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Heterosis, Combining Ability, Genetic Diversity and their Interrelationship in Pigeonpea [*Cajanus cajan* (L.) Millspaugh]

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ABSTRACT

Background: The development of superior hybrids is must to break the existing yield plateau (< 800 kg/ha) in pigeonpea and hence, the genetic mechanism governing the heterosis in pigeonpea must be decoded.

Methods: The present study was laid down using randomized block design during *kharif* 2018-19 at GBPUAT, Pantnagar with 36 genotypes (8 parents and 28 F_1 hybrids) of pigeonpea. The estimates of combining ability were evaluated by using the Griffing's, Method II, Model I. The observations recorded for yield and related traits were subjected to the estimation of genetic diversity (GD) using the D^2 statistics. The correlation between heterosis and different parameters *viz.,* parental mean (PM), specific combining ability (SCA), mean of general combining ability (MGCA) and genetic diversity (GD) were estimated by using Pearson's correlation.

Result: High estimates of SCA variance and more than unity (>1) average degree of dominance for all the characters indicated the presence of over dominance. The SCA followed by MGCA were found to be most reliable parameters to predict the heterosis. The parents having high x low or high x high *per se* performance, good x poor GCA effects and with medium genetic diversity resulted in high frequency of heterotic hybrids.

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

INTRODUCTION

The exploitation of heterosis resulted in the development of several high-yielding hybrids in various crops. In pulses the research on hybrid breeding started first in faba bean followed by pigeonpea and soybean (Bond *et al.,* 1966 and Palmer *et al.,* 2010). The success however, had come only from pigeonpea when India developed first genetic male sterility (GMS) based pigeonpea hybrid ICPH-8 in 1991 (Saxena *et al.,* 1992). Recently a new early maturing pigeonpea hybrid IPH 15-03 has been released for commercial cultivation for North West Plain Zone (NWPZ) of India (Saxena *et al.,* 2021). The global productivity of pigeonpea remained stagnant at around 800 kg/ha and became a major challenge for its breeders to further improve it. Hybrid varieties have the potential to break this yield plateau (Bohra *et al.,* 2020).

The scanty knowledge about genetic mechanism governing heterosis remains a major issue in hybrid breeding. The magnitude of heterosis relies on the combination of parental genotype which together emerged as a heterotic combination. In order to choose the lines which produce superior heterotic combinations without making all possible crosses among them, different methods including parental *per se* performance, SCA effects, GCA effects and genetic diversity had been tried (Huang *et al.,* 2015). The *per se* performance of parents may be is used as a parameters as it is assumed that, in general, the parents having high yield produce a large frequency of high yielding hybrids as compared to low yielding parents (Mohammadi *et al.,* 2008). The presence of genetic diversity between the parents used in hybridization is considered as an important parameter for obtaining significant heterosis in hybrids (Tecklewold and Becker, 2006). Combining ability was also used by several workers to predict the extent of heterosis (Devi and Singh, 2011). Hence the present study was conducted with the objectives (i) to estimate combining ability and heterosis in pigeonpea (ii) to estimate the magnitude of genetic diversity among the parents and to measure correlation between *per se* performance of parents, combining ability, genetic diversity and heterosis.

MATERIALS AND METHODS

Plant materials and field experiments

The eight elite pigeonpea genotypes *viz.,* UPAS 120, Pusa 992, Pant A 421, Pant A 477, RKPV 492-01, Pusa 2017-1, Pusa 2013-1 and Pusa 2013-2 were crossed in half diallel fashion during the *kharif* 2017-18 to produce 28 F_1's. Thus, the 36 genotypes including 8 parents and 28 F_1's, were grown during *kharif* 2018-19 at N.E.B. C.R.C, of GBPUAT,

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Pantnagar (Uttarakhand) using randomized block design with three replications. The observations were recorded for eight different characters including days to 50 per cent flowering, days to maturity, plant height (cm), number of primary branches/plant, number of pods/plant, number of seeds/pod, 100-seed weight (g) and seed yield/plant (g).

