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RESEARCH ARTICLE

Frequency of Heterotic Hybrids in Relation to Parental Genetic Divergence and General Combining Ability in Dolichos Bean

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Abstract Though F_1 hybrids are not the immediate cultivar option, development of heterotic F_1 hybrids is relevant from view point of deriving pure lines, the only cultivar choice in dolichos bean, a predominantly self-pollinated grain legume crop species. Heterotic F_1 generates a high frequency of productive derivatives in F_3 and later generations as compared to non-heterotic F_1. The criteria such as combining ability and genetic diversity between parents are being commonly used to develop heterotic hybrids. In this context, an investigation was carried out at University of Agricultural Sciences, Bengaluru, India, to test the predictability of frequency of heterotic hybrids based on parental *gca* effects and genetic diversity in dolichos bean. The 48 F_1 hybrids generated by crossing 12 lines and 4 testers were evaluated along with their parents for 6 quantitative characters. The overall *gca* status (high and low) of each parent and overall *sca* and heterotic status (high and low) of each hybrid for 6 characters were determined. Based on overall *gca* status and genetic divergence of parents, the hybrids were grouped into different classes. The hybrids involving parents contrasting for overall *gca* status and/or those involving parents with intermediate genetic divergence were more frequently heterotic than those involving comparable *gca* status with extreme genetic divergence. Thus, there exists a limit to parental divergence for the occurrence of heterosis. It is hence, desirable to involve parents with intermediate genetic divergence and contrasting *gca* effects to recover higher frequencies of heterotic hybrids for economic traits in dolichos bean.

Keywords Overall *gca* status · Overall *sca* status · Genetic divergence · Dolichos bean

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Introduction

Harnessing heterosis is the preferred approach to enhance productivity potential of crop species where development of F_1 hybrids is technically and economically feasible. However, development and deployment of F_1 hybrids in dolichos bean is constrained by non-availability of suitable pollination control system leaving pure lines as the only cultivar option. Dolichos bean is one of the important food grain legume extensively grown in southern Karnataka, India [1]. It is predominantly grown for fresh grains, for use as a vegetable and to a limited extent as split dhal [2]. It is a self-pollinated crop with 2n = 22 chromosome [3]. Pedigree selection is the commonly used breeding method to develop pureline cultivars in dolichos bean as is vogue in other grain legumes. The breeder is often constrained to select a few F_1s from among a large number of crosses to derive superior purelines. Therefore, development and use of an objective criterion for selecting a few potential F_1 to maximise the frequency of superior pure lines would help to increase the pace and efficiency of dolichos bean breeding.

The heterotic F_1's generated a high frequency of productive derivatives in F_3 and later generations as compared to non-heterotic F_1s in *Brassica compestris* and groundnut

[4]. Therefore, identification of heterotic hybrids is relevant in dolichos bean as far as deriving superior purelines is concerned. In this context, choice of parents for developing high frequency of heterotic hybrids is another issue often debated by plant breeders. Considering theoretical analysis of single gene systems with two or multiple alleles [5] and two gene systems [6], phenotypic/genetic diversity has been very commonly used criterion for choosing parents for developing heterotic hybrids [4, 7]. However, when diverse parents are crossed, heterosis is not always found to occur [8]. Combining ability (CA) is another criteria which has been being used as one of the criteria for choosing the parents for producing higher frequency of heterotic hybrids. Practical utility of CA lies in the performance prediction of hybrids [9]. Apart from providing an objective criterion for choosing parents, CA also provides useful clues about mode of action of genes controlling economically important traits. Being based on first degree statistics, the greatest advantage of CA approach for genetic analysis is that it is statistically robust and genetically neutral and hence applicable to crops irrespective of their mode of reproduction [10]. Under these premises, an attempt was made to arrive at a simple and rational criteria for the choosing the parents for developing high frequency of heterotic hybrids using experimental data from dolichos bean.

Material and Methods

Plant Material and Experimental Design

The material for the study consisted of 4 recombinant inbred lines such as RIL 21, RIL 25, RIL 60 and RIL 180 derived from the cross HA 4 × CPI 31113 designated as testers and 12 phenotypically diverse inbred lines of which two released varieties (HA 3 and HA 4), six advanced breeding lines (HA 11-3, HA 10-8, FPB 3, FPB 8, FPB 15 and FPB 21) and four recombinant inbred lines RIL 11, RIL 162, RIL 185 and RIL 332 designated as lines (Table 1). The 12 inbred lines were crossed with four testers in a line × tester mating design [11] to synthesize 48 F_1s during 2012 rainy season. The 48 F_1 progenies and their parents were evaluated in a randomised block design in a single row of 3 m length in two replications during 2013 and 2014 rainy seasons at the experimental plots of Department of Genetics and Plant Breeding, University of Agricultural Sciences (UAS), Bengaluru, India. The experimental plots are located at 12°58′ latitude north, 77°35′ longitude east and an altitude of 930 meters above sea level.

