Generation Mean Analysis to Estimate Genetic Parameters for Different Traits in Two Crosses of Corn Inbred Lines at Three Planting Densities

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ABSTRACT

The choice of an efficient breeding procedure depends to a large extent on knowledge of the genetic system controlling the character to be selected. The objective of this study was to determine genetic parameters for yield and other traits including some of the yield components under three planting densities, using analysis of generation means (P_1, P_2, F_1, F_2, BC_1 and BC_2) derived from crosses of B73 with Mo17 and K74/1 inbred lines of corn. Analysis of variance reinforced the hypothesis that interaction of plant density on generation means depends on evaluating genotypes and the kind of trait. Generation mean analysis suggested that both additive and dominance effects were important for most of the traits evaluated in this study, but dominance had a more pronounced effect. Epistasis affected the expression of nine traits in both crosses at three planting densities. Expression of epistasis and genetic parameters differed in the two crosses and were influenced by plant density. Plant densities interacted more strongly with epistasis gene action than with additive or dominance gene action in both crosses.

Keywords: Additive, Dominance, Epistasis, Gene action, Heritability, Maize, Variance components.

INTRODUCTION

The choice of an efficient breeding program depends to a large extent on knowledge of the type of gene action involved in the expression of the character. Whereas dominance gene action would favor the production of hybrids, additive gene action indicates that standard selection procedures would be effective in bringing about advantageous changes in character (Edwards *et al.*, 1975). Information on genetic variances, levels of dominance, and the importance of genetic effects have contributed to a better understanding of the gene action involved in the expression of heterosis (Wolf and Hallauer, 1997). Maize breeders have successfully exploited heterosis for grain yield by crossing inbred lines to develop desirable

hybrids. However, the nature of gene action involved in the expression of heterosis for the grain yield of elite maize hybrids remains unresolved.

The frequent occurrence of a nonallelic interaction in quantitative traits reveals their existence in the inheritance of quantitative characters. Much of the information on epistasis stems from studies in cross-pollinated crops probably because of the major role of heterosis in these crops and the possible relationship between hybrid vigor and epistasis (Ketata *et al.*, 1976). The importance of epistasis for gene controlling grain yield in the breeding population of maize is not well understood. Most statistical models for estimating gene effects assume epistasis to be of limited importance. This assumption has

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been used in the estimation of heritability and the number of genes affecting quantitative traits. Theoretical comparisons have shown that estimates of genetic parameters may be biased greatly if epistasis is present, and expectations based on such parameters may lead to erroneous expectations of response to selection (Eta-Ndu and Openshaw, 1999; Templeton, 2000).

The importance of nonallelic interaction on the expression of several agronomic traits has been reported in a number of instances. Wolf and Hallauer (1977) reported that an epistatic effect could contribute to the expression of heterosis for specific hybrids. They showed that additive by additive effects were not significant for grain yield whereas additive by dominance and dominance by dominance effects were significant. In the study of Darrah and Hallauer (1972), the additive by additive and dominance by dominance effects for yield components (ear length, ear diameter and number of kernel per row) were greater than plant height and ear height. Hallauer (1990) reported that since inbreeding is conducted simultaneously with hybrid evaluations, favorable epistatic gene combinations can ultimately be fixed in the inbred lines. Also, since maize breeders use related inbreds or at least inbreds from the same heterotic pattern as the parents of source populations, they would tend to maintain favorable epistatic gene combinations, especially linked epistatic combinations. Epistasis could also explain why it has been difficult to develop improved recoveries from some maize inbreds (Melchinger *et al.*, 1988; Lamkey *et al.*, 1995).

A few studies have indicated that epistasis was not a significant component of genetic variability in the maize population (Silva and Hallauer, 1975; Ketata *et al.*, 1976; Hinze and Lamkey, 2003). Other studies, however, have shown that epistatic effects are important for the specific combination of inbred lines (Darrah and Hallauer, 1972;

Wolf and Hallauer, 1977; Moreno-Gonzalez and Dudley, 1981; Lamkey *et al.*, 1995; Chen *et al.*, 1996; Hinze and Lamkey, 2003). Hallauer and Miranda (1988) concluded that epistasis variance is not an important contributor to the genetic variance for yield in maize. It seems that epistasis for complex traits, such as yield, must exist, but realistic estimates of additive by additive epistasis have not been obtainable. Hence, either the genetic models used are inadequate or epistasis variance is small relative to the total genetic variance of the maize population (Hallauer and Miranda, 1988). Biometric methods that use mean comparison rather than variance component estimation (for example, generation mean analysis and triple test cross) have regularly indicated that epistatic effects are important for grain yield in maize (Eta-Ndu and Openshow, 1999; Lamkey *et al.*, 1995; Moll and Stuber, 1971; Wolf and Hallauer, 1977).

Genotype $\times$ environment interaction is a major factor in the genetic study of quantitative traits because it complicates the interpretation of genetic experiments and makes predictions difficult. The bias caused by these interactions in the estimates of the various genetic parameters is of unknown magnitude and direction and may not be the same for each parameter (Gamble, 1962a, c). Planting densities, which can be considered as different environments, could affect interrelationships among agronomic traits measured on generations of the same or different crosses, and bias the estimates of genetic parameters (Adetimirin *et al.*, 2001; Hallauer and Miranda, 1988)

The objectives of this study were: (1) To estimate and compare genetic parameters for different traits using P_1, P_2, F_1, F_2, BC_1 and BC_2 generations of crosses between B73 and Mo17, and between B73 and K74/1 inbred lines, evaluated over three planting densities (environments), and (2) to study the effect of different environments (planting densities) on the estimates of genetic parameters.

MATERIALS AND METHODS

Genetic Materials and Experimental Procedure

Generation means of two crosses, i.e. B73×Mo17 and B73×K74/1 were analyzed to estimate the genetic parameters for different traits in three plant densities. Inbred B73 was a selection from Iowa Stiff Stalk Synthetic (BSSS) after five cycles of half-sib recurrent selection for grain yield (Russell, 1972). Inbred Mo17 was derived by selection from the single cross of inbred lines CI187-2 and C103 (Zuber, 1973). Inbred K74/1 is an Iranian Inbred line derived from introduced germplasms from Yugoslavia and is widely used as parent of single crosses grown in Iran. The six generations $(P_1, P_2, F_1, F_2, BC_1$ and $BC_2)$ of each cross were evaluated in a separate randomized complete block design with 3 replications at 3 plant densities (70000, 105000, 140000 plant ha^{-1}) at the Experimental Field of Seed and Plant Improvement Institute at Karaj, Iran, in 2001. The site is at 35°, 50′ N latitude; 50°, 58′ E longitude; and 1300 m elevation, with maximum and minimum temperatures of 38°C and 25°C during the growing season. The experimental units contained four rows for non-segregating generations $(P_1, P_2$ and $F_1)$, and six rows for F_2, BC_1 and BC_2 generations. Each row was 4 m long and 0.75 m wide. The planting date was May, 11, 2001. Fertilizer treatments were 150 kg ha^{-1} of N applied prior to planting, plus and additional of 100 kg ha^{-1} of N topdressing after ear emergence. In each replication, observations were recorded on 10 random plants of P_1, P_2 and F_1 and on 50 plants of F_2, BC_1, and BC_2. Nine traits including anthesis (days from planting to anthesis), plant and ear heights (from soil surface to the collar of the flag leaf and primary ear node in cm, respectively), kernel rows, kernel per row, kernel depth (difference between ear and cob diameters in mm), grain yield per plant (14% moisture in g), 100-seed weight(g), and cob dry weight(g), were measured.

