



Heterosis, Combining Ability and Their Inter-Relationship for Morphological and Quality Traits in Yellow Maize (*Zea mays* L.) Single-Crosses Across Environments

T. N. Bhusal^{*)} and G. M. Lal

Department of Genetics and Plant Breeding, Sam Higginbottom University of Agriculture Technology and Sciences, Allahabad-211007, Uttar Pradesh, India

ARTICLE INFO

Keywords:

Combining ability
Heterosis
Morphological traits
Pearson's correlation
Quality traits

Article History:

Received: December 8, 2018

Accepted: January 23, 2020

*) Corresponding author:

E-mail: tnagr01@gmail.com

ABSTRACT

The research aimed to study heterosis, combining ability and performance along with their inter-relationship across three environments. Variance due to general (GCA) and specific combining abilities (SCA) and their interaction with environment was found to be significant for most of studied traits. For all the studied traits but ASI (Anthesis-silking interval), HI (Harvest index) and starch content, additive gene action was highly important than non-additive gene action for their expression as reflected by Baker's ratio which was near to unity. CML439, R13-1-1 and Tarun83-1-3-2 were the best general combiner for starch, protein and oil, respectively. R13-1-17, CML439 and Tarun83-1-3-2 were good general combiner for maturity characters and harvest index while TSK 196 and TSK 197 were good general combiner for cob length, cob girth, number of grains/row and grain yield. DMR9047×R13-1-17 and POP31Q×Tarun83-1-3-2 showed desirable heterosis and SCA effect for maturity characters. Regarding to SCA and heterosis, the prominent hybrids for grain yield were TSK197×R13-1-10, TSK194×POP31Q, DMR9047×POP31Q and R13-1-1×DMR9047. SCA established stronger relationship with per se performance of grain yield and quality traits than mid-parent (MPH) and best-parent heterosis (BPH), reflecting that an improvement in selection of SCA will results in an indirect improvement of MPH and BPH of hybrids.

INTRODUCTION

Globally, maize (*Zea mays* L.; $2n = 20$) is the third important food crop after rice and wheat in terms of area and production. It has multifaceted uses as food, feed and basic raw materials for number of industries such as oil, food, protein, alcoholic beverages, starch, sweeteners, and biofuels. Demand of maize is exponentially increasing worldwide, especially as feed in poultry and pig industries. The major challenges like changes in environments, decrease in land fertility, limited resources, high demand, etc. put thrust over maize production. Heterosis breeding is one of the most potential approaches to combat the threats of maize production.

Heterosis expresses the superiority of F_2 s over their standard and better parents, but fails to identify the possible causes of the superiority

of hybrid (Amiruzzaman, Islam, Hasan, Kadir, & Rohman, 2013). Farmers merely preferred hybrids to other varieties due to their yield potential. The success of hybrid development is fundamentally depended on the genetic variability in the base population and the development of superior inbreds. In a conventional breeding approach, potential inbred lines are important to be identified for hybridization and cross to expand the variability of genetic for the superior genotypes selection (Hallauer & Miranda Filho, 1988). Combining ability plays an important role in crop improvement such as maize, as it helps to identify potential parents that can be used for producing hybrids and synthetics (Vasal, 2000). To assist research on hybrid development, the information about heterotic patterns and combining ability among gene pools and populations are needed (Beck, Vasal, & Crossa, 1990). A sound breeding

ISSN: 0126-0537 Accredited First Grade by Ministry of Research, Technology and Higher Education of The Republic of Indonesia, Decree No: 30/E/KPT/2018

Cite this as: Bhusal, T. N., & Lal, G. M. (2020). Heterosis, combining ability and their inter-relationship for morphological and quality traits in yellow maize (*Zea mays* L.) single-crosses across environments. *AGRIVITA Journal of Agricultural Science*, 42(1), 174–190. <http://doi.org/10.17503/agrivita.v42i1.2089>

program needs the nature of gene actions controlling quantitative traits and a basis for selecting good combiners as reflected by a high general combining ability (GCA) effect and superior hybrids as reflected by a high specific combining ability (SCA) effect (Soriana Viana & de Pina Matta, 2003). Knowledge of genetic architecture of characters is necessary for developing and implying appropriate breeding procedures, which leads the plant breeder to develop new commercial crop varieties. Differences of GCA are attributed to additive effects, the interaction of additive \times additive and higher-order interactions of additive genetic effects in the base population. While, differences in SCA effects attributed to non-additive genetic variance arising from dominance and epistatic genetic effects (Sherpa et al., 2014; Sprague & Tatum, 1942). The information on variation ascribed to genetic differences and also on the association among various quantitative traits is significant in a crop improvement program (Gardner, 1963). Combining ability studies help to extract ideas about the nature of gene action for particular traits, which in turn being useful for a breeder to select the diverse parents and hybrid combinations. In the hybrid production, diallel cross analysis has been adopted extensively to decide the abilities of parental lines combination to screen out superior parent (Fry, 2004; Griffing, 1956a; Hayman, 1954). In addition, genetic parameters can be estimated by the diallel cross analysis related to combining ability and the dominance relationship indication studied using F_1 hybrids with or without reciprocals. Many researchers like Abdel-Moneam, Sultan, Sadek, & Shalof (2014), El-Badawy (2013), Guerrero et al. (2014) and Umar, Ado, Aba, & Bugaje (2014) used diallel cross method to estimate heterosis and combining ability effects in maize. Selection could be effective to improve the traits like grain yield controlled by additive gene effects. Some researchers reported the preponderance role of additive genetic effects on grain yield (Badu-Apraku et al., 2016; Bekeko et al., 2018) while others stated the significant role of non-additive genetic effects (Bello & Olawuyi, 2015; Estakhr & Heidari, 2012; Seymour et al., 2016) or importance of both additive and non-additive genetic effects (Hefny, 2010; Njeri et al., 2017; Shiri, Aliyev, & Choukan, 2010). Also, if these crops were exploited properly through heterosis breeding, the quality traits give the high economic importance of this crop.

For the formulation of effective hybrid breeding

programs, the information on nature and magnitude of gene action is helpful, which can be understood through combining ability analysis. Besides, economic heterosis is useful for selecting hybrids having commercial value. Identification of parental lines that can be used in promising hybrid development is the most costly and time-consuming process in the maize breeding phase. Establishment of the significant relationship among heterosis, combining ability and mean performance of hybrid in field experiments make the process easier to screen out superior hybrids in advance. Many researcher works in this direction and found significant association of heterosis with mean performance and combining ability with heterosis and mean performance of grain yield of maize (Balestre, Von Pinho, Souza, & Lima, 2008; Bhusal & Lal, 2017; Devi & Singh, 2011; Ndhlela et al., 2015). The selection of hybrids based on heterosis and combining ability coupled with higher per se performance in the field will probably produce satisfied yield when in commercial use. Information on combining ability and heterosis is very helpful to plant breeders for formulating hybrid breeding programs. Therefore, the present investigation with a 10×10 half diallel cross was done to estimate heterosis and combining ability estimates of maize for different morphological and quality traits and further, to do association analysis among the hybrid performance.

MATERIALS AND METHODS

Forty-five experimental hybrids, ten parents and three commercial hybrids as check, i.e. Kaveri-2020, DHS-42 and Kanchan were grown by randomized block design and replicated three times during monsoon, 2014 under three environments, i.e. normal sowing (July 15) with high fertilization dose (180:80:50 N:P:K kg/ha) (E_1), late sowing (July 25) with normal fertilization dose (120:60:40 N:P:K kg/ha) (E_2) and very late sowing (August 5) with low fertilization dose (60:40:30 N:P:K kg/ha) (E_3). The 45 F_1 's, were developed through diallel crosses of ten early to intermediate inbred lines of maize namely R13-1-10, R13-1-17, CML439, Tarun83-1-3-2, POP31Q, DMR9047, TSK196, R13-1-1, TSK194 and TSK197 during winter, 2013-14. A detailed description of the parent materials is presented in Table 1.

The Center of Field Experimentation, Genetics and Plant Breeding Department, Sam Higginbottom University of Agriculture Technology

and Science (SHIATS), Allahabad was chosen as the research site. It was located at the elevation of 98 m asl at 28.87°N latitude and 81.54°E longitude. The region has a sub-tropical climate (1-2°C in winter to 48°C in summer) with average annual precipitation of 1013.4 mm. The weather conditions experienced by crops from July to November 2014 are presented in Table 2.

