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LIMITS TO GENETIC DIVERGENCE FOR OCCURRENCE OF HETEROSIS—EXPERIMENTAL EVIDENCE FROM CROP PLANTS

V. ARUNACHALAM AND A. BANDYOPADHYAY

National Research Centre, Indian Agricultural Research Institute, Regional Station, Rajendranagar, Hyderabad-500 030

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ABSTRACT

Two experiments in groundnut (*Arachis hypogaea* L.) and one in rapeseed (*Brassica campestris* L.) involving varying number of crosses made to diallel and line × tester designs were studied with the aim of relating genetic divergence among parents with the frequency and magnitude of heterosis in the F_1 generation. A method was devised to delineate the divergence among parents into four divergence classes, DC1, DC2, DC3 and DC4. Heterosis was computed as per cent improvement over the value of better parent, for three important components of yield in each crop. Genetic divergence was measured by D^2 statistic. If m is the mean and s the standard deviation of divergence values (given by D^2) among parents, it was postulated that two parents whose genetic divergence falls between (m-s) and (m+s), i.e., in the classes, DC2 or DC3, when crossed will have higher chances of producing high frequency and magnitude of heterosis when compared to a cross whose parental divergence falls outside the limits, (m-s, m+s).

Heterosis is of direct relevance for developing hybrids in cross-pollinated crops. But it is also of importance in self-pollinated crops. In view of the fact that large F_2 populations of every cross studied in F_1 cannot be screened for further breeding, the breeder is often constrained to select a few crosses in F_1. In that context, heterosis may be a key parameter for selection. Recent studies in groundnut (Pungle, 1983) show that heterotic F_1's generate a higher frequency of productive derivatives in F_5 and later generations when compared to non-heterotic F_1's.

It is increasingly realised that crosses between divergent parents usually produce greater heterosis than those between closely related ones as was pointed out long time ago by Hayes and Johnson (1939) and East and Hayes (1942). In practical situations, it can be reasoned that heterosis occurs because of parental divergence. But when divergent parents are crossed, heterosis is not found to occur always (Cress, 1966). It is essential therefore to explore the possible limits to parental divergence within which there are reasonably high chances for occurrence of heterosis.

This paper is an attempt in this regard using experimental data from groundnut (*Arachis hypogaea* L.) and rapeseed (*Brassica campestris* var. brown *sarson*).

MATERIALS AND METHODS

In groundnut, the two experiments were diallel crosses with reciprocals, one involving 15 parents (GF) ane the other 10 parents (GT). The parents were chosen primarily on their yield performance, geographic origin or resistance to diseases, especially rust and leaf spots. The diallel crosses were evaluated in randomised blocks designs for combining ability and heterosis in F_1 generation. The genetic divergence among the parents was measured by Mahalanobis' D^2 statistic (Rao, 1952).

The experiment in rapeseed (BS) involved 60 single crosses made between 10 female and 6 male parents in a line × tester design and studied in the same manner as in groundnut.

Three important yield components were considered in each crop—pod yield (PW), 100-kernel weight (TW) and shelling percentage (SP) in groundnut and length of main axis (LM), number of siliquae on main axis (SM) and number of seeds per siliqua (SS) in rapeseed. Heterosis was calculated in all the experiments as the percent improvement of F_1 over better parent for every character.

A method was devised to delineate parental divergence in four divergence classes (DC). To take into account the variable magnitude of variation in parental divergence in various experiments, the mean (m) and standard deviation (s) of the values of divergence were calculated. The divergence classes were defined as follows :

DC1 : $D^2 >$ or $= (m+s)$
DC2 : $D^2 < (m+s)$ and $>$ or $= m$
DC3 : $D^2 >$ or $= (m\text{-}s)$ and $< m$
DC4 : $D^2 < (m\text{-}s)$

It may be noted that in this set-up, DC1 and DC4 are the extremely divergent classes in either direction. This method was found to be the best of the 3 methods tried. ~~(see 'Discussion')~~.

For each cross, the divergence class to which the D^2 value between their perents belonged was established. The number of crosses (n) falling in each divergence class, the proportion of crosses showing positive values of heterosis (p) and the mean for each character over such crosses(x)were computed, Since, in this process even a very low positive value of heterosis which may not be of great importance would get included, it was decided to set a norm for heterosis and obtain frequnecies of crosses showing heterosis greater than or equal to the norm. The norm (k) was taken to be the mean heterosis value of these crosses with positive value of heterosis for that character. The proportion of crosses (q) showing a heterosis value greater than or equal to k and the mean (y) for each character over such crosses were also worked out. In addition, the maximum value of heterosis recorded in each divergence class for each character was noted.