Data Analysis

Data were subjected to combined analysis of variance over planting densities for each cross using a general linear model and generation and generation × plant density sum of squares were partitioned to different orthogonal contrasts (Tables 1 and 2). A quantitative generation mean analysis was performed separately for each plant density. The trait means for each generation, across replication within each density, were obtained and different 2, 3, 4, and 5 parameter models were fitted by weighted least square analysis or joint scaling test (Mather and Jinks, 1982). Mather and Jinks (1982) model describes the phenotype in terms of the mid-parental values [m], additive effects [d], dominance effects [h], and additive by additive [i], additive by dominance [j], and dominance by dominance [l] epistatic interaction effects. (Mather and Jinks, 1982; Shonnard and Gepts, 1994). The generation means and their expectations were weighted by using the reciprocal of the variance of generation means (1/ V_X) (Warnock *et al.*, 1998; Mansure *et al.*, 1993; Mather and Jinks, 1982; Shonnard and Gepts, 1994). The goodness of fit was tested by a chi-square with 4, 3, 2 and 1 degrees of freedom; i.e. the number of available generations minus the number of estimated parameters (Cukadar-Olmedo and Miller, 1997). The significance of parameters was tested with related standard errors at 1% and 5% probability levels.

Broad-sense (h_b^2) and narrow-sense (h_n^2) heritabilities were estimated using the variance component method (Wright, 1968) and variances of F_2 and back cross generations (Warner, 1952), respectively, as:

$$h_b^2 = \{V_{F2} - [(V_{P1} + V_{P2} + 2V_{F1})/4]\}/V_{F2}$$
$$h_n^2 = [V_{F2} - (V_{BC1} + V_{BC2})/2]/V_{F2}$$

Response to selection was estimated with 5% selection intensity (i) (Selection differential, k=2.06) as:

$$R = i \times h_n^2 \times \sqrt{V_{F2}}$$

Heterosis was calculated as F_1 mean deviation from mid-parental performances. Variance components (additive, dominance and environment) were estimated as described by Mather and Jinks (1982) using the following equations;

$D = 4\ V_{F2} - 2\ (V_{BC1} + V_{BC2})$

$H = 4\ (V_{B1} + V_{B2} - V_{F2} - V_E)$

$E_W = 0.25\ (V_{P1} + V_{P2} + 2V_{F1})$

In these formulae, V stands for variance and the subscripts refer to generations. E_W, D, and H are variances of environment, additive and dominance effects, respectively.

RESULTS

The combined analysis of variance over plant densities indicated highly significant differences (P < 0.01) among plant densities for anthesis, kernel per row, seed yield per plant and cob weight in both crosses (Tables 1 and 2). Also differences among plant densities for plant height, kernel rows and 100-seed weight were significant (P< 0.05) in cross B73×Mo17 but not significant in cross B73×K74/1. Plant density differences for ear height and kernel depth were non-significant in both crosses. There were significant differences among generations (P < 0.01) for all traits in both crosses.

Significant generation × plant density interaction effects were found for anthesis, plant height, kernel per row, seed yield per plant, cob weight and ear height in cross B73×Mo17 (Table 1). None of the characters showed significant generation × plant density interaction in cross B73×K74/1, except anthesis (Table 2). Therefore, differences between parents (P_1 *vs* P_2) that reveal additive effects were significant for all traits except ear height and kernel depth in cross B73×Mo17 and anthesis and 100-seed weight in cross B73×K74/1. The interaction effects (P_1 *vs* P_2) × plant density were non-significant for all traits in both crosses, except for anthesis in cross B73×K74/1 which resulted in a non-significant P_1 *vs* P_2 mean square for this trait. Heterosis was significant for all traits in both crosses except 100-

seed weight in cross B73×Mo17 and kernel row number in cross B73×K74/1. The interaction effects of heterosis × plant density were non-significant for all traits in both crosses, except kernel per row in cross B73×Mo17. In other words, ranking of the estimates of heterosis was the same at different planting densities. Generally, most of the interaction mean squares involving planting density were significant. Therefore, generation mean analysis was performed separately for each plant density.

The generations' performances for cross B73 × Mo17 and cross B73 × K74/1 at different planting densities are presented in Tables 3 and 4. Traits responded differentially to planting densities. Also some of the characteristics studied showed more variation among generations. For example, grain yield per plant and the number of kernels per row had relatively more variations. With a few exceptions, the trend of decreased performance with increased planting density was consistent for all characteristics in all generations of the two crosses. Mo17 had more grain yield per plant, kernel per rows and 100-seed weight, but B73 was superior with respect to the other traits. K74/1 outperformed B73 with respect to grain yield per plant, kernel per row, kernel rows and cob weight, but performed almost similar to B73 for the other traits at all planting densities, except for plant height.

For cross B73 × Mo17 at all planting densities, F_1 and F_2 mean performances were greater than the top parents for all traits except kernel rows, 100-grain weight and anthesis. Both F_1 and F_2 means were close to superior parents for kernel rows and to inferior parents for 100-seed weight. For anthesis, F_1 mean was lower than the earlier maturing parent but F_2 mean was greater than F_1. All the generation means for 100-seed weight were close to the inferior parent. Both BC generation means were greater than the superior parent for all the traits, except the BC_1 grain yield per plant and kernel per row means which were close to superior parent.

Table 1. Analysis of variance for nine traits of P_1, P_2, F_1, F_2, BC_1 and BC_2 generations derived from cross B73×Mo17.