The seeds of each of the F_1 progeny and their parents were sown and seedlings were thinned 15 days after sowing maintaining spacing of 0.45 m between rows and 0.2 m between plants within a row. A total of 15 plants were maintained in each row. All the recommended crop production practices were followed to raise the experimental plants.

Collection of Data

The data were collected on 5 randomly chosen plants in each of the 48 F_1 progenies and parents and in each replication on days to first flowering (DFF), racemes/plant (RP), pods/plant (PP), pod weight/plant (PWP), seed weight/plant (SWP) and fresh pod weight/plant (FPWP). DFF was recorded as the number of days from sowing to first flowering and averaged. RP was recorded as the average number of racemes/inflorescence borne on 5 plants. PP was recorded as the average number of sun-dried pods borne on 5 plants. PWP was recorded as average weight (grams) of sundried pods harvested from 5 plants and SWP was recorded as the average weight (grams) of hand-shelled sun-dried seeds from dry pods harvested from 5 plants. FPWP was recorded as the average weight of fresh pods harvested from a different set of 5 randomly selected plants.

Statistical Analysis

The mean of quantitative traits of two replications were used for statistical analysis. Non-significant mean squares due to hybrids × years provided statistical validity to pool the 2-year data on quantitative traits. The individual year-wise as well as pooled data were used for combining ability (CA) analyses [11] using computer software program Windowstat 8.0 (developed by Indostat services 18.0, Ameerpet, Hyderabad, India). General combining ability (*gca*) effects of 4 testers and 12 lines and specific combining ability (*sca*) effects of 48 F_1 hybrids and variances due to *gca* and *sca* effects were estimated [11]. Better parent heterosis (BPH) of 48 F_1 hybrids was estimated for each of the 6 characters as following.

$$\mathrm{BPH} = \left(\frac{\bar{\mathrm{F}}_1 - \mathrm{B\bar{P}}}{\mathrm{B\bar{P}}}\right) \times 100$$

where $\bar{\mathrm{F}}_1$ = Quantitative trait (QT) mean of $\bar{\mathrm{F}}_1$, $\mathrm{B\bar{P}}$ = Mean of better parent.

As quantitative traits are correlated either positively or negatively, it is usual to find, for a particular parent and a hybrid, *gca* effects and *sca* effects, BPH, respectively in the desirable direction for some characters and in the undesirable direction for others. Hence, the overall status of parents with respect to their *gca* effects and the hybrids with respect to their *sca* effects and BPH across six characters were determined [12]. As per the procedure suggested by [12], the determination of overall status of

Table 1 Pedigree and characteristic features of experimental genetic material of dolichos bean used in the study

Sl. no	Nature of genetic material	Pedigree		Characters				
		Male	Female	Days to flowering	Racemes/plant	Pods/plant	Pod weight/plant (g)	Seed weight/plant (g)
Inbred lines								
A. Released varieties								
1	HA 4	Magadi local	HA 3	45 ± 2	High	High	High	High
2	HA 3	US 67-31	HA 1	45 ± 2	High	High	High	High
B. Recombinant inbred lines								
3	RIL 162	CPI 31113	HA 4	50 ± 2	High	High	High	High
4	RIL 185	CPI 31113	HA 4	50 ± 2	High	High	High	High
5	RIL 11	CPI 31113	HA 4	54 ± 2	Low	Low	Low	Low
6	RIL 332	CPI 60216	HA 4	50 ± 2	Moderate	Moderate	Moderate	Moderate
C. Advanced breeding lines								
7	FPB 3 (10-31)	NA	NA	47 ± 2	High	High	High	High
8	FPB 8 (10-41)	NA	NA	48 ± 2	High	High	High	High
9	FPB 15	NA	NA	47 ± 2	High	High	High	High
10	FPB 21	NA	NA	50 ± 2	High	High	High	High
11	HA 11-3	NA	NA	47 ± 2	High	High	High	High
12	HA 10-8	NA	NA	48 ± 2	High	High	High	High
Testers								
1	RIL 21	CPI 31113	HA 4	46 ± 2	Low	Low	Low	Low
2	RIL25	CPI 31113	HA 4	46 ± 2	Low	Low	Low	Low
3	RIL 60	CPI 31113	HA 4	60 ± 2	High	High	High	High
4	RIL 180	CPI 31113	HA 4	50 ± 2	High	High	High	High

NA Parentage of the advanced breeding lines is not available

parents with respect to their *gca* effects and the hybrids with respect to their *sca* effects and BPH across all characters should be based on only significant *gca, sca* and heterotic effects. The consideration of only significant *gca, sca* and heterotic effects results in loss of information on several parents and crosses. To overcome such shortcoming, we considered the estimates of *gca, sca* and heterotic effects irrespective of their statistical significance. The modified procedure is described as under.