Statistical analysis

The analysis of variance for eight characters was carried out as given by Fisher (1920). The combining ability was evaluated by Griffing's (1956), Method II, Model I (Fixed effects). If the GCA and SCA effects were significant in desirable direction than these effects were considered as good (G) and those significant towards undesirable direction were considered as poor (P) while non-significant effects were designated as average (A). Similarly in case of *per se* (PM) performance if mean of line is found above overall parental mean than such lines were considered as good (G) but if mean of a parental line was below the overall parental mean than these lines were classified as poor (P). The heterosis over mid parent (MPH) and better parent (BPH) were estimated for seed yield and the significance of heterosis was tested with t test. The GCA effects obtained from both parental lines of a hybrid were averaged to determine the mean GCA (MGCA) effect of the parents (Kumar *et al.,* 2015). The genetic diversity was estimated for various yield and related traits by using the D^2 statistics (Mahalanobis, 1936) and for preparation of clusters, Tocher's method as proposed by Rao (1952) was used. By using the method of Arunachalam (1984) the parents were classified into three diversity classes *i.e.* low, medium and high. The Pearson's correlation coefficients were used to estimate the relation between PM, SCA, MGCA, GD, MPH and BPH. To estimate the combining ability and heterosis and Mahalanobis D^2 statistics data were analysed using the INDOSTAT software (IndoStat Inc. Hyderabad, India).

RESULTS AND DISCUSSION

Estimation of combining ability

A close perusal of Table 1 indicated that genotypic differences were significant for all characters which indicated the preponderance of sufficient genetic variability. The diallel ANOVA indicated that MSS due to GCA effects were highly significant ($p<0.01$) for all the characters, however, SCA effects were significant for all the characters except for number of seeds per pod (Table 2). The significance of GCA and SCA indicated the presence of additive and non-additive gene actions. For all characters the estimates of SCA variance were found to be higher than the corresponding GCA variance indicating the presence of non additive gene action. Average degree of dominance was found to be more than unity for all the characters which indicated the presence of over dominance. The presence of dominance gene effect in governing these characters was also reported earlier by Gedam *et al.* (2013) and Tikle *et al*. (2016). The parent Pant A 421 and Pant A 477 can be ranked as the best parent as they had a good GCA effects for all yield attributes except

Table 1: Analysis of variance in randomized block design for different biometrical traits in pigeonpea.

Source of variation	Df	MSS							
		DF	DM	PH	NPB	NPP	NSP	HSW	SYP
Replication	2	0.04	0.06	3.18	1.56	167.53	0.01	0	13.03
Genotypes	35	32.84**	63.44**	1381.43**	15.29**	2756.77**	0.51**	2.49**	333.02**
Error	70	0.03	0.03	82.27	0.97	52.6	0.05	31.75	9.29
CD		0.48	0.52	25.64	2.78	20.50	0.62	0.19	8.61
CV		0.37	0.23	7.07	14.58	7.63	9.48	1.37	11.97

Where, DF= Days to 50% flowering, DM= Days to maturity, PH= Plant height, NPB= Number of primary branches, NPP= Number of pods per plant, NSP= Number of seeds per pod, HSW= 100-seed weight and SYP =seed yield per plant; *, ** Significant at 5% and 1% level of probability respectively.

Table 2: Diallel analysis of variance for different biometrical traits in pigeonpea.