Source	df	Grain yield per plant	Kernel per row	Kernel row number	100-Seed weight	Kernel depth	Cob weight	Plant height	Ear height	Anthesis
Plant density	2	73614.50 **	1270.63 **	17.96 *	707.68 *	0.02	2216.70 **	12200.10 *	2692.70	46.88 **
Rep/Plant density	6	1782.67	39.63	2.95	104.76	0.02	23.07	1548.62	623.48	2.43
Generations	5	49489.80 **	3297.43 **	490.00 **	1048.30 **	0.51 **	481.24 **	30497.68 **	23893.58 **	202.26 **
Homogeneous (Hom.)	2	72584.20 **	3940.35 **	712.63 **	867.97 **	0.61 **	691.92 **	24908.45 **	21899.05 **	222.80 **
P_1 vs. P_2	1	11903.40 *	1493.57 **	1394.45 **	1369.84 **	0.14	1044.39 **	2776.90 *	76.00	96.80 **
F_1 vs. $(P_1+P_2)/2$	1	133265.00 **	6387.12 **	30.82 **	366.08	1.08 **	339.45 *	47040.00 **	43722.00 **	348.81 **
Heterogeneous (Het.)	2	48342.00 **	4067.82 **	503.51 **	804.56 **	0.44 **	98.10	26917.65 **	12168.70 **	3.04
BC_1 vs. BC_2	1	92320.00 **	7909.14 **	1007.00 **	1600.66 **	0.79 **	73.39	28611.70 **	19534.70 **	2.45
F_2 vs.$(BC_1+BC_2)/2$	1	4365.00	226.49 *	0.02	8.46	0.10	122.81	25223.60 **	4802.70 **	3.63
Hom. vs Het.	1	5596.60	470.81 **	17.69 *	1896.47 **	0.46 **	826.17 **	48836.20 **	51332.40 **	559.59 **
Generations × Plant density	10	14527.30 **	408.64 **	4.16	190.30	0.08	227.91 **	1787.63 **	735.78 *	24.45 **
Hom.× Plant density	4	3920.15	175.76 *	1.58	16.65	0.06	21.48	112.80	86.20	5.12
$(P_1$ vs. $P_2) ×$ Plant density	2	632.25	25.59	2.45	32.71	0.05	0.51	66.35	22.80	2.52
$[F_1$ vs.$(P_1+P_2)/2] ×$ Plant density	2	7208.05	325.93 **	0.71	0.58	0.07	42.45	159.25	149.60	7.72
Het.× Plant density	4	30636.25 **	779.53 **	7.24	413.47 **	0.10	450.03 **	3770.05 **	1716.13 **	52.69 **
$(BC_1$ vs $BC_2) ×$ Plant density	2	58940.00 **	1364.14 **	5.88	671.75 **	0.18 *	715.61 **	6623.10 **	2519.65 **	64.95 **
$[F_2$ vs $(BC_1+BC_2)/2] ×$ Plant density	2	2332.50	194.92 *	8.61	155.20	0.03	184.45	917.00	912.55	40.42 **
(Hom. vs Het.) × Plant density	2	3523.70	132.65	3.14	91.28	0.09	196.55	1172.45	74.25	6.61
Generations×Rep/Plant density	30	2345.03	45.85	3.06	92.47	0.04	73.68	504.67	293.12	3.90

* and ** Significant at P<0.05 and P<0.01 probability levels, respectively.

Table 2. Analysis of variance for nine traits of P_1, P_2, F_1, F_2, BC_1 and BC_2 generations derived from cross B73×K74/1.

Source	df	Grain yield per plant	Kernel per row	Kernel row number	100-Seed weight	Kernel depth	Cob weight	Plant height	Ear height	Anthesis
Plant density	2	71039.00**	1248.22**	58.79	131.35	0.17	3770.14**	382.05	880.00	52.85**
Rep/Plant density	6	2394.17	61.75	18.70	52.02	0.13	88.98	840.53	262.02	4.13
Generations	5	103788.80**	2261.50**	592.29**	788.06**	0.97**	2195.08**	22390.96**	10691.84**	354.09**
Homogeneous (Hom.)	2	204586.00**	4543.87**	579.39**	262.21*	2.09**	2262.95**	47658.40**	23210.75**	583.84**
P_1 vs. P_2	1	151206.00**	2901.64**	1155.20**	169.22	0.55*	4069.94**	6612.70**	2753.40**	0.20
F_1 vs. $(P_1+P_2)/2$	1	257966.00**	6186.09**	3.59	355.20*	3.63**	455.96**	88704.20**	43668.00**	1167.47**
Heterogeneous (Het.)	2	32466.50**	882.24**	813.18**	486.14**	0.25	1541.87**	2523.50*	1867.35**	166.73**
BC_1 vs. BC_2	1	58974.00**	1639.04**	1554.99**	959.90**	0.42*	2747.13**	4558.50**	3477.07**	326.40**
F_2 vs.$(BC_1+BC_2)/2$	1	5959.00	125.43	71.38	12.38	0.08	336.62*	488.54	257.61	7.05
Hom. vs Het.	1	44839.00**	455.32*	176.30**	2443.61**	0.16	3365.76**	11591.00**	3303.00**	269.32**
Generations × Plant density	10	6221.30	146.73	13.04	111.71	0.13	92.15	578.96	443.40	83.78**
Hom.× Plant density	4	4333.75	111.21	14.70	63.95	0.15	55.92	396.90	328.13	58.50**
(P_1 vs. P_2) × Plant density	2	2533.50	72.45	16.47	23.25	0.25	67.37	614.00	329.05	114.20**
[F_1 vs.$(P_1+P_2)/2$] × Plant density	2	6134.00	149.97	12.94	104.65	0.05	44.47	179.75	327.20	2.81
Het.× Plant density	4	6613.75	149.11	4.16	212.14*	0.10	105.57	1018.65	615.15	23.22*
(BC_1 vs BC_2) × Plant density	2	10290.00*	191.88	7.79	374.54**	0.16	118.17	1127.84	1140.43*	28.86*
[F_2 vs $(BC_1+BC_2)/2$] × Plant density	2	2937.00	106.35	0.54	49.75	0.04	92.98	909.45	89.85	17.58
(Hom. vs Het.) × Plant density	2	9211.50	212.98	27.47	6.35	0.17	137.77	63.70	330.45	255.44**
Generations×Rep/Plant density	30	2952.37	92.88	13.69	60.97	0.10	57.82	521.91	297.40	6.61

* and ** Significant at $P<0.05$ and $P<0.01$ probability levels, respectively.

Table 3. Observed mean of P_1, P_2, F_1, F_2 BC_1 and BC_2 generations for nine characters in three plant densities for cross B73×Mo17.

Traits	Plant density	P_1	P_2	F_1	F_2	BC_1	BC_2
Grain yield per plant (g)	D1	82.74± 27.92	103.51± 29.43	157.69± 33.37	124.48± 52.31	104.21± 42.51	146.69± 50.05
	D2	76.83± 28.81	96.02± 25.46	143.13± 31.26	111.30± 47.86	95.53± 42.00	100.69± 45.51
	D3	67.36± 22.92	76.18± 27.55	116.21± 31.19	85.26± 42.23	79.47± 39.32	92.60± 42.30
Kernel per row	D1	19.47± 4.77	25.08± 6.04	36.22± 5.98	29.17± 9.01	24.60± 8.55	33.08± 9.35
	D2	18.23± 5.49	25.37± 5.47	32.77± 6.50	27.88± 9.27	22.28± 8.62	27.47± 9.39
	D3	17.38± 4.43	21.92± 7.33	28.69± 6.18	23.07± 9.04	21.74± 8.18	25.86± 9.01
Kernel row number	D1	17.33± 1.60	11.83± 0.97	15.20± 1.63	15.25± 2.12	16.08± 2.11	13.78± 1.71
	D2	16.80± 1.54	11.60± 1.02	14.80± 1.60	14.87± 2.06	16.04± 1.92	13.79± 1.84
	D3	17.07± 1.55	11.07± 1.14	15.00± 1.55	14.30± 2.02	15.45± 1.91	13.66± 1.86
100-Seed weight (g)	D1	28.96± 2.92	34.94± 3.75	28.85± 4.10	28.03± 5.13	26.42± 4.08	32.13± 4.88
	D2	27.84± 3.22	33.12± 3.73	28.45± 4.12	26.79± 4.59	26.26± 4.40	26.00± 4.10
	D3	26.34± 3.45	30.64± 5.39	26.72± 3.50	25.76± 4.64	23.39± 4.53	25.94± 4.36
Kernel depth (mm)	D1	0.97± 0.15	0.98± 0.14	1.16± 0.08	1.07± 0.24	1.10± 0.20	1.12± 0.20
	D2	1.04± 0.14	0.95± 0.11	1.13± 0.08	1.08± 0.25	1.01± 0.25	1.12± 0.17
	D3	1.03± 0.13	0.94± 0.10	1.06± 0.09	1.04± 0.25	1.04± 0.24	1.09± 0.19
Cob weight (g)	D1	18.29± 4.53	13.29± 3.90	19.26± 4.82	19.41± 7.14	18.39± 6.54	22.28± 7.05
	D2	15.49± 4.34	10.86± 3.76	16.20± 4.59	16.94± 6.93	16.66± 6.62	14.44± 6.60
	D3	14.61± 4.14	9.79± 3.63	15.14± 4.39	14.22± 6.65	12.74± 6.70	12.78± 5.94
Plant height (cm)	D1	158.43± 10.30	152.90± 10.25	186.32± 8.31	183.64± 18.73	166.41± 17.32	181.67± 18.25
	D2	160.00± 10.12	150.37± 6.87	183.50± 8.11	186.35± 15.91	174.12± 16.07	174.66± 14.40
	D3	146.80± 10.81	138.40± 9.62	167.63± 9.51	173.99± 15.48	159.03± 15.72	177.06± 14.43
Ear height (cm)	D1	75.17± 9.10	72.53± 10.30	103.33± 7.21	101.21± 18.44	90.89± 13.74	101.25± 15.69
	D2	76.00± 9.25	74.93± 7.99	102.90± 8.63	104.90± 15.45	97.07± 11.86	100.14± 14.85
	D3	71.30± 9.51	71.10± 6.68	95.27± 9.21	94.72± 14.08	86.89± 12.32	101.41± 13.10
Anthesis	D1	70.60± 0.50	69.60± 0.50	67.40± 0.67	70.63± 3.64	71.67± 4.00	70.61± 3.20
	D2	71.13± 0.69	69.37± 0.65	68.40± 0.56	70.48± 2.66	70.96± 2.70	70.89± 2.47
	D3	71.63± 0.49	70.00± 0.69	69.13± 0.63	72.15± 2.29	71.13± 2.17	71.93± 2.17

