Gene action for some agronomic traits in maize (*Zea mays* L.)

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ABSTRACT

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Seven maize inbred lines were crossed in a complete diallel cross design at the Seed and Plant Improvement Institute, Karaj, Iran, during the 2006 growing season. The parents and 42 F_1 hybrids were grown in the research field of Islamic Azad University of Firoozabad, Firoozabad, Iran, using a Randomized Complete Block Design (RCBD) with three replications, during the 2007 growing season. The Hayman method was used for data analysis. Results indicated over-dominance gene effects for days from silking to physiological maturity, days from anthesis to physiological maturity, plant height, kernel depth, number of rows per ear and grain yield. The most appropriate strategy for the exploitation of these effects is to obtain hybrid cultivars and evaluate these characteristics in hybrid combinations. The gene effect for days from emergence to physiological maturity and number of kernels per row was complete dominance, suggesting that reciprocal recurrent selection would be effective. Ear leaf area and ear length were controlled by partial dominance, indicating that additive gene effects were more important than non-additive gene effects for controlling the inheritance of these traits. Therefore, improvement of these traits through selection of breeding materials is highly feasible. Broad-sense heritability ranged between 47.4% and 89.4% for days to physiological maturity and number of rows per ear; however, narrow-sense heritability varied between 7.3% and 50.6% for days from anthesis to physiological maturity and ear leaf area, respectively. Non-additive gene effects were predominant for controlling the majority of traits.

Key words: diallel cross, grain yield, narrow-sense heritability, broad-sense heritability, physiological maturity

INTRODUCTION

Maize (*Zea mays* L.), a multipurpose crop, plays an important role in cropping systems throughout the world. Advances in maize genomics, breeding and production have had significant impact on the lives of a large proportion of the world's population (Xu and Crouch, 2008). Balancing consumer demand for various end-uses of maize and different maize production practices will be critical for maintaining sustainability of cropping systems, food security, feed and fodder supply, and bioenergy demands (Ortiz *et al*., 2006). The objective of maize population improvement is to increase the frequency of favorable alleles while maintaining genetic variation. These improved populations can then serve as a potential source of superior inbred lines and inhibit development of a possible genetic ceiling for future hybrid improvement (Duvick, 1992; Kannenberg and Falk, 1995). The diallel mating design is an important tool used by plant breeding programs to obtain information on trait inheritance (Fry, 2004; Griffing, 1956; Hayman, 1954a).

Jones and Frey (1960) stated that heritability of a trait approaches its maximum in successive generations following hybridization. Furthermore, the presence of additive gene effects for a trait indicates the presence of additive variation, which means that selection could be successful for the trait (Fehr, 1991; Gamble, 1962). Based on a seven-parent inbred diallel of white maize for grain yield and yield components (ear length, ear diameter and shelling [%]), Ojo *et al*. (2007) reported that hybrid means were significantly higher than parental means for all traits except shelling (%). Additive gene action was more important than non-additive gene action for grain yield.

Ottaviano and Camussi (1981) examined several agronomic traits in 45 F_1 hybrids (10×10 diallel cross) to study their genetic relationships with grain yield. They reported that ear size components (number of rows per ear and number of kernels per row) were positively correlated to grain yield, and

that number of kernels per row made the most important contribution.

Saeed *et al.* (2000) performed a 6×6 diallel cross analysis in maize according to Hayman (1954a,b) and Jinks (1954). Vr/Wr graphs indicated that number of kernels per row, 100-grain weight and grain yield per plant were controlled by over-dominance type of gene action, while number of rows per ear was controlled by additive gene action. Vidal-Martinez *et al.* (2001) reported that they found gene effects rather than environmental effects in the expression of grain yield components in maize. Dominance gene effects were also the most important contributors to the inheritance of grain yield and its components.

The mode of inheritance of kernel number per row number was reported to be partial dominance, whereas over-dominance was of greater importance for grain yield, number of kernels per row and 100-grain weight (Srdić *et al.*, 2007). Ali *et al.* (2007) reported that additive genetic variance was important for grains per ear and 1000-grain weight, and that non-additive gene action was involved in plant height, ear height, days to silking and days to maturity. Perez-Velasquez *et al.* (1996) showed that number of kernels per row was controlled by additive gene action, while number of rows per ear, 100-grain weight and grain yield per plant were conditioned by over-dominance gene action. Kumar and Gupta (2003) reported that the additive and dominance components were highly significant for days to tasselling, days to maturity, plant height, main cob height from ground level, number of cobs per plant and 100-kernel weight. The estimates of heritability were higher for days to tasselling and cobs per plant. Days to maturity, plant height, main cob height from ground level and 100-kernel weight exhibited moderate heritability. Ali *et al.* (2007) reported that grain yield and its components showed lower broad-sense heritability than plant height, ear height and flowering traits.

The objective of this study was to estimate genetic parameters for grain yield and its components, as well as other traits, in seven maize inbred lines to be used in maize hybrid development programs.

