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Gene action, heterosis and combining ability studies for economic traits in diallel crosses of lentil (*Lens culinaris* Medikus.)

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ABSTRACT

Diallel analysis was used to understand the nature of gene effects to determine the nature, magnitude and direction of heterosis and to identify promising single cross based on mean performance, heterosis, GCA and SCA effect and to dissect the kind of gene action governing the economic traits in lentil. Eight lentil parents and their 28 F_{1S} (excluding reciprocals) along with 2 checks were evaluated. Among parents, investigation of highest gca effects illustrated that PL 406 and L 4188 were good general combiners for most of yield. Cross PL 7 x PL 406 showed better parent as well as standard heterosis over check for maximum number of traits *viz.*, harvest index, pods per cluster, seeds per pod and secondary branches per plant and yield. Both additive and non-additive gene actions were involved in governing the inheritance of traits. This study suggests, even parents with poor GCA possess the potential to produce heterotic crosses. The manifestation of high amount of heterosis for seed yield and component traits by a large number of crosses suggest for the need to maintain heterozygosity in the population for maximum expression of the traits in desired direction.

Key words: Additive gene action, Diallel, Dominant gene action, GCA, Heterosis, Lentil, SCA, Yield.

INTRODUCTION

Lentil (*Lens culinaris* Medikus.) is one of the oldest and most important grain legume crop cultivated in India. In India area under lentil was 13.90 lakh hectares with a production of 10.93 lakh tonnes (DPD, Bhopal, Twelfth Plan (T.E. 2012-15). In terms of production Uttar Pradesh is on first ranked 34.36% followed by Madhya Pradesh (30.73%) and Bihar (17.35%) (Anonymous, 2016). Lentil has the third-highest level of protein (20-25%), by weight, of any legume or nut, after soybean and hemp (Callaway, 2004). Low productivity of lentil may be attributed to a number of factors (Kumar and Sahu, 2013). Yield is the ultimate product of action and interaction between yield components which are governed by a large number of gene having small effects and are greatly influenced by environment, the effect of small individual genes cannot be estimated, and only cumulative effect of the genes can be estimated for any of the attributes. The information on the nature of gene action could be helpful in predicting the effectiveness of selection in a population. Estimates of genotypic variance and phenotypic variance are used by plant breeders to estimate heritability. For developing elite strains, the identification of genetically superior parents is an important prerequisites. An erroneous choice of parents at this stage may undo a meticulously planned and well executed programme. Combining ability analysis is one of the powerful tools available to estimate the combining ability effects and aids in selecting the desirable parents and crosses for the exploitation of heterosis. Studies on heterosis have been well represented in black gram (Thamodharan *et al*., 2016), pea (Nageshwar *et al*., 2017) and green gram (Reddy *et al*., 2011), therefore, the present investigation was carried out with the specific objectives to estimate GCA and SCA variance, to determine the nature, magnitude and direction of heterosis in F_1 hybrid combinations to identify the promising single cross lentil hybrids.

MATERIALS AND METHODS

The present investigation was undertaken with eight (PL 7, PL 8, PL 6, PL 4, PL 406, L 4188, PL 084, and L 4147) lentil inbred lines which were initially screened for various desired characters. These inbred lines were grown for their seed multiplication and crossed in all possible combinations in a half diallel fashion (one way single crosses) to produce F_{1S} during *Rabi*,2013-14 at N. E. Borlaug Crop Research Centre, Pantnagar. The 28 F_{1s} were evaluated next year along with parents and two checks (DPL 62 and PRECOZ) in randomized complete block design in three replications. For a comprehensive analysis of data recorded

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on various quantitative characters and estimation of certain genetic parameters the statistical analysis using ANOVA was followed and subjected to test the significance of the various quantitative characters. Combining ability analysis in diallel analysis was done following the method given by Griffing (1956).