Table 4. Observed mean of P_1, P_2, F_1, F_2 BC$_1$ and BC$_2$ generations for nine characters in 3 plant densities for crosses B73×K74/1.

Traits	Plant density	P$_1$	P$_2$	F$_1$	F$_2$	BC$_1$	BC$_2$
Grain yield per plant (g)	D1	76.02 ± 33.20	142.91 ± 32.52	195.00 ± 37.54	116.20 ± 52.31	108.06 ± 50.91	125.39 ± 49.35
	D2	63.15 ± 28.41	122.62 ± 39.64	163.05 ± 36.94	95.67 ± 44.33	104.34 ± 39.03	108.29 ± 44.25
	D3	58.67 ± 20.10	106.20 ± 45.36	143.45 ± 36.00	87.22 ± 41.92	75.78 ± 37.98	103.07 ± 40.27
Kernel per row	D1	16.20 ± 5.55	24.93 ± 4.53	33.07 ± 5.21	25.07 ± 9.03	23.12 ± 8.95	26.35 ± 8.40
	D2	13.80 ± 4.64	22.97 ± 5.66	27.40 ± 5.19	22.36 ± 7.75	23.64 ± 6.95	24.54 ± 7.87
	D3	13.18 ± 3.48	19.37 ± 6.37	25.22 ± 6.13	20.92 ± 7.59	19.48 ± 7.33	23.45 ± 7.21
Kernel row number	D1	16.87 ± 2.08	22.67 ± 2.37	19.80 ± 1.85	18.64 ± 3.11	17.61 ± 2.66	20.53 ± 3.43
	D2	16.80 ± 1.63	22.13 ± 2.34	19.87 ± 1.90	18.43 ± 3.04	17.67 ± 2.68	20.34 ± 3.24
	D3	16.60 ± 1.19	20.67 ± 2.49	18.93 ± 2.10	17.41 ± 3.14	16.73 ± 3.18	19.01 ± 2.90
100-Seed weight (g)	D1	27.28 ± 4.09	25.76 ± 3.35	30.07 ± 2.72	24.89 ± 5.08	25.77 ± 4.59	22.89 ± 4.04
	D2	26.88 ± 3.08	25.92 ± 3.11	29.30 ± 3.32	23.95 ± 4.34	25.35 ± 4.23	23.52 ± 3.74
	D3	27.49 ± 3.01	24.15 ± 2.65	29.06 ± 3.02	22.85 ± 3.96	23.06 ± 3.95	21.57 ± 3.88
Kernel depth (mm)	D1	0.92 ± 0.24	0.91 ± 0.20	1.23 ± 0.08	1.06 ± 0.24	1.04 ± 0.23	1.08 ± 0.23
	D2	0.89 ± 0.15	0.97 ± 0.19	1.17 ± 0.11	1.07 ± 0.23	1.06 ± 0.21	1.06 ± 0.20
	D3	0.82 ± 0.16	1.08 ± 0.13	1.14 ± 0.12	1.02 ± 0.26	0.94 ± 0.22	1.03 ± 0.21
Cob weight (g)	D1	22.07 ± 4.98	33.97 ± 7.92	32.49 ± 6.52	24.45 ± 8.73	23.16 ± 7.82	26.39 ± 8.72
	D2	18.30 ± 4.41	26.13 ± 9.02	24.26 ± 6.17	19.14 ± 8.23	20.10 ± 7.23	22.49 ± 8.51
	D3	17.62 ± 3.57	26.42 ± 8.31	23.77 ± 7.04	17.70 ± 7.51	15.97 ± 6.57	20.82 ± 7.88
Plant height (cm)	D1	159.67 ± 14.04	147.83 ± 8.67	198.13 ± 9.13	165.29 ± 16.49	162.82 ± 13.29	161.37 ± 17.39
	D2	162.47 ± 11.98	150.90 ± 9.79	195.07 ± 10.57	163.21 ± 15.52	160.00 ± 14.72	166.11 ± 15.49
	D3	167.33 ± 9.19	154.37 ± 10.45	193.43 ± 11.12	162.25 ± 14.95	157.35 ± 13.82	166.19 ± 15.47
Ear height (cm)	D1	81.30 ± 9.77	73.53 ± 8.87	111.53 ± 9.66	84.59 ± 12.54	84.51 ± 11.66	84.60 ± 12.67
	D2	84.53 ± 12.03	74.03 ± 7.89	103.93 ± 8.62	86.15 ± 12.32	85.20 ± 10.72	89.02 ± 12.74
	D3	86.57 ± 9.16	81.37 ± 12.93	106.13 ± 8.45	83.55 ± 11.87	81.47 ± 10.22	89.35 ± 12.18
Anthesis	D1	71.47 ± 0.51	74.67 ± 0.96	68.33 ± 0.48	71.04 ± 2.92	71.55 ± 2.32	71.57 ± 3.00
	D2	75.33 ± 0.48	74.33 ± 0.48	70.33 ± 0.48	72.06 ± 2.70	72.69 ± 2.95	71.09 ± 1.84
	D3	76.33 ± 0.48	74.33 ± 0.48	71.33 ± 0.48	72.75 ± 2.60	72.95 ± 2.21	70.93 ± 2.23

For cross B73×K74/1, the F_1 means for all the traits at all planting densities were greater than the superior parent with the exception of kernel rows, cob weight and anthesis. For anthesis all the generation means were lower than or close to the earlier maturing parent. For kernel rows, cob weight, grain yield per plant, and plant height all the generation means (except F_1 for two last traits) were between parental means. For kernel depth, all the generation means exceeded the superior parent means. For ear height and kernel per row F_2, BC_1 and BC_2 means were close to the superior parent.