MATERIALS AND METHODS

Seven maize inbred lines, 1 = K18, 2= K3218, 3 = K1264.1, 4 = MO17, 5 = K19,6 = K74.1 and 7 = K3653.5, were crossed in a complete diallel cross design at the Seed and Plant Improvement Institute, Karaj, Iran, in the 2006 growing season. The inbred lines differed in phenotypic expression of different agronomic traits. The parents and the 42 F_1 hybrids were grown in the research field of Islamic Azad University of Firoozabad (28° 35'N, 52° 40'E and 1327 m above sea level) using a randomized complete block design with three replications in the 2007 growing season. Seed was hand-sown, 3-4 seeds per hill. Each genotype was sown in one 6-m row with 20 cm between plants and 75 cm row spacing. At the 3-4 leaf stage, hills were thinned, leaving only one plant per hill. Prior to planting, 300 kg ha^{-1} of ammonium phosphate and 200 kg ha^{-1} urea were applied, and an additional 200 kg ha^{-1} urea were top dressed at the 7-9 leaf stages. The following observations were made and recorded: days from emergence to physiological maturity (number of days from 50% plant emergence to when 50% of plants reached physiological maturity), days from silking to physiological maturity, days from anthesis to physiological maturity, plant height (from the soil surface to the node below the tassel), ear leaf area (calculated as: A = W × L × 0.75, where A= area of ear leaf in square centimeters, W= width of ear leaf in centimeters and L= length of ear leaf in centimeters), ear length (the length of an husked ear from the bottom to the tip), kernel depth (ear diameter minus cob diameter divided by two), number of rows per ear, number of kernels per row and grain yield. Grain yield was adjusted to 14% grain moisture content.

Statistical analysis was performed for diallel data following Hayman (1954a,b). The significance of t^2 value indicates failure of hypothesis (Singh and Chaudhary, 1985). The second test for the adequacy of the additive-dominance model is regression coefficient analysis. Failure of this test can mean that: (1) non-allelic interaction (epistasis) is present; (2) genes are not independent in their action, or (3) there is non-random association among parents.

The genetic components of variation were calculated by Dial98 software using the procedures of Hayman (1954a,b) and Jinks and Hayman (1953) as follows:

$$\text{Average degree of dominance} = (H_1/D)^{\frac{1}{2}}$$

$$h^2_{bs} = \frac{0.5\,D + 0.5\,H_1 - 0.25\,H_2 - 0.5\,F}{0.5\,D + 0.5\,H_1 - 0.25\,H_2 - 0.5\,F + E},$$

$$h^2_{ns} = \frac{0.5\,D + 0.5\,H_1 - 0.5\,H_2 - 0.5\,F}{0.5\,D + 0.5\,H_1 - 0.25\,H_2 - 0.5\,F + E}$$

where h^2_{bs} = broad-sense heritability and h^2_{ns} = narrow-sense heritability.

Reciprocal effects were also partitioned to maternal and non-maternal effects. The correlation between the parental lines (Y_r) and V_r+W_r indicates direction of dominance according to Hayman (1954a,b), as follows:

$$r = \frac{Cov\ (Y_r,\ V_r + W_r)}{\sqrt{(Var_{Y_r} . Var_{V_r + W_r})}}$$

A negative value of the correlation coefficient (r) indicates dominant genes, whereas a positive value indicates recessive genes are responsible for the phenotypic expression of the trait.

RESULTS AND DISCUSSION

The analysis of variance showed significant differences between the parents and the F_1 hybrids for all the traits (Table 1). Therefore, the Hayman-Jinks model could be used for genetic analysis. The non-significant t^2 values showed fulfillment of diallel assumptions. The additive-dominance model is thus an adequate description of data for traits (Table 2).

The regression coefficient (b) differed significantly from unity (1-b) for days from emergence to physiological maturity and days from silking to physiological maturity; the assumptions of the Hayman-Jinks model were therefore not fulfilled, which makes the model only partially adequate for these traits. The regression coefficient (b) differed significantly from zero (b-0) for days from anthesis to physiological maturity, plant height, ear length, kernel depth, number of rows per ear and number of kernels per row, indicating that non-allelic interactions and epistasis were not important for these traits. Estimates of regression coefficients were not significantly different from zero (b-0) for ear leaf area and grain yield, which indicated the presence of epistasis. However, the fact that the regression coefficients

showed a non-significant difference from unity (1-b) confirmed the validity of the assumption and, therefore, the absence of epistasis was also confirmed.

Hayman's analysis revealed that the additive (a) and dominance (b) components were highly significant for almost all traits, indicating the importance of both of these components (Table 3). These results were in accordance with findings reported by Rezaei and Roohi (2004) for plant height, number of kernels per row, ear length and grain yield.

All traits except days from emergence to physiological maturity showed directional dominance (b_1). Days from emergence to physiological maturity, days from silking to physiological maturity, days from anthesis to physiological maturity, kernel depth, number of rows per ear, number of kernels per row and grain yield traits showed a significant b_2 component, implying asymmetry in gene distribution and dominance effects common to the progeny of a particular parent (b_2). All traits except days from silking to physiological maturity, days from anthesis to physiological maturity and ear leaf area showed dominance effects specific to particular crosses (b_3). There were significant differences between maternal effects (c) and non-maternal reciprocal effects (d) for kernel depth, number of rows per ear, number of kernels per row and grain yield (Table 3). Similar results were reported by Rezaei and Roohi (2004).