RESULTS AND DISCUSSION

Combining Ability Analysis

Analysis of variance for combining ability: Study of analysis of variance for combining ability revealed that GCA and SCA mean squares were significant for most of the characters under study (Table 1) and indicating that both additive and non-additive gene actions were involved in governing the inheritance of traits. Thus, the desirable GCA effects observed for different characters may serve as a guide-line in sorting out outstanding parents with favourable alleles for different component traits. Though, both additive and non-additive gene actions were significant for most of traits, higher magnitude of specific combining ability variances (s^2SCA) than general combining ability variances (s^2GCA) showed that the non-additive gene action was preponderant (Table 1). Results presented earlier by Kumar and Srivastava (2007); Sood *et al.* (2007) and Vanda *et al.* (2013) also indicated preponderance of non-additive gene effects in the expression of various quantitative traits. In contrast significantly higher values of GCA (General Combining Ability) than that of the values of variance of SCA depicted the role of additive type of gene action Abbas *et al.* (2016).

General combining ability studies: The estimate of GCA effect of parental lines for different characters (Table 2) revealed that none of the parental line was excellent in GCA

Table 1: Analysis of variance for combining ability.

Character	Mean Squares Source of Variation			σ^2GCA	σ^2SCA	GCA/ SCA Ratio
DF	GCA D f (7)	SCA D f (28)	Error D f(70)			
Days to 50% Flowering	13.35***	13.67***	2.66	0.0322	11.0084	0.0029
Days to Maturity	56.04***	43.15***	4.29	5.1756	38.8679	0.1332
Primary Branches/ Plant	5.80***	7.66***	0.12	0.5684	7.5432	0.0754
Secondary Branches/Plant	5.57***	9.95***	0.11	0.5463	9.8412	0.0555
Plant Height (cm)	13.18***	24.82***	1.31	1.1877	23.5107	0.0505
Pods/ Plant	86.58***	152.26***	1.33	8.5242	150.925	0.0565
Seeds/ Pod	0.04	0.19***	0.05	0.0012	0.1383	0.0084
Pods/ Cluster	0.20***	0.17***	0.04	0.0162	0.1339	0.121
100 Seed Weight (g)	0.50***	1.21***	0.03	0.0467	1.1855	0.0394
Yield/ Plot (g)	58.80***	143.50***	8.71	5.0088	134.7876	0.0372
Biological Yield	2509.74***	2047.45***	202.54	230.7199	1844.912	0.1251
Harvest Index	66.43***	119.95***	2.42	6.4002	117.5302	0.0545

Significance Level * = <.05, ** = <.01 and *** = <.001

Table 2: Estimates of general combining ability effects of parents.

Parent	Days to 50% Flowering	Days to Maturity	Primary Branches / Plant	Secondary Branches / Plant	Plant Height (cm)	Pods/ Plant	Seeds/ Pod	Pods/ Cluster	100 Seed Weight (g)	Yield/ Plot (g)	Biological Yield	Harvest Index
PL 7	0.56	-2.45***	0.21*	0.60***	-0.88*	1.86***	-0.09	0.04	0.12*	-1.22	-20.34***	1.57**
PL 8	0.59	3.32***	-0.48***	0.71***	0.96**	1.61***	-0.04	0.22***	-0.27***	0.57	5.64	0.07
PL 6	-0.31	3.68***	-0.78***	-1.25***	0.79*	-4.72***	0.05	-0.16**	-0.24***	-3.70***	14.35**	-3.70***
PL 4	0.99*	-0.98	-0.74***	-0.27**	0.49	-0.34	-0.01	-0.14*	-0.05	-0.63	7.75	-2.99***
PL 406	1.43**	-1.48*	1.46***	0.94***	-1.67***	0.30	-0.04	0.15*	0.18***	3.70***	-15.58***	3.91***
L 4188	0.06	0.85	0.32**	0.19	-0.69*	4.50***	0.04	-0.01	0.40***	3.13***	25.23***	-1.57**
PL 084	-1.84***	-0.98	-0.44***	-0.65***	-0.69*	-3.43***	0.09	-0.15*	-0.02	-0.93	-5.34	1.18*
L 4147	-1.48**	-1.95**	0.46***	-0.27**	1.71***	0.22	-0.01	0.05	-0.10*	-0.92	-11.71**	1.53**
SE (gi)	1.14	1.45	0.24	0.23	0.80	0.81	0.15	0.14	0.12	2.06	9.95	1.09
SE (gi-gj)	1.72	2.19	0.36	0.35	1.21	1.22	0.23	0.21	0.18	3.12	15.05	1.65