The estimates of *gca* effects of parents, *sca* effects and BPH of hybrids were ranked by assigning lowest rank for the parent or the cross which manifested the highest *gca*/*sca* effects and BPH, respectively in desirable direction. The highest rank was assigned for parent or the cross which manifested the lowest *gca*/*sca* effects and BPH, respectively in desirable direction. The ranks obtained by the parent/hybrid were summed up across all the characters to arrive at a total score for each of the parent/cross. Further, the mean of the total scores of all the parents or crosses across the traits was computed which was used as the final norm to ascertain the status of a parent or a hybrid for their *gca*/*sca* effects and BPH. The parent/hybrid whose total rank exceeded the final norm were given low (L) overall *gca*/*sca*/BPH status, respectively. On the other hand, the parent or a hybrid, whose total rank was less than the final norm were given high (H) overall *gca*/*sca*/BPH status, respectively.

Based on the overall *gca* status of parents, crosses were classified into HH (both the parents in a cross with high overall *gca* status), HL (one parent with high and the other parent with low overall *gca* status) and LL (both the parents with low overall *gca* status) categories.

Genetic divergence between the parents of 48 F_1's was estimated by Mahalanobis D^2 statistic [13]. The mean (m) (604.54), lowest (16.76), highest (1757.01) and standard deviation (s) (441.84) of D^2 statistic were calculated, and were used to delineate parental divergence into four divergent classes (DC) [4]. Divergence classes were defined as follows.

$$\mathrm{DC\,1}: D^2 \geq (m + s)$$

$$\mathrm{DC\,2}: m \geq D^2 \geq (m + s)$$

$$\mathrm{DC\,3}: (m - s) \geq D^2 < m$$

$$\mathrm{DC\,4}: D^2 > (m - s)$$

where, DC 1 and DC 4 represent the extremely divergent classes in either direction.

Correlation of Hybrid per se Performance with Sum of Parental gca Effects

From two year pooled data, Pearson's correlation coefficient of hybrid *per se* performance with sum of *gca* effects of parents were estimated for all the six quantitative traits [14].

Relationship of Parental Divergence and gca Status with Hybrid Heterosis and sca Status

The total number of hybrids and those with high overall *sca* and heterotic status falling into each of the 4 parental divergence classes (DC 1, DC 2, DC 3 and DC 4) and 3 parental *gca* classes (HH, HL/LH and LL) were counted. Based on this information, given a hybrid with high overall *sca* and heterotic status, conditional probability that it belongs to each of the 4 parental divergence and 3 parental *gca* classes were estimated [12].

Results and Discussion

Analysis of Variance for Combining Ability

Significant mean sum of squares due to line effect for days to first flowering, dry seed weight plant^{-1} and fresh pod weight plant^{-1}, and those due to tester effect and line × tester (L × T) effects for all the traits suggested importance of both *gca* and *sca* effects for these traits were considered for the study (Table 2). The significance of the interaction arising from line effect with year for days to first flowering and L × T interaction effect with the years for all the traits except for days to first flowering and fresh pod weight plant^{-1} suggested differential response of the alleles controlling these traits to differences in weather variables that prevailed during experimental period in the two different years. The significant line effect × year first-order interaction suggested the necessity of selecting lines that are relatively more stable across years for their *gca* effects. The significant line × tester × year second-order interaction justifies evaluating hybrids across years to identify stable hybrids.

