents × E	14	41.50**	20.66**
Hybrids × E	110	48.51**	26.38**
P vs H × E	2	17.85	18.02*
Error	378	15.12	10.46
Parents × Reps/E	42	10.47	8.86
Hybrids × Reps/E	330	15.84	10.79
P vs H × Reps/E	6	7.74	3.40

* $P \leqq 0.05$ ** $P \leqq 0.01$

Table 3. Analysis of variance for combining ability

Item	df	P	PY
GCA	7	52.53**	21.14**
SCA	28	3.81**	2.47**
RCE	28	12.05**	5.54**
Error	378	1.68	1.16
Components			
$\frac{1}{7}\sum_i g_i^2$		3.18	1.25
$\frac{1}{28}\sum_{ij} s_{ij}^2$		2.13	1.31

** $P \leqq 0.01$

The analysis of variance for combining ability (Table 3), when the entries were summed over all environments, showed that variances due to general combining ability (GCA), specific combining ability (SCA) and reciprocal cross effect (RCE) were significant for both the characters. Further, the higher magnitude of estimated variance due to GCA, $\frac{1}{7}\sum_i gi^2$, over that of SCA, $\frac{1}{28}\sum_{ij} s_{ij}^2$, indicated the preponderance of additive genetic variance for number of pods; but, the reverse was true for pod yield.

The estimates of gca and sca effects with regard to the parental lines and their F_1 hybrids are given in Table 4. For number of pods F 334-AB-14 was the best and Pearl the poorest general combiner; the mean values and the gca effects of the parents showed identical trends, and the estimate of their correlation ($r = 0.98 \pm 0.08$) was observed to be significant. The sca effect of most of the parents indicated that they transmit desirable genes uniformly to all of their hybrids for this character. The hybrid TG 17 × Lin-yueh-tsao recorded the highest and F 334-AB-14 × Pearl the lowest sca effect. For pod yield, M 13 was the best general combiner while TG 17 was the poorest one. The gca effects of the parents as such could be related to their mean values because of the existence of positive correlation ($r = 0.89 \pm 0.19$) between them. Significant sca effect was found in Lin-yueh-tsao and F 334-AB-14 indicating that these parents were involved in some specific combinations rather than being uniform in the transmission of desirable genes for pod yield. Highest sca effect was recorded by U4-47-7 × Pearl while both of the parents showed negative gca effect.

The analyses of variance of the diallel table (Hayman 1954a) are given in Tables 5 and 6 and the test statistics for graphical analysis are presented in Table 7. For number of pods, additive gene effects 'a', maternal effects 'c' and item 'd' were clearly involved in the in-

Table 4. Estimates of general and specific combining ability effects. Values below the diagonal relate to number of pods and those above the diagonal to pod yield

	g_i	s_{ii}	s_{ij}								g_i	s_{ii}
			1	2	3	4	5	6	7	8		
1.	−1.57**	−0.50		1.58**	0.10	−1.10	0.02	1.00	−0.47	−1.11	1.28**	−0.02
2.	2.19**	−2.59*	3.27**		−0.65	−0.62	−0.02	0.25	0.55	1.25	0.34	−2.34*
3.	0.35	−0.86	−0.24	−0.87		−0.15	−1.17	0.59	0.28	1.89**	−0.66**	−0.89
4.	0.90**	−1.33	−1.25	1.10	−0.88		1.35*	1.72*	−0.60	1.19	0.09	−1.78
5.	−0.96**	−0.77	0.24	−0.34	−1.49	1.65*		0.98	−0.06	−1.19	−1.00**	0.08
6.	2.53**	−1.92	0.27	0.11	1.32	2.46**	0.69		−0.43	−1.77**	1.32**	−2.34*
7.	0.84**	0.36	−0.58	−0.78	0.91	−1.08	0.47	−0.59		0.45	1.94**	0.27
8.	−2.61**	1.18	−1.21	0.10	2.11**	−0.67	−0.46	−2.34**	1.29		−0.74**	−0.71
SE(±)	0.30	1.13									0.25	0.94
C.D. 0.05	0.90				2.20				1.83		0.75	

* $P \leqq 0.05$ ** $P \leqq 0.01$

Table 5. Analysis of variance over individual environment

Item	df	P			PY		
		E_1	E_2	E_3	E_1	E_2	E_3
a	7	289.26**,****	83.96**,****	290.11**	65.09*,****	48.53**,****	176.36**,****
b	28	53.35**,****	16.36**,****	22.50	31.86**,****	8.97**,***	12.96
b1	1	82.31***	2.22	4.21	99.17****	5.64	8.19
b2	7	39.98**,***	5.72	18.55	16.99**	4.51	9.98
b3	20	56.59**,****	20.79**,****	24.80	33.69**,****	10.89**,***	14.24
c	7	230.70**,****	55.27**,****	317.46**	76.36**,****	13.90***	149.90**,****
d	21	26.79*	20.64**,****	38.78**	19.64	17.27**,****	27.82**,****
Block interactions							
B×a	14	21.91	9.25	16.36	15.98	8.97	10.84
B×b	56	17.23	5.51	28.27	10.51	3.95	17.50
B×b1	2	18.18	3.78	1.24	5.55	0.69	3.95
B×b2	14	7.59	8.66	22.86	3.47	5.13	21.85
B×b3	40	20.56	4.50	31.52	13.22	3.70	16.66
B×c	14	24.01	12.17	10.16	16.21	5.41	7.81
B×d	42	14.18	7.67	14.89	12.19	6.17	11.40
Pooled	126	17.49	7.39	20.48	12.31	5.41	13.65