Significance Level * = <.05, ** = <.01 and *** = <.001

effects for all the characters studied. This results suggested that use of multiple parent participation through multiple crossing to effect substantial improvement in yield and its components. Use of multiple parents for yield improvement has been suggested in the studies of Tamoli (2011). Parental line PL 406 was ranked as the best parent as it had a good general combining ability. Line PL 406 was found to be a good general combiner for all the traits except for days to 50% flowering, pods per plant, biological yield and seeds *per se*. The parents having good GCA effects for yield also had good GCA effects for other yield contributing components, consequences has been revealed by Singh and Singh (2003) and Kumar and Srivastava (2007). Exploitation of outstanding parents in breeding programme is thus, expected to bring about substantial shift in the gene frequency of yield traits towards desired direction and will thereby provide elegant scope for improvement of these traits through selection.

Specific combining ability studies: In self-pollinated crops the additive x additive type of interaction is also feasible in later generations and can be exploited for the improvement of grain yield and related traits (Tamoli, 2011). The crosses with highest SCA effects and per se performance have been summarized (Table 3). The cross PL 8 x PL 6 (poor x poor) was identified as the best cross for primary branches per plant as per SCA effects and *per se* performance. Both the parents have poor GCA effects for the same character, yet they combine well together. Likewise, for secondary branches per plant the cross PL 7 x PL 406 (good x good) was been recognized as the best cross and has the highest SCA effects and *per se* performance as well. For plant height, PL 4 x PL 406 (average x good) has been recognized as the best cross and has the highest SCA effects and *per se* performance. The cross PL 7 x PL 084 (good x poor) had the highest SCA effect as well as *per se* performance for pods per plant. For yield per plot the cross PL 8 x PL 6 (average x poor) was the best cross based on highest SCA effects. Such studies have also been done by Kumar *et al*. (1996) and Abbas *et al*. (2016). Two poor combiners resulting into crosses with high positive *sca* effects might be due to better nicking ability of the parents. The poor general combiners tended to produce significant *sca* effects in the hybrids, where in the parental combinations provided environment for full expression of genes controlling this trait, though the parent themselves would not express any superiority. Thus among all the crosses PL 8 x PL 6, PL 7 x PL 084, PL 7 x PL 406, PL 4 x PL 406, PL 406 x L 4147 and L 4188 x PL 084 were ranked as the best crosses as they had good specific combining ability for maximum number of yield attributes including high *sca* effects for yield. This was notable that all these crosses had good SCA for yield per plot also (Table 4). These crosses can be further evaluated to produce promising hybrids. Thus transgressive segregants were expected in segregating generations. No correspondence between *per se* performance and GCA (Table 3) for rest of the traits might be due to the preponderance of non-additive gene effects. Therefore, the high mean performance of the parents may not be transferable to the progenies uniformly in such cases. The G X G (PL 7 x PL 406, PL 7 x PL 084, PL 406 x L 4147) parental combinations can be exploited through simple breeding procedures and (G/A X P or P X G/A PL 6 x L 4147, PL 4 x PL 406, L 4188 x PL 084, PL 8 x PL 6) combinations will require specific breeding procedures that provide opportunity for recombination and accumulation of desired genes in addition to breaking the undesirable linkages.

Heterotic advantage: Combinations that registered high yield *per se* along with significant positive SCA and Heterbeltiotic as well as standard heterotic responses for

Table: 3 Correspondence of per se performance and SCA effects of best cross in F_1 generation.

Character	Best cross (per se)	Best cross (SCA effect)	GCA of parents in specific crosses
Days to 50% Flowering	PL 084 x L 4147 (71.33)	PL 8 x L 4188 (-6.81)	A x A
Days to Maturity	PL 7 x PL 406 (113.33), PL 406 x L 4147 (113.33)	PL 8 x L 4188 (-9.93)	P x A
Primary Branches/ Plant	PL 8 x PL 6 (11.48)	PL 8 x PL 6 (7.15)	P x P
Secondary Branches/ Plant	PL 7 x PL 406 (15.81)	PL 7 x PL 406 (5.76)	G x G
Plant Height (cm)	PL 4 x PL 406(21.31)	PL 4 x PL 406 (-9.22)	A x G
Pods/ Plant	PL 7 x PL 084 (63.11)	PL 7 x PL 084 (25.58)	G x P
Seeds/ Pod	PL 8 x PL 6 (2.56)	PL 7 x PL 406 (0.7)	A x A
Pods/ Cluster	PL 8 x PL 406 (2.89)	PL 6 x L 4147 (0.64)	A x A
100 Seed Weight (g)	L 4188 x L 4147 (4.88)	PL 8 x PL 6 (2.59)	P x P
Biological Yield	PL 6 x L 4188 (275.67)	PL 7 x PL 406 (18.65)	P x P
Harvest Index	PL 8 x PL 6 (48.56)	PL 8 x PL 084 (95.43)	A x G
Yield/ Plot (g)	PL 7 x PL 406 (57.37)	PL 8 x PL 6 (24.84)	A x P