Source of variation	Df	DF	DM	PH	NPB	NPP	NSP	HSW	SYP
					MSS				
Parents	7	60.52**	100.17**	1303.28**	2.61	1753.62**	0.55**	2.82**	194.80**
Hybrids	27	23.06**	32.65**	1327.40**	12.60**	2805.71**	0.52**	2.49**	365.47**
Parents *vs* Hybrid	1	103.19**	637.77**	3387.02**	176.78**	8457.54**	0.13	0.08	424.34**
GCA	7	42.53**	64.03**	795.26**	8.18**	3354.81**	0.67**	3.25**	428.04**
SCA	27	3.05**	10.42**	376.80**	4.33**	309.96**	0.05	0.22**	31.75**
					Variances				
σ^2GCA		0.0002	0.003	7.199	0.0845	4.6023	0.0042	0.0004	0.8127
σ^2SCA		0.0232	0.0282	67.647	0.7943	43.24	0.0391	0.0039	7.6373
$\sqrt{\sigma^2}$SCA/2σ^2GCA		7.6157	2.1679	2.1189	2.1679	2.1673	4.6547	2.2079	2.1676

plant height for Pant A 421 and number of seeds per pod for Pant A 477 (Table 3). A critical analysis of Table 3 indicated that the parents that were showing good GCA for seed yield per plant also showing positive and significant GCA effects for yield related traits and hence provides a clue that the combining ability for seed yield may be under the influence of combining ability of its components. Therefore, to increase yield in pigeonpea simultaneous improvement in yield components is also required. The hybrids Pant A 421 x RKPV 492-01 exhibited good SCA effects for maximum number of traits *i.e.* six including seed yield (Table 4). In case of seed yield, out of twenty eight hybrids, seventeen and six hybrids exhibited significant and positive MPH and BPH respectively.

Estimation of magnitude of genetic diversity among parents

The estimation of genetic diversity among parents revealed that four different clusters were present (Table 5). The cluster I was largest and contain five parents while the cluster II, III and cluster IV each contains single genotype. The inter

Table 3: General combining ability effects of parents for different biometrical traits.

Parents	DF	DM	PH	NPB	NPP	NSP	HSW	SYP
UPAS 120	1.62**(P)	3.37**(P)	7.84**(G)	1.12** (G)	13.08** (G)	0.08(A)	-0.34**(P)	1.53(A)
Pusa 992	-0.45** (G)	1.37**(P)	-1.99 (A)	-0.22(A)	2.18(A)	0.02(A)	0.33** (G)	2.29*(G)
Pant A 421	-1.48**(G)	-1.2**(G)	-13.26**(P)	1.18** (G)	33.52** (G)	0.52**(G)	0.33**(G)	13.39**(G)
Pant A 477	-0.28**(G)	-0.33**(G)	10.41** (G)	0.85** (G)	9.42** (G)	0.08(A)	0.41** (G)	2.66**(G)
RKPV 492-01	4.35**(P)	3.63**(P)	4.11(A)	-0.82**(P)	-21.02**(P)	-0.08(A)	0.53**(G)	-4.57**(P)
Pusa 2017-1	-0.42**(G)	-1.4**(G)	7.31**(G)	-1.02**(P)	-9.72**(P)	-0.28**(P)	0.32**(G)	-7.18**(P)
Pusa 2013-1	-1.78**(G)	-2.43**(G)	-3.16(A)	-0.58(A)	-8.88**(P)	-0.02(A)	-0.55**(P)	-3.67**(P)
Pusa 2013-2	-1.55**(G)	-3.00**(G)	-11.26**(P)	-0.52(A)	-18.58**(P)	-0.32**(P)	-1.04**(P)	-4.44**(P)

G= Good, P= Poor and A= Average

Table 4: Specific combining ability effects in hybrids for different biometrical traits.

