HETEROSIS IN RELATION TO GENETIC DIVERGENCE AND SPECIFIC COMBINING ABILITY IN GROUNDNUT (ARACHIS HYPOGAEA L.)

V. ARUNACHALAM¹, A. BANDYOPADHYAY¹, S. N. NIGAM² and R. W. GIBBONS²

¹National Research Centre, IARI Regional Station, Rajendranagar, Hyderabad 500030, India ²Groundnut Improvement Program, International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru P.O. 502324, Andhra Pradesh, India

Received 1 February 1983

INDEX WORDS

Arachis hypogaea, genetic divergence, heterosis, combining ability, diallel crosses, D^2 statistic.

SUMMARY

The frequency and magnitude of heterosis were examined in relation to genetic divergence among parents in two diallel cross experiments in groundnut. The parents were grouped into clusters based on their divergence. The range, mean and standard deviation of the intra- and inter-cluster divergence were used to define four divergence classes. The frequency of heterotic crosses and the magnitude of heterosis for yield and its components were found to be higher in crosses between the parents in intermediate divergence classes than extreme ones. The results agreed well with the overall status of the specific combining ability of these crosses.

INTRODUCTION

Genetic divergence, as one of the criteria of selection of parents is, in general, considered in plant breeding as a mean to generate crosses which segregate in later generations into genotypes transgressing the performance of the better parent (Murty et al., 1962; Timothy, 1963). However, transgression or F_1 heterosis does not always occur when divergent lines are crossed (Cress, 1966; Matzinger & Wernsman, 1967; Busbice & Rawlings, 1974). Genetic background for transgression or heterosis has been studied for characters governed by a single gene with two or multiple alleles or two linked loci (Falconer, 1964; Cress, 1966; Arunachalam, 1977). It has been shown (Arunachalam, 1977) that not only pure dominance and its interactions but additive \times additive epistasis also can cause heterosis.

 F_1 heterosis is of direct interest for developing hybrids in cross-pollinated crops, but it is also of importance in self-pollinated crops. Such heterotic crosses may produce desirable transgressive segregants in advanced generations. Thus when an initial choice of parents has to be made to obtain heterosis it is important to ascertain the level of parental divergence. It was shown earlier that very high or very low parental divergence failed to result in heterosis in triticale (Srivastava & Arunachalam, 1977).

In an earlier paper Arunachalam et al. (1982) reported about the heterotic potential of single crosses in groundnut in two diallels, one with 15 parents (15-DL), selected essentially for productivity, and the other with 10 parents (10-DL), some of which

were resistant to some foliar diseases. Heterosis in the F_1 diallel crosses was evaluated for 15 characters in relation to the general combining ability (gca) of the parents.

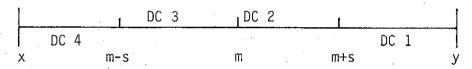
Data from these experiments were used to study the levels of parental divergence.

MATERIALS AND METHODS

Information on the parents used in the two diallel crosses is given in Table 1. Other details of the experiments were reported in Arunachalam et al., 1982.

The following procedure was used to classify the parental genetic divergence in four divergenc classes (DC1, DC2, DC3 and DC4).

- 1. Based on the divergence between the parents, as measured by the D^2 statistic, the parents were grouped into distinct clusters (Table 1) using TOCHER's method described by RAO (1952). The intra- and inter-cluster distance, D, were calculated.
- 2. The mean (m) and standard deviation (s) of those intra- and inter-cluster D-values were computed. Of course, an intra-cluster D-value is not available for clusters containing a single variety. The minimum (x) and the maximum (y) values among the intra- and inter-cluster distance were also determined.
- 3. Using m and s the range of intra- and inter-cluster D-values was divided into four divergence classes.



For example, in 10-DL, 10 parents were grouped into 6 clusters of which 4 contained a single variety each (Table 1). Obviously intra-cluster D-values for those 4 clusters did not exist. Thus there were 15 inter-cluster but only 2 intra-cluster D-values. Their mean, m, was equal to 12.9, s = 3.8, x = 4.9, and y = 19.6.

The four intervals for the four divergence classes are then:

DC1 = 16.70 to 19.60; DC2 = 12.90 to 16.69; DC3 = 9.10 to 12.89; DC4 = 4.90 to 9.09.

In the same manner, the intra- and inter-cluster D-values for 15-DL, which ranged from 4.0 to 22.4, with m = 13.4 and s = 4.5, were assigned to divergence classes.