The additive component (D) was significant for ear leaf area, ear length, number of kernels per row

Table 1. Analysis of variance for different traits in 7×7 diallel crosses of maize

S.O.V.	df	Days from emergence to physiological maturity	Days from silking to physiological maturity	Days from anthesis to physiological maturity	Plant height	Ear leaf area	Ear length	Kernel depth	Number of rows per ear	Number of kernels per row	Grain yield
						Mean of squares					
Replications	2	62.56**	55.84 ns	116.47*	13591.01 ns	5032.47 ns	59.45**	0.19**	13.17**	105.83 ns	0.23*
Genotypes	48	21.33**	52.03**	50.58**	1398.56**	23216.76 ns	16.02**	0.09**	16.18**	73.78**	0.46*
Error	96	11.94 ns	24.89 ns	28.33 ns	569.32 ns	2819.22 ns	4.25 ns	0.02 ns	1.57 ns	23.34 ns	0.05 ns
Total	146										
%CV		2.48	7.37	7.34	13.45	11.08	13.63	20.85	8.42	17.81	11.65

* and **: Significant at the 5% and 1% levels of probability, respectively.
ns: Not significant.

Table 2. Scaling tests of the additive-dominance model (t^2 test and regression analysis) for different traits in 7×7 diallel crosses of maize

Traits	t^2 test	b± SE	H0: b=0	H1: b=1	Conclusions
			Regression analysis (t value of b)		
Days from emergence to physiological maturity	2.27 ns	0.418±0.204	2.05 ns	2.85*	Model was partially adequate due to t^2 test
Days from silking to physiological maturity	2.78 ns	0.345±0.203	1.70 ns	3.23*	Model was partially adequate due to t^2 test
Days from anthesis to physiological maturity	1.58 ns	0.5952±0.214	2.78*	1.89 ns	Model was adequate shown by both tests
Plant height	0.67 ns	0.767±0.167	4.6**	1.40 ns	Model was adequate shown by both tests
Ear leaf area	0.68 ns	0.385±0.279	1.38 ns	2.20 ns	Model was adequate shown by both tests
Ear length	0.0001 ns	0.8861±0.323	2.74*	0.35 ns	Model was adequate shown by both tests
Kernel depth	1.97 ns	0.667±0.246	2.71*	1.35 ns	Model was adequate shown by both tests
Number of rows per ear	0.03 ns	0.861±0.334	2.58*	0.42 ns	Model was adequate shown by both tests
Number of kernels per row	0.19 ns	0.971±0.225	4.31**	0.09 ns	Model was adequate shown by both tests
Grain yield	1.09 ns	0.609±0.693	0.88 ns	0.56 ns	Model was adequate shown by both tests

* and **: Significant at the 5% and 1% levels of probability, respectively.
ns: Not significant.

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Table 3. Hayman's analysis of variance for different traits in 7×7 diallel crosses of maize

		Mean of squares							
S.O.V.	df	Days from emergence to physiological maturity	Days from silking to physiological maturity	Days from anthesis to physiological maturity	Plant height	Ear leaf area	Ear length	Kernel depth	Number of rows per
Replications	2	62.59 **	75.01 ns	116.42 *	13587.16 **	2584.75 ns	55.95 **	0.19 **	13.
a	6	61.63 **	76.03 *	59.86 ns	1757.13 **	79066 **	64.17 **	0.15 **	51
b	21	20.08 *	79.76 **	71.03 **	2273.68 **	20953.12 **	12.85 **	0.08 **	13.
b_1	1	4.22 ns	421.88 **	473.15 **	29369.63 **	321591 **	97.32 **	0.30 **	67.
b_2	6	14.87 ns	113.76 **	73.72 *	68.31 ns	7039.71 ns	4.07 ns	0.09 **	14.
b_3	14	23.44 *	40.75 ns	41.16 ns	1283.41 *	5441.87 ns	10.59 **	0.06 **	9.
c	6	8.46 ns	25.03 ns	23.21 ns	644.19 ns	8264.91 ns	4.36 ns	0.10 **	9.
d	15	12.09 ns	11.81 ns	29.21 ns	331.84 ns	4546.38 ns	4.21 ns	0.06 **	8.
Error	96	11.94	28.19	28.33	569.34^s	3911.97	4.42	0.02	
Total	146								

* and **: Significant at the 5% and 1% levels of probability, respectively.
ns: Not significant.