Seeds of each genotype was propagated by a single row of 3.0 m length with an inter-row spacing of 0.60 m and in-row spacing of 0.20 m. A maximum of two seeds per hill was planted and thinned to a single plant per hill at three weeks after planting. To maintain the healthy crops, the practices of standard agronomy were applied.

Different quantitative traits namely days to 50% tasseling, days to 50% silking, anthesis-silking interval, days to 50% maturity, cob length, cob girth, number of grain rows/cob, number of grains/row, 100 seed weight (g), grain yield/plant (g) and harvest index (%) were studied. For traits like days to 50% tasseling, days to 50% silking and days to 50%

maturity, data were recorded on visual observation on plot basis while five competitive plants from middle of each row for every genotype and in each replication were selected to take data for other traits. Anthesis-silking interval was computed by deducing days to 50% tasseling from days to 50% silking.

The starch content (%) of each genotypes was estimated by anthrone reagent method of Clegg (1956), protein content (%) by Lowry method (Lowry, Rosebrough, Farr, & Randall, 1951) and oil content according to AOAC (1975).

Griffing Model 1, Method 2 (Griffing, 1956b) was used for combining ability analysis, followed by heterosis evaluation by the method of Turner Jr (1953) for mid-parent heterosis (MPH) and Muñoz et al. (2014) for best-parent heterosis (BPH). Finally, the nature and magnitude of association among MPH, BPH, SCA and mean values of hybrids were evaluated using Pearson's correlations coefficients. The Baker ratio (Baker, 1978) was estimated to highlight the relative importance of additive or non-additive gene action for different characters.

Table 1. Pedigree and characteristics of parental lines used in hybridization

Genotypes	Pedigree	Principle characteristics		
		Maturity	Seed color	Seed texture
R13-1-10	R9303	Early	Yellow	Flint
R13-1-17	R9303	Early	Yellow	Flint
CML439	SA5-C2HC (26×21)-4-3-7-5-BBBBBB	Intermediate	Yellow	Semi-dent
Tarun83-1-3-2	---	Early	Yellow	Flint
POP31Q	P31DMR#1-55-2-3-2-1-BBBBBBB	Early	Yellow	Semi-flint
DMR9047	VEH-11-1	Intermediate	Yellow	Flint
TSK196	R9906	Early	Yellow	Flint
R13-1-1	R2005	Early	Yellow	Flint
TSK194	R9901	Early	Yellow	Flint
TSK197	R2007-1	Early	Yellow	Flint

Table 2. Weather conditions during monsoon, 2014 at Allahabad, India

Month	Temperature (°C)		Total Rainfall (mm)
	Minimum	Maximum	
July	28.11	36.35	202.80
August	28.35	35.75	164.30
September	26.40	35.55	45.40
October	22.37	33.57	110.60
November	15.17	31.53	0.00

RESULTS AND DISCUSSION

Variation in Morphological and Quality Traits

The mean square estimates for environment (E) was significant ($P < 0.05$) for 50% tasseling (T), 50% silking (S), 50% maturity (M), anthesis-silking interval (ASI), cob length (CL), cob girth (CG), number of grain rows/cob (RC), number of grains/row (GR), 100 seed weight (100SW) and grain yield/plant (GY), but not harvest index (HI), starch, protein and oil based on Analysis of Variance (ANOVA) (Table 3). Mean square estimates for genotype (G) was significant ($P < 0.05$) for GY and other morphological and quality traits studied (Table 3). The significant mean square of E and G for GY and other traits across environments showed the presence of diverse environments and sufficient genetic variability among inbred lines and single cross hybrids. The non-significant variance observed for HI, starch, protein and oil suggested that these traits were consistent across environments. Except starch, protein and oil, the genotypes \times environments interactions ($G \times E$) for 50%T, 50%S, 50%M, ASI, CL, CG, RC, GR, 100SW, GY and HI were significant ($P < 0.05$) which suggest the magnitudes of these traits in genotypes were different across three environments. The $G \times E$ interaction effects were larger for GY, HI and GR than others. These urges to consider genotype by environment effects while formulating breeding strategies. About the existence of genotype by environment effects for different agronomic and quality traits was also reported by Estakhr & Heidari (2012), Kumar et al. (2014), and Zare, Choukan, Heravan, Bihamta, & Ordoorkhani (2011). The non-significant $G \times E$ for starch, protein and oil suggested that expression of these traits was consistent across all research environments to highlight that there would be feasible to do the selection by early generation testing.

The significant ($P < 0.05$) mean squares for GCA and SCA for 50%T, 50%S, 50%M, CL, CG, GR, 100SW, GY, HI, starch, protein and oil (Table 3) indicated the presence of both additive gene and non-additive gene action in the inheritance of the respected traits across environments. Mean square of GCA was non-significant ($P < 0.05$) for ASI and RC, but mean square of SCA was significant ($P < 0.05$) for these traits (Table 3) pointed out the non-additive gene action played

a role in the inheritance of the traits. The present finding is in line with Badu-Apraku et al. (2015), Estakhr & Heidari (2012), Owusu et al. (2017) and Rajitha, Babu, Mohammad, & Rao (2014) that reported the significant mean squares of GCA and SCA for GY and other agronomic traits could be attributed to the action of both additive and non-additive gene action. They also confirmed that the traits improvement could be reached through hybridization, backcrossing, and recurrent methods of selection.

The greater mean squares of GCA over SCA for GY and almost other agronomic and quality traits suggested that the preponderance of additive gene action and that GCA played important role than SCA for the expression of these traits. The relative importance of additive and non-additive gene action is also reflected by Baker ratio. Baker ratio was near to unity for all agronomic and quality traits besides ASI, HI and starch content (Table 3), which suggest additive gene effect was highly important than non-additive gene effect in modulating the expression of these traits. The closer the ratio is to unity, the greater the predictability of progeny performance based on GCA effects alone (Baker, 1978). Moreover, high additive gene action indicates higher heritability and lesser environmental influences (Hakizimana, Ibrahim, Langham, Haley, & Rudd, 2004). The considerably high GCA effects suggested that preliminary selection for the relative potential of the parents used in hybrid breeding could be accomplished effectively by crossing to a few tester lines and comparing the performance of the hybrids in multi-environments, while improvement of morphological and quality traits may be possible by utilizing biparental mating, followed by recurrent selection in case of significant effect due to SCA (Alika & Ojomo, 1996). Even though several reports have emphasized the importance of additive variance in grain yield variation (Badu-Apraku et al., 2016; Bekeko et al., 2018) in some studies grain yield was found to be controlled by non-additive (Bello & Olawuyi, 2015; Estakhr & Heidari, 2012; Seymour et al., 2016) or both additive and non-additive gene action (Shiri, Aliyev, & Choukan, 2010). Ali et al. (2018) reported over-dominance type of gene action played an important role in the inheritance of earliness and yield traits in maize at different locations.

The magnitude of GCA×E mean squares were significant for all morphological traits, therefore, additive variances influenced by the effects of environments and also indicates the variation in combining abilities of inbred lines. The SCA×E mean squares were also significant for all morphological traits, indicates the effect of environments on non-additive type of genetic component or dominant variance was important and also pointed out that yield performance of the evaluated single-crosses was not consistent across the environment. This highlights G×E effects would present challenges in breeding materials for different environments which highlights the need to use multi-environments in the estimation of genetic effects. However, both GCA×E and SCA×E mean squares were non-significant for quality traits (Table 3) which suggested that the expression of these traits was consistent across the environment.

Estimates of General Combining Ability

The estimates of GCA effects of the parents are presented in Table 4. The significant ($p < 0.05$) positive GCA's for 50%T and 50%S were observed in inbred lines R13-1-10, POP31Q, DMR9047, TSK196 and TSK197, while significant ($p < 0.05$) negative GCA's were observed for R13-1-17, CML439 and Tarun83-1-3-2. Significant positive ($p < 0.05$) GCA's for ASI were observed for R13-1-10, CML439, POP31Q, TSK196 and R13-1-1. On the other hand, significant ($p < 0.05$) negative GCA's effects for ASI were found in Tarun83-1-3-2, DMR9047 and TSK197. Significant ($p < 0.05$) positive GCA's for 50% M were found in inbred lines R13-1-10, POP31Q and TSK197, while significant ($p < 0.05$) negative GCA's were observed for R13-1-17, CML439 and Tarun83-1-3-2 (Table 4). For days to tasseling, silking, maturity and ASI, negative estimates are considered desirable, since they were to be associated with earliness. Therefore, the use of the genotypes as parents would be valuable to formulate efficient breeding program for earliness. Furthermore, shorter ASI helped to escape from abiotic stresses and impacted on greater possibilities of seed setting. Thus, inbred lines Tarun83-1-3-2, DMR9047 and TSK197 are the best combiners for reducing ASI and would be appropriate for breeding for short ASI hybrids with greater seed setting.

