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Research Article

Genetics of ear traits and grain yield in quality protein maize (*Zea mays* L.)

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Abstract

Hayman's component analysis was employed to ascertain the gene actions conditioning the ear related traits *viz.*, ear length, ear diameter, kernel rows per ear, kernels per row and grain yield per plant in quality protein maize. Eight yellow seeded quality protein maize (QPM) inbred lines were crossed in diallel mating design, including reciprocals. The inbreds and their 56 crosses were evaluated in randomized block design with 3 replications across the three environments. Significant differences among genotypes observed for all the traits over the environments. Influence of epistasis found for all the traits in one or more seasons except ear length. Ear length exhibited importance of additive gene effects across the seasons. Over-dominance showed in all the characters. The range of narrow sense heritability was low over the environments for most of the traits i.e. for ear length (15.1-19.3%), ear diameter (12.1-17.7%), kernels per row (23.6-30.5%) and grain yield per plant (13.6-19.5%) whereas kernel rows per ear exhibited moderate narrow sense heritability ranging from 44.3-66.5% over the environments. In general, narrow sense heritability estimates were higher in *rabi* environment as compared to *kharif* environment
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Key words:
Maize, Component analysis, gene action, diallel, QPM, heritability.

Introduction:

Maize or corn (*Zea mays* L.) is the third most important cereal crop worldwide, after wheat and rice. It is not only important in human nutrition, but also plays a significant role in animal feed and as raw material for manufacture of various industrial products *viz.* corn starch, maltodextrins, corn oil, corn syrup and products of fermentation and distillation industries. Many developing countries rely on maize as a primary staple which meets the protein and calorie requirements of its human population (Vasal, 2002).Despite its importance in human food and as industrial raw material, it is deficient in two essential amino acids, *viz.*, lysine and tryptophan (Osborne and Mendel, 1914) lowering its nutritional value. This limitation was overcome with the subsequent discovery of *opaque*-2 gene which led to the development of quality protein maize (Vasal, 2001).

Development of superior QPM inbred lines for commercial use in hybrid combination is one of the major goals of today's maize improvement programme. In the process of selection of parental lines, fixation of selection criteria is one of the crucial tasks that often a plant breeder encounters. Harvestable 'grain yield' is usually the primary trait for improvement. However, it is a complex quantitative character governed by poly-genes, which are highly influenced by environmental fluctuations. A number of characters are associated directly or indirectly with this and various approaches have been used to explain yield as a function of different traits (Johnson, 1973). Therefore selection for yield components would be more useful than yield *per se*. Further, the study of genetic makeup of such quantitative traits is essential in deciding proper methodology for their improvement along with yield.

In order to formulate an effective breeding strategy, the sound knowledge of nature and magnitude of gene actions conditioning the traits is a prerequisite. Thus the present study was conducted over three seasons (environments), to have a reliable estimates of the various components of genetic variation for traits related to ears/cobs and grain yield in a set of elite QPM inbred lines.

Material and Methods

Eight diverse yellow QPM inbred lines [HUZQPM 10, HUZQPM 9, CML 163, CML 169, CML 451(P2), HKI 193-1, VQL 1 and VQL 16] were procured from All India Co-ordinated Research Project on Maize running at Department of Genetics and Plant Breeding, Institute of Agricultural Sciences, Banaras Hindu University, Varanasi (UP), India. All possible single crosses, including reciprocals (total 56 crosses), were made in diallel mating design.

Eight QPM inbreds, their 56 crosses along with 2 standard checks were grown in compact family randomized block design (RBD) with 3 replications during two post rainy seasons (*rabi*-2011 and *rabi*-2012) and one rainy season (*kharif*-2012) at Agricultural Research Farm of Banaras Hindu University.

Data were collected on ear related traits, namely ear length (cm), ear diameter (cm), number of kernel rows per ear, and number of kernels per row, and grain yield per plant (g). For grain yield per plant, fresh weight of all ears from a plot was obtained after harvest, leaving two border plants from both sides. Later on it was adjusted at 15% moisture and 80% shelling as follows:

$$Grain\ yield = \frac{Fresh\ ear\ weight \times 0.8 \times (100 - Actual\ \ moisture\ \ \%)}{85}$$

Here, actual moisture per cent was measured with the help of electronic moisture meter by taking shelled kernel samples from the bulk of harvested ear of each treatment. Grain yield per plot was divided by the number of plants in individual plots in each replication to get grain yield per plant.