Table 4. Estimation of statistical indices and genetic parameters for different traits in 7×7 diallel crosses of maize

Parameters	Days from emergence to physiological maturity	Days from silking to physiological maturity	Days from anthesis to physiological maturity	Plant height	Ear leaf area	Ear length	Kernel depth
D	5.533 ns ±5.151	9.71 ns ±12.511	9.657 ns ±12.459	63.41 ns ±169.114	16401.776 ** ±2607.061	8.797 ** ±3.244	0.004 ns ±0.01
F	-0.513 ns ±7.26	25.531 ns ±22.203	17.462 ns ±20.715	-295.822 ** ±196.901	-115.7 ns ±2577.962	3.025 ns ±3.646	0.009 ns ±0.018
H_1	6.104 ns ±7.571	54.759 * ±23.996	39.276 ns ±21.538	1016.919 ** ±389.657	13534.73 ** ±2777.381	5.543 ns ±3	0.055 ** ±0.021
H_2	5.565 ns ±5.314	34.77 * ±15.272	28.855 * ±14.461	1143.967 ** ±364.219	13244.27 ** ±2456.407	5.685 ns ±3.456	0.039 ** ±0.014
h^2	-1.121 ns ±3.66	64.605 ns ±35.491	72.954 ns ±39.109	4708.738 ** ±1326.806	55723.77 ** ±10273.83	15.22 * ±6.924	0.045 ns ±0.028
E	3.98 ** ±0.568	9.396 ** ±1.281	9.444 ** ±1.373	189.781 ** ±25.925	992.413 ** ±132.169	1.472 ** ±0.207	0.008 ** ±0.001
$[H1/D]^{1/2}$	1.05	2.375	2.107	4.005	0.908	0.794	3.557
h^2/H_2	-0.235	2.168	2.95	4.802	4.909	3.123	1.36
$H_2/4H_1$	0.228	0.159	0.184	0.228	0.245	0.205	0.177
h^2_{bs}	0.481	0.534	0.474	0.641	0.886	0.742	0.652
h^2_{ns}	0.299	0.103	0.073	0.1	0.506	0.493	0.239
KD/KR #	0.915	3.48	2.625	0.264	0.992	1.553	1.871
r (Y_r, W_r+V_r)	-0.287	-0.938	-0.841	-0.874	-0.758	0.339	-0.502

#: $(\sqrt{4DH1}+F)/(\sqrt{4DH1}-F$.
* and **: Significant at the 5% and 1% levels of probability, respectively.
ns: Not significant.

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and grain yield, whereas the dominance component (H_1) of genetic variance was significant for all traits except days from emergence to physiological maturity, days from anthesis to physiological maturity, ear length and number of kernels per row (Table 4).

The value of (H_1) was higher than that of (D), revealing that non-additive gene effects were more important than additive gene effects for all the traits except ear length. The significant value of additive component (D) and the non-significant values of dominance components (H_1) and (H_2) for ear length indicated stability in the additive variance of this trait; it can thus be improved through simple selection procedures. The overall dominance effect was determined by h^2 estimates, which gave the total sum over all the loci in a heterozygous state. This was positive and significant for plant height, ear leaf area, ear length, number of rows per ear and grain yield, indicating that dominance is largely unidirectional. The value of the degree of dominance $(H_1/D)^{1/2}$ was less than unity for ear leaf area and ear length, indicating the existence of partial dominance for these traits. However, it was almost equal to unity for days from emergence to physiological maturity and number of kernels per row, revealing the existence of complete dominance. On the other hand, it was more than unity for other traits, indicating the existence of over-dominance, which can be utilized for developing hybrid varieties.

These results are in agreement with reports by other researchers about predominance of non-additive gene effects for days from silking to physiological maturity (Zare *et al.,* 2008), plant height (Irshad-Ul-Haq *et al.,* 2010; Akbar *et al.,* 2008; Alam *et al.,* 2008), grain depth (Zare *et al.,* 2008), number of rows per ear (Vidal-Martinez *et al.,* 2001; Saeed *et al.,* 2000; Ismail, 1996) and grain yield (Irshad-Ul-Haq *et al.,* 2010; Ali *et al.,* 2007; Srdić *et al.*, 2007; Bhatnagar *et al.,* 2004; Prakash and Ganguli, 2004; Rezaei and Roohi, 2004). Muraya *et al. (*2006) reported predominance of additive gene effects for ear leaf area and ear length. However, equal importance of additive and non-additive gene effects for number of kernels per row was reported by other researchers (Kumar *et al.,* 1998; Debnath *et al.,* 1988; Debnath *et al.,* 1989), and for days from emergence to physiological maturity by Kumar and Gupta (2003).

In contrast to the findings of this study, other researchers reported predominance of additive gene effects for plant height (Vacaro *et al.,* 2002), number of rows per ear (Srdić *et al.,* 2007) and grain yield (Ojo *et al.,* 2007; Vacaro *et al.,* 2002).

The component F determines the relative frequencies of dominant and recessive alleles in the parents. Positive but non-significant values of F for most of the traits indicated almost symmetrical gene distribution with a small excess of dominant alleles in the parents. This was also confirmed by the ratio $[(\sqrt{4DH_1} + F)/(\sqrt{4DH_1} - F)]$, which was greater than unity for most traits, indicating an asymmetrical distribution of positive and negative alleles among the parents. The significant positive value of F and the ratio of the number of total dominant genes to the number of recessive genes was greater than unity for grain yield, suggested that dominant genes were excessive in the parents. Secanski *et al.* (2004) reported comparable results for grain yield.

