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Elucidation of Genetic Mechanism Governing Heterosis in Pigeonpea [*Cajanus cajan* (L.) Millspaugh]

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ABSTRACT

Background: The findings of the present research will provide an indepth understanding of important parameters contributing to heterosis in pigeonpea.

Methods: Combining ability effects and heterosis of crosses were determined among 45 hybrids developed by crossing 10 elite pigeonpea genotypes in half diallel fashion. The combining abilities were estimated by using Griffing's, Method II and Model I.

Result: The SCA followed by MGCA (mean general combinig ability of parents) were observed as the most reliable parameters to predict heterosis. High *per se* performance of parents and high genetic diversity does not lead to high heterosis. The parents having high × low *per se* performance, good × poor GCA effects and medium genetic diversity resulted in high frequency of heterotic hybrids. The results indicated that the hybrid Paras × PA 624 exhibited maximum mid parent, better parent and standard heterosis for seed yield.

Key words: Combining ability, Genetic diversity, Heterosis, Pigeonpea.

INTRODUCTION

Heterosis results in more than 60% yield advantage in pigeonpea hybrids (Saxena *et al.,* 2006). However, the major milestone in pigeonpea hybrid breeding was achieved in the year 2010 when India released world's first commercial pigeonpea hybrid ICPH-8 which was soon followed by release of other commercial hybrids like ICPH 3762 and ICPH 2740. These developments revealed that in pigeonpea crop sufficient heterosis is available and there is an urgent need to exploit heterosis for breaking the yield plateau (<800 kg/ha). The genetic mechanism of heterosis still remains unclear to a large extent. The magnitude of heterosis depends on the relative performance of the inbred parents (Betran *et al.,* 2003) and hence mean yield of parents can be used as an important factor in heterosis prediction. Combining ability is widely used by several workers in pigeonpea to compare performance of lines in hybrid combinations (Singh and Singh, 2009). Heterosis may increase with increase in genetic diversity but greater divergence between parents not always results in heterosis (Moll *et al.,* 1965). The present study was conducted with the aim to measure interrelationship between combining ability, *per se* performance of parents, genetic diversity and heterosis.

MATERIALS AND METHODS

Experimental material and field trial

The 10 elite pigeonpea genotypes (Pusa 992, Paras, UPAS 120, PA 620, PA 623, PA 624, PA 625, PA 627, PA 626 and PA 622) were crossed in half diallel fashion during *kharif* 2017-18 at N.E.B.C.R.C. of Pantnagar to develop the 45 F_1's. Thus, the experimental material consisted of 56 genotypes including 10 parents, 45 F_1 hybrids and one check (Pant A 291). The 45 hybrids along with their parents and check variety were grown during the *kharif* 2018-19 in randomized block design with three replications. The observations were recorded on five randomly selected competitive plants of each genotypes from each replication on characters *viz.,* plant height (cm), number of primary branches/ plant, number of secondary branches/plant, number of pods/plant, pod length (cm), number of seed/ pod, 100-seed weight (g) and seed yield/plant (g). However, the data on number of days to 50 per cent flowering and number of days to maturity were taken on whole plot basis.

Statistical analysis

The combining abilities were evaluated by using Griffing's, (1956), Method II, Model I (Fixed effects). The GCA effects

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of both parents of hybrid were averaged to determine the mean GCA (MGCA) effect of the parents (Kumar *et al.,* 2015). The mean of *per se* performance of both parents of a hybrid (PM) and the mean grain yield of F_1's (HMY) were also calculated. Further, heterosis over mid parent (MPH %), better parent (BPH %) and standard check variety (SH %) were estimated to determine the different types of heterosis for seed yield per plant. The data recorded for various yield and attributing attributes were subjected to the estimation of morphological genetic diversity (GD) using the D^2 statistics (Mahalanobis, 1936). The clusters were prepared by following Tocher's method as proposed by Rao (1952). The genetic diversity classes were prepared by using method suggested by Arunachalam (1984). Parents were classified as good (G), average (A) and poor (P) combiners on the basis their overall GCA effects. If the GCA effects were significant in desirable direction then the parents were considered as good general combiner (G) and those significant towards undesirable direction were poor general combiner (P) while non-significant effects were designated as average general combiner (A). Similarly, crosses were also classified as good (G), average (A) and poor (P). The Pearson's correlation coefficients among PM, HMY, MGCA, SCA, GD, MPH%, BPH% and SH% were also calculated.

