

## Research Article



# Heterosis and Inbreeding Depression for Grain Yield Variables in Indigenous Maize Germplasm

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**Abstract** | Heterosis is one of the greatest practical contributions of genetics to the agricultural world and has its most significant expression in maize than other cereal crops. Exploitation of this phenomenon of superior performance of  $F_1$  progeny over their parents not only transfigured maize breeding schemes but also constituted the foundation of maize seed industry. Evaluation of *per se* performance of parental lines and estimation of heterosis and inbreeding depression are prerequisites to start hybrid development program. In this context, we explored heterosis and inbreeding depression in indigenous maize germplasm comprising inbred lines NCMLQ<sub>4</sub>, NCMLQ<sub>2</sub>, NCMLD<sub>1</sub>, NCMLD<sub>2</sub>, NCMLD<sub>3</sub>, and NCMLD<sub>4</sub>. These genotypes were crossed to get ten  $F_1$  hybrid combinations, which were used to develop three generations  $F_2$ ,  $BC_1$  and  $BC_2$ . Heterosis (in  $F_1$ ) and inbreeding depression (in  $F_2$ ,  $BC_1$  and  $BC_2$ ) were quantified for traits including shelling percentage, kernels per row, kernel rows per ear, and 100-grain weight and grain yield. Non-additive gene action was evident for shelling percentage, kernels per row and 100-grain weight and grain yield for which both heterosis and inbreeding depression were expressed by crosses like NCMLQ<sub>2</sub> × NCMLD<sub>2</sub> and NCMLQ<sub>2</sub> × NCMLD<sub>4</sub>. The parental lines used in above  $F_1$  hybrids could prove useful in exploitation of heterosis and development of hybrids.

**Editor** | Tahir Sarwar, The University of Agriculture, Peshawar, Pakistan.

**Received** | February 15, 2015; **Accepted** | December 08, 2015; **Published** | December 12, 2015

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**Citation** | Kiani, T. T., M. Hussain and H. Rahman. 2015. Heterosis and inbreeding depression for grain yield variables in indigenous maize germplasm. *Sarhad Journal of Agriculture*, 31(4): 217-223.

**DOI** | <http://dx.doi.org/10.17582/journal.sja/2015/31.4.217.223>

**Keywords** | Maize, Heterosis, Inbreeding depression, Grain yield, Non-additive gene action

## Introduction

Maize is undeniably the most completely domesticated of field crops and since its domestication, purposeful attempts have been made to enhance its yield. Consequently, open-pollinated varieties having distinct characters were developed and can still be seen under cultivation in developing countries. However, the discovery of hybrid vigor or “heterosis” in maize has revolutionized the breeding work being carried out. Exploitation of this phenomena of superior performance of progeny ( $F_1$  generally) with

respect to their parents not only transfigured maize breeding schemes but also constituted the foundation of maize seed industry (Acquaah, 2007). The hybrid vigor is one of the greatest practical contributions of genetics to the agricultural world and has its most significant expression in maize, as compared to other cereal crops, which is being explored intensively by maize breeders and seed production companies (Paterniani, 2001).

G.H. Shull's publication in early 1908 “the composition of a field of maize” marked the beginning of the

exploitation of heterosis in plant breeding. He reported that inbred lines of maize showed general deterioration in yield and vigor (inbreeding depression), but when crossed, the yield of hybrids exceeded that of the varieties from which the inbreds were derived. Furthermore, they not only had vigor restored greatly but also possessed an increased level of uniformity (Shull, 1908; Crow, 1998).

Shull in 1909 drew the pure-line method in maize breeding proposing the use of continuous selfing to develop homozygous lines that would be of use in hybrid production. This combination of inbreeding and hybridization created the basis of maize improvement and became standard in maize breeding programs (Shull, 1909; Acquaah, 2007). Due to higher yields, uniformity of hybrids, ability to incorporate favourable qualitative traits and be adapted to different habitats, especially length of growing season, the change from open-pollinated to hybrid maize was amazingly rapid (Crow, 1998). The impact of this paradigm shift is clearly evident from global maize yield and production statistics.