The significantly positive ($p < 0.05$) GCA for CL was observed for R13-1-10, POP31Q, TSK196 and TSK197. On the other hand, the significantly ($p < 0.05$) negative GCA effect for CL was found in R13-1-17, CML439 and DMR9047. The significantly ($p < 0.05$) positive GCA for CG was found in inbred lines CML439, TSK196, R13-1-1 and TSK197, while the significantly ($p < 0.05$) negative GCA was observed for R13-1-17, Tarun83-1-3-2, DMR9047 and TSK194. The significantly positive ($p < 0.05$) GCA for RC was observed for CML439 and TSK197. On the other hand, the significantly ($p < 0.05$) negative GCA effect for RC was found in Tarun83-1-3-2 and POP31Q. The significantly ($p < 0.05$) positive GCA for GR was found in inbred lines R13-1-10, TSK196, TSK194 and TSK197, while the significantly ($p < 0.05$) negative GCA was observed for R13-1-17, CML439 and DMR9047 (Table 4). For CL, CG, RC and GR, positive estimates are highly desirable and those inbred lines having significantly positive GCA estimates for these traits suggest that these inbred lines could transmit favorable alleles to their progenies to improve these traits.

The significantly positive ($p < 0.05$) GCA for 100SW was observed for R13-1-10, CML439, Tarun83-1-3-2, POP31Q and TSK196. On the other hand, the significantly ($p < 0.05$) negative GCA effect for 100SW was found in R13-1-17, DMR9047 and TSK194 (Table 4). The significantly ($p < 0.05$) positive GCA for HI was found in inbred lines R13-1-17, CML439 and Tarun83-1-3-2, while the significantly ($p < 0.05$) negative GCA was observed for R13-1-10, POP31Q, DMR9047, R13-1-1 and TSK194 (Table 4). The significantly ($p < 0.05$) positive GCA for GY was observed for inbred lines R13-1-10, CML439, Tarun83-1-3-2, POP31Q, TSK196, R13-1-1 and TSK197. On the other hand, the significantly ($p < 0.05$) negative GCA for GY was found in inbred lines R13-1-17, DMR9047 and TSK194. Positive estimates of GCA is also highly desirable for 100SW, HI and GY. The significantly positive GCA for 100SW, HI and GY indicated that selection of traits for improvement through hybridization is possible as also reported by Owusu et al. (2017). Inbred lines R13-1-10, CML439, Tarun83-1-3-2, POP31Q, TSK196, R13-1-1 and TSK197 could be used as parents for breeding to improve GY through hybridization as these parental lines could transmit favorable alleles to their progenies.

Table 3. Mean squares for the combined ANOVA for different morphological and quality traits of maize across all environments

Sources of variation	df	Morphological traits											Quality traits		
		50%T	50%S	ASI	50%M	CL	CG	RC	GR	100SW	GY	HI	Starch	Pro-tein	Oil
Environ-ments (E)	2	379.15**	1024.03**	159.52**	1622.74**	872.02**	181.35**	192.23**	5808.24**	828.57**	72219.38**	3093.17	0.04	0.07	0.00
Reps/Env.	6	0.55	5.63**	6.19**	3.23	76.31**	0.24	1.92	203.93	0.13	3384.59**	997.52*	83.09**	0.50**	0.00
Genotypes (G)	54	67.98**	71.13**	0.65**	79.11**	27.59**	8.42**	8.24**	179.32**	72.49**	1672.76**	354.82**	237.14**	9.12**	2.87**
GCA ^a	9	170.89**	177.99**	0.66	234.39**	42.45**	15.29**	10.94	263.80**	192.70**	1896.15**	201.42*	75.33**	13.59**	8.09**
SCA ^b	45	47.40**	49.75**	0.65**	48.05**	24.62**	7.05**	7.70**	162.42**	48.44**	1628.08**	385.50**	269.50**	8.23**	1.83**
GxE	108	2.28**	2.87**	0.35**	3.43**	4.43**	1.28**	3.10*	32.66**	8.64**	232.11**	56.37**	0.03	0.00	0.03
GCAxE	18	3.04**	4.24**	0.31**	5.59**	3.73**	1.92**	4.58**	34.25**	5.06**	292.32**	68.96**	0.05	0.00	0.04
SCAxE	90	2.12**	2.59**	0.35**	2.99*	4.57**	1.15**	2.80	32.35**	9.35**	220.06**	53.85**	0.02	0.00	0.03
Error	324	1.01	1.02	0.04	2.20	2.92	0.70	2.30	17.19	0.11	6.52	2.40	0.29	0.00	0.19
Baker ratio		0.88	0.88	0.67	0.91	0.78	0.81	0.74	0.76	0.89	0.70	0.51	0.36	0.77	0.90

Remarks: * and ** significant at 0.05 and 0.01 probability levels, respectively; ^a GCAxE was used to test the significance of MS of GCA, ^b SCAxE was used to test the significance of MS of SCA. Note. 50%T = Days to 50% tasseling, 50%S = Days to 50% silking, ASI = Anthesis-silking interval (days), 50%M = Days to 50% maturity, CL = Cob length (cm), CG = Cob girth (cm), RC = No. of rows/cob, GR = No. of grains/row, 100 SW = 100 seed weight (g), GY = Grain yield/plant (g), HI = Harvest index (%)

Table 4. Estimates of general combining ability (gca) of parents for different agro-morphological and quality traits in maize across environments

Parents	50%T	50%S	ASI	50%M	CL	CG	RC	GR	100SW	GY	HI	Starch	Protein	Oil
R13-1-10	1.24 **	1.32 **	0.08 **	1.04 **	0.44 *	0.08 ns	0.03 ns	0.67 *	0.27 **	0.78 **	-0.82 **	-0.66 **	0.07 **	-0.25 **
R13-1-17	-0.62 **	-0.64 **	-0.03 ns	-0.91 **	-0.73 **	-0.46 **	-0.28 ns	-1.85 **	-1.14 **	-5.53 **	0.45 **	0.06 ns	0.04 ns	0.26 **
CML439	-1.39 **	-1.35 **	0.05 *	-1.49 **	-0.45 **	0.40 **	0.44 **	-1.01 **	0.55 **	2.81 **	1.94 **	1.44 **	-0.42 **	-0.44 **
Ta-run83-1-3-2	-2.64 **	-2.76 **	-0.12 **	-2.41 **	-0.23 ns	-0.18 *	-0.34 *	-0.09 ns	0.48 **	1.21 **	2.41 **	0.51 **	0.02 ns	0.37 **
POP31Q	0.69 **	0.77 **	0.08 **	1.23 **	0.44 *	0.07 ns	-0.58 **	-0.35 ns	2.52 **	1.12 **	-0.87 **	0.90 **	-0.36 **	0.05 ns
DMR9047	0.99 **	0.91 **	-0.08 **	-0.21 ns	-1.15 **	-0.52 **	0.11 ns	-2.76 **	-2.10 **	-8.88 **	-1.94 **	0.07 ns	-0.29 **	-0.30 **
TSK196	0.49 **	0.57 **	0.08 **	0.01 ns	0.51 **	0.42 **	0.18 ns	0.88 **	1.05 **	3.30 **	0.21 ns	0.42 **	-0.38 **	0.15 **
R13-1-1	0.13 ns	0.19 ns	0.06 *	-0.13 ns	0.23 ns	0.20 **	-0.06 ns	0.65 ns	0.02 ns	1.97 **	-0.50 **	-0.76 **	0.51 **	-0.19 **
TSK194	-0.17 ns	-0.20 *	-0.03 ns	0.09 ns	0.09 ns	-0.44 **	0.14 ns	1.35 **	-1.51 **	-1.34 **	-1.12 **	-0.90 **	0.42 **	0.10 **
TSK197	1.27 **	1.18 **	-0.09 **	2.79 **	0.85 **	0.42 **	0.35 *	2.51 **	-0.13 ns	4.55 **	0.25 ns	-1.07 **	0.38 **	0.25 **
Gi	0.09	0.09	0.02	0.14	0.16	0.08	0.14	0.38	0.03	0.23	0.14	0.05	0.001	0.04
Gi-Gj	0.14	0.14	0.03	0.20	0.23	0.11	0.21	0.56	0.05	0.35	0.21	0.07	0.001	0.06