The procedure for analysis of variance for the crosses and parents was followed as suggested by Panse and Sukhatme (1967). The variances for different sources of variations were utilized against error variance for ‘F-test’ at 5% and 1% level of significance. Diallel component analysis (Hayman, 1954) was performed with the help of statistical software Windostat v.8.5 (Windostat Services, Hyderabad, A.P., India).

Results and Discussion

Analysis of variance (ANOVA) for all the traits, over the environments, exhibited significant differences among environments, genotypes and genotype × environment interaction (Table 1). Significant genotype × environment interaction suggested the differential response of genotypes over the environments, thus a separate analysis for each environment was carried out in order to assess the reliable estimates of various genetic components. Separate analysis for individual environment could also help in selection of traits which exhibit consistency in gene action, thus those traits could be reliably utilized in breeding programme irrespective of the environments. Analysis of variance for all the traits in three growing environments indicated significant differences among the treatments, i.e. 8 parents and 56 diallel set of crosses including reciprocals (Table 2). Significant variation among the yield traits in maize was earlier reported by Unay et al. (2004), Hussain et al. (2009), Wattoo et al. (2009), Haq et al. (2009), Zare et al. (2011), Kumar et al. (2012), Dawod et al. (2012) and Sarac and Nedelea (2013a).

The validity of assumptions for diallel analysis was tested by ‘t^2’ test (Hayman, 1954). Most of the traits exhibited non-significant value for t^2 over the environments (Table 3), except ear diameter (*rabi*-2012), kernels per row (*kharif*-2012) and grain yield per plant (*rabi*-2012). The significance of t^2 values indicated that at least one of the assumptions was not fulfilled; however none of the traits exhibited significance of t^2 values in more than one enviroment. Most of the traits exhibited significant deviation of regression coefficient between array variances and co-variances ‘b’ from zero during *rabi* environments, except ear diameter and grain yield per plant in *rabi*-2011 and ear length in *rabi*-2012. However, in *kharif* environment only ear length and kernels per row exhibited significant departure of ‘b’ from zero. The non-significant deviation of ‘b’ from unity was observed for most of the traits during *rabi* environments suggesting absence of epistasis, except ear diameter and grain yield per plant. However, during *kharif* environment ear diameter, kernel rows per ear and kernels per row exhibited significant deviation of ‘b’ from unity, suggesting influence of non-allelic interactions. Significant ‘t^2’ values for ear diameter, kernels per row and grain yield per plant, along with non-significant deviation of ‘b’ from zero and significant departure of ‘b’ from unity was also reported by Subramanian and Subbaraman (2006).

The components of genetic variation were estimated for all the traits, in each season and results are presented in Table 4. Ear length exhibited significant estimates of additive genetic component D, over the seasons, whereas other traits exhibited significance of additive components in either one or two environments. For grain yield per plant additive component was not significant over the environments. The estimate of dominance genetic component (H_1) and dominance component due to proportion of positive and negative genes (H_2) were significant for all the traits in all the environments. This indicated that both additive and non-additive type of gene action is important for ear length but for other traits dominance gene effect is primarily responsible for their conditioning. A pronounced effect of additive genetic effects in the inheritance of ear length, kernel rows per ear and kernels per row was reported by Haq et al. (2009) in contrast to the present findings. Dawod et al. (2012) reported relatively higher estimates of dominance components than additive component for kernel rows per ear, kernels per row and grain yield in line with the present findings. The estimates of net dominance effect were positive and significant for all the traits, in all the seasons, indicating importance of dominant genes for all the traits.

The estimated values of F were non-significant for most of the traits, over the environments, which indicated the relatively symmetrical distribution of dominant and recessive alleles (Table 4). For ear length, estimate of F was positive and significant (*rabi*-2012) and for kernel rows per ear the estimate of F was negative and significant (*rabi*-2012), indicating that these traits are governed by an excess of dominant and recessive genes, respectively. However, it is of little importance since the estimates of F was not consistently significant over the environments. Similar to the present findings Unay et al. (2004) also reported non-significant estimates of F for grain yield, suggesting nearly equal distribution of dominant and recessive genes among the parents. However, significant estimates of F for ear length and grain yield per plant and non-significant estimate for ear diameter was reported by Subramanian and Subbaraman (2006). The estimate of environmental component of variation was significant for kernel rows per ear during *rabi* environments suggesting the role of environment for this trait. Significant role of environment for kernel rows per ear was also reported by Khodarahmpour (2011).