Inbreeding depression, however, is the conceptual opposite of heterosis and it is the loss of vigor following related mating. Inbreeding depression is due to reduction in heterozygosity in contrast to heterosis which is often viewed as maximizing heterozygosity (Kaeppeler, 2012). The extent of inbreeding depression and homozygosity achieved through self-pollination to develop maize inbred lines and exploitation of heterosis by crossing those lines are two main steps that lead to the development of desired hybrids. In the light of above, the present study aimed at quantifying heterosis and inbreeding depression in indigenous maize germplasm and also to identify parental lines to be used for hybrid development in future maize breeding programs.

## Materials and Methods

For heterosis estimates, maize inbred lines NCMLQ<sub>4</sub>, NCMLQ<sub>2</sub>, NCMLD<sub>1</sub>, NCMLD<sub>2</sub>, NCMLD<sub>3</sub>, and NCMLD<sub>4</sub> were inter crossed to have ten F<sub>1</sub> combinations viz:

NCMLQ<sub>4</sub> × NCMLQ<sub>2</sub>, NCMLQ<sub>4</sub> × NCMLD<sub>1</sub>, NCMLQ<sub>4</sub> × NCMLD<sub>2</sub>, NCMLQ<sub>4</sub> × NCMLD<sub>3</sub>, NCMLQ<sub>4</sub> × NCMLD<sub>4</sub>, NCMLQ<sub>2</sub> × NCMLD<sub>1</sub>, NCMLQ<sub>2</sub> × NCMLD<sub>2</sub>, NCMLQ<sub>2</sub> × NCMLD<sub>3</sub>, NCMLQ<sub>2</sub> × NCMLD<sub>4</sub>, NCMLD<sub>3</sub> × NCMLD<sub>4</sub>. For inbreeding estimates, we developed three generations

of each cross viz; F<sub>2</sub> (by selfing of F<sub>1</sub> plants), BC<sub>1</sub> (by backcrossing F<sub>1</sub> with parent-1) and BC<sub>2</sub> (by backcrossing F<sub>1</sub> with parent-2). All six parents with their four generations i.e. F<sub>1</sub>, F<sub>2</sub>, BC<sub>1</sub> and BC<sub>2</sub> were planted in randomized complete block design having three replications following optimum agronomic practices. Data for grain yield and ear traits like shelling percentage, kernels per row, kernel rows per ear, and 100-grain weight were recorded. Thirty guarded plants were used to take data of parents and F<sub>1</sub>s, 210 plants of F<sub>2</sub> and 45 plants of back-crosses. The study was carried out during spring 2009 at National Agricultural Research Centre (NARC), Islamabad, Pakistan

## Statistical analysis

Analysis of variance was conducted to check significant differences among generations used for estimation of heterosis and inbreeding depression. Mid-parent (MP) and better parent (BP) heterosis were calculated by using the following formulae (Nadarajan and Gunasekaran, 2008):

$$\text{Mid - parent heterosis\%} = \left( \frac{F_1 - \text{Midparent value}}{\text{Midparent value}} \right) \times 100$$

$$\text{Better - parent heterosis \%} = \left( \frac{F_1 - \text{Betterparent value}}{\text{Betterparent value}} \right) \times 100$$

Standard errors for both these estimates were calculated as (Nadarajan and Gunasekaran, 2008):

$$S.E. \text{ for mid - parent heterosis} = \sqrt{\left( \frac{3}{2r} \times \text{error mean square} \right)}$$

$$S.E. \text{ for better - parent heterosis} = \sqrt{\left( \frac{3}{2r} \times \text{error mean square} \right)}$$

where  $r$  is number of replications.  $t$ -test was used to check significance of heterosis estimates where ' $t$ ' values were calculated as (Nadarajan and Gunasekaran, 2008):

Mid-parent heterosis:

$$t_{calc} = \frac{F_1 - MP}{S.E}$$

Better-parent heterosis:

$$t_{calc} = \frac{F_1 - BP}{S.E}$$

Estimates were found significant when these  $t_{calc}$  values were greater than  $t_{tabulated}$  values at 5% probability.