Different 3 to 6 parameter models showed the best fits to generation means of different traits, planting density, and cross combinations (Tables 5 and 6). In cross B73×Mo17, additive effects were significant for all traits in all plant densities, except ear height in all plant densities, and kernel depth in low plant density. Non-significancy in those cases may be ascribed to large error variance (Edwards *et al.*, 1975). In cross B73×K74/1, except for ear height in high plant density, kernel depth in low and intermediate plant densities, and 100-seed weight in low plant density, the other additive effects were significant. As is shown in Tables 3 and 4, some of the additive effects were negative. The negative or positive signs for additive effects depend on which parent is chosen as P_1 (Cukadar-Olmedo and Miller, 1997; Edwards *et al.*, 1975). The additive effects for grain yield per plant were much greater in cross B73×K74/1 than cross B73×Mo17, but for the other traits were almost of the same magnitude.

Dominance effects were positive and significant in cross B73×Mo17 for all traits at all planting densities, except for anthesis in high planting density, plant height in low and high planting densities, ear height and 100-seed weight at low planting density. Also, in this cross, negative and significant dominance effects were estimated for plant height and kernel per row at an intermediate planting density, grain yield per plant, 100-seed weight in intermediate and high planting densities. In cross B73×K74/1, domi-

nance effects were significant for all traits at all planting densities, except ear height at low and intermediate planting densities and kernel depth at high planting density. Also in this cross, dominance effects were significant and negative for anthesis, plant height and 100-seed weight at all planting densities, grain yield per plant and cob weight at low and high planting densities, and ear height at high planting density.

As it is shown in Tables 5 and 6, different types of epistasis interaction effects were found for different trait, cross and planting density combinations. With the exception of anthesis for B73×Mo17 at high planting density, all the other signs of [h] and [l] type of epistasis were opposite, indicating duplicate non-allelic gene interactions. For plant height at all planting densities of cross B73×Mo17 and anthesis at high planting densities of both crosses, a six parameter model had the best fit to the data. This finding suggested that more generations are needed for a more exact estimate of genetic parameters for plant height.

The estimates of additive, dominance, and environment components of variance, broad-sense and narrow-sense heritabilities, genetic gain from selection and heterosis for different traits in different planting densities are presented in Table 7. By increase planting density, in cross B73×Mo17, for grain yield per plant, 100-seed weight and ear height, and in cross B73×K74/1 for 100-seed weight, the additive variance was decreased but the dominance variance was increased for grain yield per plant, 100-seed weight, and ear height, causing lower broad and narrow sense heritability estimates and also response to selection. Likewise the average degree of dominance was decreased by the increase of plant density. In cross B73× Mo17 the additive variances for anthesis and kernel rows were increased in higher planting densities, but the dominance variances were decreased. The same results were observed for anthesis, ear height and kernel depth in cross B73×K74/1. In cross B73× K74/1 both additive and dominance

Table 5. Estimates of gene effects with standard errors and χ^2 values of the fitted models for nine traits in three plant densities for cross B73×Mo1.

Traits	Plant density	m	d	h	i	j	l	χ^2
Grain yield per plant	D1	93.04 ± 3.33 **	-10.38 ± 3.70 **	64.42 ± 6.57 **	-	-64.06 ± 12.96 **	-	0.04
	D2	138.90 ± 18.94 **	-8.15 ± 2.88 **	-114.63 ± 45.16 *	-52.30 ± 18.60 **	-	118.85 ± 28.85 **	0.52
	D3	69.16 ± 2.95 **	-6.95 ± 2.69 **	-37.43 ± 5.89 **	-	-	-	7.43
Kernel per row	D1	22.15 ± 0.63 **	-2.78 ± 0.70 **	13.77 ± 1.22 **	-	-11.46 ± 2.49 **	-	0.28
	D2	34.03 ± 3.74 **	-4.08 ± 0.59 **	-23.32 ± 9.02 **	-12.23 ± 3.67 **	-	22.06 ± 5.83 **	1.67
	D3	19.62 ± 0.66 **	-2.86 ± 0.61 **	8.26 ± 1.27 **	-	-	-	3.75
Kernel row number	D1	15.18 ± 0.11 **	2.58 ± 0.14 **	-	-0.69 ± 0.21 **	-	-	2.97
	D2	15.01 ± 0.11 **	2.48 ± 0.13 **	-	-0.79 ± 0.21 **	-	-	3.94
	D3	14.04 ± 0.16 **	2.99 ± 0.17 **	0.90 ± 0.31 **	-	-2.41 ± 0.56 **	-	1.77
100-Seed weight	D1	27.22 ± 1.12 **	-2.99 ± 0.43 **	1.68 ± 1.70 **	4.74 ± 1.20 **	-5.42 ± 1.34 **	12.56 ± 1.94 **	0.03
	D2	30.48 ± 0.45 **	-2.64 ± 0.45 **	-14.59 ± 1.75 **	-	5.87 ± 1.33 **	16.29 ± 3.07 **	2.15
	D3	32.95 ± 1.92 **	-2.38 ± 0.39 **	-22.52 ± 4.69 *	-4.37 ± 1.83	-	-	0.27
Kernel depth	D1	0.98 ± 0.02 **	-0.01 ± 0.02 ns	0.32 ± 0.07 **	-	-	-0.14 ± 0.06 *	4.35
	D2	0.10 ± 0.01 **	0.04 ± 0.02 **	0.14 ± 0.02 **	-	-0.31 ± 0.06 **	-	0.73
	D3	0.10 ± 0.01 **	0.05 ± 0.01 **	0.08 ± 0.02 **	-	-0.22 ± 0.06 **	-	5.60
Cob weight	D1	15.79 ± 0.55 **	2.50 ± 0.55 **	13.56 ± 2.27 **	-	-12.70 ± 1.91 **	-10.09 ± 2.45 **	1.74
	D2	16.55 ± 0.35 **	2.28 ± 0.43 **	-	-3.45 ± 0.68 **	-	-	0.81
	D3	12.02 ± 0.45 **	2.39 ± 0.50 **	2.66 ± 0.88 **	-	-4.58 ± 1.77 **	-	5.60
Plant height	D1	194.07 ± 7.49 **	2.77 ± 1.33 *	-33.96 ± 17.88 *	-38.41 ± 7.37 **	-36.06 ± 4.89 **	26.21 ± 11.01 *	0.00
	D2	203.02 ± 6.38 **	4.82 ± 1.12 **	-47.15 ± 15.27 **	-47.83 ± 6.28 **	-10.72 ± 4.17 **	27.63 ± 9.51 **	0.00
	D3	166.39 ± 6.28 **	4.20 ± 1.32 **	29.16 ± 15.17	-23.79 ± 6.14 **	-44.45 ± 4.37 **	-27.92 ± 9.65 **	0.00
Ear height	D1	100.51 ± 2.93 **	1.28 ± 1.25	3.16 ± 3.83	-26.36 ± 3.32 **	-22.99 ± 4.21 **	-	0.91
	D2	104.98 ± 0.73 **	-0.55 ± 0.90	-	-29.31 ± 1.44 **	-	-	6.24
	D3	71.20 ± 1.06 **	0.10 ± 1.06	68.39 ± 4.37 **	-	-29.28 ± 3.62 **	-44.32 ± 4.69 **	0.18
Anthesis	D1	70.10 ± 0.64 **	0.51 ± 0.06 **	6.05 ± 0.71 **	-	-	-8.75 ± 0.73 **	3.25
	D2	70.25 ± 0.09 **	0.88 ± 0.09 **	3.98 ± 0.57 **	-	-1.68 ± 0.62 **	-5.83 ± 0.56 **	2.86
	D3	73.31 ± 0.90 **	0.82 ± 0.08 **	-0.45 ± 2.13	-2.49 ± 0.90 **	-3.25 ± 0.52 **	-3.73 ± 1.28 **	0.00