	$P \leqq 0.05$	$P \leqq 0.01$
Each item tested against its own block interaction	*	**
All items tested against the pooled block interaction MS	***	****

heritance of this character in individual as well as over all environments. The dominance effect detected in E_1 was attributable to directional dominance 'b1', to differences in the distribution of dominant alleles among the parents 'b_2' and to specific combining ability effects 'b_3'. In E2, the overall 'b' term was significant but of its components only 'b3' achieved significance level suggesting the presence of dominance which in the absence of 'b1' would be ambidirectional in nature. Additive, maternal and reciprocal effects interacted with environments. Interaction of dominance effects with environments was due to the interaction of specific combining ability effects with environments. The statistical tests using Wr and Vr were performed to investigate whether an additive-dominance model was appropriate. But this character did not satisfy the tests, involving the consistency of (Wr–Vr) over arrays and agreement of the regression slope with unity. This suggested that simple dominance was not an adequate explanation of the non-additivity and does not allow the estimation of the components of variation D, H_1, H_2, F and E. Each of the arrays 3 and 7 had extreme values of (Wr–Vr), therefore sub diallel tables, were prepared after removing them individually and to-

Table 6. Pooled analysis of variance with mean squares

Item	df	P	PY
a	7	472.80**, ****	190.22**, ****
b	28	34.27**, ****	22.21**, ****
b1	1	53.03*	76.97**, ****
b2	7	17.25	13.79
b3	20	39.28**, ****	22.42*, ****
c	7	361.01**, ****	120.03**, ****
d	21	24.31*, ***	26.44**, ****
a × E	14	95.26**, ****	49.89**, ****
b × E	56	28.97**, ****	15.79*, ****
b1 × E	2	17.85	18.02*
b2 × E	14	23.50	8.84
b3 × E	40	31.45*, ****	18.10*, ****
c × E	14	121.21**, ****	60.06**, ****
d × E	42	30.95**, ****	19.14*, ****
Pooled	126	47.25****	25.61****
B × a/E	42	15.84	11.93
B × b/E	168	17.01	10.65
B × b1/E	6	7.74	3.40
B × b2/E	42	13.04	10.15
B × b3/E	120	18.86	11.19
B × c/E	42	15.45	9.81
B × d/E	126	12.24	9.92
Pooled	378	15.12	10.46

	P≦0.05	P≦0.01
Each item tested against its own block interactions within environments	*	**
All items tested against the pooled block interaction within environments MS	***	****

Table 7. The test statistics for the estimates of components of genetic variance

	bWr/Vr	SEb(±)	t_b	t_{b-1}	t^2
P	0.54	0.10	5.40**	4.54**	10.25**
PY	0.27	0.30	0.90	2.48*	0.46

* P≦0.05 **P≦0.01

gether. The regression coefficients were 0.55, 0.63 and 0.62 respectively which differed significantly from zero as well as from unity.

For pod yield, the significant 'a' and 'c' mean squares revealed the presence of additive genetic variation and maternal effects respectively in individual as well as overall environments. Except E3, non-additive genetic variation was detected; in E1 it was due to directional dominance 'b1', asymmetry of gene distribution 'b2' and interaction between specific genotypes 'b3'; in E2 non-additive variation was due to interaction between specific genotypes which in the absence of 'b1' would not be unidirectional. Item 'd' did not reach significance in E1. Additive and maternal effects and reciprocal differences interacted with environments. Interaction of non-additive effects with environments was due to directional dominance and due to interactions between specific genotypes. There was contradictory evidence whether the genetic control of this trait followed the additive-dominance model. The (Wr–Vr) differences were consistent over eight arrays. On the other hand the regression coefficient of Wr on Vr deviated significantly from unity but not from zero indicating the presence of non allelic interactions and/or the absence of dominance effects. Hence, further analysis was abandoned.

Discussion

In groundnut, there has been no previous attempt to select parents on the basis of D^2 statistics, to develop a full diallel and to test it over a number of environments. This experiment was a large one in terms of genotypes included and the design differs from those of most previously reported experiments. In the previous experiments, genotypes were grown over one or two environments (Parker et al. 1970; Wynne et al. 1970, 1975; Garet 1976; Gibori et al. 1978) and inferences were derived from results based on individual environment.