The differences in combining ability of parents and their interaction with years have been reported in azukibean [15] and rajmesh [16] for seed weight plant^{-1}, winter wheat [17], *Pisum sativum* [18] and in maize [19] for most traits considered for the study. Predominance of *sca* variance for most of the traits in both years indicated greater importance of non-additive (non-fixable) mode of action of genes controlling these traits. The predominance of *sca* variance is expected as the material used for the analysis has undergone intense selection for traits considered for the study. This is because with selection all the variation due to additive genetic effects exhausted leaving only variance due to non-additive gene effects [20]. Similar results have been reported in dolichos bean for racemes plant^{-1} [21, 22]. Importance of non-additive gene action for pod and seed weight plant^{-1} have been

Table 2 Analysis of variance of combining ability for quantitative traits in dolichos bean

Source of variation	df	Days to flowering	Racemes plant^{-1}	Pods plant^{-1}	Dry pod weight plant^{-1}	Dry seed weight plant^{-1}	Fresh pod weight plant^{-1}
Replications	1	13.55	0.05	126.12	66.92	112.81	1.18
Years	1	291.56**	0.33	2819.88**	1752.63**	5.59	5569.17**
Replication × years	1	99.48*	2.82	281.33*	288.64	493.47**	190.28
Crosses	47	166.72**	16.38**	1624.76**	1143.61**	398.87**	1528.72**
Line effect	11	415.85**	15.80	1181.72	1066.03	471.00*	1805.05*
Tester effect	3	267.28*	48.40*	10722.46**	6558.73**	2150.36**	7909.15**
Line × tester effect	33	74.54**	13.67**	945.38**	677.18***	215.60**	856.57**
Years × crosses	47	28.67*	10.69**	184.20**	224.61**	96.56**	381.11**
Years × line effect	11	47.90*	6.29	152.70	181.10	50.65	245.54
Years × tester effect	3	39.01	18.53	315.36	284.33	182.06	273.62
Years × L × T effect	33	21.31	11.45**	182.78**	233.68**	104.09**	436.07**
Pooled error	94	17.76	1.80	59.18	122.38	51.68	92.06
σ^2 GCA		10.24	0.96	184.39	115.65	39.55	149.45
σ^2SCA		15.14	3.06	223.41	141.43	42.59	195.48
σ^2 GCA/σ^2SCA		0.68	0.31	0.83	0.82	0.93	0.76

* Significant at $P = 0.05$

** Significant at $P = 0.01$

reported in common bean [23], field pea [24], faba bean [25] and rajmesh [16].

Predominance of dominant action of genes renders selection in early generation ineffective. One or 2 cycles of bi-parental mating in F_2 generations not only reduce dominance gene effects but also convert un-exploitable potential into exploitable free variability [26–28] which enables rapid genetic gain from selection in dolichos bean. This is because, probability of genes being in dispersion phase (which result in reduction in trait mean) minimised by F_2 inter-se mating [29]. Bulking segregating populations up to F_6 generation followed by pedigree selection is considered as an effective strategy to derive superior purelines [30–33].

Trait-wise Parental gca Effects and Hybrid sca and Heterosis

Both lines and testers differed widely in their abilities to combine in the cross combinations for all the traits (data not provided). The differences in *gca* effects are attributable to differences in frequencies of genes with the additive effects [5]. The differences in gene frequencies among the lines and testers suggest their significant genotypic differences, thus justifying their selection for the present study. As expected, different lines and testers were desirable general combiner in both direction and magnitude for different traits. Thus, no single line or a tester was a desirable combiner for all the traits. As it is true with respect to lines and testers for *gca* effects, the hybrids differed significantly for their *sca* and better-parent heterotic effects. These results indicate that while performance of a few hybrids is attributable only to their parental genes with additive effects, that of other hybrids is attributable to non-additive effects of their parental genes in addition to their additive effects [34]. It should however, be noted that the estimates of *gca* and *sca* effects are relative to and are dependent on particular set of parents included in the experiment.

Similar to lines and testers with respect to their *gca* effects, the different hybrids displayed desirable *sca* and heterotic effects for different traits. For instance, lines such as HA 3, FPB 21 and HA 4 were desirable general combiners for days to flowering, HA 10-8, RIL 185 and HA 11-3 were desirable general combiners for fresh pod weight plant^{-1} (Table 3). Similarly, hybrids such as RIL 332 × RIL 180, RIL 185 × RIL 21 and RIL 162 × RIL 60 were desirable specific combinations for days to first flowering, HA 10-8 × RIL 60, RIL 332 × RIL 180 and FPB 21 × RIL 180 were desirable specific combinations for fresh pod weight plant^{-1} (Table 4). These results lend support to the use of the method suggested [3] to determine *gca* status of parents, and *sca* and heterotic status of hybrids across the 6 traits considered for the study.