Hybrids	DF	DM	PH	NPB	NPP	NSP	HSW	SYP
UPAS 120 × Pusa 992	-0.96**(G)	-1.77**(G)	11.05(A)	1.08(A)	9.34(A)	-0.08(A)	0.01(A)	9.43**(G)
UPAS 120 × Pant A 421	-1.93**(G)	-3.20**(G)	-1.02(A)	2.68**(G)	18.68**(G)	0.09(A)	-0.22**(P)	-2.33(A)
UPAS 120 × Pant A 477	-0.13(A)	-2.07**(G)	11.98(A)	0.35(A)	-11.89(A)	-0.15(A)	-0.13*(P)	0.40(A)
UPAS 120 × RKPV 492-01	-0.10(A)	1.96**(P)	14.61(A)	0.35(A)	8.88(A)	0.02(A)	0.08(A)	-3.37(A)
UPAS 120 × Pusa 2017-1	-1.66**(G)	-1.67**(G)	22.08**(G)	0.88(A)	15.58**(G)	0.22(A)	-0.24**(P)	-2.10(A)
UPAS 120 × Pusa 2013-1	0.04(A)	-2.30**(G)	3.55(A)	1.45(A)	3.74(A)	-0.05(A)	0.06(A)	2.07(A)
UPAS 120 × Pusa 2013-2	0.14(A)	-3.40**(G)	-5.35(A)	0.38(A)	14.11*(G)	0.25(A)	0.09(A)	0.83(A)
Pusa 992 × Pant A 421	-0.86**(G)	-1.20**(G)	36.48**(G)	-1.32(A)	-6.76(A)	0.15(A)	-0.03(A)	-3.43(A)
Pusa 992 × Pant A 477	0.27(A)	-2.07**(G)	28.48**(G)	0.35(A)	-4.32(A)	-0.08(A)	0.13*(G)	0.30(A)
Pusa 992 × RKPV 402-01	-0.70**(G)	-0.04(A)	-5.89(A)	0.01(A)	-5.22(A)	0.09(A)	0.41**(G)	0.20(A)
Pusa 992 × Pusa 2017-1	2.07**(P)	1.00**(P)	-28.75**(P)	2.21**(G)	1.14(A)	0.29(A)	0.35**(G)	-2.53(A)
Pusa 992 × Pusa 2013-1	-1.56**(G)	1.03**(P)	-5.62(A)	1.11(A)	9.31(A)	0.02(A)	-0.31**(P)	2.63(A)
Pusa 992 × Pusa 2013-2	-2.46**(G)	-1.40**(G)	9.15(A)	0.38(A)	16.01**(G)	-0.35(A)	0.02(A)	2.07(A)
Pant A 421 × Pant A 477	-1.03**(G)	-0.50*(G)	5.41(A)	0.28(A)	14.68*(G)	0.09(A)	0.46**(G)	7.87**(G)
Pant A 421 × RKPV 492-01	-2.66**(G)	-2.47**(G)	-57.29**	2.28**(G)	22.78**(G)	-0.08(A)	0.54**(G)	6.77**(G)
Pant A 421 × Pusa 2017-1	0.10(A)	-2.44**(G)	-1.49(A)	1.48(A)	19.14**(G)	0.12(A)	0.95**(G)	5.03(A)
Pant A 421 × Pusa 2013-1	0.47**(P)	-1.40**(G)	10.31(A)	0.05(A)	8.31(A)	-0.15(A)	0.12(A)	4.53(A)
Pant A 421 × Pusa 2013-2	-0.43*(G)	0.50*(P)	18.08*(G)	1.31(A)	0.01(A)	0.49*(G)	0.31**(G)	12.63**(G)
Pant A 477 × RKPV 492-01	-2.86**(G)	-3.34**(G)	-7.29(A)	1.95*(G)	14.88*(G)	0.02(A)	0.26**(G)	-2.83(A)
Pant A 477 × Pusa 2017-1	-0.10(A)	-0.30(A)	-2.15(A)	2.15*(G)	16.58**(G)	0.22(A)	-0.92**(P)	2.77(A)
Pant A 477 × Pusa 2013-1	-0.73**(G)	0.73**(P)	0.31(A)	-1.62(A)	16.08**(G)	-0.05(A)	0.31**(G)	5.27*(G)
Pant A 477 × Pusa 2013-2	1.04**(P)	0.30(A)	-4.25(A)	3.98**(G)	16.44**(G)	0.25(A)	0.04(A)	-0.97(A)
RKPV 492-01 × Pusa 2017-1	2.27**(P)	-1.27**(G)	11.15(A)	-1.19(A)	1.34(A)	-0.28(A)	0.22**(G)	-2.67(A)
RKPV 492-01 × Pusa 2013-1	0.64(A)	-3.90**(G)	11.28(A)	0.05(A)	-20.16**(P)	0.12(A)	-0.65**(P)	-3.17(A)
RKPV 492-01 × Pusa 2013-2	-1.60**(G)	-3.67**(G)	19.38**(G)	-0.69(A)	-23.12**(P)	-0.25(A)	-0.79**(P)	-0.40(A)
Pusa 2017-1 × Pusa 2013-1	-0.60**(G)	-1.20**(G)	-3.92(A)	-0.75(A)	-6.12(A)	-0.01(A)	-0.20**(P)	-2.23(A)
Pusa 2017-1 × Pusa 2013-2	-0.83**(G)	-1.64**(G)	0.51(A)	-2.15*(P)	-7.76(A)	-0.38(A)	-0.67**(P)	-2.80(A)
Pusa 2013-1 × Pusa 2013-2	-0.46**(G)	-0.60**(G)	-7.02(A)	2.08*(G)	-9.26(A)	0.02(A)	0.23**(G)	-4.30(A)