The divergence classes were ranked for their relative order of importance on the basis of the values of p, x, q and y separately. However, the relative order could vary in each case, also in each experiment and for each character. In order to come to a final conclusion jointly on the ranking based on p, x, q and y, a scoring process was adopted. The divergence class which gave the highest value of p was allotted a score 1, the next best a score 2 and so on. Whenever there was a tie, the classes involved in the tie received the same score. The scores over p and x were added across the three characters to obtain a final score for each divergence class (Tables 2 and 4). Similar procedure was adopted for q and y (Tables 3 and 5). It must be noted that the divergence class with the lowest total score will be the most desirable one with high frequency of heterotic crosses and high average magnitude of heterosis.

RESULTS

The range of D^2 was substantial in all the experiments (Table 1) justifying their arrangement in four divergence classes.

Heterosis was considered separately for direct and reciprocal crosses in the groundnut dialles, GF and GT. The divergence class DC2 obtained the top

TABLE 1

Mean (m). Standard deviation (sd) and range of divergence values

	m	sd	maximum D^2	minimum D^2
GF	165.61	111.75	528.00	9.34
GT	158.00	92.88	383.00	17.96
BS	5.18	3.98	19.03	0.51

TABLE 2

Proportion of crosses with positive heterosis and their average magnitude for 4 divergence classes in groundnut

	DC	n	PW			TW			SP			Score
			p	x	t	p	x	t	p	x	t	
	1	18	39	41	120	17	18	24	11	15	20	15
GFD	2	27	37	79	196	37	25	104	33	9	35	12
	3	44	57	37	153	39	11	33	16	13	47	14
	4	16	31	30	72	31	16	47	19	11	15	19
	1	18	17	44	83	17	4	10	0	0	0	22
GFR	2	27	37	48	116	33	29	94	30	14	63	11
	3	44	57	37	113	41	13	32	23	6	15	15
	4	16	44	30	65	50	25	51	56	10	26	12
	1	7	86	47	108	15	19	19	15	1	0	15
GTD	2	11	1	254	254	16	3	3	0	0	0	19
	3	20	65	66	208	25	25	44	30	7	20	10
	4	7	71	46	164	14	23	23	14	8	8	16
	1	7	57	103	320	14	84	84	15	24	24	15
GTR	2	11	82	121	273	36	48	113	55	15	19	10
	3	20	90	78	315	25	33	56	20	12	16	15
	4	7	71	66	135	43	10	15	14	6	6	20

t = maximum heterosis observed in the class; for other symbols, see text rank based on the total score across p and x or q and y in 15-parent diallel direct crosses (GFD), 15-parent diallel reciprocal crosses (GFR) and 10-parent diallel reciprocal crosses (GTR) while DC3 was on top in the case of 10-parent diallel direct crosses (GTD), However DC3 occupied second position in GFD and GTR based on p, x (Tables 2 and 3). But highest heterosis for each character was recorded by either DC2 or DC3 in most of the cases (cf. values of t in Table 2).

TABLE 3

Proportion of crosses showing more than overall average heterosis and average magnitude given by those crosses for characters in 4 divergence classes in groundnut

	DC	n	PW		TW		SP		Score
			q	y	q	y	q	y	
	1	18	11	88	11	24	7	21	15
GFD	2	27	22	120	22	37	11	20	9
	3	44	14	85	7	29	5	29	16
	4	16	6	72	6	47	6	15	20
	1	11	6	83	0	0	0	0	22
GFR	2	27	15	91	11	70	11	29	9
	3	44	25	64	7	25	5	14	16
	4	16	13	52	31	36	19	18	13
	1	7	43	87	0	0	0	0	17
GTD	2	11	1	254	0	0	0	0	17
	3	20	20	124	20	29	15	13	9
	4	7	14	164	14	23	14	8	13
	1	7	14	320	14	84	14	24	13
GTR	2	11	45	198	18	85	36	17	9
	3	20	20	224	15	46	10	15	16
	4	7	29	120	0	0	0	0	22

For symbols, see text.

In the case of brown sarson, DC3 got the top rank based on p and x or q and y, followed by DC2. However DC4 was as good as DC3 based on p and x and as DC2 based on q and y. It must be noted that in this experiment, several zero values were encountered and the values of p, x, q and y were much lower than those in the experiments with groundnut (Tables 4 and 5). The large number of zero values, in particular, might be responsible for equating DC4 with DC2 or DC3.

The judgement on the importance of various divergence classes would become more precise if the results were based on a large number of crosses.

TABLE 4

Proportion of crosses showing positive heterosis and average magnitude of characters in 4 divergence classes in brown sarson

		LM			SM			SS			
DC	n	p	x	t	p	x	t	p	x	t	Score
1	12	0	0	—	8	1	1	33	9	13	17
2	11	9	22	22	0	0	—	36	7	9	15
3	30	10	6	10	17	14	30	30	9	28	12
4	7	14	5	5	0	0	—	43	13	15	12

t=maximum heterosis observed in the class; for other symbols, see text.