Remarks: * and ** significant at 0.05 and 0.01 probability levels, respectively; ns = non-significant. Note. 50%T = Days to 50% tasselling, 50%S = Days to 50% silking, ASI = Anthesis-silking interval (days), 50%M = Days to 50% maturity, CL = Cob length (cm), CG = Cob girth (cm), RC = No. of rows/cob, GR = No. of grains/row, 100 SW = 100 seed weight (g), GY = Grain yield/plant (g), HI = Harvest index (%)

The significantly positive ($p < 0.05$) GCA for starch content was observed for CML439, Tarun83-1-3-2, POP31Q and TSK196. On the other hand, the significantly ($p < 0.05$) negative GCA effect for starch content was found in R13-1-10, R13-1-1, TSK194 and TSK197. The significantly ($p < 0.05$) positive GCA for protein content was found in inbred lines R13-1-10, R13-1-1, TSK194 and TSK197, while the significantly ($p < 0.05$) negative GCA was observed for CML439, POP31Q, DMR9047 and TSK196. The significantly positive ($p < 0.05$) GCA for oil content was observed for R13-1-17, Tarun83-1-3-2, TSK194 and TSK197. On the other hand, the significantly ($p < 0.05$) negative GCA effect for oil content was found in CML439, DMR9047 and R13-1-1 (Table 4). For starch, protein and oil content, positive GCA effects is desirable and inbred lines with significantly positive GCA effects could be included in maize breeding scheme to produce hybrids with good quality.

The parents with highest GCA values have a high contribution in the expression of their respective progeny performance and the effects of additive type are important (Guerrero et al., 2014). Recurrent selection is a way to exploit the proportion of additive genetic variance available (Preciado-Ortiz, Terrón-Ibarra, Gómez-Montiel, & Robledo-González, 2005). Lines with greater general combining ability effects could be used effectively for synthetic varieties development (Rahman et al., 2013).

Estimates of Specific Combining Ability and Heterosis

Estimates of SCA and heterosis for top five hybrids are presented in Table 5. Hybrids were superior over commercial checks in their performance for the studied traits. Among selected top five hybrids, earlier tasseling and silking along with shorter ASI were observed for POP31Q×Tarun83-1-3-2 and TSK194×Tarun83-1-3-2. These hybrids have significantly ($p < 0.05$) negative MPH, BPH and SCA, which is desirable for improvement of these traits. Also, they were derived from parents having Poor×Good and Average×Good GCA effects for days to 50% tasseling and ASI and Poor×Good and Good×Good GCA effects for days to 50% silking. Hybrids TSK197×CML439, TSK196×R13-1-17 and TSK197×POP31Q show shorter ASI accompanied with significantly ($p < 0.05$) negative MPH, BPH and SCA (Table 5) than commercial checks varieties. ASI is a trait used mostly in screening genotypes

for tolerance to stresses especially for drought tolerance (Lu et al., 2010) and low N tolerance (Dass et al., 2010). However, early maturity was observed in hybrid DMR9047×R13-1-17 derived from parents with Average×Good GCA effects for days to 50% maturity and the hybrid has significant ($p < 0.05$) negative MPH, BPH and SCA (Table 5). Singh, Singh, Singh, Shahi, & Rao (2013) obtained desirable hybrids developed by crossing parents having high×high, high×low GCA effects for days to 50% tasseling, high×high, high×low, low×high GCA effects for day to 50% silking and high×high, high×low GCA effects for days to 50% maturity.

The significantly ($p < 0.05$) positive BPH, MPH and SCA were recorded for CL, CG, RC, GR, grain yield, HI, starch and protein content in selected top five hybrids (Table 5). The longest CL, more GR and highest grain yield were found in TSK197×R13-1-10 and developed by crossing parents with Good×Good GCA effects for CL, GR and grain yield. Other high yielding hybrids (TSK196×CML439, TSK194×POP31Q, DMR9047×POP31Q and R13-1-1×DMR9047) were derived by crossing parents with Good×Good, Poor×Good and Good×Poor GCA effects for grain yield. These hybrids exhibited significantly ($p < 0.05$) positive BPH, MPH and SCA, thus, would augmented grain yield when used. Hybrid TSK197×CML439 has larger cob diameter and more RC, which was developed by crossing parent with Good×Good GCA effects for CG and RC. Hybrids TSK196×CML439 and TSK197×Tarun83-1-3-2 were made by a cross between parents with Good×Good and Good×Poor GCA effects for CG and Average×Good and Good×Poor GCA effects for RC and showed significantly ($p < 0.05$) positive MPH and SCA for both CG and RC. These hybrids would increase diameter and RC and consequently enhanced grain yield. In maize, CL is a prominent trait having much effect on grain yield and the only one trait which affect ear characters like grain number and to lesser degree of grain weight (Herczegh, 1970) while CG particularly effects on the grain rows per cob, grain size and ultimately to grain yield.

The significantly ($p < 0.05$) positive MPH, BPH and SCA were observed for 100 seed weight in Tarun83-1-3-2×R13-1-10, TSK196×POP31Q and TSK197×Tarun83-1-3-2 which were derived from crossing parents of Good×Good and Average×Good GCA effects for 100 seed weight (Table 5).

Table 5. Performance of promising hybrids for different agro-morphological and quality traits in maize across environments

Single cross hybrids	Mean	MPH	BPH	SCA	GCA effects (Female×Male)	Single cross hybrids	Mean	MPH	BPH	SCA	GCA effects (Female×Male)
a. Days to 50% tasseling											
POP31Q× Ta-run83-1-3-2	46.33	-10.32 **	-17.75 **	-3.84 **	Poor×Good	POP31Q× Ta-run83-1-3-2	48.56	-10.63 **	-18.31 **	-4.22 **	Poor×Good
TSK194× Ta-run83-1-3-2	46.33	-7.95 **	-13.67 **	-2.98 **	Average×Good	TSK194× Ta-run83-1-3-2	48.56	-7.90 **	-13.64 **	-3.24 **	Good×Good
Tarun83-1-3-2×CML439	47.67	-1.37 ns	-4.02 **	-0.42 **	Good×Good	Tarun83-1-3-2×CML439	50.22	-1.42 ns	-4.65 **	-0.43 **	Good×Good
DMR9047× R13-1-17	48.00	-16.03 **	-17.24 **	-4.50 **	Poor×Good	DMR9047× R13-1-17	50.56	-15.19 **	-16.05 **	-4.48 **	Poor×Good
POP31Q× CML439	48.00	-9.43 **	-14.79 **	-3.42 **	Poor×Good	POP31Q× CML439	50.56	-9.81 **	-14.95 **	-3.63 **	Poor×Good
b. Days to 50% silking											
c. Anthesis-silking interval (days)											
POP31Q× Ta-run83-1-3-2	2.22	-16.70 **	-28.62 **	-0.38 **	Poor×Good	DMR9047× R13-1-17	78.67	-9.28 **	-9.34 **	-4.30 **	Average×Good
TSK194× Ta-run83-1-3-2	2.22	-7.05 ns	-13.17 **	-0.27 **	Average×Good	POP31Q× Ta-run83-1-3-2	79.00	-5.26 **	-10.00 **	-3.90 **	Poor×Good
TSK197× CML439	2.22	-20.10 **	-26.00 **	-0.37 **	Good×Poor	Tarun83-1-3-2×CML439	79.67	-1.26 ns	-3.28 **	-0.51 **	Good×Good
TSK196× R13-1-17	2.22	-20.10 **	-26.00 **	-0.47 **	Poor×Average	CML439× R13-1-17	79.67	-5.79 **	-8.17 **	-2.01 **	Good×Good
TSK197× POP31Q	2.33	-17.76 **	-25.08 **	-0.30 **	Good×Poor	TSK196× DMR9047	80.00	-5.51 **	-7.66 **	-3.88 **	Average×Average
d. Days to 50% maturity											
e. Cob length (cm)											
TSK197× R13-1-10	16.46	44.99 **	38.80 **	2.23 **	Good×Good	TSK196× CML439	13.25	19.39 **	13.93 **	1.00 **	Good×Good
TSK197× TSK196	15.91	22.90 **	13.37 *	1.61 **	Good×Good	TSK197× CML439	13.05	22.40 **	21.32 **	0.80 **	Good×Good
TSK194× R13-1-10	15.81	50.26 **	45.80 **	2.33 **	Average×Good	TSK197× POP31Q	12.71	19.48 **	18.13 **	0.79 **	Good×Average
TSK197× TSK194	15.30	38.76 **	29.07 **	1.42 **	Good×Average	TSK197× Ta-run83-1-3-2	12.57	17.48 **	16.83 **	0.90 **	Good×Poor
R13-1-1× DMR9047	15.08	41.66 **	9.78 ns	3.05 **	Average×Poor	TSK194× POP31Q	12.50	25.70 **	18.96 **	1.44 **	Poor×Average