Inbreeding estimates for each generation were computed as under (Talebi et al., 2010):

$$ID \% = \left( \frac{F_1 - F_2}{F_1} \right) \times 100, \left( \frac{F_1 - BC_1}{F_1} \right) \times 100, \left( \frac{F_1 - BC_2}{F_1} \right) \times 100$$

Similarly  $t_{calc}$

$$\frac{Estimated\ ID\%}{S.E.M(F_1) + S.E.M(F_2)}, \frac{Estimated\ ID\%}{S.E.M(F_1) + S.E.M(BC_1)}, \frac{Estimated\ ID\%}{S.E.M(F_1) + S.E.M(BC_2)}$$

These were compared with  $t_{tabulated}$  at 5% to determine the significance of inbreeding depression estimates in each of three generations where S.E.M = Standard Dev/no. of observations.

## Results and Discussion

Analysis of variance showed significant differences among generations for traits under study viz; shelling percentage, kernels per row, kernel rows per ear and 100-grain weight and grain yield thereby data was pursued for further analysis (Table 1). Mid-parent and better parent heterosis estimates were computed for all traits which showed varied level of significance corresponding to each cross (Table 2). Inbreeding depression estimates were determined as expressed by three generations  $F_2$ ,  $BC_1$  and  $BC_2$  of all crosses and results are appended in Table 3. The inconsistent display of inbreeding depression along with the varied expression of heterosis by different crosses gave a hint towards selection of the parental lines for development of hybrids. The point of emphasis here is that the measures of heterosis are phenotype-dependent or, in other words, trait specific. It is therefore, recommended that studies to understand mechanisms of heterosis must be conducted and inferred with respect to specific traits (Kaeppler, 2012). In early 1900s, E. M. East recognized the deleterious effects of inbreeding but was not convinced of the idea of exploitation of heterosis and development of hybrids because the inbred lines were generally very weak, producing little seed and hence the increased cost of seed production negated any increments in yield (Crow, 1998). However, modern day breeders emphasize more on development of parental inbred lines that have greater vigor, greater seed yields and, thus, commercially viable. Hence, our efforts for development of superior inbred lines and exploitation of heterosis for larger commercial gains are more focused now on understanding of underlying genetic make-up of these germplasm resources.

Results of heterosis estimates showed that besides positive heterosis, i.e. heterosis in desired direction, many crosses showed significant negative heterosis over mid-parent and better parent for grain yield, shelling percentage, kernels per row, kernel rows per ear and 100-grain weight. For grain yield, although heterosis was expressed as high as 20.62 percent by hybrid NCMLQ<sub>2</sub> × NCMLD<sub>2</sub>, 15.33 percent by NCMLD<sub>3</sub> × NCMLD<sub>4</sub> and 10.89 percent by NCMLQ<sub>4</sub> × NCMLQ<sub>2</sub> over mid-parental values however, remained non-significant statistically. Positive heterosis for this trait have also been reported by Geeta et al. (2001), Bajaj et al. (2007), Amiruzzaman et al. (2011), Ikramullah et al. (2011), Jain and Bharadwaj (2014), whereas Rozende and Souza (2000) reported low heterosis for grain yield.