The h^2/H_2 ratio denotes an approximate number of genes or groups of genes controlling the traits, i.e., exhibiting dominance, and was more than one for all the traits except days from emergence to physiological maturity, which most likely was underestimated. This may be attributed to the differences in the intensity of of dominant genes effects as well as dependence on their direction and cancellation effects. Jinks (1954) stated that a non-random distribution of genes may bring about this discrepancy. The estimates of the $H_2/4H_1$ ratio were close to the expected value of 0.25 for days from emergence to physiological maturity, plant height, ear leaf area and grain yield, suggesting symmetrical distribution of positive and negative dominant genes among the parents. For days from silking to physiological maturity, days from anthesis to physiological maturity, ear length, kernel depth, number of rows per ear and number of kernels per row, the value of this ratio was far from the expected value, revealing an asymmetrical distribution of positive and negative genes among the parents. This was also confirmed by the correlation between parental order of dominance (W_r+V_r) and parental measurement (Y_r), suggesting that negative genes were more frequent than positive genes in the parents, as the r values were negative for most traits. The positive r values for ear length and grain yield indicated positive effects of the alleles controlling these traits. The results were in agreement with Irshad-Ul-Haq *et al.* (2010), who demonstrated that positive and negative alleles were distributed equally at the loci, indicating dominance in the parental genotypes for grain yield.

Estimates of broad-sense heritability for all traits (Table 4) showed that number of rows per ear, ear leaf area and grain yield had the highest heritability (0.894, 0.886 and 0.857, respectively). Lower estimates of broad-sense heritability were observed for ear length, number of kernels per row, kernel depth and plant height (0.742, 0.673, 0.652 and 0.641,

respectively). This implied a high estimate of genetic variance and a low estimate of environmental variance for these traits in maize genotypes. These findings are in agreement with reports by Arbelbide and Bernardo (2004) and Kumar and Gupta (2003) for plant height. Days from silking to physiological maturity, days from emergence to physiological maturity and days from anthesis to physiological maturity had moderate heritability (0.534, 0.481 and 0.474, respectively). Other researchers indicated moderate heritability for days from emergence to physiological maturity (Kumar and Gupta, 2003) and days from silking to physiological maturity (Choi *et al.*, 1995). Contrary to these results, estimates for narrow-sense heritability varied between 7.3% and 50.6% for days from anthesis to physiological maturity and ear leaf area, respectively. This was caused by a low proportion of additive variance expressed for these traits. Therefore, direct selection for these traits would not be effective. These results are in agreement with the findings of Rezaei and Roohi (2004).

The distribution of parents along the regression line of Wr on Vr, and the sign and amount of intercepts for all traits are presented in Fig. 1 to 10. A zero, positive or negative intercept indicates complete, partial or over-dominance gene action, respectively. Parents closer to the origin possess more dominant alleles and those farther from the origin contain more recessive alleles for the respective traits.

The regression line for days from emergence to physiological maturity intercepted the W_r axis close to the origin and denoted both additive and dominance gene effects, with complete dominance controlling the inheritance of this trait (Fig. 1). This was confirmed by the degree of dominance (Table 4). It was noticed that inbred line K18 possessed maximum dominant genes, as evidenced by its position nearest the origin, while inbred line K1264.1 was farther away from the origin, indicating it had recessive genes. Malik *et al.* (2004) have also reported a similar type of gene action for days from emergence to physiological maturity.
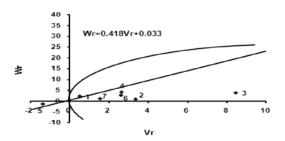
The regression line for days from silking to physiological maturity cut the W_r axis below the origin in the negative zone, suggesting the over-dominance type of gene action (Fig. 2); this is also supported by the greater than unity $(H_1/D)^{1/2}$ ratio (Table 4). The distribution of array points along the regression line indicated that inbred line K19, being closest to the origin, contains maximum dominant genes, while inbred line K18, being farthest from the origin, had maximum recessive genes. Zare *et al.* (2008) also reported the over-dominance type of gene action for this trait.