Table 3 Desirable general combiners for quantitative traits in dolichos bean

Traits	Desirable general combiners			
	Lines	Estimates of *gca*	Testers	Estimates of *gca*
Days to flowering	HA 3	−5.46**	RIL 25	−1.82*
	FPB 21	−5.27**	RIL 21	−1.22*
	HA 4	−4.36**		
Racemes plant^{-1}	RIL 185	1.71**	RIL 60	1.27**
	FPB 15	1.23**	RIL 21	0.11
	HA 10-8	0.87**		
Pods plant^{-1}	RIL 185	13.55**	RIL 60	22.25**
	HA 10-8	12.65**		
	RIL 162	12.07**		
Dry pod weight plant^{-1}	RIL 185	20.29**	RIL 60	17.21**
	HA 10-8	9.54**		
	FPB 3	6.43*		
Dry seed weight plant^{-1}	RIL 185	13.30**	RIL 60	9.90**
	HA 10-8	5.47**		
	FPB 3	4.90**		
Fresh pod weight plant^{-1}	HA 10-8	20.68**	RIL 60	18.42**
	RIL 185	17.03**		
	HA 11-3	6.67**		

* Significant at $P = 0.05$

** Significant at $P = 0.01$

Parental Overall gca Status, Hybrid Overall sca and Heterotic Status

Six of the 12 lines and two of the four testers displayed high overall *gca* status and the remaining exhibited low overall *gca* status (Table 5). Similarly, 50% of the hybrids displayed high overall *sca* and heterotic status (Tables 6, 7). The similar results of parents with high and low overall *gca* status and hybrids with low and high overall *sca* and heterotic status have also been reported in *Brassica campestris* [35] and sesame [36, 37]. The lines and testers with overall high *gca* status could be preferentially used to develop hybrids from which it is more likely to derive high frequency of superior purelines. Similarly, the hybrids with high overall *sca* status are suggested for preferential use in deriving desirable purelines.

Table 4 Desirable specific combinations based on sca effect and better parent heterosis (BPH) for quantitative traits in dolichos bean

Traits	Crosses	Estimates of *sca*	Crosses	Estimates of BPH
Days to flowering	RIL 11 × RIL 60	−6.95**	FPB 21 × RIL 60	−20.34**
	RIL 185 × RIL 21	−5.66**	HA 3 × RIL 60	−17.98**
	RIL 332 × RIL 180	−4.82*	RIL 11 × RIL 25	−17.50**
	FPB 3 × RIL 180	−4.55*	HA 11-3 × RIL 60	−17.06**
	FPB 21 × RIL 60	−4.02*	HA 4 × RIL 60	−16.64**
Racemes plant^{-1}	HA 11-3 × RIL 180	3.24**	FPB 15 × RIL 60	118.96**
	RIL 185 × RIL 21	2.42**	RIL 185 × RIL 21	90.71**
	HA 10-8 × RIL 60	2.31**	HA 3 × RIL 60	74.55**
	FPB 15 × RIL 60	2.18**	HA 10-8 × RIL 60	72.47**
	HA 3 × RIL 60	2.03**	RIL 11 × RIL 21	72.00**
Pods plant^{-1}	HA 10-8 × RIL 60	28.74**	HA 10-8 × RIL 60	163.26**
	RIL 185 × RIL 25	28.66**	RIL 185 × RIL 25	142.05**
	RIL 162 × RIL 60	28.13**	RIL 162 × RIL 60	136.97**
	HA 4 × RIL 21	22.32**	FPB 3 × RIL 60	136.67**
	FPB 3 × RIL 60	20.74**	RIL 11 × RIL 21	109.26**
Dry pod weight plant^{-1}	RIL 185 × RIL 25	31.87**	RIL 185 × RIL 25	194.98**
	HA 10-8 × RIL 60	26.43**	RIL 11 × RIL 25	188.02**
	RIL 162 × RIL 60	16.01**	RIL 11 × RIL 21	182.62**
	FPB 3 × RIL 60	14.35**	RIL 332 × RIL 21	169.51**
	RIL 332 × RIL 21	14.05**	RIL 185 × RIL 21	119.80**
Dry seed weight plant^{-1}	RIL 185 × RIL 25	21.05**	RIL 11 × RIL 25	267.58**
	HA 10-8 × RIL 60	12.57**	RIL 11 × RIL 21	256.98*8
	FPB 3 × RIL 60	9.45**	RIL 185 × RIL 25	209.17**
	RIL 162 × RIL 60	7.64*	RIL 332 × RIL 21	142.45**
	FPB 15 × RIL 25	6.90*	RIL 332 × RIL 25	128.50*8
Fresh pod weight plant^{-1}	RIL 185 × RIL 25	25.60**	RIL 11 × RIL 21	150.35**
	HA 10-8 × RIL 60	24.85**	RIL 332 × RIL 21	138.33**
	FPB 21 × RIL 180	23.54**	RIL 11 × RIL 25	127.42**
	FPB 3 × RIL 60	19.54**	RIL 185 × RIL 25	79.15*8
	FPB 15 × RIL 25	16.54**	HA 10-8 × RIL 60	79.07**