For shelling percentage, cross combination NCMLQ<sub>4</sub> × NCMLD<sub>2</sub> expressed significant heterosis over mid-parent (11.09%) and NCMLQ<sub>2</sub> × NCMLD<sub>4</sub> over both mid-parent (21.30%) and better parent (18.69%). Heterosis for this trait was also found in studies by Ravikant et al. (2006) and Jain and Bharadwaj (2014). For kernels per row, NCMLQ<sub>2</sub> × NCMLD<sub>2</sub> showed high level of heterosis (13.60%) but remained nonsignificant. On the contrary, studies by Jain and Bharadwaj (2014), Geeta et al. (2001) and Malik et al. (2004) reported heterosis for this character. No hybrid combination displayed positive heterosis for kernel rows per ear in contrast to Jain and Bharadwaj (2014) who reported heterosis for grain rows per cob as did Geeta et al. (2001) and Kara et al. (2001).

However, for 100-grain weight, significant positive heterosis was shown by NCMLQ<sub>4</sub> × NCMLD<sub>1</sub> over mid-parent (16.42%) and by NCMLQ<sub>4</sub> × NCMLD<sub>2</sub>, NCMLQ<sub>2</sub> × NCMLD<sub>4</sub> over both mid-parent (40.01%, 37.10%, respectively) and better-parent (17.84%, 35.25%, respectively). Significant heterosis was also found for this trait by Bajaj et al. (2007), Jain and Bharadwaj (2014), Kara et al. (2001), Dickert and Tracy (2002) and Malik et al. (2004).

It is to be considered here that yield is a complex trait that manifests itself through interaction of the plant with the environment from planting until harvest. Moreover, being quantitative in nature, yield is determined by a large number of genes each individually having a small incremental effect on its total expression. Furthermore, heterosis expressed by hybrids

**Table 1: Mean squares for various traits in maize**

Source of variation	d.f.	Mean square values														
		Grain yield			Shelling %			Kernels per row			Kernel rows			100 grain weight		
		F <sub>2</sub>	BC <sub>1</sub>	BC <sub>2</sub>	F <sub>2</sub>	BC <sub>1</sub>	BC <sub>2</sub>	F <sub>2</sub>	BC <sub>1</sub>	BC <sub>2</sub>	F <sub>2</sub>	BC <sub>1</sub>	BC <sub>2</sub>	F <sub>2</sub>	BC <sub>1</sub>	BC <sub>2</sub>
Replications	2	318.63	207.2	139.68	91.56*	80.04*	89.97*	11.29	19.98	32.12*	3.57*	1.70*	2.05*	4.41*	30.42	21.93
Generations	25	277.94*	349.71*	426.26*	62.23*	99.25*	104.07*	188.74*	43.85*	60.13*	1.22*	1.70*	1.93*	25.74*	340.03*	396.26*
Error	50	105.41	66.116	66.86	17.37	17.04	19.12	12.07	9.70	4.77	0.32	0.40	0.36	15.4	19.02	15.78