RESULTS AND DISCUSSION

Estimation of combining ability and heterosis

The analysis of variance revealed that mean sum of squares due to GCA and SCA effects were highly significant indicating that both additive and non-additive gene action are involved in governing inheritance of seed yield (Table 1). The σ^2 SCA were found to be higher than σ^2 GCA, indicating preponderance of non-additive gene effects. The presence of non-additive gene effects indicated that heterosis breeding will be rewarding in increasing seed yield. Phad *et al.,* (2007) also reported that dominance gene effect was involved in controlling seed yield. The results of heterosis estimation revealed that hybrid Paras × PA 624 showed maximum MPH, BPH and SH of 227.71%, 183.33% and 175.68% respectively (Table 2).

Table 1: The ANOVA for seed yield/plant (g) in pigeonpea.

Source of variation	Df	MSS
Replication	2	68.01
Treatment	54	2472.59**
Parent	9	136.74**
Hybrid	44	2106.88**
Parent *vs* hybrid	1	39586.07**
GCA	9	637.01**
SCA	45	861.63**
Error	108	4.95
σ^2 GCA		52.67
σ^2 SCA		856.62
$\sqrt{\sigma^2 SCA / 2\sigma^2 GCA}$		2.85

*Significant at 5% level, **Significant at 1% level.

Estimation of genetic diversity

The analysis of genetic diversity revealed presence of four different clusters (Table 3). The cluster I showed maximum mean for plant height (232.5), number of secondary branches (15.1), number of pods/plant (211.6) and seed yield/plant (52.1) hence the genotypes in this cluster can be used as donors for these traits. The cluster II was found to be the earliest maturing cluster (126.5) with highest number of primary branches (14.0). The cluster III was found had highest mean for pod length (5.2), number of seed per pods (4.5) and 100 seed weight (9.2).

Relationship between different parameters and heterosis

The MPH, BPH and SH were found to be perfectly positively correlated with each other (Table 4). The SCA effects were found to be positively and significantly correlated with the MPH (r=0.899**), BPH (r=0.918**) and SH (r=0.939**) respectively (Table 4). The significant linear regression of SCA effects and very high R^2 value further revealed that SCA was good determinant of heterosis (Fig 1). The regression analysis of SCA effects on heterosis indicated that 80.90%, 84.34%, 88.17% variation in MPH, BPH and SH is due to SCA (Fig 1). A critical analysis of Table 5 indicated that out of the 45 hybrids, 42 hybrids exhibited significant MPH, BPH and SH. Out of these 42 heterotic hybrids, 21 hybrids exhibited good SCA, 13 hybrids exhibited poor SCA and 8 hybrids exhibited average SCA effects. A critical analysis of Table 6 indicated that good SCA effects showed highest heterotic frequency (50.00%) followed by poor SCA (30.95%) and average SCA (19.05%) effects. These results clearly indicated that highest frequency of hybrids (50%) was reported in case of crosses having good SCA. The results indicated that SCA is the most important factor for determination of heterosis and is supported by Pandey *et al.,* (2015). The MGCA effects were found to be positively and significantly correlated with MPH (r=0.504**), BPH (r=0.526**) and SH (r=0.532**) respectively. The significant linear regression of MGCA on MPH, BPH and SH and high R^2 value revealed that MGCA was also a good determinant of heterosis (Fig 2). The regression analysis of MGCA effects on heterosis indicated that 25.41%, 27.73% and 28.38%, variation in MPH, BPH and SH is due to MGCA effects. The highest heterotic frequency (47.62%) was observed by crossing parents having good × poor combination while the poor × poor (7.15%) combination showed the least heterotic frequency. The good × good parental combination produce (23.81%) heterotic frequency. These results indicated that if the parents had good × poor GCA effects than it results in high heterotic frequency, however, the parents having good × good GCA effects produces a moderate level of heterotic hybrids. In present study, the mean GCA of both parents (MGCA) also emerged as another important factor which can be used in predicting the heterosis. The present study revealed that the GCA

Table 2: The estimates of different parameters for seed yield/plant.