4. For each of the 15 characters, the desirable direction for improvement was considered. The actual heterosis occurring in each F_1 was calculated as the percent improvement over the value of the better parent. This was done only if the F_1 exceeded the better parent in the desired direction significantly (at 5% level of significance), as determined by a t-test. For each heterotic cross the divergence class to which the intraor inter-cluster D-value of their parents belonged was established. For example, the F_1 from the cross Chalimbana \times EC 76446 (292), which was heterotic for 2 characters was obtained from parents whose D-value belonged to DC1 (see Table 2). Thus the frequency with which heterotic crosses could be associated with divergence classes was determined. The mean heterosis value and the range of heterosis values of crosses associated with each divergence class were obtained (Table 3).

The procedure, as detailed in Arunachalam & Bandyopadhyay (1979), was fol-

GENETIC DIVERGENCE IN GROUNDNUT

Table 1. Clusters, based on genetic divergence, of parents involved in two diallel crosses in groundnut.

	Cluster	Parents	Botanical Group*	GCA**	·
15-parent	1	Robut 33-1	VB	H	
diallel		TG 16	SB	L	
G.2		Florunner	VR	$\mathbf{L}_{;}$	•
	2 .	Pol. 2	SB	Ľ	
		Argentine	SB	H	
		GAUG 1	SB	L	
	3	M 13	VR	H	
		MK 374	VB	Н	
		NC Ac 2731	VR	H	·
		Shantung KU No.	203 SB	Η .	
	4	Gangapuri .	VL	L	
		MH 2	VL	${f L}$	
	5	NC Ac 1107-	. VB	H	The second second
	6	NC Ac 2768	VB	L	
	7 -	28-206	VB	H	
10-parent	1 .	Robut 33-1	VB .	Н	
diallel		Mani Pintar	VB	H	•
		PI 298115	VB	H	•
	2	PI 259747	VL	L	
	•	EC 76446 (292)	VL	H	
		NC Ac 17090	VL	L	•
	3	87/4/7	VB	L	
	4	Makulu Red	VB	L	
	5	Chalimbana	VR	H	
	6	Chico	SB	L	

^{*}SB = Spanish Bunch; VL = Valencia; VB = Virginia Bunch; VR = Virginia Runner

lowed to determine the specific combining ability (sca) status over all 15 characters as high (H) or low (L). The procedure consisted, in brief, of the following:

i) As in the case of heterosis, the desirable direction of improvement of each character was considered in the case of sca also.

Table 2. Information on five heterotic crosses in a 10-parent diallel cross in groundnut.

Cross	Number of characters for which the F	Cluster to parents b		Corresponding intra- or inter-cluster	Diver- gence class
	was heterotic	female	male	D value	Class .
Chalimbana × EC 76446 (292)	2	5	2	17.12	1
Mani Pintar × Chalimbana	4 .	1	5	13.67	2
Robut 33-1 × EC 76446 (292)	2	1	2	9.75	3
PI 298115 × PI 259747	3	1	2	· 9.75	3
Robut 33-1 × Mani Pintar	1 .	1	1	7.70	4
NC Ac 17090 × PI 259747	1 .	2	2	4.90	4

^{**} H = High; L = Low

4

03

84

24

27

Table 3. Average heterosis in F₁ in relation to divergence between parents in groundnut.

5		,					1									
	DC	SH^3	N N	LA	$S\Gamma$	FT	PB	SB	MS	VS	MP	RP	SP	TW		SY
	115-DL ¹	m ²	. 1	41	. 1	10	=======================================	ı	10	ı	1		1	·	1	ı
		- 1	1.	36-46	ı	1	1	1	ı			1	1	ı		1
		nh –	٠,	7	1	_	_	1	_				ı	ı		!
	10-DL	n L	27	42	1	1	1	7.1	· I			06	ı	84		284
		- -	T	2968	I	1	1	64-80	ı			88-92	1			
		– qu		9	ı	1	1	ω,	J			2 ·	į			_
	215-DL	– m	. 33	36	43	12	. 82	180	14			76	1	73		151
		- -	ı	27-44	25-65	9–17	71–93	95–273	1			38-119	1	36-104		68-22
		- qu	7	4	. 2	6	2	Ś	—				ı			9
	10-DL	m 37	20	47	36	12		62	ı			, <u>6</u>	1	7.		217
		- I	1,	36-70	32–39	ı	1	59-64	ı			80-106	1	44-113		53-32
		nh 1		9	7.	_	!	7	.I			5	ı	· ~		4
	315-DL	m 47	24 ·	41	46	12	. 63	63	18			71	55	52		. 06
		r 41–53	21–28	41-41	34-58	9-20	36-94	34-111	1			41 - 106	47-63	31–94		39-18
		n h 2	4	7	7	11	13.	. 5	_			9	2	4		12
	10-DL	m 67.	. 22	40	1	23	84	155	1			94	1	40		164
		r 25–106	17-30	23-52	ı	, I ·	63-118	100-205	ı			38-138	1	27-55		46-34
		nh 5	∞	S	I	_	9	3	ı			6	1	7		10
	415-DL	- m	ı	39		12	55.	49	ı			1	26	40		73
		 -	1	34-43	1	1114	38-75	1	1			ı	1	29-97		43–10
		- qu	i	7	!	S	m		1			1	_			3
	10-DL	_ m	31	ı	1	41	53	112	1			1	1	1		51
			1	1	1	I		46-293	1			1	1	1		1
		uh –	_	ı	1	_		2	1			. · . . · .	1	1		_

m = Average heterosis (in %), r = Range of heterosis (in %); nh = Number of crosses showing significant heterosis. 15-DL = 15 parent diallel; 10-DL = 10 parent diallel; DC = Divergence class.