The regression line for days from anthesis to physiological maturity intercepted the W_r axis in the negative zone, revealing over-dominance gene action (Fig. 3); this was confirmed by the degree of dominance (Table 4). From the position of the array points on regression line, it was observed that inbred lines K3653.5 and MO17, being nearest to the origin, appeared to have maximum dominant genes, while inbred line K18, being farther away from the origin, had recessive gene action for this trait. Wang *et al.* (1999) showed predominance of additive gene effects for this trait. The differences in these reports may be due to the different genetic materials studied under different experimental conditions.
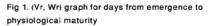
For plant height, the regression line passed the W_r axis below the origin, indicating over-dominance gene action (Fig. 4), which is evidenced by the greater than unity $(H_1/D)^{1/2}$ ratio (Table 4). Based on the array points on the regression line, inbred line MO17 had maximum dominant genes, being closest to the origin, while inbred line K3653.5 possessed recessive genes, as evidenced by its distant position from the origin. These results for plant height are in accordance with those reported by Wattoo *et al.* (2009), Kumar *et al.* (2005), and Prakash and Gunguli (2004). However, the findings of Singh and Roy (2007) revealed that additive gene action was involved in the inheritance of plant height, which disagrees with the results of this study. This disagreement may be due to the difference in the genetic materials used and the environmental conditions under which the experiments were conducted.
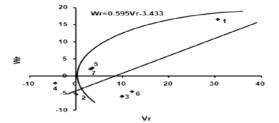
For ear leaf area, the regression line intercepted the W_r axis above the origin, which indicated additive gene action with partial dominance for this trait (Fig. 5), due to prevalence of recessive genes. It was noticed that inbred lines K18 and K74.1 possessed maximum dominant genes, as evidenced by their position nearest to the origin, while inbred line K3218, being farther away from the origin, had recessive genes. Hussain (2009) reported a similar type of gene action for ear leaf area.
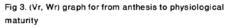
The (W_r, V_r) regression line for ear length intercepted the W_r axis above the origin, indicating the importance of additive gene action with partial dominance (Fig. 6). The relative distribution of inbred lines along the regression line revealed that inbred line K19, being closer to the origin, carried the most dominant genes for the trait, whereas inbred line K3218, being farther away from the origin, possessed the maximum recessive genes. These results are in agreement with the findings of Sofi (2007) and Saeed and Saleem (2000).
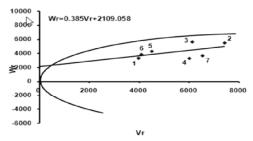
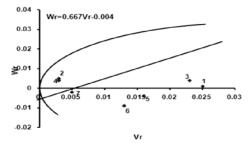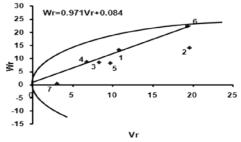The regression line for kernel depth intercepted

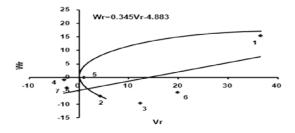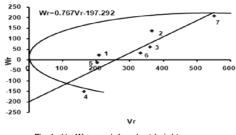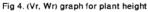Fig 1. (Vr, Wr) graph for days from emergence to physiological maturity

Fig 2. (Vr, Wr) graph for days from silking to physiological maturity

Fig 3. (Vr, Wr) graph for from anthesis to physiological maturity

Fig 4. (Vr, Wr) graph for plant height

Fig 5. (Vr, Wr) graph for area of ear leaf

Fig 6. (Vr, Wr) graph for ear length

Fig 7. (Vr, Wr) graph for kernel depth

Fig 8. (Vr, Wr) graph for number of rows per ear
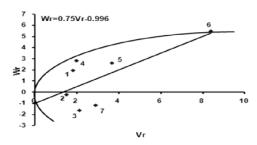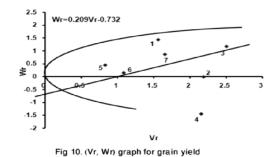
Fig 9. (Vr, Wr) graph for number of kernels per row

Fig 10. (Vr, Wr) graph for grain yield

the Wr-axis below the origin, revealing over-dominance gene action (Fig. 7). The results of graphic and genetic components analyses were in agreement, and the $(H_1/D)^{1/2}$ ratio also suggested the presence of over-dominance (Table 4). Based on the location of their regression lines, inbred lines K3218 and MO17, being closer to the origin, were found to have maximum dominant genes, whereas inbred line K18, being farthest from the origin, contained the most recessive genes (Fig. 7). Zare *et al.* (2008) reported over-dominance gene action for kernel depth.

The regression line intercepted the Wr-axis below the origin for number of rows per ear, indicating the over-dominance type of gene action (Fig. 8), which was also evidenced by the greater than unity $(H_1/D)^{1/2}$ ratio (Table 4). The position of the array points, closer to the origin, showed that inbred line K3218 had the maximum dominant genes, whereas inbred line K74.1 possessed recessive genes, as revealed by their distant position from the origin (Fig. 8). Given that the remaining genotypes occupied central positions, it was speculated that they had equal frequencies of dominant and recessive genes (Fig. 8). Wattoo *et al.* (2009) and Saleem *et al.* (2002) reported comparable results for number of rows per ear.

As shown in Fig. 9, the line of unit slope cut the limiting parabola close to the origin, indicating additive and dominance gene effects, with complete dominance controlling the inheritance for number of kernels per row. This was also confirmed by degree of dominance (Table 4). The dispersion of parental arrays along the regression line showed that inbred line K3653.5 had maximum dominant genes, since it lay farthest from the origin on the extreme end towards the origin, whereas inbred lines K74.1 and K3218 had the maximum recessive genes, as they were at the farthest end of the regression line (Fig. 9). Hussain (2009), however, reported the over-dominance type of gene action for number of kernels per row. The differences in these reports could be because the studies observed different genetic materials under different experimental conditions.

The regression line for grain yield was of unit slope and intercepted the Wr-axis below the origin, indicating over-dominance for this trait (Fig. 10). Both graphic and genetic component analyses indicated the over-dominance type of gene action, as the $(H_1/D)^{1/2}$ ratio was greater than unity and $D < H_1$. The distribution of array points along the regression line indicated that inbred line K19 was close to the origin and had the maximum number of dominant genes, whereas inbred line K1264.1 was farthest from the origin and carried the maximum number of recessive alleles. These findings confirm reports by

Wattoo *et al.* (2009), Secanski *et al.* (2004), Rezaei and Roohi (2004), Betran *et al.* (2003), Saleem *et al.* (2002) and Saeed *et al.* (2000) for grain yield.