TABLE 5

Proportion of crosses showing more than overall average heterosis and average magnitude given by those crosses for 3 characters in 4 divergence classes in brown sarson

DC	n	LM		SM		SS		
		q	y	q	y	q	y	Score
1	12	0	0	0	0	17	12	15
2	11	9	22	0	0	10	9	13
3	30	3	10	10	23	10	17	10
4	7	0	0	0	0	25	15	13

For symbols, see text.

Since our primary interest was on the relationship between parental divergence and heterosis, it would be worthwhile to pool the scores obtained for p, x and q, y in each experiment and over all the evperiments. The results clearly showed the superiority of DC2 and DC3 in both the groundnut diallels, GF and GT, and when pooled over them (G). These results were found true in the experiment on rapeseed (BS) and when pooled over all the experiments (T) as well (Table 5).

DISCUSSION

The experimental evidence provided in the two crops has suggested a consistent relationship between parental divergence and F_1 heterosis. The relationship was arrived at by a method with adequate precautions to ensure its validity.

TABLE 6

Scores based on heterosis in 4 divergence classes

DC	1			2			3			4		
	a	b	s	a	b	s	a	b	s	a	b	s
GFD	15	15	30	12	9	21	14	16	30	19	20	39
GFR	22	22	44	11	9	20	15	16	31	12	13	25
GF	37	37	74	23	18	41	29	32	61	31	33	64
GTD	15	17	32	19	17	36	10	9	19	16	13	29
GTR	15	13	28	10	9	19	15	16	31	20	22	42
GT	30	30	60	29	26	55	25	25	50	36	35	71
G	67	67	134	52	44	96	54	57	111	67	68	135
BS	17	15	32	15	13	28	12	10	22	12	13	25
T	84	82	166	67	57	124	66	67	133	79	81	160

a=Score based on p, x; b=score on q, y;
s=a+b; GFD=Direct crosses of GF; GFR=Reciprocal crosses of GF; GTD=Direct crosses of GT; GTR=Reciprocal crosses of GT; G=over GF and GT; T=over all experiments; for other symbols, see text.

The logic of this method was evaluated in the light of two others that could be conceived in this context. In the first, the divergence classes were so defined as to contain equal number of crosses. The D^2 values were arranged in descending order of magnitude. Starting from the top, the total number of D^2 values were divided into four equal parts to provide the divergence classes, DC1 to DC4.

In the second, the total range of D^2 values was divided into 4 equal parts. The divergence classes were so set up that the range of D^2 values in each of them was equal. For example, in the case of GF (Table 1), the total range of D^2=528.00 - 9.34=518.66. The range for each divergence class was therefore= 518.66/4=129.67. The divergence classes were then defined as :

DC1 :	D^2-values in the range	528.00 to 398.33
DC2 :	,,	398.32 to 268.65
DC3 :	,,	268.64 to 138.97
DC4 :	,,	138.96 to 9.29

However, the number of crosses falling in each divergence class would be unequal.

Both these methods could not score over the method used in this paper, since they did not take into consideration the varying magnitudes and variance of D^2-values from experiment to experiment and from crop to crop.

Further to take into account unequal number of crosses and heterotic ones, falling in various divergence classes, the percentage of heterotic crosses, p and q were used as parameters in the decision process. In addition, both the general level of heterosis (given by average heterosis value of those crosses showing positive heterosis) and a selected level (over a norm defined by overall mean heterosis) provided by the values x and y were considered in conjunction. While the former would take into account the magnitude of F_1 improvement over better parent, however slight it might be, the latter would give weightage to those F_1's showing substantial improvement whose F_2's a breeder would like to search on priority for desirable transgressive segregants (refer Pungle, 1983 for experimental evidence on groundnut in this connectian).

The results ~~have than~~ brought out the consistent superiority of DC2 and DC3 over DC1 or DC4 as far as occurrence of a high proportion of heterotic crosses or of a high value of heterosis was concerned. Studies on triticale (Srivastava and Arunachalam, 1977) support these results, though delineation of divergence classes was not made there as precisely as in this study. The concept that there are limits to parental divergence for optimum expression of heterosis was also set by past studies on crosses among divergent geographic races in maize (Moll, Lonnqvist, Fortuno and Johnson, 1965). ~~The present~~ study provides sufficient ground for conceiving those limits and for the hypothesis in general that——if m and s are the mean and standard deviation of the values of divergence (given by D^2) among parents, the chances for the occurrence of a high frequency of heterotic crosses and with high values of heterosis are more when the parents are chosen to have their divergence in the interval (m—s, m+s) compared to the crosses between parents whose divergence falls outside that interval.

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