'SH = Seeding height; NL = Number of leaves; LA = Leaf Area; SL = Specific leaf weight [= (Dry weight of NL)/LA]; FT = Flowering time; PB = Number of primary branches; SB = Number of secondary branches; MS = Mean number of seeds in pod; VS = Variance of seed number in pods; MP = Per cent of mature pods [= (Number of mature pods/Total number of pods) × 100]; RP = Recovery percentage = [Number of mature pods/(Total number of pods + Number of aerial pegs)] × 100; SP = Shelling percentage; TW = 100-kernel weight; PY = Pod yield; SY = Seed yield; Dashes indicate that no heterosis was observed for that character in that class. ii) The sca effects were tested whether they were significantly different from zero on either side by a two-tailed t-test at 5% level of significance.

iii) k, the mean-value of all the significant sca effects, was calculated.

iv) k was used as the norm. Significant sca effects whose values were greater than or equal to k, received a score +1; those significant effects which were less than k received a score -1; all non-significant effects received a zero score.

v) A final sca score was obtained for each cross by addition of the individual scores for each character. The mean across the crosses was calculated. A cross whose final score was greater than or equal to this mean was allotted a High (H) overall sca status and one whose final score was less than this mean, a Low (L) overall sca status.

The crosses were grouped into the classes H or L based on their overall sca status. The frequency of crosses falling in each of these 2 sca classes was scored for each individual divergence class.

RESULTS

As reported earlier (Arunachalam et al., 1981), 7 clusters were formed from the parents of 15-DL and 6 from those of 10-DL (Table 1).

The mean and standard deviation of intra- and inter-cluster D-values were 13.4 and 4.5 respectively in 15-DL which were comparable to the corresponding values of 12.9 and 3.8 in 10-DL except that 10-DL had 17 D-values and 15-DL 25.

The average heterosis for 15 characters in the 4 divergence classes is given in Table 3. DC 3 showed significant heterosis for 14 and 10 characters and DC 2 for 11 and 12 characters in 15-DL and 10-DL, respectively. DC 1 showed heterosis for 5 and 7 characters and DC 4 for 10 and 6 characters in 15-DL and 10-DL, respectively. The frequency of heterotic crosses, the range of heterosis and the average heterosis were similarly high for individual characters in DC 3 and DC 2 (Table 3).

Heterosis occurring in DC 1 (though in a low frequency) could be explained by the high parental divergence associated with that divergence class. Such explanation is impossible for the heterosis occurring in DC 4 which had the lowest parental divergence. It was then found necessary to relate heterosis in the various divergence classes with the sca status of the crosses. It was found (Table 4) that 45 and 48% of the total heterotic crosses had high overall sca status in 15- and 10-DL respectively. Of the 40 heterotic crosses with high and 49 with low overall sca in 15-DL, DC 3 accounted for 19 and 22 and DC 2 for 14 and 15 crosses respectively, followed only by DC 1 or DC 4. Similar was the trend in 10-DL (Table 4). The number of crosses made in each divergence class was different; it was, however, much higher in DC 2 and DC 3 as compared to DC 1 or DC 4 (Table 4). The high number of heterotic crosses found in DC 2 and DC 3 was thus based on large frequencies of crosses made in them. This lends further support to the general superiority of DC3 and DC2 mentioned earlier.

The occurrence of as high as 7 heterotic crosses in 15-DL in DC 4 with the lowest parental divergence and low sca may seem to be unusual. But 6 of them showed heterosis for only one character and 1 for two characters. Further, only 4 crosses showed more than 35% heterosis. They were NC Ac 2731 × M 13 (38% for PB, number of primary branches), NC Ac 2731 × MK 374 (62% for PY, pod yield), Pol. 2 × Argen-

Table 4. Frequency of heterotic crosses in relation to its sca and parental divergence in groundnut.