G= Good, A= Average, P= Poor

Table: 4 Summary for specific combining ability (SCA) of crosses for different characters

Diallel crosses	Days to 50% Flowering	Days to Maturity	Primary Branches/ Plant	Secondary Branches/ Plant	Plant Height (cm)	Pods/ Plant	Seeds/ Pod	Pods/ Cluster	100 Seed Weight (g)	Yield/ Plot (g)	Biological Yield	Harvest Index	Overall good
PL 7 x PL 8	A	G	P	A	G	P	P	A	A	A	A	P	2
PL 7 x PL 6	A	A	A	G	P	P	A	P	A	A	G	P	2
PL 7 x PL 4	A	A	A	P	P	P	A	A	A	P	A	P	-
PL 7 x PL 406	G	G	G	G	P	A	G	G	G	G	A	G	9
PL 7 x L 4188	A	P	P	P	A	P	P	P	P	P	P	A	-
PL 7 x PL 084	G	G	G	G	G	G	G	G	G	G	A	A	10
PL 7 x L 4147	P	A	P	P	A	P	P	P	P	P	A	A	-
PL 8 x PL 6	A	G	G	G	G	G	G	G	G	G	P	G	10
PL 8 x PL 4	A	A	A	G	P	A	A	A	P	A	A	A	1
PL 8 x PL 406	A	P	P	P	P	P	A	G	P	P	G	P	2
PL 8 x L 4188	G	G	P	P	A	P	G	A	P	P	A	P	3
PL 8 x PL 084	P	P	P	G	P	P	A	P	P	A	G	P	2
PL 8 x L 4147	A	P	P	G	P	P	A	A	P	A	A	A	1
PL 6 x PL 4	G	P	P	A	A	G	A	P	P	P	P	A	2
PL 6 x PL 406	A	G	P	P	A	G	A	A	P	P	P	A	2
PL 6 x L 4188	A	G	P	G	A	A	P	A	P	A	G	P	3
PL 6 x PL 084	A	A	P	A	A	P	A	A	A	P	A	P	-
PL 6 x L 4147	P	A	P	P	A	P	A	G	P	G	G	P	3
PL 4 x PL 406	G	G	G	G	G	G	A	A	G	G	A	A	8
PL 4 x L 4188	A	A	P	G	A	P	P	G	P	A	A	A	2
PL 4 x PL 084	A	G	P	P	A	P	A	A	P	P	P	P	1
PL 4 x L 4147	A	A	G	P	G	G	A	P	G	P	P	G	5
PL 406 x L 4188	A	G	G	G	A	G	G	A	G	A	A	A	6
PL 406 x PL 084	A	P	P	P	P	P	P	A	A	P	A	P	-
PL 406 x L 4147	A	G	G	G	G	G	A	P	G	G	A	G	8
L 4188 x PL 084	A	G	G	G	G	G	A	A	G	G	P	G	8
L 4188 x L 4147	G	A	G	G	G	G	A	A	G	A	P	A	6
PL 084 x L 4147	G	A	P	G	P	P	A	A	P	P	A	P	2

Table 5: Heterotic crosses for various characters.