Genetic components of variance, broad- and narrow-sense heritability, and graphic analysis revealed that days from silking to physiological maturity, days from anthesis to physiological maturity, plant height, kernel depth, number of rows per ear and grain yield were controlled by over-dominance gene actions. The most appropriate strategy for the exploitation of these gene effects in maize breeding programs is to develop hybrids and evaluate these traits in hybrid combinations.

In contrast, ear leaf area and ear length were governed by additive gene effects; therefore, improvement of these traits through selection is highly feasible (Jagtap, 1986). The importance of both additive and non-additive gene effects for days from emergence to physiological maturity and number of kernels per row suggested that reciprocal recurrent selection would be an effective approach for improving these traits (Popi and Kannenberg, 2001).

REFERENCES

Akbar, M., M. Saleem, F. M. Azhar, M. Y. Ashraf, and R. Ahmad. 2008. Combining ability analysis in maize under normal and high temperature conditions. J. Agric. Res. 46(1): 261-277.

Alam, A. K. M. M., S. Ahmed, M. Begum, and M. K. Sultan. 2008. Heterosis and combining ability for grain yield and its contributing characters in maize. Bangladesh J. Agric. Res. 33(3): 375-379.

Ali, G., A. C. Rather, A. Ishfaq, S. A. Dar, S. Wani, and M. N. Khan. 2007. Gene action for grain yield and its attributes in maize (*Zea mays* L.). Int. J. Agric. Sci. 3(2): 278.

Arbelbide, M., and R. Bernardo. 2004. Random mating before selfing in maize BC_1 populations. Crop Sci. 44: 401-404.

Betran, F. J., J. M. Ribaut, D. Beck, and D. Gonzalez de Leon. 2003. Genetic diversity, specific combining ability, and heterosis in tropical maize under stress and non-stress environments. Crop Sci. 43: 797-806.

Bhatnagar, S., F. J. Betrán, and L. W. Rooney. 2004. Combining abilities of quality protein maize inbreds. Crop Sci. 44: 1997-2005.

Choi, K. J., M. S. Chin, K. Y. Park, H. S. Lee, J. H. Seo, and D. Y. Song. 1995. Heterosis and heritability of stay-green characters. Maize Genetics Cooperation Newsletter 69: 122-123.

Debnath, S. C., K. R. Sarkar, and D. Singh. 1988. Combining ability estimates in maize (*Zea mays* L.). Annals of Agric. 9: 37-42.

Debnath, S. C., K. K. Sarker, and D. Singh. 1989. Combining ability estimates in maize. J. Agri. Res. 9: 37-42.

Duvick, D. N. 1992. Genetic contributions to advances in yield of U.S. maize. Maydica 37: 69–79.

Fehr, W. R. 1991. Principles of cultivar development. Theory and techniques. MacMillan Publishing Co. 536 pp.

Fry, J. D. 2004. Estimation of genetic variances and co-variances by restricted maximum likelihood using

PROC MIXED. Pp. 7–39. *In* A. R. Saxton (ed.). Genetic analysis of complex traits using SAS. Books by Users Press, SAS Inst., Cary, NC.

Gamble, E. E. 1962. Gene effects in corn (*Zea Mays* L.). II. Relative importance of gene effects for plant height and certain attributes of yield. Can. J. Plant Sci. 42: 349-358.

Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing system. Aust. J. Biol. Sci. 9: 463-493.

Hayman, B. I. 1954a. The analysis of variance of diallel tables. Biometrics 10: 235-244.

Hayman, B. I. 1954b. The theory and analysis of diallel crosses. Genetics 39: 789-809.

Hussain, I. 2009. Genetics of drought tolerance in maize (*Zea mays* L.). Ph.D. thesis. University of Agriculture, Faisalabad, Pakistan. 201 pp.

Irshad-Ul-Haq, M., S. U. Ajmal, M. Munir, and M. Gulfaraz. 2010. Gene action studies of different quantitative traits in maize. Pak. J. Bot. 42(2): 1021-1030.

Ismail, A. A. 1996. Gene action and combining ability for flowering and yield in maize under two different sowing dates. Assiut J. Agri. Sci. 27: 91-105.

Jagtap, D. R. 1986. Combining ability in upland cotton**.** Indian J. Agric. Sci. 12: 833-840.

Jinks, J. L. 1954. The analysis of continuous variation in a diallel cross of *Nicotiana rustica*. Genet. 39: 767-788.

Jinks, J. L., and B. I. Hayman. 1953. A survey of the genetical basis of heterosis in a variety of diallel crosses. Heredity 9: 223-238.

Jones, K. R., and K. J. Frey. 1960. Heritability percentages and degrees of dominance for quantitative characters in oats. State J. Sci. 35: 49-58.

Kannenberg, L. W., and D. E. Falk. 1995. Models for activation of plant genetic resources for crop breeding programs. Can. J. Plant Sci. 75: 45-53.

Kumar, A., M. G. Gangashettiand, and A. Kumar. 1998. Gene effects in some metric traits of maize. Annals of Agric. Biol. Res. 3: 139-143.