G = Good, P=Poor and A=Average.

cluster distance was greater than the intra cluster distance indicating sufficient genetic diversity among the genotypes. The maximum inter cluster distance was found between cluster II and IV (90.676) and minimum between cluster III and IV (43.013). Thus the parents used in present study exhibited considerable amount of genetic diversity. The existence of large morphological diversity in pigeonpea was also reported earlier by Verma *et al.* (2018).

Relationship between PM, SCA, MGCA, MPH and BPH for seed yield

Both MPH and BPH (r=0.87*) were significantly and positively correlated with each other (Table 6 and Table 7). The SCA effects were positively and significantly correlated with the MPH (r=0.91**) and BPH (r=0.81**), respectively. The significant linear regression of SCA effects on MPH and BPH and very high R^2 value further revealed that SCA was a good determinant of heterosis (Fig 1). In case of MPH, out of 17 heterotic hybrids, 12 hybrids (70.58%) exhibited average SCA and 5 hybrids (29.41%) exhibited good SCA effects (Table 8). In case of BPH, out of six hybrids, 4 hybrids had good SCA (66.66%) while two hybrids (33.33%) had average SCA. Present finding indicated that high frequency of heterotic hybrids were obtained if crosses possessed average or good SCA. These results further indicated that SCA is the most important factor for determination of heterosis and is supported by earlier findings of Pandey *et al.* (2015). This strong relationship may be due to the reason

Table 5: Average intra (diagonal) and inter cluster distance (D^2values) for pigeonpea parental genotypes.

Clusters	I	II	III	IV
I (Pusa 992, Pant A 421, Pant A 477, Pusa 2017-1 and Pusa 2013-1)	31.189	55.050	51.173	59.590
II (Pusa 2013-2)		0	57.395	90.676
III (UPAS 120)			0	43.013
IV (RKPV 492-01)				0

Table 6: The estimates of parental mean (PM), mean general combining ability (MGCA), Genetic Distance (GD), Mid parent heterosis (MPH) and Better parent heterosis (BPH) for seed yield.