Hybrids	PM	HMY	MGCA	SCA	GD	MPH	BPH	SH
Pusa 992 × Paras	50.0	72	4.49	-16.73**	1638.76	44.00**	38.46**	45.95**
Pusa 992 × UPAS 120	51.0	65	-4.945	-4.87*	122.857	27.45**	25.00**	31.76**
Pusa 992 × PA 620	51.5	102.33	2.53	17.52**	1638.76	98.71**	96.79**	107.43**
Pusa 992 × PA 623	49.5	101.33	1.975	17.63**	1638.76	104.03**	94.87**	105.41**
Pusa 992 × PA 624	43.5	131	5.35	40.55**	420.668	201.15**	151.92**	165.54**
Pusa 992 × PA 625	49.5	91.67	5.515	0.88	1638.76	85.19**	76.28**	85.81**
Pusa 992 × PA 627	43.0	131	3.015	45.21**	420.668	203.47**	151.92**	165.54**
Pusa 992 × PA 626	51.5	78	0.85	-3.45	395.178	50.97**	50.00**	58.11**
Pusa 992 × PA 622	52.5	81	7.905	-14.56**	395.178	54.29**	52.83**	64.19**
Paras × UPAS 120	49.0	62	-7.125	-3.51	1638.76	26.53**	24.00**	25.68**
Paras × PA 620	49.5	92	0.35	11.55**	184.336	85.86**	80.39**	86.49**
Paras × PA 623	47.5	95	-0.205	15.66**	184.336	99.30**	97.92**	92.57**
Paras × PA 624	41.5	136	3.17	49.91**	811.11	227.71**	183.33**	175.68**
Paras × PA 625	47.5	68	3.335	-18.42**	184.336	43.16**	41.67**	37.84**
Paras × PA 627	41.0	60	0.835	-21.42**	811.11	45.75**	25.00**	21.62**
Paras × PA 626	49.5	95	-1.33	17.91**	641.578	91.28**	85.06**	92.57**
Paras × PA 622	50.5	129	5.725	37.80**	641.578	155.45**	143.40**	161.49**
UPAS 120 × PA 620	50.5	51	-9.085	-10.59**	395.178	0.99	0.00	3.38
UPAS 120 × PA 623	48.5	78.33	-9.64	17.85**	1638.76	60.96**	56.67**	58.78**
UPAS 120 × PA 624	42.5	88	-6.265	20.77**	420.668	107.06**	76.00**	78.38**
UPAS 120 × PA 625	48.5	70.33	-6.1	2.77	1638.76	45.02**	40.67**	42.57**
UPAS 120 × PA 627	42.0	58	-8.6	-4.56**	420.668	37.55**	16.00**	17.57**
UPAS 120 × PA 626	50.5	35	-10.765	-23.23**	395.178	-30.92**	-31.82**	-29.05**
UPAS 120 × PA 622	51.5	71	-3.71	-1.34	395.178	37.86**	33.96**	43.92**
PA 620 × PA 623	49.0	60	-2.165	-15.42**	184.336	22.03**	17.65**	21.62**
PA 620 × PA 624	43.0	100	1.21	17.83**	811.11	132.56**	96.08**	102.70**
PA 620 × PA 625	49.0	128	1.375	45.49**	184.336	161.22**	150.98**	159.46**
PA 620 × PA 627	42.5	115	-1.125	37.49**	811.11	169.53**	125.49**	133.11**
PA 620 × PA 626	51.0	38.33	-3.29	-34.84**	641.578	-25.08**	-25.32**	-22.30**
PA 620 × PA 622	52.0	69.33	3.765	-17.95**	641.578	33.33**	30.82**	40.54**
PA 623 × PA 624	41.0	71.33	0.655	-9.73**	811.11	73.28**	50.70**	44.59**
PA 623 × PA 625	47.0	65	0.82	-16.40**	184.336	37.81**	37.32**	31.76**
PA 623 × PA 627	40.5	75	-1.68	-1.40	811.11	83.67**	58.45**	52.03**
PA 623 × PA 626	49.0	120	-3.845	47.94**	641.578	143.24**	133.77**	143.24**
PA 623 × PA 622	50.0	84	3.21	-2.17	641.578	67.44**	58.49**	70.27**
PA 624 × PA 625	41.0	111	4.195	22.85**	811.11	170.73**	136.17**	125.00**
PA 624 × PA 627	34.5	57	1.695	-26.15**	252.047	64.42**	62.86**	15.54**
PA 624 × PA 626	43.0	77.33	-0.47	-1.48	363.243	79.15**	50.65**	56.76**
PA 624 × PA 622	44.0	84	6.585	-8.92**	363.243	90.91**	58.49**	70.27**
PA 625 × PA 627	40.5	111.33	1.86	27.85**	811.11	173.77**	136.88**	125.68**
PA 625 × PA 626	49.0	65	-0.305	-14.15**	641.578	32.20**	26.62**	31.76**
PA 625 × PA 622	50.0	125.33	6.75	32.08**	641.578	150.67**	136.48**	154.06**
PA 627 × PA 626	42.5	81.33	-2.805	7.19**	363.243	89.88**	58.44**	64.87**
PA 627 × PA 622	43.5	112.33	4.25	24.08**	363.243	157.25**	111.95**	127.70**
PA 626 × PA 622	52.0	125	2.085	41.08**	20.544	139.62**	135.85**	153.38**

Table 3: Average intra (diagonal) and inter cluster distance (D^2 values) for pigeonpea parental genotypes.