* and **: Significant at P<0.05 and P<0.01 probability levels, respectively.

Table 6. Estimates of gene effects with standard errors and χ^2 values of the fitted models for nine traits in three plant densities for cross B73×K74/1.

Traits	Plant density	m	d	h	I	j	l	χ^2
Grain yield per plant	D1	109.58 ± 4.24 **	-27.82 ± 3.42 **	-57.96 ± 17.34 **	-	-	143.37 ± 18.75 **	5.04
	D2	27.58 ± 9.88 **	-29.07 ± 4.43 **	130.71 ± 15.08 **	63.24 ± 10.81 **	49.04 ± 13.01 **	-	2.30
	D3	83.60 ± 3.99 **	-25.49 ± 3.20 **	-39.35 ± 15.48 *	-	-	99.21 ± 17.06 **	0.58
Kernel per row	D1	16.22 ± 1.69 **	-4.04 ± 0.55 **	16.24 ± 2.40 **	4.14 ± 1.85 *	-	-	4.24
	D2	18.70 ± 0.58 **	-4.65 ± 0.67 **	9.34 ± 1.11 **	7.84 ± 2.16 **	-	-	6.01
	D3	16.63 ± 0.56 **	-3.50 ± 0.51 **	9.14 ± 1.14 **	-	-	-	1.62
Kernel row number	D1	17.39 ± 0.59 **	-2.92 ± 0.22 **	2.34 ± 0.84 **	2.33 ± 0.67 **	-	-	0.36
	D2	16.97 ± 0.59 **	-2.67 ± 0.21 **	2.87 ± 0.85 **	2.48 ± 0.65 **	-	-	0.04
	D3	15.77 ± 0.63 **	-2.09 ± 0.20 **	3.02 ± 0.92 **	2.86 ± 0.68 **	-	-	1.23
100-Seed weight	D1	26.52 ± 0.48 **	0.76 ± 0.48 ns	-11.71 ± 1.76 **	-	4.32 ± 1.39 **	15.26 ± 1.63 **	1.33
	D2	26.39 ± 0.40 **	1.05 ± 0.30 **	-11.45 ± 1.55 **	-	-	14.36 ± 1.64 **	5.98
	D3	25.81 ± 0.37 **	1.60 ± 0.28 **	-16.52 ± 1.43 **	-	-	19.78 ± 1.52 **	1.95
Kernel depth	D1	0.90 ± 0.02 **	-0.02 ± 0.021 ns	0.33 ± 0.03 **	-	-	-	1.95
	D2	0.94 ± 0.02 **	-0.02 ± 0.02 ns	0.24 ± 0.03 **	-	-	-	3.27
	D3	0.95 ± 0.02 **	-0.11 ± 0.02 **	-0.04 ± 0.07 ns	-	-	0.22 ± 0.07 **	4.10
Cob weight	D1	27.49 ± 0.82 **	-4.73 ± 0.64 **	-16.04 ± 3.13 **	-	-	21.04 ± 3.28 **	0.15
	D2	14.11 ± 1.74 **	-3.17 ± 0.65 **	10.36 ± 2.61 **	7.73 ± 1.94 **	-	-	1.58
	D3	22.15 ± 0.72 **	-4.59 ± 0.59 **	-17.57 ± 2.81 **	-	-	19.19 ± 3.22 **	0.97
Plant height	D1	167.08 ± 6.63 **	4.06 ± 1.15 **	-38.19 ± 15.92 *	-14.16 ± 6.43 *	-	69.24 ± 10.00 **	3.65
	D2	156.68 ± 1.41 **	5.78 ± 1.41 **	-12.70 ± 5.47 *	-	-23.81 ± 4.49 **	51.09 ± 5.58 **	0.01
	D3	160.85 ± 1.27 **	6.48 ± 1.27 **	-28.27 ± 5.14 **	-	-30.72 ± 4.23 **	60.85 ± 5.54 **	0.10
Ear height	D1	77.42 ± 1.21 **	3.88 ± 1.21 **	-5.52 ± 4.64 ns	-	-7.94 ± 3.70 *	39.64 ± 4.86 **	0.00
	D2	79.28 ± 1.31 **	5.25 ± 1.31 **	5.46 ± 4.80 ns	-	-17.94 ± 3.77 **	19.19 ± 4.68 **	0.62
	D3	83.97 ± 1.45 **	2.60 ± 1.45 ns	-18.69 ± 5.09 **	-	-20.57 ± 3.88 **	40.86 ± 4.75 **	2.54
Anthesis	D1	73.07 ± 0.10 **	-1.60 ± 0.10 **	-1.91 ± 0.61 **	-	3.33 ± 0.65 **	-2.82 ± 0.58 **	3.35
	D2	74.83 ± 0.06 **	0.50 ± 0.06 **	-7.08 ± 0.52 **	-	2.30 ± 0.57 **	2.58 ± 0.52 **	0.42
	D3	78.57 ± 0.99 **	1.00 ± 0.06 **	-16.07 ± 2.30 **	-3.24 ± 0.99 **	2.04 ± 0.53 **	8.83 ± 1.35 **	0.00

* and ** Significant at P<0.05 and P<0.01 probability levels, respectively.

Table 7. Estimates of broad-sense (h^2b) and narrow-sense heritabilities (h^2n), genetic advance(GA), environmental(Ew), additive(D) and dominance(H) genetic variances, and heterosis(Het.), for cross(I) B73×Mo17 and cross (II) B73×K74/l.