Hybrids	PM	MGCA	GD	GD class	MPH	BPH
1	82.17	1.91	51.173	M	28.84**	28.36**
2	81.67	7.46	51.173	M	13.33**	2.41
3	82.17	2.10	51.173	M	11.03**	8.96*
4	87.17	-1.52	43.013	M	-8.50**	-15.67**
5	80.83	-2.83	51.173	M	-5.22	-18.66**
6	80.33	-1.07	51.173	M	11.39**	-1.49
7	81.17	-1.46	57.395	M	10.04**	-5.97
8	79.50	7.84	31.189	L	13.04**	1.81
9	80.00	2.48	31.189	L	12.98**	11.28**
10	85.00	-1.14	59.590	M	2.44	-5.26
11	78.67	-2.45	31.189	L	-3.93	-17.29**
12	78.17	-0.69	31.189	L	15.25**	2.26
13	79.00	-1.08	55.050	M	15.79**	-0.75
14	79.50	8.03	31.189	L	38.31**	22.89**
15	84.50	4.41	59.590	M	28.32**	7.83
16	78.17	3.11	31.189	L	26.72**	0
17	77.67	4.86	31.189	L	30.11**	5.42
18	78.50	4.48	55.050	M	50.96**	18.67**
19	85.00	-0.96	59.590	M	-2.48	-8.53*
20	78.67	-2.26	31.189	L	12.89**	-1.55
21	78.17	-0.51	31.189	L	25.00**	12.40**
22	79.00	-0.89	55.050	M	10.71**	-3.88
23	83.67	-5.88	59.590	M	-14.83**	-21.24**
24	83.17	-4.12	59.590	M	-9.26**	-13.27**
25	84.00	-4.51	90.676	H	0	-7.96
26	76.83	-5.43	31.189	L	-6.53	-9.71*
27	77.67	-5.81	55.050	M	-6.81	-7.29
28	77.17	-4.06	55.050	M	-4.04	-7.77

Here 1 to 28 represents hybrids from UPAS 120 × Pusa 992 to Pusa 2013-1 × Pusa 2013-2; L= Low, M= Medium, H= High that both SCA and heterosis are function of non- additive gene action. The MGCA effects were found to be positively and significantly correlated with MPH (r=0.76**) and BPH (r=0.69**), respectively. The significant linear regression of MGCA on MPH and BPH along with high R^2 value revealed that MGCA was also a good determinant of heterosis (Fig 2). A close perusal of Table 8 indicated that in case of MPH highest heterotic frequency (52.94%) was observed by crossing parents having good x poor GCA effects combination while the poor x poor GCA combination showed no heterotic frequency. The good x good and good x average combination each produced 17.64% heterotic frequency while poor x average produced 11.76 % heterotic frequency. In case of BPH the good x good, good x average and good x poor each showed a heterotic frequency of 33.33 %. These results further indicated that if the parents had good x poor GCA effects, it results in yielding high heterosis frequency, however, the parents having good x good and good x average GCA effects produced a moderate level of heterotic hybrids. The present study revealed that the GCA effects of parental lines have potential application in hybrid development programmes and supported the earlier findings of Saxena and Sawargaonkar (2014). The PM was found to be negatively and non-significantly correlated with the MPH

Table 7: The Pearson's correlation between different parameters under study for seed yield.

Parameters	PM	SCA	MGCA	GD	MPH	BPH
PM	1					
SCA	-0.18	1				
MGCA	-0.05	0.51**	1			
GD	0.55**	-0.15	-0.32	1		
MPH	-0.30	0.91**	0.76**	-0.28	1	
BPH	-0.22	0.81**	0.69**	-0.24	0.87**	1

Table 8: The heterotic frequency obtained in different class.

Parameters	Classes	Number of heterotic hybrids		Heterotic frequency percent	
		MPH	BPH	MPH	BPH
SCA	Poor	0	0	0	0
	Average	12	2	70.58	33.33
	Good	5	4	29.41	66.66
GCA	G × G	3	2	17.64	33.33
	G × A	3	2	17.64	33.33
	G × P	9	2	52.94	33.33
	P × P	0	0	0	0
	P × A	2	0	11.76	0
GD Class	High	0	0	0	0
	Medium	9	3	52.94	50
	Low	8	3	47.05	50
Per se performance of parents	H × H	6	4	35.29	66.66
	H × L	11	2	64.70	33.33
	L × L	0	0	0	0