Table 5. (continue)

Single cross hybrids	Mean	MPH	BPH	SCA	GCA effects (Female×Male)	Single cross hybrids	Mean	MPH	BPH	SCA	GCA effects (Female×Male)
a. No. of rows/cob											
TSK197× CML439	15.33	26.60 **	21.05 **	1.87 **	Good×Good	TSK197× R13-1-10	33.00	74.45 **	72.17 **	5.81 **	Good×Good
TSK194× TSK196	14.89 **	24.10 **	24.08 **	1.89 **	Average×Average	TSK197× TSK194	32.00	68.42 **	66.96 **	4.13 **	Good×Good
R13-1-1× DMR9047	14.67 **	28.15 **	19.99 **	1.95 **	Average×Average	TSK197× TSK196	30.61	38.43 **	22.16 **	3.21 **	Good×Good
TSK196× CML439	14.22 **	20.76 **	18.53 **	0.93 **	Average×Good	TSK194× POP31Q	29.83	65.24 **	58.41 **	4.82 **	Good×Average
TSK197× Ta-run83-1-3-2	13.78 **	15.88 **	8.76 ns	1.09 **	Good×Poor	TSK197× R13-1-1	29.83	45.14 **	35.96 **	2.67 **	Good×Average
c. 100 seed weight (g)											
Tarun83-1-3-2× R13-1-10	25.87 **	32.96 **	17.91 **	3.91 **	Good×Good	TSK197× R13-1-10	75.89	157.91 **	156.52 **	19.26 **	Good×Good
TSK196× POP31Q	25.47 **	13.19 **	1.60 *	1.36 **	Good×Good	TSK196× CML439	75.07	53.82 **	52.91 **	18.00 **	Good×Good
TSK197× POP31Q	25.17 **	21.48 **	0.40 ns	2.24 **	Average×Good	TSK194× POP31Q	73.89	160.91 **	106.69 **	22.49 **	Poor×Good
DMR9047× POP31Q	25.03 **	25.06 **	-0.19 ns	4.06 **	Poor×Good	DMR9047× POP31Q	66.17	178.60 **	85.08 **	24.31 **	Poor×Good
TSK197× Ta-run83-1-3-2	24.43 **	29.49 **	14.33 **	3.54 **	Average×Good	R13-1-1× DMR9047	65.11	104.67 **	25.52 **	22.40 **	Good×Poor
e. Harvest index (%)											
TSK194× Ta-run83-1-3-2	43.22 **	76.69 **	35.84 **	8.36 **	Poor×Good	DMR9047× POP31Q	78.33	29.13 **	28.30 **	13.62 **	Average×Good
TSK194× POP31Q	42.84 **	99.45 **	69.62 **	9.82 **	Poor×Poor	TSK197× R13-1-17	78.11	27.86 **	26.49 **	15.39 **	Poor×Average
DMR9047× R13-1-17	42.10 **	121.02 **	67.51 **	9.92 **	Poor×Good	TSK194× POP31Q	74.30	22.04 **	21.71 **	10.57 **	Poor×Good
TSK194× R13-1-10	41.87 **	101.47 **	70.62 **	10.44 **	Poor×Poor	TSK196× DMR9047	71.30	16.57 **	14.86 **	7.08 **	Good×Average
TSK197× R13-1-10	41.16 **	55.91 **	49.59 **	7.15 **	Average×Poor	R13-1-1× R13-1-17	70.17	13.39 **	10.78 **	7.14 **	Poor×Average

Table 5. (continue)

Single cross hybrids	Mean	MPH	BPH	SCA	GCA effects (Female×Male)	Single cross hybrids	Mean	MPH	BPH	SCA	GCA effects (Female×Male)
a. Protein content (%)											
TSK194× R13-1-1	10.48	34.17 **	27.14 **	2.33 **	Good×Good	TSK197× Ta-run83-1-3-2	5.44	11.32 **	11.32 **	0.64 **	Good×Good
R13-1-1× R13-1-10	9.75	28.33 **	24.67 **	1.96 **	Good×Good	POP31Q× Ta-run83-1-3-2	5.22	18.91 **	6.75 ns	0.61 **	Average×Good
TSK194× R13-1-10	9.16	14.05 **	11.17 **	1.45 **	Good×Good	TSK197× R13-1-17	5.11	7.58 *	4.50 ns	0.41 **	Good×Good
TSK197× R13-1-1	8.17	-4.91 **	-16.67 **	0.06 ns	Good×Good	TSK194× R13-1-1	5.11	27.75 **	10.85 *	1.01 **	Good×Poor
POP31Q× R13-1-17	8.04	7.25 **	-9.05 **	1.14 **	Poor×Average	TSK196× Ta-run83-1-3-2	5.11	14.31 **	4.57 ns	0.40 **	Good×Good

Remarks: * and ** significant at 0.05 and 0.01 probability levels, respectively; ns = non-significant; MPH = mid-parent heterosis; BPH = best-parent heterosis; SCA = specific combining ability; GCA = general combining ability

Owing to this, these were the potential hybrids to increase seed weight and consequently increase grain yield/plant. Hybrid TSK197×Tarun83-1-3-2 has highest harvest index along with significantly ($p < 0.05$) positive MPH, BPH and SCA effects for harvest index and these was derived from the cross of Poor×Good GCA parents for harvest index. Other selected hybrids were derived from the crosses of parents with Poor×Poor, Poor×Good and Average×Poor GCA effects for harvest index and they also exhibited significantly ($p < 0.05$) positive MPH, BPH and SCA effect for harvest index. Among the selected top hybrids for grain yield, TSK197×R13-1-10 and TSK194×POP31Q only expressed higher harvest index and positive heterosis and SCA effects for harvest index while DMR9047×POP31Q exhibited heavier seed and positive SCA effects for 100 seed weight (Table 5). These hybrids also showed significant positive economic heterosis for yield and yield attributing traits. Therefore, these hybrids could impact positive effect to enhance the grain yield of maize while taking them in the breeding plan for accelerating grain yield. Kamara, El-Degwy, & Koyama (2014), Rahman et al. (2013), and Ruswandi et al. (2015) also worked out in heterosis and combining ability using F1s and reported significant heterosis and high positive specific combining ability for yield and yield attributing traits along with high per se performance for grain yield. Singh, Singh, Singh, Shahi, & Rao (2013) obtained superior hybrids developed by crossing parents having high×low, high×high GCA effects for ear length, high×high, low×high GCA effects for ear diameter, high×low for kernel rows/ear, high×low, low×high, high×high GCA effects for kernel/row and high×low, high×high GCA effects for grain yield. Rajitha, Babu, Mohammad, & Rao (2014) also found hybrids with high SCA effects were resulted from high×low, low×low and high×high GCA combinations for yield and their trait components.

In this study, hybrids DMR9047×POP31Q and TSK197×R13-1-17 have higher starch content along with significantly positive MPH, BPH and SCA. They were developed from the crosses of Average×Good and Poor×Average parents for GCA starch content. Other selected hybrids were derived by crossing parents of Poor×Good, Good×Average and Poor×Average GCA effects for starch content. Hybrids TSK194×R13-1-1, R13-1-1×R13-1-10 and TSK194×R13-1-10 exhibited higher protein content and showed significantly positive MPH, BPH and

SCA. These hybrids were developed by crossing parents with Good×Good GCA effects for protein content. Likewise, hybrid TSK197×Tarun83-1-3-2 has highest oil content along with significantly positive MPH, BPH and SCA effects and these was made by crossing parents with Good×Good GCA effects for oil content. Hybrid TSK194×R13-1-1 showed significant positive MPH, BPH and SCA for both protein and oil content and was developed by crossing parent with Good×Good GCA effects for protein content and Good×Poor GCA effects for oil content (Table 5). These hybrids could be put in advance selection schemes to produce hybrids with special quality (i.e., high starch, protein and oil) in maize. For hybrid development, the greater specific line on combining ability effects could be applied (Rahman et al., 2013). Hybrids containing special quality (e.g., high starch, protein & oil) are used for extraction of high quality starch for textile and pharmaceutical industry, high quality protein and amino acid for pharmaceutical, biochemical and industrial uses and also good quality oil with high polyunsaturated fatty acid. Among the top hybrids, Mahesh, Wali, Gowda, Motagi, & Uppinal (2013) found high×high GCA effects for starch content, high×low GCA effects for protein content and high×high GCA effects for oil content. Similarly, Khan, Dubey, Vadodariya, & Patel (2014) obtained highest SCA values from the crossing of parents having poor×poor and good×poor GCA nature.