Traits	Plant density	h^2b I	h^2b II	h^2n I	h^2n II	R I	R II	Ew I	Ew II	D I	D II	H I	H II	Het. I	Het. II
Grain yield per plant	D1	0.65	0.55	0.42	0.16	36.70	15.12	968.22	1244.43	2319.76	892.48	2431.97	4183.07	0.69	0.78
	D2	0.63	0.35	0.33	0.23	28.82	21.84	858.05	1277.01	1490.45	899.36	2747.67	955.23	0.66	0.76
	D3	0.55	0.28	0.13	0.26	13.27	25.37	807.43	1263.41	464.00	900.60	2976.18	175.08	0.62	0.74
Kernel per row	D1	0.60	0.68	0.02	0.15	1.52	11.33	32.65	26.42	3.87	24.90	186.44	170.74	0.63	0.61
	D2	0.58	0.55	0.11	0.16	7.65	11.62	36.13	26.85	19.20	19.55	160.97	93.57	0.50	0.49
	D3	0.54	0.45	0.19	0.16	15.03	12.28	37.44	31.95	30.43	18.94	116.18	64.77	0.46	0.55
Kernel row number	D1	0.51	0.57	0.36	0.06	10.27	1.91	2.20	4.19	3.22	1.07	2.70	19.88	0.04	0.00
	D2	0.50	0.58	0.34	0.09	9.83	3.12	2.12	3.85	2.93	1.70	2.68	18.28	0.04	0.02
	D3	0.48	0.58	0.27	0.13	7.75	4.68	2.14	4.11	2.18	2.49	3.47	18.12	0.07	0.02
100-Seed weight	D1	0.47	0.59	0.46	0.55	17.34	23.04	14.05	10.70	24.19	28.27	0.55	3.81	-0.10	0.13
	D2	0.31	0.45	0.29	0.30	10.12	11.30	14.54	10.30	12.09	11.39	2.11	11.22	-0.07	0.11
	D3	0.24	0.45	0.16	0.04	6.06	1.46	16.37	8.58	7.03	1.28	6.65	25.72	-0.06	0.13
Kernel depth	D1	0.75	0.55	0.58	0.25	26.59	11.76	0.01	0.03	0.07	0.03	0.04	0.07	0.19	0.34
	D2	0.82	0.62	0.53	0.48	25.10	21.50	0.01	0.02	0.07	0.05	0.07	0.03	0.14	0.26
	D3	0.84	0.73	0.50	0.68	24.70	36.30	0.01	0.02	0.06	0.09	0.08	0.01	0.08	0.20
Cob weight	D1	0.60	0.43	0.19	0.20	14.02	14.74	20.56	43.14	18.86	30.55	83.81	71.38	0.22	0.16
	D2	0.61	0.35	0.19	0.16	15.62	14.13	18.76	44.24	17.81	21.62	81.68	50.83	0.23	0.09
	D3	0.61	0.20	0.18	0.14	17.74	11.90	17.23	45.21	16.27	15.36	75.26	14.23	0.24	0.08
Plant height	D1	0.75	0.60	0.20	0.24	27.10	4.91	87.28	109.77	137.19	130.06	779.80	389.07	0.20	0.29
	D2	0.72	0.52	0.16	0.10	14.80	2.03	70.29	115.66	81.84	49.98	568.12	400.88	0.18	0.24
	D3	0.59	0.51	0.10	0.07	11.28	1.41	97.55	110.21	47.97	33.12	472.16	386.81	0.18	0.20
Ear height	D1	0.78	0.43	0.72	0.11	27.10	3.44	73.18	90.18	491.03	35.41	85.66	196.98	0.40	0.44
	D2	0.69	0.41	0.49	0.17	14.80	5.12	74.56	88.88	232.95	52.80	190.99	146.11	0.36	0.31
	D3	0.62	0.30	0.37	0.21	11.28	6.04	76.23	98.44	145.96	58.20	195.70	53.45	0.34	0.26
Anthesis	D1	0.97	0.95	0.03	0.31	0.27	2.64	0.35	0.41	0.68	5.31	50.33	21.83	-0.04	-0.06
	D2	0.95	0.97	0.11	0.35	0.87	2.69	0.38	0.23	1.59	5.09	23.67	18.15	-0.03	-0.06
	D3	0.93	0.97	0.20	0.55	1.32	4.05	0.38	0.23	2.11	7.45	15.17	11.28	-0.02	-0.05

variances for kernel per row and cob weight were decreased with increase of planting densities. For the other traits very small changes were detected in genetic variances with an increase in planting densities.

Broad sense heritability estimates ranged from 0.24 (100-seed weight at high planting density) to 0.97 (anthesis at low planting density) in cross B73×Mo17, and from 0.20 (cob weight at a high planting density) to 0.97 (anthesis at all plant densities) in cross B73×K74/1.

Narrow-sense heritabilities ranged from 0.02 (kernel per row at low planting density) to 0.72 (ear height at low planting density) in cross B73×Mo17, and from 0.04 (100-seed weight at high planting densities) to 0.68 (kernel depth at high planting density) in cross B73×K74/1. For grain yield per plant, kernel rows, and ear height, greater estimates of narrow-sense heritability and consequently greater gain from selection were found in cross B73×Mo17. In contrast, these estimates were greater in cross B73×K74/1 for anthesis and kernel per row. Genetic advance ranged from 0.27 (anthesis at low planting density) to 36.70 (grain yield per plant at low planting density) in cross B73×Mo17, and from 1.41 (plant height at high planting densities) to 36.30 (kernel depth at high planting density) in cross B73×K74/1.

Based on variations in additive and dominance variance, broad sense heritability decreased at higher planting densities for both crosses, except for kernel depth and cob weight in cross B73×Mo17 and anthesis, kernel depth and kernel row number in cross B73×K74/1.

Narrow sense heritability and also genetic advance decreased at higher planting densities in cross B73×Mo17 except for anthesis and kernel per row but it increased in cross B73×K74/1 except for plant height, 100-seed weight and cob weight.

Absolute estimates of heterosis ranged from 0.02 (anthesis at high planting density) to 0.69 (grain yield per plant at low planting density) in cross B73×Mo17, and from 0.00 (kernel rows at low planting density) to 0.78

(grain yield per plant at low planting density) in cross B73 × K74/1.

DISCUSSION

In both crosses, the dominance effects were greater than the additive effects for all characters at all planting densities, except kernel rows at high planting density of cross B73×Mo17 and low planting density of cross B73×K74/1. Some studies have indicated the importance of the dominance effect for yield in corn (Guei and Wassom, 1992; Malvar *et al.*, 1996). Gamble (1962a and b) reached the same conclusion in evaluating some ear characteristics in different crosses. The contribution of the parents to dominance effects varied according to trait and planting density. The sign for dominance effect is a function of the F_1 mean value in relation to the mid-parental value and indicates which parent is contributing to the dominance effect (Cukadar-Olmedo and Miller, 1997).

The possibility that epitasis accounts for a significant proportion of the genetic variance of quantitative traits has been investigated extensively. Our results showed that, besides the additive and dominance genetic effects, epistatic components have also contributed to genetic variations for most of the characters studied. However, their relative magnitudes vary for different traits and under different plant densities. In such a situation, the appropriate breeding method is the one that can effectively exploit the three types of gene effects simultaneously. Lamkey *et al.* (1995) found that unlinked additive by additive epistasis accounted for at least 21% of the variation among test cross generation means derived from elite maize inbred lines. Under highly productive environmental conditions, dominance effects have accounted for most of the variability in yield, with epistasis having a small and significant influence on the final performance of different generations.