\* Significant at 5%

**Table 2: Mid and better parent heterosis estimates for grain yield and other yield attributes in maize**

Generations	Grain yield			Shelling %			Kernels per rows			Kernel rows per ear			100 Grain Weight		
	Mean	MP Het-erosis %	BP Het-erosis %	Mean	MP Het-erosis %	BP Het-erosis %	Mean	MP Het-erosis %	BP Het-erosis %	Mean	MP Het-erosis %	BP Het-erosis %	Mean	MP Het-erosis %	BP Het-erosis %
PARENTS	NCMLQ <sub>4</sub>	68.59		66.98		39.92		12.71		37.30					
	NCMLQ <sub>2</sub>	64.19		67.23		34.18		12.67		41.25					
	NCMLD <sub>1</sub>	53.18		71.12		40.81		15.14		39.04					
	NCMLD <sub>2</sub>	51.71		76.91		32.84		13.72		54.59					
	NCMLD <sub>3</sub>	51.75		78.63		38.39		14.84		62.47					
	NCMLD <sub>4</sub>	80.91		64.33		47.96		14.09		40.14					
	Q <sub>2</sub> XQ <sub>2</sub>	73.61	10.89	7.33	68.28	1.75	1.57	35.63	-3.85	-10.76	12.51	-1.44	-1.58	32.02	-18.47*
	Q <sub>2</sub> XD <sub>1</sub>	62.89	3.30	-8.30	69.48	0.62	-2.30	39.88	-1.21	-2.29	13.66	-1.89	-9.77*	44.44	16.42*
	Q <sub>2</sub> XD <sub>2</sub>	46.71	-22.35	-31.9*	79.93	11.09*	3.92	35.65	-2.02	-10.71	12.69	-4.00	-7.54*	64.32	40.01*
	Q <sub>2</sub> XD <sub>3</sub>	63.50	5.53	-7.42	69.91	-3.98	-11.09*	42.74	9.14	7.05	13.11	-4.84	-11.68*	38.27	-23.28*
F <sub>1</sub> HYBRIDS	Q <sub>2</sub> XD <sub>4</sub>	74.90	0.21	-7.42	64.43	-1.87	-3.81	45.03	2.48	-6.11	13.10	-2.21	-7.02*	35.65	-7.91
	Q <sub>2</sub> XD <sub>1</sub>	61.29	4.44	-4.51	67.49	-2.43	-5.10	38.80	3.47	-4.93	13.59	-2.29	-10.25*	35.46	-11.68
	Q <sub>2</sub> XD <sub>2</sub>	69.90	20.62	8.90	62.84	-12.81*	-18.30*	38.07	13.60	11.37	12.50	-5.30	-8.92*	31.72	-33.80*
	Q <sub>2</sub> XD <sub>3</sub>	61.05	5.32	-4.88	69.61	-4.55	-11.48*	37.47	3.25	-2.41	13.60	-1.15	-8.37*	36.44	-29.74*
	Q <sub>2</sub> XD <sub>4</sub>	49.48	-31.79*	-38.84*	79.79	21.30*	18.69*	37.82	-7.92	-21.15*	13.14	-1.79	-6.74*	55.79	37.10*
	D <sub>3</sub> XD <sub>4</sub>	76.50	15.33	-5.45	65.54	-8.31*	-16.65*	47.36	9.69	-1.25	12.78	-11.69*	-13.92*	41.02	-20.04*

\* Significant against *t* tabulated at 5% probability.



**Table 3:** *Inbreeding depression estimates for various traits as manifested in  $F_2$ ,  $BC_1$  and  $BC_2$  generations*