	Cluster I	Cluster II	Cluster III	Cluster IV
Cluster I (PA 626 and PA 622)	20.544	641.578	395.178	363.243
Cluster II (PA 620, PA 623, PA 625 and Paras)		184.336	1638.756	811.110
Cluster III (Pusa 992 and UPAS 120)			122.857	420.668
Cluster IV (PA 624 and PA 627)				252.047

effects of parental lines have potential application in hybrid development programmes and supported the findings of Fan *et al.,* (2014). The SCA and MGCA emerged as the independent parameters in present study since they exhibited poor relationship (r=0.209). The parental mean (PM), was found to be negatively and non-significantly correlated with the better parent (r=-0.250) and standard heterosis (r=-0.112), however with the mid parent heterosis (r=-0.387**) it was negatively and significantly correlated. The linear regressions of PM on heterosis were also found to be non-significant. These results suggested that parental mean was not a reliable criteria to predict heterosis. The highest frequency of heterotic hybrids (59.52%) was reported when parents having high and low mean were crossed *i.e.* high × low combination. The negligible correlation of parental mean with all the other studied parameters further indicated that the parental mean had not exhibited any role in determination of heterosis, combining ability, genetic diversity as well as *per se* performance of the hybrids in pigeonpea. Hence the parental mean cannot be used as sole determinant of heterosis as well as parental selection for hybridization. These results supported the earlier findings of Hallauer, (1990); Lee *et al.,* (2007) in maize. The genetic distance (GD) was found to be negatively and non-

Table 4: The Pearson's correlation between different parameters for seed yield/plant.

Parameters	PM	HMY	MGCA	SCA	GD	MPH	BPH	SH
PM	1	-0.111^{ns}	-0.057^{ns}	-0.106^{ns}	0.097^{ns}	-0.387**	-0.250^{ns}	-0.112^{ns}
HMY		1	0.533**	0.939**	0.006^{ns}	0.955**	0.980**	1**
MGCA			1	0.209^{ns}	-0.049^{ns}	0.504**	0.526**	0.532**
SCA				1	0.027^{ns}	0.899**	0.918**	0.939**
GD					1	-0.010^{ns}	-0.003^{ns}	0.006^{ns}
MPH						1	0.977**	0.956**
BPH							1	0.980**
SH								1

*Significant at 5% level, **Significant at 1% level.

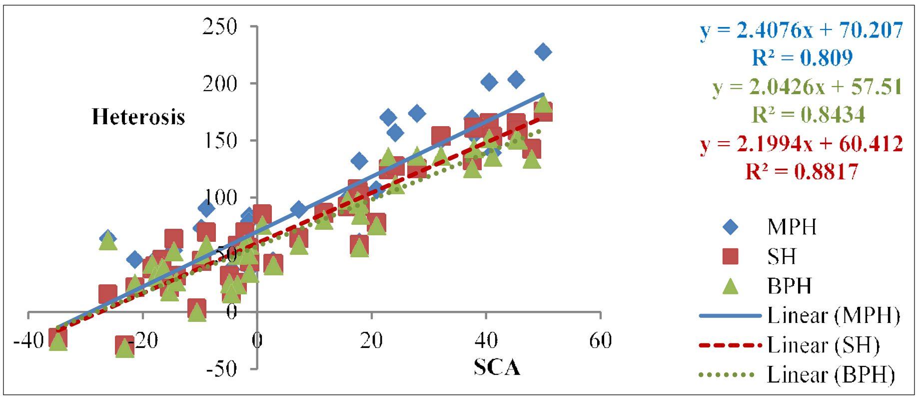

Fig 1: Relation between specific combining ability (SCA) and heterosis.