Proportions of components of genetic variations were calculated and results are presented in Table 5. The average degree of dominance indicated over-dominance for all the traits, over the environments. This suggested the importance of non-additive type of gene action for all the traits. Over-dominance for ear traits and grain yield, similar to present findings was also reported by Turgut et al. (1995), Unay et al. (2004), Subramanian and Subbaraman (2006), Wattoo et al. (2009), Haq et al. (2010), Kumar et al. (2012), Dawod et al. (2012) and Sarac and Nedelea (2013a, 2013b). In contrast to the present findings, partial dominance for grain yield (Hussain et al., 2009), ear length (Zare et al., 2011), ear diameter, kernel rows per ear and kernels per row (Khodarahmpour, 2011) was also reported.

The ratio of $H_2/4H_1$ was close to the expected value of 0.25 for most of the traits, over the environments, except ear length (*rabi*-2012) and kernel rows per ear (*rabi*-2012 & *kharif*-2012) (Table 5). This indicated relatively symmetrical distribution of positive and negative dominant genes for most of the traits among the parents. Consistent with the present finding, Subramanian and Subbaraman (2006), Haq et al. (2010) and Kumar et al. (2012) also reported nearly symmetric distribution of positive and negative dominant genes for ear related traits and grain yield. Khodarahmpour (2011) reported asymmetric distribution of genes for kernels rows per ear which supports the present finding about this trait in two out of three environments (*rabi*-2012 and *kharif*-2012). Zare et al. (2011) observed values of $H_2/4H_1$ away from 0.25, showing asymmetric distribution of positive and negative dominant genes for kernel rows per ear and kernels per row in their material being not in consonance with the present findings.

The values of KD/KR were higher than one for most of the traits, except kernel rows per ear (*rabi* environments), suggesting an excess of dominant genes conditioning most of the traits (Table 5). Similar to the present findings the prevalence of dominant genes for ear related traits and grain yield was reported by Unay et al. (2004), Subramanian and Subbaraman (2006), Zare et al (2011) and Kumar et al. (2012), whereas, Haq et al. (2010) reported prevalence of recessive genes for grain yield per plant.

The number of dominant genes or groups of genes was observed to be 2-4 for ear length, 3-4 for ear diameter, 3 for kernel rows per ear, 4 for kernels per row and 3 for grain yield per plant (Table 5). Earlier reports for grain yield indicated nearly 2 (Zare et al., 2011) to 4 (Turgut et al., 1995; Unay et al., 2004; Sarac and Nedelea, 2013b) dominant genes/genes blocks associated with the inheritance of the grain yield, which were in close correspondence with the present findings. However, 6 to 7 dominant genes/genes blocks for grain yield have also been reported (Subramanian and Subbaraman, 2006; Zare et al., 2011; Kumar et al., 2012). Nearly 4 genes for ear length, 3-4 genes for ear diameter and 2 genes each for kernel rows per ear and kernels per row were also reported (Turgut et al., 1995; Subramanian and Subbaraman, 2006; Zare et al., 2011), which are in close agreement to the number of genes estimated in present investigation for above traits, whereas, Subramanian and Subbaraman (2006) reported nearly 7 dominant genes or group of genes controlling the inheritance of kernels per row.

The narrow sense heritability estimates were highest for kernel rows per ear (44.3-66.5%) followed by kernels per row (23.6-30.5%), over the environments (Table 5). The moderate heritability estimates for kernel rows per ear suggested effectiveness of selection for improvement of this trait. Ear length, ear diameter and grain yield per plant exhibited low heritabilities (of the order of 10-20%) over the seasons suggesting lower selection efficiency for this trait among the present material. The perusal of heritability estimates indicated that the magnitude of heritabilities for all the traits were higher during *rabi* environments as compared to *kharif* environments, suggesting the differences among the genotypes were more pronounced during *rabi*, which may be helpful in discrimination among genotypes while practicing selection. Low narrow sense heritability for grain yield (~10%) was reported by Khodarahmpour (2011), Zare et al. (2011) and Sarac and Nedelea (2013b), which reveals relatively less genetic variation for yield in their material, being in agreement to the present findings. In close accordance with the present findings, Zare et al. (2011) also reported moderate narrow sense heritability estimates for kernel rows per ear (48.4%) and kernels per row (43.7%). Like present findings, Subramanian and Subbaraman also reported low heritability for ear length (9.8%) and ear diameter (12.7%).