Generations		Grain Yield		Shelling %		No of Kernels per Row		No. of Kernel Rows per ear		100 Grain Weight	
		Means	ID %	Means	ID %	Means	ID %	Means	ID %	Means	ID %
PARENTS	NCMLQ <sub>4</sub>	68.59		66.98		39.92		12.71		37.30	
	NCMLQ <sub>2</sub>	64.19		67.23		34.18		12.67		41.25	
	NCMLD <sub>1</sub>	53.18		71.12		40.81		15.14		39.04	
	NCMLD <sub>2</sub>	51.71		76.91		32.84		13.72		54.59	
	NCMLD <sub>3</sub>	51.75		78.63		38.39		14.84		62.47	
$F_1$ HYBRIDS	NCMLD <sub>4</sub>	80.91		64.33		47.96		14.09		40.14	
	Q <sub>4</sub> X Q <sub>2</sub>	73.61		68.28		35.63		12.51		32.02	
	Q <sub>4</sub> X D <sub>1</sub>	62.89		69.48		39.88		13.66		44.44	
	Q <sub>4</sub> X D <sub>2</sub>	46.71		79.93		35.65		12.69		64.32	
	Q <sub>4</sub> X D <sub>3</sub>	63.50		69.91		42.74		13.11		38.27	
	Q <sub>4</sub> X D <sub>4</sub>	74.90		64.43		45.03		13.10		35.65	
	Q <sub>2</sub> X D <sub>1</sub>	61.29		67.49		38.80		13.59		35.46	
	Q <sub>2</sub> X D <sub>2</sub>	69.90		62.84		38.07		12.50		31.72	
	Q <sub>2</sub> X D <sub>3</sub>	61.05		69.61		37.47		13.60		36.44	
	Q <sub>2</sub> X D <sub>4</sub>	49.48		79.79		37.82		13.14		55.79	
$F_2$ GENERATION	D <sub>3</sub> X D <sub>4</sub>	76.50		65.54		47.36		12.78		41.02	
	Q <sub>4</sub> X Q <sub>2</sub>	49.66	32.54*	69.71	-2.10	27.55	22.66*	13.20	-5.53*	27.32	14.66*
	Q <sub>4</sub> X D <sub>1</sub>	68.45	-8.84*	66.45	4.36*	26.46	33.65*	12.85	5.95*	25.37	42.92*
	Q <sub>4</sub> X D <sub>2</sub>	58.36	-24.9*	72.15	9.72*	25.49	28.50*	13.19	-3.98*	27.38	57.43*
	Q <sub>4</sub> X D <sub>3</sub>	56.21	11.47*	72.29	-3.40*	20.30	52.49*	13.63	-3.98*	26.97	29.54*
	Q <sub>4</sub> X D <sub>4</sub>	51.65	31.05*	71.00	-10.20*	24.63	45.31*	13.59	-3.71*	27.23	23.62*
	Q <sub>2</sub> X D <sub>1</sub>	65.18	-6.35	69.34	-2.74	27.34	29.53*	13.29	2.22*	25.52	28.02*
	Q <sub>2</sub> X D <sub>2</sub>	49.87	28.66*	68.67	-9.28*	25.32	33.48*	13.22	-5.78*	25.24	20.44*
	Q <sub>2</sub> X D <sub>3</sub>	53.35	12.62*	71.03	-2.04	23.72	36.68*	13.03	4.20*	26.68	26.77*
	Q <sub>2</sub> X D <sub>4</sub>	67.49	-36.4*	66.96	16.08*	24.60	34.95*	13.41	-2.03*	26.67	52.20*
$BC_1$ GENERATION	D <sub>3</sub> X D <sub>4</sub>	68.99	9.82*	71.97	-9.81*	28.21	40.43*	13.27	-3.84*	27.81	32.21*
	Q <sub>4</sub> X Q <sub>2</sub>	58.21	20.92*	66.31	2.89	40.41	-13.43*	13.20	-5.53*	29.93	6.53*
	Q <sub>4</sub> X D <sub>1</sub>	54.96	12.61*	61.16	11.98*	41.96	-5.23*	12.75	6.70*	44.17	0.61
	Q <sub>4</sub> X D <sub>2</sub>	45.66	2.24	69.88	12.57*	35.92	-0.77	13.22	-4.25*	63.33	1.54
	Q <sub>4</sub> X D <sub>3</sub>	65.30	-2.84	61.62	11.86*	38.47	9.98*	13.95	-6.43*	40.61	-6.12*
	Q <sub>4</sub> X D <sub>4</sub>	79.87	-6.64	61.98	3.79	43.99	2.30	15.18	-15.85*	35.24	1.18
	Q <sub>2</sub> X D <sub>1</sub>	57.95	5.44	68.99	-2.22	42.25	-8.91*	13.47	0.85*	36.21	-2.13
	Q <sub>2</sub> X D <sub>2</sub>	73.41	-5.02*	70.05	-11.48*	38.47	-1.04	13.36	-6.91*	28.42	10.41*
	Q <sub>2</sub> X D <sub>3</sub>	67.10	-9.91*	65.87	5.38*	39.65	-5.82*	12.80	5.91*	36.49	-0.15
	Q <sub>2</sub> X D <sub>4</sub>	48.38	2.23	71.85	9.95*	38.96	-3.03*	13.60	-3.48*	58.87	-5.53
$BC_2$ GENERATION	D <sub>3</sub> X D <sub>4</sub>	78.12	-2.12	80.70	-23.13*	45.00	4.99*	13.88	-8.68*	38.82	5.37*
	Q <sub>4</sub> X Q <sub>2</sub>	59.27	19.49*	69.67	-2.03	36.21	-1.63	12.32	1.50*	30.73	4.02
	Q <sub>4</sub> X D <sub>1</sub>	54.92	12.68*	65.88	5.19*	34.94	12.38*	12.51	8.39*	45.59	-2.59
	Q <sub>4</sub> X D <sub>2</sub>	46.70	0.02	79.15	0.97	36.05	-1.13	13.71	-8.08	68.92	-7.15*
	Q <sub>4</sub> X D <sub>3</sub>	72.09	-13.53*	70.62	-1.01	42.50	0.55	14.87	-13.44	36.14	5.57*
	Q <sub>4</sub> X D <sub>4</sub>	85.80	-14.55*	62.47	3.04	45.10	-0.16	14.68	-12.06	36.53	-2.47
	Q <sub>2</sub> X D <sub>1</sub>	58.53	4.51	71.47	-5.90*	35.42	8.70*	13.50	0.63*	36.64	-3.34*
	Q <sub>2</sub> X D <sub>2</sub>	80.02	-14.49*	82.28	-30.94*	39.73	-4.35*	12.76	-2.11	27.23	14.17*
	Q <sub>2</sub> X D <sub>3</sub>	68.72	-12.56*	64.73	7.01*	39.64	-5.79*	13.45	1.11*	39.84	-9.35*
	Q <sub>2</sub> X D <sub>4</sub>	47.30	4.41	63.38	20.56*	38.96	-3.02*	13.60	-3.48	64.44	-15.50*
$BC_2$ GENERATION	D <sub>3</sub> X D <sub>4</sub>	83.10	-8.63*	72.60	-10.76*	50.04	-5.66*	13.88	-8.62	40.97	0.14