As good general combiners (i.e., good×good GCA), high SCA effects resulting from crosses both parents may be attributed to additive×additive gene action (Dey, Singh, Bhatia, Parkash, & Chandel, 2014). Good×Good GCA combiner is more desirable for commercial hybrid developments. Not always only two good general combiners involved in better specific combining hybrids, but two poor combiners may also ensue to good specific combination. In current research, some of the superior hybrids were from both parents with good×good general combiner or either one of the parents with high GCA effects (good×poor or poor×good) or parents that are poor×poor combiners for different traits, which implies that parents with either high GCA or low GCA would have a higher chance of having excellent complementarity with other parents as found by Seymour et al. (2016). The high SCA effects derived from crosses including good×poor general combiner parents (Dey, Singh, Bhatia, Parkash, & Chandel, 2014; Milić et al., 2011) may be ascribed to favorable epistatic effects of poor general combiner and

additive effects of the good general combiner parent. Low×low crosses that produces the high SCA effects (Chigeza, Mashingaidze, & Shanahan, 2014; Dey, Singh, Bhatia, Parkash, & Chandel, 2014), it's may be related to dominance×dominance type of non-allelic gene interaction creating over dominance thus being non-fixable (Wassimi, Isleib, & Hosfield, 1986). The non-fixable could be shown by the high yield of such crosses, and its could be exploited by heterosis breeding.

Association Analysis

The Pearson's correlation and regression analysis were performed for different hybrid performance parameters. The correlation coefficients of per se performance with MPH and BPH were ranged from 0.29 (BPH of 100 seed weight) to 0.86** (MPH of rows/cob). The per se performance established significant association with MPH and BPH of days to 50% tasseling, days to 50% silking, days to 50% maturity, ASI, CL, CG, RC, GR, 100 SW, grain yield, HI, starch, protein and oil (Table 6). The results were in consonant with the findings of Balestre, Von Pinho, Souza, & Lima (2008). The significantly positive association between MPH, BPH and per se performance in maize was also obtained by Devi & Singh (2011) and Ndhlela et al. (2015). Similar results as presented by Balestre, Von Pinho,

Souza, & Lima (2008) and Devi & Singh (2011), MPH and BPH were found as key determinant of hybrids per se performance in present research.

The correlation coefficient of SCA with MPH, BPH and mean values was varied from 0.68** (BPH of 100 seed weight) to 0.98** (mean value of starch content). The SCA had significant association with MPH, BPH and per se performance of hybrids for days to 50% tasseling, days to 50% silking, days to 50% maturity, ASI, CL, CG, RC, GR, grain yield, HI, starch, protein and oil (Table 6). The significantly positive correlation of SCA with MPH, BPH and per se performance was also reported by Devi & Singh (2011) and Ndhlela et al. (2015). Our study revealed that SCA, as suggested by Devi & Singh (2011) and Ndhlela et al. (2015), is a good predictor for agronomical and quality traits of maize. A significantly positive association among SCA, MPH, BPH and per se performance is an indicator that SCA can be used to predict MPH and BPH during selection under all conditions. SCA was found as a good predictor of heterosis and per se performance under both optimum and drought conditions by Ndhlela et al. (2015). In our study, SCA established stronger relationship with per se performance of grain yield and quality traits than MPH and BPH, reflecting that the improvement in selection of SCA will results in an indirect improvement of MPH and BPH of hybrids.

Table 6. Inter-relationship among mean performance (MP), BPH, MPH and SCA of different morphological and quality traits in maize

Traits	r(MP, BPH)	r(MP, MPH)	r(SCA, MP)	r(SCA, BPH)	r(SCA, MPH)
Days to 50% tasseling	0.78**	0.62**	0.75**	0.80**	0.91**
Days to 50% silking	0.82**	0.64**	0.76**	0.81**	0.91**
ASI	0.69**	0.77**	0.92**	0.81**	0.87**
Days to 50% maturity	0.81**	0.79**	0.78**	0.83**	0.89**
Cob length	0.75**	0.69**	0.86**	0.80**	0.86**
Cob girth	0.62**	0.59**	0.78**	0.77**	0.86**
Number of rows/cob	0.85**	0.86**	0.89**	0.83**	0.87**
Number of grains/row	0.83**	0.69**	0.85**	0.81**	0.84**
100 seed weight	0.29ns	0.38**	0.69**	0.68**	0.82**
Grain yield	0.62**	0.53**	0.88**	0.73**	0.75**
Harvest index	0.69**	0.62**	0.94**	0.81**	0.79**
Starch content	0.74**	0.85**	0.98**	0.81**	0.90**
Protein content	0.79**	0.83**	0.88**	0.85**	0.91**
Oil content	0.64**	0.69**	0.78**	0.86**	0.93**

Remarks: ** = significant at 0.01 probability levels; ns = non-significant; MP = mid-parent; BPH = best-parent heterosis; MPH = mid-parent heterosis; SCA = specific combining ability

CONCLUSION

TSK 196 and TSK 197 were good general combiner for cob length, cob girth, no. of grains/row and grain yield. In addition, TSK197×R13-1-10, TSK194×POP31Q, DMR9047×POP31Q and R13-1-1×DMR9047 exhibited highest specific combining ability and heterosis for grain yield, indicating the best promising single cross for improvement of grain yield. These hybrids also showed highest grain yield than the commercial hybrids namely Kaveri-2020, DHS-42 and Kanchan. The significant correlation of mean performance of morphological and quality traits with heterosis and combining ability pointed out that the selection of genotypes based on these parameters would help in improvement of grain yield and attributing characters in maize. Improvement in selection of SCA would indirectly improve heterosis of hybrids as it made significant relationship with mean performance, BPH and MPH of maize.

ACKNOWLEDGEMENT

The authors would like to thank Prof. (Dr.) S. Marker and Dr. Harish Chandra Singh for their support in the completion of the research by providing experimental materials and academic guidelines.