* Significant at $P = 0.05$

** Significant at $P = 0.01$

Correlation of Hybrid per se Performance with Sum of Parental gca Effects

One of the utilities of CA of the parents is their predictive power of hybrid per se performance in the absence of significant hybrid *sca* effects. CA provides empirical summary of quantitative traits and reasonable basis for assessing breeding value of parental lines and for forecasting the performance of untested hybrids but yet make no genetic assumptions [34, 38, 39]. In the present study, despite significant differences in *sca* effects of hybrids, *gca* effects of parents retained fairly high predictability of hybrid *per se* performance as is evident from higher coefficient of determination of sum of the parental *gca* effects with hybrid per se performance (Fig. 1). Prediction of hybrid heterosis based on parental gca effects would save substantial resources and time and thus help enhance the pace and efficiency of dolichos bean breeding. The utility of parental *gca* effects for predicting hybrid per se performance has also been reported in maize [14] and winter wheat [17]. The predictive power of parental *gca* effects provide adequate support for the present attempt to explore frequency of hybrids with high overall heterosis and *sca* effects in relation to parental overall *gca* effects in dolichos bean.

Table 5 Overall general combining ability status of parents in dolichos bean

	Overall rank	Overall status
Lines[a]		
HA 3	44	L
HA 4	45	L
HA 11-3	30	H
RIL 11	53	L
RIL 185	18	H
FPB 8	61	L
FPB 15	35	H
RIL 332	46	L
FPB 3	34	H
RIL 162	48	L
HA 10-8	17	H
FPB 21	37	H
Testers[b]		
RIL 21	17	L
RIL 25	20	L
RIL 60	9	H
RIL 180	14	H

[a] Final norm: 39

[b] Final norm: 15

H = High overall *gca* status

L = Low overall *gca* status

Relationship of Overall Parental *gca* Status with Hybrid Overall *sca* and Heterosis

The number of hybrids with high (H) overall *sca* status was more in HL than either in HH or LL category. Also, the number of overall heterotic crosses was more in HL than either in HH or LL category. It may be argued that the frequencies of hybrids with high overall *sca* and heterotic status could be biased due to varying number of crosses under each category. To take into consideration, the unequal number of crosses in different categories and conditional probability of a heterotic cross found in HH, HL or LL category was computed manually as the ratio of number of heterotic crosses belonging to HH, HL or LL category to the total number of heterotic crosses. The conditional probability is independent of number of crosses under each category. It was interesting to note that given a heterotic cross, the probability of finding it to be a H × L combination was higher than the probability of finding it to be either H × H or L × L combination. Also, given a cross with high *sca* status, the probability of finding it to be a H × L combination was higher than the probability of finding it to be either H × H or L × L combination (Table 8).

Thus, the present study indicated requirement of parents with contrasting *gca* effects to realise higher frequency of heterotic hybrids. The results of the present investigation

Table 6 Overall specific combining ability status of crosses in dolichos bean

Lines	Testers							
	RIL 21 (L)		RIL 25 (L)		RIL 60 (H)		RIL 180 (H)	
	Total score	Status	Total score	Status	Total score	Status	Total score	Status
HA 3 (L)	174	L	118	H	99	H	183	L
HA 4 (L)	97	H	222	L	157	L	111	H
HA 11-3 (H)	131	H	151	L	168	L	130	H
RIL 11 (L)	151	L	114	H	172	L	123	H
RIL 185 (H)	94	H	63	H	229	L	250	L
FPB 8 (L)	229	L	180	L	111	H	57	H
FPB 15 (H)	192	L	70	H	196	L	115	H
RIL 332 (L)	87	H	172	L	227	L	74	H
FPB 3 (H)	140	H	139	H	71	H	215	L
RIL 162 (L)	119	H	210	L	51	H	224	L
HA 10-8 (H)	169	L	198	L	53	H	198	L
FPB 21 (H)	124	H	194	L	188	L	77	H

Final norm: 146

H = High overall *sca* status of crosses; L = Low overall *sca* status of crosses

(H) = High overall *gca* status of parents; (L) = Low overall *gca* status of parents