\*Significant against  $t_{tabulated}$  at 5% probability.

largely depends on the genetic divergence of the parental lines (Telebi, 2010). Therefore, we can deduce that low values of heterosis for these traits are a consequent of close relatedness of inbred lines used in this study.

Significant positive values of inbreeding depression were found for grain yield in  $F_2$  generation of crosses  $NCMLQ_4 \times NCMLQ_2$  (32.54 %),  $NCMLQ_4 \times NCMLD_3$  (11.47%),  $NCMLQ_4 \times NCMLD_4$  (31.05%),  $NCMLQ_2 \times NCMLD_2$  (28.66%),  $NCMLQ_2 \times NCMLD_3$  (12.62%) and  $NCMLD_3 \times NCMLD_4$  (9.82%). Similarly, both backcross generations ( $BC_1$  and  $BC_2$ ) of  $NCMLQ_4 \times NCMLQ_2$  and  $NCMLQ_4 \times NCMLD_1$  also expressed significant inbreeding depression for this trait. Similarly, Jain and Bharadwaj (2014) and Ahmad et al. (2010) stated inbreeding depression for grain yield.

The cross  $NCMLQ_2 \times NCMLD_4$  showed maximum significant inbreeding depression (16.08%) in  $F_2$  for shelling percentage followed by  $NCMLQ_4 \times NCMLD_2$  (9.72%) and  $NCMLQ_4 \times NCMLD_1$  (4.36%). In addition to these crosses,  $NCMLQ_4 \times NCMLD_3$  (11.86%) and  $NCMLQ_2 \times NCMLD_3$  (5.38%) displayed decreased performance for this trait in  $BC_1$ , whereas in  $BC_2$ , the cross  $NCMLQ_2 \times NCMLD_4$  again expressed highest percentage loss in performance (20.56%) as compared to other crosses. Ravikant et al. (2006) and Jain and Bharadwaj (2014) also reported inbreeding depression for shelling percentage.