REFERENCES

- Abdel-Moneam, M. A., Sultan, M. S., Sadek, S. E., & Shalof, M. S. (2014). Estimation of heterosis and genetic parameters for yield and yield components in maize using the diallel cross method. *Asian Journal of Crop Science*, 6, 101–111. <https://doi.org/10.3923/ajcs.2014.101.111>
- Ali, S., Khan, N. U., Gul, R., Naz, I., Goher, R., Ali, N., ... Saeed, M. (2018). Genetic analysis for earliness and yield traits in maize. *Pakistan Journal of Botany*, 50(4), 1395–1405. Retrieved from <https://www.semanticscholar.org/paper/GENETIC-ANALYSIS-FOR-EARLINESS-AND-YIELD-TRAITS-IN-Ali-Khan/a84290a3559725ac454912a4b2dbc2ef950840a6>
- Alika, J. E., & Ojomo, J. O. (1996). Combining ability and reciprocal effects for physico-chemical grain quality characteristics in maize. *Food Chemistry*, 57(3), 371–375. [https://doi.org/10.1016/0308-8146\(95\)00195-6](https://doi.org/10.1016/0308-8146(95)00195-6)
- Amiruzzaman, M., Islam, M. A., Hasan, L., Kadir, M., & Rohman, M. M. (2013). Heterosis and combining ability in a diallel among elite inbred lines of maize (*Zea mays* L.). *Emirates Journal of Food and Agriculture*, 25(2), 132–137. <https://doi.org/10.9755/ejfa.v25i2.6084>
- AOAC. (1975). *Official methods of analysis* (12th ed.). Washington, DC: Association of Official Analytical Chemists.
- Badu-Apraku, B., Annor, B., Oyekunle, M., Akinwale, R. O., Fakorede, M. A. B., Talabi, A. O., ... Fasanmade, Y. (2015). Grouping of early maturing quality protein maize inbreds based on SNP markers and combining ability under multiple environments. *Field Crops Research*, 183, 169–183. <https://doi.org/10.1016/j.fcr.2015.07.015>
- Badu-Apraku, B., Fakorede, M. A. B., Talabi, A. O., Oyekunle, M., Akaogu, I. C., Akinwale, R. O., ... Aderounmu, M. (2016). Gene action and heterotic groups of early white quality protein maize inbreds under multiple stress environments. *Crop Science*, 56(1), 183–199. <https://doi.org/10.2135/cropsci2015.05.0276>
- Baker, R. J. (1978). Issues in diallel analysis. *Crop Science*, 18(4), 533–536. <https://doi.org/10.2135/cropsci1978.0011183x001800040001x>
- Balestre, M., Von Pinho, R. G., Souza, J. C., & Lima, J. L. (2008). Comparison of maize similarity and dissimilarity genetic coefficients based on microsatellite markers. *Genetics and Molecular Research*, 7(3), 695–705. <https://doi.org/10.4238/vol7-3gmr458>
- Beck, D., Vasal, S., & Crossa, J. (1990). Heterosis and combining ability of CIMMYT's tropical early and intermediate maturity maize (*Zea mays* L.) germplasm. *Maydica*, 35(3), 279–285. Retrieved from <https://repository.cimmyt.org/handle/10883/1927>
- Bekeko, Z., Fininsa, C., Wegary, D., Hussien, T., Hussien, S., & Asalf, B. (2018). Combining ability and nature of gene action in maize (*Zea mays* L.) inbred lines for resistance to gray leaf spot disease (*Cercospora zaeae maydis*) in Ethiopia. *Crop Protection*, 112, 39–48. <https://doi.org/10.1016/j.cropro.2018.05.010>
- Bello, O. B., & Olawuyi, O. J. (2015). Gene action, heterosis, correlation and regression estimates in developing hybrid cultivars in maize. *Tropical Agriculture*, 92(2), 102–117. Retrieved from https://www.researchgate.net/publication/271195887_Gene_action_heterosis_correlation_and_regression_estimates_in_developing_hybrid_cultivars_in_maize
- Bhusal, T. N., & Lal, G. M. (2017). Relationship among

- heterosis, combining ability and SSR based genetic distance in single cross hybrids of maize (*Zea mays* L). *Vegetos - An International Journal of Plant Research*, 30(2), 1–10. Retrieved from https://www.researchgate.net/publication/320399132_Relationship_among_Heterosis_Combining_Ability_and_SSR_Based_Genetic_Distance_in_Single_Cross_Hybrids_of_Maize_Zea_Mays_L
- Chigeza, G., Mashingaidze, K., & Shanahan, P. (2014). Advanced cycle pedigree breeding in sunflower. II: Combining ability for oil yield and its components. *Euphytica*, 195, 183–195. <https://doi.org/10.1007/s10681-013-0985-0>
- Clegg, K. M. (1956). The application of the anthrone reagent to the estimation of starch in cereals. *Journal of the Science of Food and Agriculture*, 7(1), 40–44. <https://doi.org/10.1002/jsfa.2740070108>
- Dass, S., Manivannan, A., Kaul, J., Singode, A., Sekhar, J., & Chikkappa, G. (2010). *Inbred-hybrid technology in maize*. DMR Technical Bulletin 2010. New Delhi, India: Directorate of Maize Research. Retrieved from https://www.researchgate.net/publication/290911718_Inbred-Hybrid_Technology_in_Maize
- Devi, P., & Singh, N. K. (2011). Heterosis, molecular diversity, combining ability and their interrelationships in short duration maize (*Zea mays* L.) across the environments. *Euphytica*, 178, 71–81. <https://doi.org/10.1007/s10681-010-0271-3>
- Dey, S. S., Singh, N., Bhatia, R., Parkash, C., & Chandel, C. (2014). Genetic combining ability and heterosis for important vitamins and antioxidant pigments in cauliflower (*Brassica oleracea* var. *botrytis* L.). *Euphytica*, 195, 169–181. <https://doi.org/10.1007/s10681-013-0981-4>
- El-Badawy, M. E. M. (2013). Heterosis and combining ability in maize using diallel crosses among seven new inbred lines. *Asian Journal of Crop Science*, 5, 1–13. <https://doi.org/10.3923/ajcs.2013.1.13>
- Estakhr, A., & Heidari, B. (2012). Combining ability and gene action for maturity and agronomic traits in different heterotic groups of maize inbred lines and their diallel crosses. *Journal of Crop Science and Biotechnology*, 15, 219–229. <https://doi.org/10.1007/s12892-012-0030-1>
- Fry, J. D. (2004). Estimation of genetic variances and covariances by restricted maximum likelihood using PROC MIXED. In A. M. Saxton (Ed.), *Genetic analysis of complex traits using SAS* (pp. 11–34). Cary, NC: SAS Institute. Retrieved from <https://books.google.co.id/books?id=KUar026FM20C>
- Gardner, C. O. (1963). Estimates of genetic parameters in cross-fertilizing plants and their implications in plant breeding. In W. D. Hanson & H. F. Robinson (Eds.), *NAS-NRC Publ. 982* (pp. 225–252). Washington, DC: NAS-NRC.
- Griffing, B. (1956a). A generalised treatment of the use of diallel crosses in quantitative inheritance. *Heredity*, 10, 31–50. <https://doi.org/10.1038/hdy.1956.2>
- Griffing, B. (1956b). Concept of general and specific combining ability in relation to diallel crossing systems. *Australian Journal of Biological Sciences*, 9(4), 463–493. <https://doi.org/10.1071/bi9560463>
- Guerrero, C. G., Gallegos Robles, M. A., Luna Ortega, J. G., Castillo, I. O., Vázquez, C. V., Carrillo, M. G., ... Torres, A. G. (2014). Combining ability and heterosis in corn breeding lines to forage and grain. *American Journal of Plant Sciences*, 5(6), 1–12. <https://doi.org/10.4236/ajps.2014.56098>
- Hakizimana, F., Ibrahim, A. M. H., Langham, M. A. C., Haley, S. D., & Rudd, J. C. (2004). Diallel analysis of *wheat streak mosaic virus* resistance in winter wheat. *Crop Science*, 44, 89–92. <https://doi.org/10.2135/cropsci2004.8900>
- Hallauer, A. R., & Miranda Filho, J. B. (1988). *Quantitative genetics in maize breeding*. Ames: Iowa State University Press.
- Hayman, B. I. (1954). The analysis of variance of diallel tables. *Biometrics*, 10(2), 235–244. <https://doi.org/10.2307/3001877>
- Hefny, M. (2010). Genetic control of flowering traits, yield and its components in maize (*Zea mays* L.) at different sowing dates. *Asian Journal of Crop Science*, 2, 236–249. <https://doi.org/10.3923/ajcs.2010.236.249>
- Herczegh, M. (1970). Importance of yield components in the phenotype. In I. Kovacs (Ed.), *Akademiai Kiado* (pp. 229–236). Retrieved from <https://www.cabdirect.org/cabdirect/abstract/19701607326>
- Kamara, M. M., El-Degwy, I. S., & Koyama, H. (2014). Estimation combining ability of some maize inbred lines using line × tester mating design under two nitrogen levels. *Australian Journal of Crop Science*, 8(9), 1336–1342. Retrieved from <https://search.informit.com.au/documentSummary;dn=675939481968329;res=IELHSS>