Kumar, P., and S. C. Gupta. 2003. Genetic analysis in maize (*Zea mays* L.). J. Res. Birsa Agric. University 15(1): 107-110.

Kumar, R., M. Singh, M. S. Narwal, and S. Sharma. 2005. Gene effects for grain yield and its attributes in maize (*Zea mays* L.). National J. Plant Improvement 7(2): 105-107.

Malik, S. I., H. N. Malik, N. M. Minhas, and M. Munir. 2004. General and specific combining ability studies in maize diallel crosses. Int. J. Agri. Biol. 6(5): 856-859.

Muraya, M. M., C. M. Ndirangu, and E. O. Omolo. 2006. Heterosis and combining ability in diallel crosses involving maize (*Zea mays* L.) S$_1$ lines. Aust. J. Expt. Agric. 46(3): 387-394.

Ojo, G. O. S., D. K. Adedzwa, and L. L. Bello. 2007. Combining ability estimates and heterosis for grain yield and yield components in maize (*Zea mays* L.). J. Sustainable Development in Agric. Environment 3: 49-57.

Ortiz, R., J. H. Crouch, and M. Iwanaga. 2006. Agriculture and energy in developing countries: bio-energy and agricultural research for development. Available at: http://www.ifpri.org/pubs/catalog.htm#focus.

Ottaviano, E., and A. Camussi. 1981. Phenotypic and genetic relationships between yield components in maize. Euphytica 30(3): 601-609.

Perez-Velasquez, J. C., H. Ceballos, S. Pandey, and C. D.

Amaris. 1996. A diallel cross analysis of some quantitative characters in maize. Crop Sci. 36: 572-578.

Popi, J., and L. Kannenberg. 2001. Response to selection over 15 years of HOPE maize breeding system. Maydica 46: 93-103.

Prakash, S., and D. K. Ganguli. 2004. Combining ability for various yield component characters in maize (*Zea mays* L.). J. Res. Birsa Agric. University 16(1): 55-60.

Rezaei, A. H., and V. Roohi. 2004. Estimates of genetic parameters in corn (*Zea mays* L.) based on diallel crossing system. New directions for a diverse planet: Proceedings of the 4th International Crop Science Congress Brisbane, Australia.

Saeed, M. T., and M. Saleem. 2000. Estimates of gene effects for some important quantitative plant traits in maize diallel crosses. Pak. J. Bio. Sci. 3(7): 1138-1140.

Saeed, M. T., M. Saleem, and M. Afzal. 2000. Genetic analysis of yield and its components in maize diallel crosses (*Zea mays* L.). Int. J. Agri. Biol. 2(4): 376-378.

Saleem, M., K. Shahzad, M. Javid, and A. Ahmed. 2002. Genetic analysis for various quantitative traits in maize (*Zea mays* L.) inbred lines. Int. J. Agric. Biol. 4(3): 379-382.

Secanski, M., T. Zivanovic, G. Todorovic, and G. Surlan-Momirovic. 2004. Components of genetic variability and heritability of grain yield of silage maize. Genetika 36(2): 121-131.

Singh, R. K., and B. D. Chaudhary. 1985. Biometrical methods in quantitative genetic analysis. Kalyani Publisher. New Delhi. India. 318 pp.

Singh, P. K., and A. K. Roy. 2007. Diallel analysis of inbred lines in maize (*Zea mays* L.). Int. J. Agric. Sci. 3(1): 213-216.

Sofi, P. A. 2007. Genetic analysis of tassel and ear characters in maize (*Zea mays* L.) using triple test cross. Asian J. Plant Sci. 6: 881-883.

Srdić, J., Z. Pajić, and S. S. Mladenović-Drinić. 2007. Inheritance of maize grain yield components. Maydica 52(3): 261-264.

Vacaro, E., J. F. B. Neto, D. G. Pegoraro, C. N. Nuss, and L. D. H. Conceicao. 2002. Combining ability of twelve maize populations. Pesq. Agropec. Bras. 37: 67-72.

Vidal-Martinez, V. A., M. Clegg, B. Johnson, and R. Valdivia-Bernal. 2001. Phenotypic and genotypic relationships between pollen and grain yield components in maize. Agrociencia 35: 503-511.

Wang, G., S. K. Manjit, and O. Moreno. 1999. Genetic analyses of grain-filling rate and duration in maize. Field Crops Res. 61(3): 211-222.

Wattoo, F. M., M. Saleem, M. Ahsan, M. Sajjad, and W. Ali. 2009. Genetic analysis for yield potential and quality traits in maize (*Zea mays* L.). Am. Euras. J. Agric. and Environmental Sci. 6(6): 723-729.

Xu, J. Y., and H. Crouch. 2008. Genomics of tropical maize, a stable food and feed across the world. Pp. 333-370. *In* Genomics of Tropical Crop Plants, P. H. Moore and R. Ming (eds.). Springer, London, UK.

Zare, M., R. Choukan, E. Majidi Heravan, and M. R. Bihamta. 2008. Generation mean analysis for grain yield and its related traits in maize (*Zea mays*). Seed and Plant. 24(1): 63-81. (In Persian.)