Character	Relative heterosis	Heterobeltiosis	Standard Heterosis		Best specific combiner	Best cross with highest per se performance
			DPL 62	PRECOZ		
Days to 50% Flowering	PL 8 x L 4188 (-14.79)	PL 8 x L 4188 (-16.28)	PL 084 x L 4147 (-18.32)	PL 8 x L 4188 (-11.11)	PL 7 x PL 406 (-6.81)	PL 8 x L 4188 (72.00)
	PL 7 x PL 406 (-11.65)	L 4188 x L 4147 (-15.89)	PL 8 x L 4188 (-17.56)	PL 084 x L 4147 (-11.93)	PL 8 x L 4188 (-6.81)	PL 084 x L 4147 (71.33)
Days to Maturity	PL 6 x L 4188 (-8.23)	L 4188 x PL 084 (-13.25)	PL 406 x L 4147 (-11.69)	PL 7 x PL 406 (-7.36)	PL 8 x L 4188 (-9.93)	PL 7 x PL 406 (113.33),
	PL 8 x L 4188 (-11.36)	PL 8 x L 4188 (-12.25)	PL 7 x PL 406 (-11.69)	PL 406 x L 4147 (-7.36)	PL 8 x PL 6 (-7.09)	PL 406 x L 4147 (113.33)
Primary Branches/ Plant	PL 8 x PL 6 (95.63)	PL 8 x PL 6 (65.78)	PL 8 x PL 6 (75.14)	PL 8 x PL 6 (67.80)	PL 8 x PL 6 (7.15)	PL 8 x PL 6 (11.48)
	PL 4 x PL 406 (88.88)	PL 4 x PL 406 (60.31)	PL 4 x PL 406 (64.87)	PL 4 x PL 406 (57.96)	PL 4 x PL 406 (4.50)	PL 4 x PL 406 (10.81)
Secondary Branches/ Plant	PL 084 x L 4147 (140.60)	PL 084 x L 4147 (123.79)	PL 7 x PL 406 (154.10)	PL 7 x PL 406 (127.86)	PL 7 x PL 406 (5.76)	PL 7 x PL 406 (15.81)
	PL 406 x L 4188 (130.77)	PL 7 x PL 406 (116.72)	PL 406 x L 4188 (139.85)	PL 406 x L 4188 (115.08)	PL 406 x L 4188 (5.29)	PL 406 x L 4188 (14.93)
Plant Height (cm)	L 4188 x L 4147(-35.20)	PL 406 x L 4147 (-41.60)	PL 4 x PL 406 (-35.44)	PL 4 x PL 406 (-33.12)	PL 4 x PL 406 (-9.22)	PL 4 x PL 406(21.31)
	PL 4 x PL 406 (-33.42)	PL 4 x PL 406 (-39.09)	L 4188 x PL 084 (-30.85)	L 4188 x PL 084 (-28.37)	PL 406 x L 4147 (-7.91)	L 4188 x PL 084 (22.83)
Pods/ Plant	PL 4 x PL 406 (77.77)	PL 4 x PL 406 (57.09)	PL 7 x PL 084 (36.26)	PL 7 x PL 084 (59.22)	PL 7 x PL 084 (25.58)	PL 7 x PL 084 (63.11)
	PL 7 x PL 084 (53.97)	PL 6 x PL 406 (28.59)	L 4188 x PL 084 (20.42)	L 4188 x PL 084 (40.72)	L 4188 x PL 084 (15.61)	L 4188 x PL 084 (55.78)
Seeds/ Pod	PL 7 x PL 406 (48.50)	PL 7 x PL 406 (21.17)	PL 7 x PL 406 (9.57)	PL 7 x PL 406 (53.40)	PL 7 x PL 406 (0.70)	PL 8 x PL 6 (2.56)
	PL 406 x L 4188 (33.27)	PL 7 x PL 084 (21.17)	PL 7 x PL 084 (9.57)	PL 7 x PL 084 (53.40)	PL 7 x PL 084 (0.56)	PL 7 x PL 406 (2.56)
Pods/ cluster	PL 8 x PL 406 (33.38)	PL 8 x PL 406 (29.99)	PL 8 x PL 406 (13.04)	PL 8 x PL 406 (44.50)	PL 6 x L 4147 (0.64)	PL 8 x PL 406 (2.89)
	PL 8 x PL 6 (31.56)	PL 7 x PL 406 (24.89)	PL 7 x PL 406 (8.60)	PL 7 x PL 406 (38.83)	PL 7 x PL 406 (0.56)	PL 7 x PL 406 (2.78)
100 Seed Weight (g)	PL 406 x L 4147 (224.15)	PL 406 x L 4147 (218.01)	L 4188 x L 4147 (52.50)	L 4188 x L 4147 (41.31)	PL 8 x PL 6 (2.59)	L 4188 x L 4147 (4.88)
	L 4188 x L 4147 (130.55)	L 4188 x L 4147 (72.64)	PL 8 x PL 6 (45.62)	PL 8 x PL 6 (34.94)	L 4188 x L 4147 (2.00)	PL 8 x PL 6 (4.44)
Biological Yield	PL 8 x PL 084 (120.32)	PL 8 x PL 084 (111.76)	PL 6 x L 4188 (166.51)	PL 6 x L 4188 (170.39)	PL 7 x PL 406 (18.65)	PL 6 x L 4188 (275.67)
	PL 6 x L 4147 (92.83)	PL 6 x L 4147 (74.15)	PL 8 x PL 084 (130.44)	PL 8 x PL 084 (133.79)	PL 6 x L 4188 (93.46)	PL 8 x PL 084(238.36)
Harvest Index	PL 8 x PL 6 (41.97)	PL 7 x PL 406 (29.38)	PL 8 x PL 6 (18.68)	PL 8 x PL 6 (26.29)	PL 8 x PL 084 (95.43)	PL 8 x PL 6 (48.56)
	PL 7 x PL 406 (33.39)	PL 406 x L 4147 (27.60)	PL 7 x PL 406 (17.76)	PL 7 x PL 406 (25.31)	L 4188 x PL 084 (17.64)	PL 7 x PL 406 (48.18)
Yield/ Plot (g)	PL 7 x PL 406 (44.49)	PL 7 x PL 406 (36.22)	PL 7 x PL 406 (35.84)	PL 7 x PL 406 (46.30)	PL 7 x PL 406 (18.65)	PL 7 x PL 406 (57.37)
	PL 406 x L 4147 (34.59)	PL 406 x L 4147 (26.81)	PL 406 x L 4147 (26.45)	PL 406 x L 4147 (36.18)	PL 8 x PL 6 (17.32)	PL 406 x L 4147 (53.41)