All crosses exhibit significant inbreeding depression for kernels per row in  $F_2$  ranging from 52.49% by  $NCMLQ_4 \times NCMLD_3$  to 22.66 % by  $NCMLQ_4 \times NCMLQ_2$ . Only  $NCMLQ_4 \times NCMLD_3$  (9.98%) and  $NCMLD_3 \times NCMLD_4$  (4.99%) replicated this decline in  $BC_1$ ,  $NCMLQ_4 \times NCMLD_1$  (12.38%) and  $NCMLQ_2 \times NCMLD_1$  (8.70%) in  $BC_2$ . Inbreeding depression with respect to this trait was also noted in crosses studied by Jain and Bharadwaj (2014)).

Three crosses demonstrated significant inbreeding for no. of kernel rows per ear across all segregating generations under study viz;  $NCMLQ_4 \times NCMLD_1$  (5.95% in  $F_2$ , 6.70% in  $BC_1$ , 8.39% in  $BC_2$ ),  $NCMLQ_2 \times NCMLD_1$  (2.22% in  $F_2$ , 0.85% in  $BC_1$ , 0.63% in  $BC_2$ ) and  $NCMLQ_2 \times NCMLD_3$  (4.20% in  $F_2$ , 5.91% in  $BC_1$ , 1.11% in  $BC_2$ ). These results are in agreement with those reported by Jain and Bharadwaj

(2014) and Ahmad et al. (2010).

Reduction in 100-grain weight was recorded for all crosses in  $F_2$ . This reduction was apparent in  $BC_1$  for only three crosses;  $NCMLQ_4 \times NCMLQ_2$  (6.53%),  $NCMLQ_2 \times NCMLD_2$  (10.41%) and  $NCMLD_3 \times NCMLD_4$  (5.37%).  $NCMLQ_2 \times NCMLD_2$  experienced consistent depression for 100 grain weight having being estimated significantly in  $BC_2$  (14.17%) also. Ahmad et al. (2010) and Jain and Bharadwaj (2014) also illustrated inbreeding depression for this plant attribute. Apart from these estimates, significant negative estimates were also demonstrated for crosses in generations studied.

Non-additive gene action can be assumed responsible for the traits when the hybrid combinations exhibit high heterosis followed by a high inbreeding depression in  $F_2$  generation (Jain and Bharadwaj (2014)). So it can be inferred that the parents of such crosses possess dominant genes responsible for traits under study, as evident by high heterosis (although non-significant in some cases), followed by high inbreeding depression. This also authenticates our earlier diallel study involving these line where we reported non-additive (dominance) gene action for grain yield, shelling percentage and 100 grain weight (Hussain et al., 2014). This gene action will prove fruitful in exploiting heterosis and developing hybrid cultivars using these particular inbred lines.

However, those hybrid combinations which showed high heterosis coupled with low inbreeding depression could be used to develop superior inbred lines which could be further exploited in hybridization programs. This has also been suggested by Banerjee and Kole (2011) and Jain and Bharadwaj (2014).

## Conclusion

As discussed earlier, heterosis should be considered in the context of a specific trait. Furthermore, non-additive gene action becomes evident when a cross expresses high heterosis in  $F_1$  and inbreeding depression in  $F_2$ . This type of gene action is of particular interest for breeders to take advantage of heterosis and develop hybrids. Hence, we also focused our attention under the light of these two factors i.e. trait specific heterosis and non-additive gene action. The crosses  $NCMLQ_2 \times NCMLD_2$  expressed heterosis and inbreeding depression for grain yield and kernels per row. Thus,

these parents could be used in hybrid development. On the other hand, cross NCMLQ<sub>2</sub> × NCMLD<sub>4</sub> demonstrated heterosis and inbreeding depression for shelling percentage and 100-grain weight. Therefore, these parental lines could prove useful in exploitation of heterosis for these traits.

## Authors' Contribution

Tauseef Taj Kiani analysed the data and made a rough draft of the manuscript while Mozammil Hussain conducted research conduct, recorded and compiled data. Hidayat ur Rahman made final draft of the manuscript and reviewed it.

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