Of the different statistical methods of diallel analysis employed, first of all Griffing (1956a) and Hayman (1954a) methods were used initially to detect and evaluate non-additive genetic variance. The Wr/Vr graphs in Hayman (1954b) analysis were subsequently used in differentiating the distribution of dominant and recessive alleles in the pure lines. The mean squares for some common items estimated by combining ability analysis and Hayman's approach were similar. Further, variance due to b_1 was equivalent to the comparison 'parents vs hybrids', and the reciprocal cross effects were equivalent to maternal effects, c, plus residual reciprocal effects, d.

In the genetic analyses the validity of estimates and inferences derived from Hayman's approach depend upon the fulfilment of the basic assumptions of the analysis. In this context, two broad general tests, regression of Wr on Vr and the consistency of (Wr–Vr) over arrays, were employed. The graphical analysis detected the failure of assumption(s). The only possible test of a specific assumption was that of reciprocal differences among crosses; for this, the analysis of variance of reciprocal effects clearly demonstrated significant differences.

To aquire insight into the genetic architecture of these two traits, let us have a look at the basic concepts on which these two methods operate. Hayman's (1954b) approach is based on genetical methods of gene action and provides additional statistics to those supplied by the analysis of variance of the diallel table. These analyses provide a detailed description of the relative genetic properties of the inbred lines. Combining ability approach is based on the statistical methods of gene action. Griffing (1956a, b, 1958) stressed the statistical concept of general and specific combining ability in conjunction with loss of some genetic information since the inbred lines themselves are neglected; the genetic variation was expressed in terms of only two statistical parameters, i.e., the variances due to general and specific combining abilities which consequently restricted the genetic variability to only two components of variation; this approach was restricted to F1 families. The two methods operate under similar assumptions given by Hayman (1954b). The regression line in the Wr/Vr graph, in the presence of non-allelic interactions, will have a slope deviating from unity, therefore, making interpretation of the graph impossible. Griffing's approach provides, neither any test nor estimate of epistasis; instead, these effects, if present, as clearly indicated by Griffing, form a specific part of the variances due to general and specific combining ability. In every generation of selfing, the contribution of dominance as well as interactions involving dominance would decrease by one half. But the specific combining ability effects will not vanish because they measure additive × additive effects even if the material has become homozygous.

With regard to an Wr/Vr graph, the expectations for the two statistics of F1 generation are:

$$\mathrm{Wri} = \tfrac{1}{2}\mathrm{D} - \tfrac{1}{4}\mathrm{F} \quad \text{and} \quad \mathrm{Vri} = \tfrac{1}{4}\mathrm{D} + \tfrac{1}{4}\mathrm{H}_1 - \tfrac{1}{4}\mathrm{F}\,.$$

In the absence of dominance ($h = 0$), within the limits of sampling error, all the Wri and Vri would cluster at a single point where $\mathrm{Vri} = \tfrac{1}{4}\mathrm{D} = \tfrac{1}{4}\mathrm{VP}$ and $\mathrm{Wri} = \tfrac{1}{2}\mathrm{D} = \tfrac{1}{2}\mathrm{VP}$. At this point the regression line forms a tangent to the limiting parabola and will have a non-significant regression value. In the presence of detectable non-allelic interactions it is not possible to draw conclusive results from the graphs. It is obvious that each method provides unique information about the nature of genetic system, and together they more clearly resolve the mechanisms of inheritance better than do each alone.

For both the traits, the 8 × 8 diallel population does not appear to fulfil all the assumptions underlying diallel analysis. Thus a simple genetic basis of quantitative variation was found to be inadequate. When such discrepancies occur, one routinely manipulates his data to salvage as much information as possible by eliminating those arrays which cause most of the discrepancies. If non-allelic inter-actions are the sole cause of disturbance, removal of one or two parents showing such interaction is often enough to make the remaining diallel data conform to an additive-dominance model not complicated by epistasis and correlated gene distribution. For number of pods, however, no sufficient improvement of the Wr/Vr graph was achieved by the application of array elimination technique. In an attempt to discover whether the epistasis postulated was general to all the parents, or was a property of only a few, omission of one or two supposedly epistatic parents did not restore the rectilinear relation between Wr and Vr with unit slope. The results suggested that a model more complex than one or two epistatic parents superimposed on an additive-dominance scheme of gene action must be invoked to describe the genetic basis of parental difference of this character. The genic system controlling this character showed very strong gene interaction effects, and these effects are on the whole advantageous in that they lead to increased number of pods.

The genetic control for pod yield in this material was not clear, for Wr was not at all a linear function of Vr. For this trait, Gibori et al. (1978) observed ambi-directional dominance and non-significant H_1; Cahaner et al. (1979) noticed dominance for a lower manifestation; Sandhu and Khehra (1976) observed larger non-additive genetic variance.

Since variances due to general and specific combining ability were highly significant for both the traits, it seemed their inheritance was conditioned by all three kinds of gene effects, i.e., additive, dominance and epistasis; further, the estimated variances due to general and specific combining ability for both of the characters were biased to an unknown degree by the presence of epistasis.

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