DC	sca	H		L		Total	
		15-DL	10-DL	15-DL	10-DL	15-DL	10-DL
1 .	h	_	4	5	6 .	5	10
· ·	t	_	4	12	10	12	14
2	h	14	6	15	9	29	15
_	t.	28	6	42	14	70	20
3	h	19	16	. 22	17	41	33
-	t.	36	24	48	20	84	44
4	ĥ	7	5	7	2 .	14	7
•	t.	22	8	22	4	44	12
Total	h	40	31	49	34	89	65
	·· t	86	42	124	48	210	90

DC = Divergence class; 15-DL = 15 parent diallel; 10-DL = 10 parent diallel; h = number of crosses heterotic for at least one character; t = number of crosses made; H = High; L = Low.

tine (42% for variance of distribution of seeds within pods) and Florunner × Argentine (76% for PB and 97% for PY). In DC 4 of 10-DL, EC 76446 (292) × PI 259747 showed heterosis with low sca for SB, number of secondary branches (81%) only and PI 298115 × Mani Pintar for PB (53%) and SB (46%). Most of the 9 crosses in DC 4 which were heterotic with low sca, involved parents one of which had high and the other low gca status (which could have resulted in parental divergence), or a parent adapted to Indian environments for a long time and another from the exotic germplasm maintained at ICRISAT.

DISCUSSION

This study shows that there is an optimum level of genetic divergence between parents to obtain heterosis in the F_1 generation. The optimum level is provided by the divergence classes 2 and 3. As such, it may not be logical to advocate the use of extremely divergent parents to obtain heterotic combinations. This study demonstrated a method of classifying parental divergence and selecting pairs of parents from intermediate classes to provide the greatest chance of obtaining heterotic F_1 's.

The method gains support from a parallel study of a 10 × 10 diallel cross in triticale (Srivastava & Arunachalam, 1977) where it was also shown that DC 1 and DC 4 contained a low frequency of heterotic crosses compared to DC 3 and DC 2. However, in that study, the divergence classes were obtained by dividing the total range of intra- and inter-cluster D-values equally. We have now found that the standard deviation of the intra- and inter-cluster D-values can be used to take into account the variation among D-values. When studies on parental divergence and heterosis on different material or crops are to be compared, it is necessary to take into account the variation in the number and magnitude of intra- and inter-cluster D-values. The suggested modification provides a standardisation.

In this study, the occurrence of differential frequencies of heterotic crosses in various divergence classes was related to parental divergence and/or specific combining ability

GENETIC DIVERGENCE IN GROUNDNUT

of the crosses. For example, about half of the total heterotic crosses had high sca to explain heterosis. The heterotic crosses which occurred in DC 4, characterised by low parental divergence, had either high sca or possessed heterosis for one character only. When the magnitude of heterosis was substantial for that character, the parents had, in general, other contrasting attributes like High vs. Low gca status or adaptation to Indian vs. exotic environments.

The results of this study were based on an *aposteriori* analysis of experimental data. Nevertheless it would be of interest to check the efficiency of selection of parents based on genetic divergence as envisaged here in other studies as well.

REFERENCES

ARUNACHALAM, V., 1977. Heterosis for characters governed by two genes. J. Genet. 63: 15-24.

ARUNACHALAM, V. & A. BANDYOPADHYAY; 1979. Are multiple cross-multiple pollen hybrids an answer for productive populations in *Brassica campestris* var. brown sarson? I. Methods for studying 'mucromphs'. Theor. appl. Genet. 54: 203–207.

ARUNACHALAM, V., A. BANDYOPADHYAY, S. N. NIGAM & R. W. GIBBONS, 1982. Heterotic potential of single crosses in groundnut (*Arachis hypogaea* L.). Oléagineux 37: 415-418.

BUSHICE, D. H. & J. O. RAWLINGS, 1974. Combining ability in crosses within and between diverse groups of alfalfa introductions. Euphytica 23: 86-94.

CRESS, C. E., 1966. Heterosis of the hybrid related to gene frequency differences between two populations. Genetics 53: 269-274.

FALCONER, D. S., 1964. Introduction to quantitative genetics. Oliver and Boyd, Edinburgh and London. 365 pp.

MATZINGER, D. F. & E. A. WERNSMAN, 1967. Genetic diversity and heterosis in *Nicotiana*. I. Interspecific crosses. Der Züchter 37: 188–191.

MURTY, B. R., G. S. Murty & M. V. Pavate, 1962. Studies on quantitative inheritance in *Nicotiana tabacum* L. Der Züchter 32: 361-369.

RAO, C. R., 1952. Advanced statistical methods in biometric research. John Wiley, New York. 390 pp.

Srivastava, P. S. L. & V. Arunachalam, 1977. Heterosis as a function of genetic divergence in triticale. Z. Pflanzenzüchtg 79: 269–275.

TIMOTHY, D. H., 1963. Genetic diversity, heterosis and the use of exotic stocks in maize in Columbia. Statistical Genetics and Plant Breeding Symposium, Raleigh, 1961, NAS-NRC Publ. 982: 581-593.