Table 7 Overall heterotic status of crosses in dolichos bean

Lines	Testers							
	RIL 21 (L)		RIL 25 (L)		RIL 60 (H)		RIL 180 (H)	
	Total score	Status	Total score	Status	Total score	Status	Total score	Status
HA 3 (L)	219	L	177	L	55	H	223	L
HA 4 (L)	179	L	251	L	100	H	191	L
HA 11-3 (H)	159	L	188	L	98	H	145	H
RIL 11 (L)	50	H	24	H	99	H	160	L
RIL 185 (H)	81	H	79	H	96	H	155	L
FPB 8 (L)	246	L	234	L	95	H	151	L
FPB 15 (H)	217	L	129	H	96	H	160	L
RIL 332 (L)	79	H	98	H	119	H	135	H
FPB 3 (H)	176	L	183	L	82	H	237	L
RIL 162 (L)	122	H	204	L	52	H	222	L
HA 10-8 (H)	171	L	205	L	62	H	175	L
FPB 21 (H)	184	L	244	L	113	H	136	H

Final norm: 147

H = High overall heterotic status of crosses; L = Low overall heterotic status of crosses

(H) = High overall *gca* status of parents; (L) = Low overall *gca* status of parents

are adequately supported by the studies of similar nature in *B. compestris* [35], pearl millet [10, 40] and sesame [36, 37].

The superiority of H × L crosses in producing high magnitude of heterosis over a number of characters, is of practical utility to a plant breeder [35]. It is worthwhile to initiate H × L type of crosses for realising hybrids with high heterosis to optimise resources. The support for the utility of CA as one of the criterion for choosing the parents comes from the theoretical results which have indicated higher heterosis in the hybrids derived from parents differing in the frequencies of the genes [8]. The parental differences in CA are attributed to differences in gene frequency [5]. By utilising exotic (temperate) × Indian (tropical) and dwarf × tall crosses, several hybrids and varieties were evolved in sorghum [41, 42].

Relationship of Parental Genetic Divergence with Hybrid Overall sca and Heterosis

The number of hybrids with high (H) overall *sca* status was more in moderately divergent classes (DC 3 and DC 2) than either in DC 1 or DC 4 class. The number of overall heterotic crosses was more in DC 3 than either in DC 4 or DC 1. To normalise unequal number of crosses in different divergent classes, conditional probability of a heterotic cross has been found in DC 1, DC 2, DC 3 or DC 4 divergence classes. Given a heterotic cross, the conditional probability of finding it to be in DC 3 class was higher than the probability of finding it to be either in DC 4 or DC 1. Similarly, given a cross with high *sca* status, the probability of finding it to be in DC 3 and DC 2 classes was higher than the probability of finding it to be either in DC 4 or DC 1 class (Table 9).

The study suggested that it is likely to realise high frequency of heterotic hybrids from parents with intermediate genetic divergence quantified as DC 2 and DC 3 classes. Thus, there is existence of limits to parental divergence and it should neither be too small nor very large for realizing higher frequencies of heterotic hybrids. Choosing the parents with moderate divergence is likely to result in high frequency of heterotic hybrids as shown in triticale [43], groundnut [44], sesame [36], sunflower [45] and chilli [46]. It is hence, desirable to involve parents with intermediate genetic divergence and contrasting *gca* effects to recover higher frequencies of heterotic hybrids for economic traits in dolichos bean.

Conclusion

The high predictive power of parental *gca* effects on hybrid heterosis would save substantial resources and time and thus help enhance the pace and efficiency of dolichos bean breeding. The hybrids involving parents contrasting for overall *gca* status and/or those involving parents with intermediate genetic divergence were more frequently heterotic than those involving comparable *gca* status with extreme genetic divergence. Thus, there exists a limit to parental divergence for the occurrence of heterosis. It is