yield may be considered ideal for use in yield improvement programme (Table 5). PL 7 x PL 406 was identified as a promising cross combination in the present investigation. The cross PL 7 x PL 406 was ranked best in all the aspects as this cross had better parent heterosis as well as standard heterosis for maximum number of traits *viz*., harvest index, pods per cluster, seeds per pod and secondary branches per plant including yield. Some of the cross combinations namely PL 8 x L 4188, PL 8 x PL 6, PL 4 x PL 406, PL 7 x PL 406, PL 406 x L 4188, PL 4 x PL 406, PL 7 x PL 084, PL 8 x PL 406, L 4188 x L 4147, PL 8 x PL 084 and PL 406 x L 4147 were noticed to be promising with respect to specific combining ability, *per se* performance and standard heterosis. These crosses also exhibited good correspondence between combining ability, *per se* performance and standard heterosis. This indicated the existence of positive association between SCA effects and heterotic response. Similar studies have been done earlier by Goyal *et al*. (1978), Rathi *et al.* (2003) and Kumar and Shrivastava (2007). This indicated the existence of positive association between SCA effects and heterotic response. However, ranking of crosses based on heterotic response (over BP) differed from ranking based on *per se* performance of several crosses. This stems from the fact that heterosis over poor and higher performing parents could result into different ranking. This means that selection of the crosses based on heterotic response over standard variety could be more realistic if these crosses were evaluated under multi location or multi seasonal trials. These crosses could be utilized for comprehensive *lentil* breeding programme. Crosses PL 8 x L 4188, PL 8 x PL 6, PL 4 x PL 406, PL 7 x PL 406, PL 406 x L 4188, PL 4 x PL 406, PL 7 x PL 084, PL 8 x PL 406, L 4188 x L 4147, PL 8 x PL 084 and PL 406 x L 4147 with high heterotic response for seed yield resulting from good combining parents could be identified as potential combinations for transgressive breeding. One of the cross namely PL 7 x PL 406 emerged as most promising cross for simultaneous improvement of seed yield as well as various other traits content. Further, the manifestation of high amount of heterosis for seed yield and component traits by a large number of crosses suggested for the need to maintain heterozygosity in the population for maximum expression of the traits in desired direction. Overall results indicated that breeding methods such as heterosis breeding or mass selection could be the most suitable option for further improvement (Sagar and Chandra, 1980, Sharma, 1991, Esmail *et al*., 1994 and Milan *et al.*, 2011).

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