T. N. Bhusal and G. M. Lal: *Quantitative Breeding on Maize*

- Khan, R., Dubey, R. B., Vadodariya, G. D., & Patel, A. I. (2014). Heterosis and combining ability for quantitative and quality traits in maize (*Zea mays* L.). *Trends in Biosciences*, 7(6), 422–424. Retrieved from [http://trendsinbiosciencesjournal.com/upload/5-793_\(RUMANA_KHAN\).pdf](http://trendsinbiosciencesjournal.com/upload/5-793_(RUMANA_KHAN).pdf)
- Kumar, R., Singode, A., Chikkappa, G. K., Mukri, G., Dubey, R. B., Komboj, M. C., ... Yadav, O. P. (2014). Assessment of genotype × environment interactions for grain yield in maize hybrids in rainfed environments. *Sabrao Journal of Breeding and Genetics*, 46(2), 284–292. Retrieved from https://www.researchgate.net/publication/286502708_Assessment_of_genotype_environment_interactions_for_grain_yield_in_maize_hybrids_in_rainfed_environments
- Lowry, O. H., Rosebrough, N. J., Farr, A. L., & Randall, R. J. (1951). Protein measurement with the Folin phenol reagent. *The Journal of Biological Chemistry*, 193, 265–275. Retrieved from <https://www.jbc.org/content/193/1/265.long>
- Lu, Y., Zhang, S., Shah, T., Xie, C., Hao, Z., Li, X., ... Xu, Y. (2010). Joint linkage-linkage disequilibrium mapping is a powerful approach to detecting quantitative trait loci underlying drought tolerance in maize. *Proceedings of the National Academy of Sciences of the United States of America*, 107(45), 19585–19590. <https://doi.org/10.1073/pnas.1006105107>
- Mahesh, N., Wali, M. C., Gowda, M. V. C., Motagi, B. N., & Uppinal, N. F. (2013). Genetic analysis of grain yield, starch, protein and oil content in single cross hybrids of maize*. *Karnataka Journal of Agricultural Science*, 26(2), 185–189. Retrieved from <http://citeseerx.ist.psu.edu/viewdoc/download?doi=10.1.1.1013.2967&rep=rep1&type=pdf>
- Milić, D., Katić, S., Karagić, Đ., Gvozdanović-Varga, J., Petrović, S., & Boćanski, J. (2011). Genetic control of agronomic traits in alfalfa (*M. sativa* ssp. *sativa* L.). *Euphytica*, 182(1), 25–33. <https://doi.org/10.1007/s10681-011-0434-x>
- Muñoz, P. R., Resende, M. F., Jr, Gezan, S. A., Resende, M. D., de Los Campos, G., Kirst, M., ... Peter, G. F. (2014). Unraveling additive from nonadditive effects using genomic relationship matrices. *Genetics*, 198(4), 1759–1768. <https://doi.org/10.1534/genetics.114.171322>
- Ndhlela, T., Herselman, L., Semagn, K., Magorokosho, C., Mutimaamba, C., & Labuschagne, M. T. (2015). Relationships between heterosis, genetic distances and specific combining ability among CIMMYT and Zimbabwe developed maize inbred lines under stress and optimal conditions. *Euphytica*, 204, 635–647. <https://doi.org/10.1007/s10681-015-1353-z>
- Njeri, S. G., Makumbi, D., Warburton, M. L., Diallo, A., Jumbo, M. D. B., & Chemining'wa, G. (2017). Genetic analysis of tropical quality protein maize (*Zea mays* L.) germplasm. *Euphytica*, 213, 261. <https://doi.org/10.1007/s10681-017-2048-4>
- Owusu, G. A., Nyadanu, D., Obeng-Antwi, K., Amoah, R. A., Danso, F. C., & Amissah, S. (2017). Estimating gene action, combining ability and heterosis for grain yield and agronomic traits in extra-early maturing yellow maize single-crosses under three agro-ecologies of Ghana. *Euphytica*, 213, 287. <https://doi.org/10.1007/s10681-017-2081-3>
- Preciado-Ortiz, R. E., Terrón-Ibarra, A. D., Gómez-Montiel, N., & Robledo-González, E. I. (2005). Componentes genéticos en poblaciones heteróticamente contrastantes de maíz de origen tropical y subtropical. *Agronomía Mesoamericana*, 16(2), 145–151. <https://doi.org/10.15517/am.v16i2.11867>
- Rahman, H., Ali, A., Shah, Z., Iqbal, M., Noor, M., & Amanullah. (2013). Line x tester analysis for grain yield and yield related traits in maize variety Sarhad-White. *Pakistan Journal of Botany*, 45(S1), 383–387. Retrieved from [https://www.pakbs.org/pjbot/PDFs/45\(S1\)/51.pdf](https://www.pakbs.org/pjbot/PDFs/45(S1)/51.pdf)
- Rajitha, A., Babu, D. R., Mohammad, L. A., & Rao, V. S. (2014). Heterosis and combining ability for grain yield and yield component traits in maize (*Zea mays* L.). *Electronic Journal of Plant Breeding*, 5(3), 378–384. Retrieved from <http://www.ejplantbreeding.org/index.php/EJPB/article/view/28>
- Ruswandi, D., Supriatna, J., Makkulawu, A. T., Waluyo, B., Marta, H., Suryadi, E., & Ruswandi, S. (2015). Determination of combining ability and heterosis of grain yield components for maize mutants based on line×tester analysis. *Asian Journal of Crop Science*, 7(1), 19–33. <https://doi.org/10.3923/ajcs.2015.19.33>
- Seymour, D. K., Chae, E., Grimm, D. G., Pizarro, C. M., Habring-Müller, A., Vasseur, F., ... Weigel, D. (2016). Genetic architecture of nonadditive inheritance in *Arabidopsis thaliana* hybrids. *Proceedings of the National Academy of Sciences of the United States of America*, 113(46), E7317–E7326. <https://doi.org/10.1073/pnas.1615268113>
- Sherpa, P., Seth, T., Shende, V. D., Pandiarana, N., Mukherjee, S., & Chattopadhyay, A. (2014).

- T. N. Bhusal and G. M. Lal: *Quantitative Breeding on Maize*
- Heterosis, dominance estimate and genetic control of yield and post harvest quality traits of tomato. *Journal of Applied and Natural Science*, 6(2), 625-632. <https://doi.org/10.31018/jans.v6i2.507>
- Shiri, M., Aliyev, R. T., & Choukan, R. (2010). Water stress effects on combining ability and gene action of yield and genetic properties of drought tolerance indices in maize. *Research Journal of Environmental Sciences*, 4(1), 75–84. <https://doi.org/10.3923/rjes.2010.75.84>
- Singh, P. K., Singh, N., Singh, A. K., Shahi, J. P., & Rao, M. (2013). Heterosis in relation to combining ability in quality protein protein maize (*Zea mays* L.). *Biolife*, 1(2), 65–69. Retrieved from https://www.researchgate.net/publication/291262135_HETEROISIS_IN_RELATION_TO_COMBINING_ABILITY_IN_QUALITY_PROTEIN_MAIZE_ZEA_MAYS_L
- Soriano Viana, J. M., & de Pina Matta, F. (2003). Analysis of general and specific combining abilities of popcorn populations, including selfed parents. *Genetics and Molecular Biology*, 26(4), 465-471. <https://doi.org/10.1590/S1415-47572003000400010>
- Sprague, G. F., & Tatum, L. A. (1942). General vs. specific combining ability in single crosses of corn. *Agronomy Journal*, 34(10), 923–932. <https://doi.org/10.2134/agronj1942.00021962003400100008x>
- Turner Jr, J. H. (1953). A study of heterosis in upland cotton II. Combining ability and inbreeding effects. *Agronomy Journal*, 45, 484–486. <https://doi.org/10.2134/agronj1953.00021962004500100007x>
- Umar, U. U., Ado, S. G., Aba, D. A., & Bugaje, S. M. (2014). Estimates of combining ability and gene action in maize (*Zea mays* L.) under water stress and non-stress conditions. *Journal of Biology, Agriculture and Helthcare*, 4(25), 247–253. Retrieved from <https://www.iiste.org/Journals/index.php/JBAH/article/view/17398>
- Vasal, S. K. (2000). Hybrid maize technology: Challenges and expanding possibilities for research in the next century. In S. K. Vasal, F. Gonzalez Cenicerros, & F. XiongMing (Eds.), *Proceedings of 7th Asian Regional Maize Workshop* (pp. 58–62). Los Baños, Laguna (Philippines): PCARRD. Retrieved from https://knowledgecenter.cimmyt.org/cgi-bin/koha/opac-detail.pl?biblionumber=6313&shelfbrowse_itemnumber=6332
- Wassimi, N. N., Isleib, T. G., & Hosfield, G. L. (1986). Fixed effect genetic analysis of a diallel cross in dry beans (*Phaseolus vulgaris* L.). *Theoretical and Applied Genetics*, 72, 449–454. <https://doi.org/10.1007/BF00289525>
- Zare, M., Choukan, R., Heravan, E. M., Bihamta, M. R., & Ordoorkhani, K. (2011). Gene action of some agronomic traits in corn (*Zea mays* L.) using diallel cross analysis. *African Journal of Agricultural Research*, 6(3), 693–703. Retrieved from https://www.researchgate.net/publication/266493793_Gene_action_of_some_agronomic_traits_in_corn_Zea_mays_L_using_diallel_cross_analysis