In conclusion, the present study indicated the importance of dominance type of genetic effects in the conditioning all the ear traits and grain yield per plant suggesting that heterosis breeding would be the more beneficial way to harvest the pronounced dominance gene effects of these traits. The low narrow sense heritability of ear length, ear diameter and gain yield per plant suggested that selection for these traits may not be effective and reliable. However, kernel rows per ear and kernels per row may be more reliable traits, which effectively respond to the selection, owing to their high heritabilities. Also, selection may be more effective during *rabi* as compared to *kharif* environments.

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Table 1. Analysis of variance for ear related traits and grain yield per plant over environments in QPM.

SV	DF	EL	ED	KR E^{-1}	K R^{-1}	GY P^{-1}
Replication	2	15.318 **	0.336 **	0.413	32.081 **	1428.271 **
Environment	2	100.819 **	6.728 **	20.112 **	1503.694 **	23346.210 **
Genotype	65	17.832 **	1.100 **	9.769 **	190.078 **	5300.042 **
Genotype × Environment	130	3.550 **	0.152 **	2.028 **	23.078 **	823.626 **
Error	394	0.828	0.044	0.666	5.701	129.32

* $p \leq 0.05$; ** $p \leq 0.01$; SV-Source of Variation; DF-Degrees of Freedom; EL-Ear Length; ED-Ear Diameter; KR E^{-1}-Kernel Rows per Ear; K R^{-1}-Kernels per Row; GY P^{-1}-Grain Yield per Plant

Table2. ANOVA of 8x8 diallel set of crosses in three growing environments in QPM.

SV	DF	Season	EL	ED	KR E^{-1}	K R^{-1}	GY P^{-1}
Replication	2	*Rabi*-2011	11.39**	0.51**	0.39	89.75**	1068.38**
		Rabi-2012	1.45	0.35**	0.47	19.81*	128.79
		Kharif-2012	7.48**	0.01	1.33	14.62	1443.59**
Treatments	63	*Rabi*-2011	7.80**	0.34**	3.41**	96.19**	3156.54**
		Rabi-2012	4.31**	0.44**	4.18**	42.92**	1703.70 **
		Kharif-2012	11.95**	0.66**	6.31**	95.78**	2068.96**
Error	126	*Rabi*-2011	0.67	0.04	0.54	4.01	111.56
		Rabi-2012	0.66	0.03	0.48	6.36	118.69
		Kharif-2012	1.09	0.05	0.97	5.45	144.80

* $p \leq 0.05$; ** $p \leq 0.01$; SV-Source of Variation; DF-Degrees of Freedom; EL-Ear Length; ED-Ear Diameter; KR E^{-1}-Kernel Rows per Ear; K R^{-1}-Kernels per Row; GY P^{-1}-Grain Yield per Plant

Table 3. Estimates of "t^2" and "b" for 8x8 diallel analysis in three growing environments in QPM.

	"t^2"			b (Slope) ± SE (b)			H_0: b=0			H_0: b=1		
Traits	*Rabi*-2011	*Rabi*-2012	*Kharif*-2012	*Rabi* - 2011	*Rabi* - 2012	*Kharif* - 2012	*Rabi* - 2011	*Rabi* - 2012	*Kharif* - 2012	*Rabi* - 2011	*Rabi* - 2012	*Kharif* - 2012
EL	0.012	0.841	0.828	0.804 ± 0.262	0.541 ± 0.223	0.562 ± 0.218	*	NS	*	NS	NS	NS
ED	2.153	32.062**	1.792	0.384 ± 0.205	0.255 ± 0.079	0.323 ± 0.223	NS	*	NS	*	**	**
KR E^{-1}	0.2	0.568	0.971	0.913 ± 0.108	0.732 ± 0.18	0.314 ± 0.257	**	**	NS	NS	NS	*
K R^{-1}	0.866	0.029	52.469**	0.617 ± 0.202	0.78 ± 0.229	0.279 ± 0.062	*	*	**	NS	NS	**
GY P^{-1}	2.89	15.343**	0.012	0.078 ± 0.213	0.289 ± 0.108	0.421 ± 0.389	NS	*	NS	**	**	NS

* $p \leq 0.05$; ** $p \leq 0.01$; NS-Non Significant; EL-Ear Length; ED-Ear Diameter; KR E^{-1}-Kernel Rows per Ear; K R^{-1}-Kernels per Row; GY P^{-1}-Grain Yield per Plant

Table 4. Components of genetic variation for 8 x 8 diallel in three growing environments in QPM.