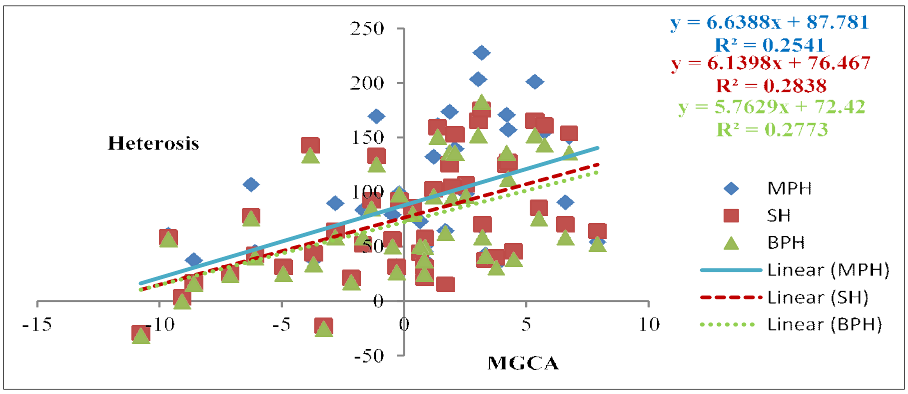

Fig 2: Relation between Mean general combining ability (MGCA) and heterosis.

significantly correlated with MPH (r=-0.010), BPH (r=-0.003) while it was positively and non-significantly correlated with SH (r=0.006). The linear regressions of GD on heterosis were found to be non-significant. The highest frequency of heterotic hybrids were produced when parents having moderate amount of diversity were crossed (83.33%) while the parents having high level of genetic diversity results in very less frequency of heterotic hybrids (14.29%) and the

Table 5: SCA and GCA effects, diversity class and parent mean class for seed yield/plant in pigeonpea.

Sr. no.	SCA	GCA	Cluster	Diversity class	Parents mean class
1	P	G × G	III × II	H	H × L
2	P	G × P	III × III	M	H × H
3	P	G × P	III × II	H	H × H
4	G	G × P	III × II	H	H × L
5	G	G × G	III × IV	M	H × L
6	A	G × G	III × II	M	H × L
7	G	G × A	III × IV	M	H × L
8	A	G × P	III × I	M	H × H
9	G	G × G	III × I	M	H × H
10	A	G × P	II × III	H	L × H
11	G	G × P	II × II	M	L × H
12	G	G × P	II × II	M	L × L
13	G	G × G	II × IV	M	L × L
14	P	G × G	II × II	M	L × L
15	P	G × A	II × IV	M	L × L
16	G	G × P	II × I	M	L × H
17	G	G × G	II × I	M	L × H
18	P	P × P	III × I	M	H × H
19	G	P × P	III × II	H	H × L
20	G	P × G	III × IV	M	H × L
21	A	P × G	III × II	H	H × L
22	P	P × A	III × IV	M	H × L
23	P	P × P	III × I	M	H × H
24	A	P × G	III × I	M	H × H
25	P	P × P	II × II	M	H × L
26	G	P × G	II × IV	M	H × L
27	G	P × G	II × II	M	H × L
28	G	P × A	II × IV	M	H × L
29	P	P × P	II × I	M	H × H
30	P	P × G	II × I	M	H × H
31	P	P × G	II × IV	M	L × L
32	P	P × G	II × II	M	L × L
33	A	P × A	II × IV	M	L × L
34	G	P × P	II × I	M	L × H
35	A	P × G	II × I	M	L × H
36	G	G × G	IV × II	M	L × L
37	P	G × A	IV × IV	M	L × L
38	A	G × P	IV × I	M	L × H
39	P	G × G	IV × I	M	L × H
40	G	G × A	II × IV	M	L × L
41	P	G × P	II × I	M	L × H
42	G	G × G	II × I	M	L × H
43	G	A × P	IV × I	M	L × H
44	G	A × G	IV × I	M	L × H
45	G	P × G	I × I	L	H × H

Where, 1 to 45 refers to hybrid Pusa 992 × Paras to PA 626 × PA 622, respectively.
(G= Good, P= Poor, A= Average, H= High, M= Medium, L= Low).

Table 6: The heterotic frequency obtained in different combining ability classes.

Parameters	Classes	Number of heterotic hybrids	Heterotic frequency per cent
SCA	P	13	30.95
	A	8	19.05
	G	21	50.00
GCA	G × G	10	23.81
	G × A	5	11.90
	G × P	20	47.62
	P × P	3	7.15
	P × A	4	9.53
Genetic diversity class	H	6	14.29
	M	35	83.33
	L	1	2.38
Per se performance of parents	H × H	7	16.67
	H × L	25	59.52
	L × L	10	23.81

(G= Good, P= Poor, A= Average) and *per se* performance classes (H= High, M= Medium, L= Low).

least frequency (2.38 %) was showed by parents belonging to low diversity class parents.

CONCLUSION

The SCA followed by MGCA emerged as most important parameters to predict the heterosis. The high parental mean and high genetic distance does not always lead to high heterosis. The parents having high × low *per se* performance, good × poor GCA effects and with medium genetic diversity may also results in high frequency of heterotic hybrids.

Conflict of interest: None.

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