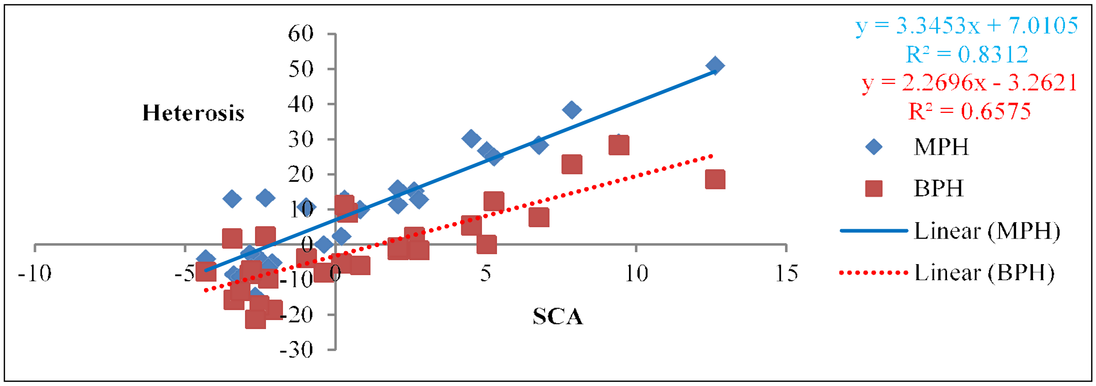

Fig 1: Relation between specific combining ability (SCA) and heterosis.

(r=-0.30) and BPH (r=-0.22) and hence it indicated that PM was not a reliable criteria to predict heterosis (Fig 3). A critical insight of Table 8 indicated that in case of mid parent highest frequency of heterotic hybrids (64.70%) was observed when parents having high and low means were crossed together *i.e.* high × low combination, the high × high combination showed 35.29% of heterotic frequency while the low × low showed no heterotic frequency for mid parent heterosis. In case of BPH highest frequency of heterotic hybrids (66.66%) was reported when parents having high and high mean were crossed *i.e.* high × high combination, the high × low combination showed 33.33% of heterotic frequency while the low x low showed no heterotic frequency for BPH. These results indicated that parental mean cannot be used as reliable parameters for heterosis estimation and supported by the findings of Devi and Singh (2011). The GD was found to be negatively and non- significantly correlated with MPH (r=-0.28) and BPH (r=-0.24). The linear regressions of GD on heterosis were found to be non-significant (Fig 4). In case of MPH the highest frequency of heterotic hybrids were produced when parents having moderate amount of diversity were crossed (52.94%) followed by parents with low diversity (47.05%) while the parents having high level of GD results in no heterotic hybrids. In case of better parent heterosis

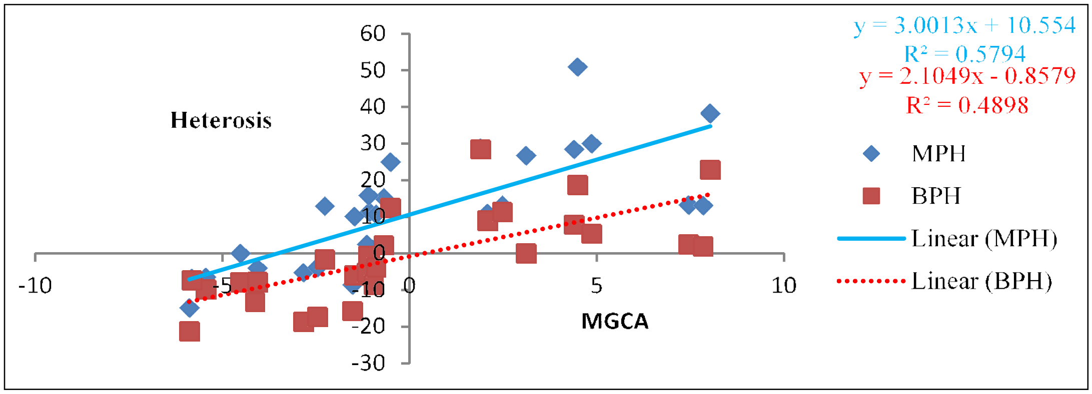

Fig 2: Relation between mean general combining ability (MGCA) and heterosis.