Component	Season	EL	ED	KR E^{-1}	K R^{-1}	GY P^{-1}
$\hat{D}$	*Rabi*-2011	1.666*	0.074	0.899**	16.43	372.58
	Rabi-2012	2.284**	0.108	0.528*	13.438**	281.136
	Kharif-2012	4.158**	0.195*	0.372	10.403	105.489
$\hat{H}_1$	*Rabi*-2011	9.868**	0.408**	1.134**	104.547**	4252.529**
	Rabi-2012	6.949**	0.591**	2.164**	44.321**	2155.177**
	Kharif-2012	14.182**	0.939**	7.567**	133.441**	2419.312**
$\hat{H}_2$	*Rabi*-2011	8.12**	0.366**	0.984**	91.231**	3582.962**
	Rabi-2012	4.856**	0.486**	1.593**	37.466**	1782.994**
	Kharif-2012	12.038**	0.78**	5.694**	109.192**	2233.59**
$\hat{h}^2$	*Rabi*-2011	24.455**	1.057**	2.292**	306.272**	9101.847**
	Rabi-2012	7.961**	1.525**	4.044**	134.248**	5214.648**
	Kharif-2012	28.459**	2.645**	15.038**	354.186**	5597.563**
$\hat{F}$	*Rabi*-2011	2.313	0.087	-0.643**	8.114	587.567
	Rabi-2012	4.169*	0.155	-0.763	12.605	454.978
	Kharif-2012	5.087	0.294	1.123	25.452	98.8
$\hat{E}$	*Rabi*-2011	0.279	0.014	0.18**	1.784	42.17
	Rabi-2012	0.225	0.013	0.158*	2.189	39.614
	Kharif-2012	0.397	0.017	0.324	1.865	55.029

* $p \leq 0.05$; ** $p \leq 0.01$; EL-Ear Length; ED-Ear Diameter; KR E^{-1}-Kernel Rows per Ear; K R^{-1}-Kernels per Row; GY P^{-1}-Grain Yield per Plant; $\hat{D}$ – variance component due to additive genetic effects; $\hat{H}_1$- variance component due to dominance deviations; $\hat{H}_2$ – estimate of dominance genetic variance due to proportion of positive and negative genes; $\hat{h}^2$ – net dominance effect; $\hat{F}$ – mean of covariance of additive and dominance effects over all the arrays; $\hat{E}$ – environmental component of variation.

Table 5. Proportion of components of genetic variation in QPM in three growing environments.

Ratio	Season	EL	ED	KR E^{-1}	K R^{-1}	GY P^{-1}
$\left[\hat{H}_1/\hat{D}\right]^{-1}$	*Rabi*-2011	2.434	2.347	1.123	2.523	3.378
	Rabi-2012	1.744	2.341	2.024	1.816	2.769
	Kharif-2012	1.847	2.194	4.507	3.582	4.789
$\hat{H}_2/4\hat{H}_1$	*Rabi*-2011	0.206	0.224	0.217	0.218	0.211
	Rabi-2012	0.175	0.205	0.184	0.211	0.207
	Kharif-2012	0.212	0.208	0.188	0.205	0.231
$\widehat{KD}/\widehat{KR}$	*Rabi*-2011	1.798	1.665	0.517	1.217	1.609
	Rabi-2012	3.195	1.884	0.474	1.696	1.826
	Kharif-2012	1.990	2.045	2.005	2.038	1.217
$\hat{h}^2/\hat{H}_2$	*Rabi*-2011	3.012	2.891	2.330	3.357	2.540
	Rabi-2012	1.640	3.140	2.538	3.583	2.925
	Kharif-2012	2.364	3.392	2.641	3.244	2.506
$\hat{h}^2\ (ns)$	*Rabi*-2011	19.3	12.1	66.5	30.5	19.5
	Rabi-2012	16.7	17.7	62.6	25.0	17.0
	Kharif-2012	15.1	12.4	44.3	23.6	13.6

EL-Ear Length; ED-Ear Diameter; KR E^{-1}-Kernel Rows per Ear; K R^{-1}-Kernels per Row; GY P^{-1}-Grain Yield per Plant; $\left[\hat{H}_1/\hat{D}\right]^{-1}$ - average degree of dominance; $\hat{H}_2/4\hat{H}_1$ - proportion of dominant genes with positive and negative effects; $\widehat{KD}/\widehat{KR}$- proportion of dominant and recessive genes; $\hat{h}^2/\hat{H}_2$ - proportion of gene(s)/gene(s) blocks exhibiting dominance; $\widehat{h^2}\ (ns)$ – narrow sense heritability estimate.