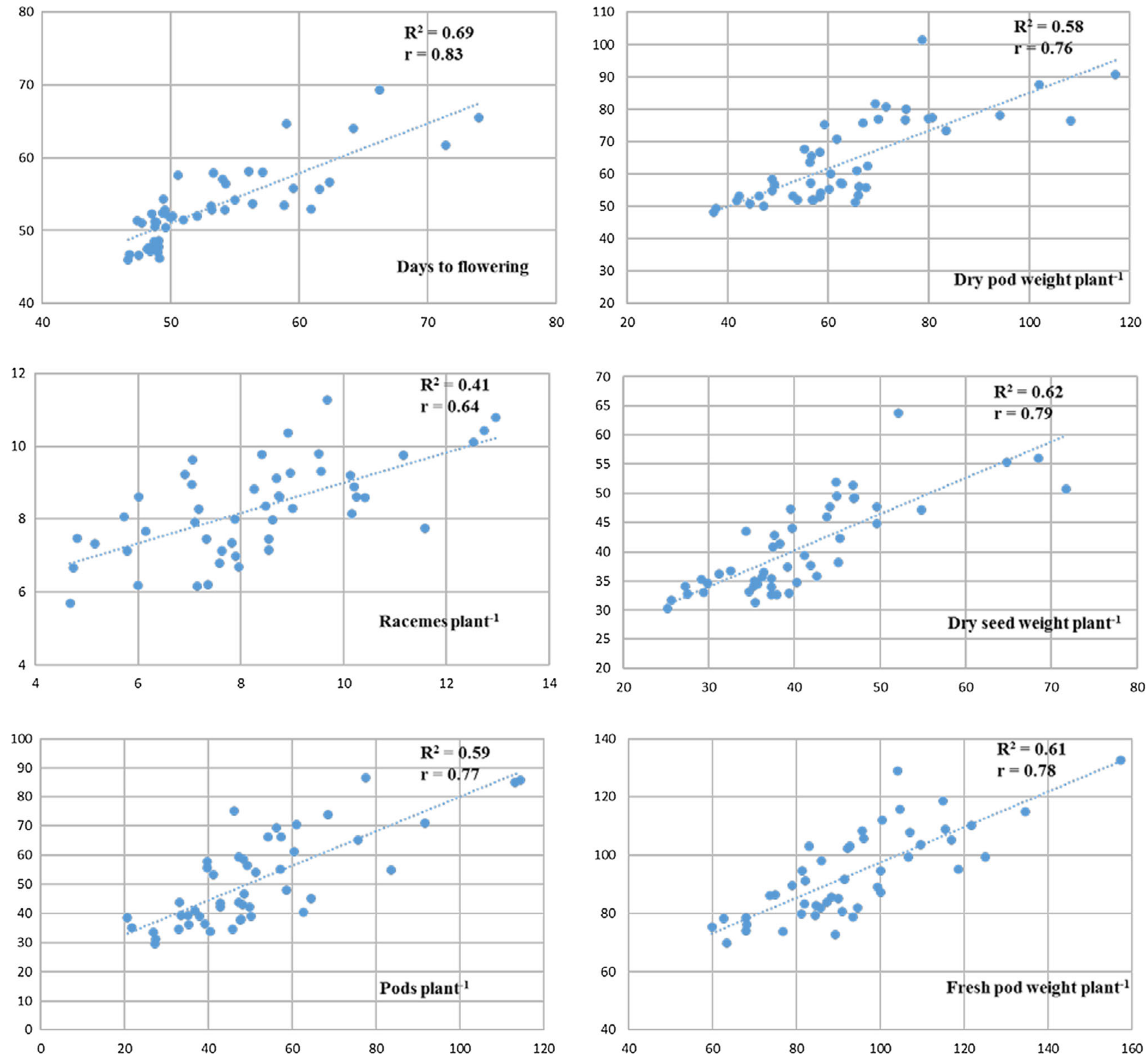

Fig. 1 Correlation between per se performance of hybrids with parental gca effects for six quantitative traits in dolichos bean. X-axis = Per se performance of hybrids; Y-axis = trait mean of all the crosses + sum of parental *gca* effects

Table 8 Distribution of crosses with high overall *sca* and heterotic status in relation to overall parental *gca* status in dolichos bean

Parental *gca* status of crosses	Number of crosses			Conditional probability that a cross with high *sca* status is found in the category	Conditional probability that a cross with high heterotic status is found in the category
	Under the category	With high (H) overall *sca* status	With high (H) heterotic status		
H × H	12	05	08	0.21	0.35
H × L/L × H	24	14	10	0.58	0.43
L × L	12	05	05	0.21	0.21

HH Both parents are high in their overall general combining ability

HL/LH One parent is high and other one is low in their overall general combining ability

LL Both parents are low in their overall general combining ability

Table 9 Distribution of crosses with high overall *sca* and heterotic status in relation to parental genetic divergence classes in dolichos bean

Parental divergence class	Number of crosses			Conditional probability that a cross with high *sca* status is found in the category	Conditional probability that a high heterotic cross is found in the category
	Under the category	With high (H) overall *sca* status	With high (H) heterotic status		
DC1	6	02	01	0.08	0.04
DC2	15	09	03	0.37	0.13
DC3	17	07	16	0.29	0.70
DC4	10	06	03	0.25	0.13

hence, desirable to involve parents with intermediate genetic divergence and contrasting *gca* effects to recover higher frequencies of heterotic hybrids for economic traits in dolichos bean.

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Compliance with Ethical Standards

Conflict of interest The authors declare that they have no conflict of interest.

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