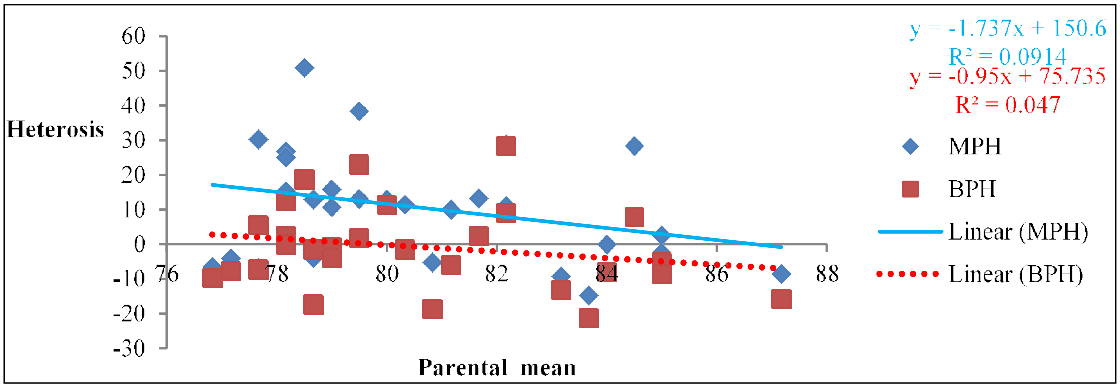

Fig 3: Relation between mean parental mean (PM) and heterosis.

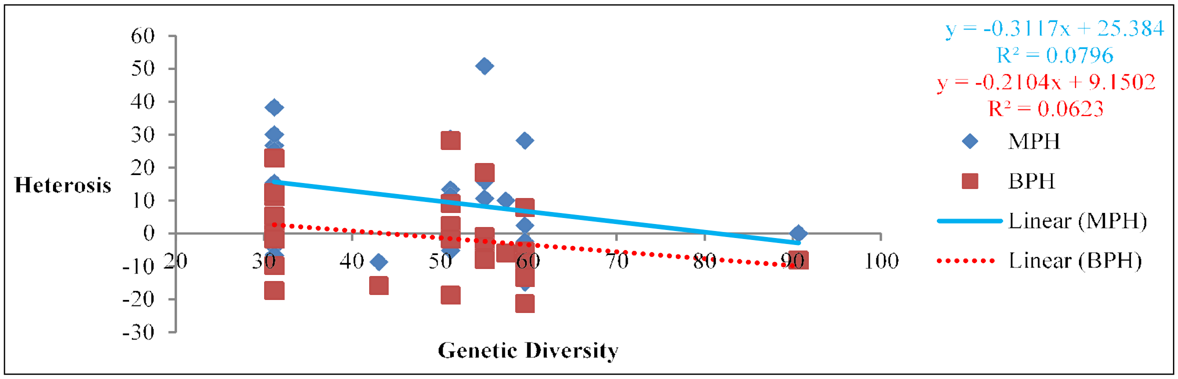

Fig 4: Relation between mean genetic diversity (GD) and heterosis.

equal frequency of heterotic hybrids (50 %) were produced when parents having moderate and low amount of diversity were crossed together. These results indicated that high genetic diversity did not lead to heterosis in pigeonpea and well supported by the findings of Pandey *et al.* (2015).

CONCLUSION

The SCA variance was higher than the corresponding GCA variance for all characters and average degree of dominance was more than unity for all the characters which indicated the presence of over dominance. The SCA and MGCA emerged as the most reliable parameters to predict the heterosis in pigeonpea. The high *per se* performance of parents and high genetic diversity does not lead to higher heterosis in pigeonpea. The parents having high x low or high x high *per se* performance, good x poor GCA effects and with medium genetic diversity resulted in high frequency of heterotic hybrids.

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