Specific combining ability is more important for selected lines than for unselected

lines, indicating the importance of dominance and epistatic effects in elite germplasm (Hallauer and Miranda, 1988). Specific crosses with epistatic effects probably have unique combinations of genes contributing to heterosis. These unique combinations are restricted to the specific cross and may be of small importance in any maize population (Hallauer and Miranda, 1988). The hybrid B73×Mo17 was a widely grown hybrid in the late 1970s and early 1980s and it is possible that favorable epistasis effects contributed to the exceptional performance of this hybrid (Lamkey *et al.*, 1995). The evidence indicates that there are net positive epistasis effects fixed in B73. This may explain why B73 has been such a widely used and successful inbred in maize breeding programs (Lamkey *et al.*, 1995; Ceballos *et al.*, 1998). Kearsey and Jinks (1968) suggested that the two parental inbreds (B73 and Mo17) have equal opportunity to contribute to the expression of additive by additive effects when averaged across all possible F_2 genotypes.

Confounding epistatic effects in the models suggested that inheritance of these traits is complex and polygenic (Warnock *et al.*, 1998; Upadhyaya and Nigam, 1998). Because one or more kinds of epistatic effects were detected for all the traits, estimates of the additive and dominance components for these traits would have been biased because of nonorthogonality if they had been estimated using procedures that assume no epistasis (Upadhyaya and Nigam, 1998). For this reason estimates of epistasis obtained are likely to be minimum value. The assumption of no epistasis is one of the most common made in quantitative genetic models (Weir and Cockerham, 1977). The amount and type of epistasis present in crop species can have major consequences on both the reliability of prediction and the design of breeding programs.

The presence of epistasis has important implications for any plant breeding program. The [i] type interaction can be fixed in inbred lines. A recurrent selection scheme, in which large populations are carried forward to later generations to allow favorable gene combinations to be in a homozygous state before practising final selection, would be the most appropriate. The other digenic interactions can be effectively exploited through the selection of lines that exhibit high levels of the trait in crosses with other inbred lines.

The signs associated with estimates of [i], [j] and [l] types of epistasis indicate the direction in which the gene effect influence the mean of the population. For [i] and [j], the sign also provides information on the association or dispersion of genes in the parents (Mather and Jinks, 1982). With two exceptions, all the other signs of [i] and [j] type of detected epistasis were negative. Also, a negative sign for any of the two parameters suggests an interaction between increasing and decreasing alleles, thus providing evidence for some level of dispersion in the inbred parents. A negative sign for each of these two parameters suggests that it should be possible further to improve the level of the corresponding traits. With one exception (anthesis at low planting density in cross B73×Mo17) all the other signs of the estimates of [l] were opposite to that of [h] in both crosses, indicating duplicate epistasis. This kind of epistasis generally hinders the improvement through selection and, hence, a higher magnitude of dominance and [l] type of interaction effects would not be expected. It also indicated that selection should be delayed after several generations of selection (single seed descent) until a high level of gene fixation is attained. Subsequent intermatings between promising lines may be important in accumulating favorable genes. Since none of the signs of the [h] were similar to the [l] type of epistasis, it was concluded that no complementary type of interaction was present in the genetic control of the studied traits.

Similarity in estimates for three planting densities was observed for additive effects in B73×K74/1 cross for most of the traits. This was true to some extent for the B73×Mo17 cross. On the other hand, the estimates of dominance effects showed considerable

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variations in magnitude and sign depending on cross, trait and planting density. Non-consistency in estimates was more pronounced for epistasis effects for most of the traits at different cross-planting densities combinations. Martine and Hallauer (1976) reported that interaction between epistatic effects and environment in maize is very important. Interactions between environment and genetic parameters depends on the number of genes involved in the inheritance of the trait and, as the number increases the influence, of the environment becomes greater (Gamble, 1969c ; Upadhyaya and Nigam, 1998). This could be one of the possible reasons for the epistasis × planting density interaction in this study. Therefore, widespread and unpredictable epistasis caused by environmental interaction reinforces the need for wide and repeated testing of maize hybrids.

By considering the three digenic epistatic effects, it was evident that epistasis was a major factor in generation × planting density interactions especially for cross B73×Mo17. This interaction was more evident for [i] type epistasis since, when generation mean analysis was conducted across planting densities, the averaging of gene effect estimates resulted in adequacy of the models without incorporating [i] type epistasis (data is not shown). Similar results that epistatic effects interact more strongly with the environment than additive and dominance gene effects have been reported for maize (Adetimirin *et al.,* 2001; Eta-Ndu and Openshaw, 1999; Gonzalez-Moreno and Dudley, 1981).

Narrow-sense heritability estimates were generally lower than broad-sense heritabilities indicating the presence of non-additive gene action. The departure from the additive-dominance model indicates that multiple genes interact to affect most of the studied traits. The low h_n^2 estimates for most traits suggested that the inheritance is complex. Although the results of this experiment may be applicable only to the germplasm used herein, the identification of dominance and epistatic effects suggest that additional research is necessary.

One advantage of generation mean analysis, compared with other mating designs such as diallel, is an increased level of sensitivity through a decreased error rate (Hallauer and Miranda, 1988). However, environmental differences may cause averages to cancel out effects for opposing directions. This may explain why the results of our experiment support the importance of nonadditive effects such as dominance.

The results of this study demonstrated that gene effects obtained by generation mean analysis differed with the different genetic backgrounds of the inbred crosses, and were also influenced by environmental conditions (planting densities). Also our results revealed the involvement of epistasis in genetic control of some of the studied planting density-traits combinations. The involvement of gene interactions for quantitative characteristics in maize has been reported previously (Darrah and Hallauer, 1972; Eta-ndu and Openshaw, 1999, Lamkey *et. al*, 1995; Morenzo-Gonzalez and Dudley, 1981; Stuber and Moll, 1971; Wolf and Hallauer, 1997).

REFERENCES

1. Adetimirin, V. O., Aken'Ova and Kim, S. K. 2001. Detection of Epistasis for Horizontal Resistance to *striga bermonthica* in Maize. *Maydica,* **46:** 27-34.
2. Ceballos, H., Pandey, S., Narro, L. and Perez-Velazquez, J. C. 1998. Additive, Dominant, and Epistatic Effects for Maize Grain Yield in Acid and Non-acid Soils. *Theor. Appl. Genet.,* **96**: 662-668.
3. Chen. L., Cui, S., Su. Y. and Chen, L. 1996. Analysis of the Gene Effect on Ear Characters in Maize. *Acta Agr. Boreali Sinica*, **11(2):** 28-32.
4. Cukadar-Olmedo, B. and Miller, J. F. 1997. Inheritance of the Stay Green Trait in Sunflower. *Crop. Sci.,* **37**: 150-153.
5. Darrah, L. L. and Hallauer, A. R. 1972. Genetic Effects Estimated from Generation Means in Four Diallel Sets of Maize Inbreds. *Crop Sci.*, **12:** 615-621.

6. Edwards, L. H., Ketata, H. and Smith, E. L. 1975. Gene Action of Heading Date, Plant Height, and Other Characters in Two Winter Wheat Crosses. *Crop Sci.,* **16:** 275-277.

7. Eta-Ndu, J. T. and Openshaw, S. J. 1999. Epistasis for Grain Yield in Two F₂ Populations of Maize. *Crop Sci.*, **39:** 346-352.

8. Gamble, E. E. 1962a. Gene Effects in Corn (Z*ea mays* L.). I. Separation and Relative Importance of Gene Effects for Yield. *Can. J. Plant Sci.,* **42:** 339-348.

9. Gamble, E. E. 1962b. Gene Effects in Corn (Z*ea mays* L.). II. Relative Importance of Gene Effects for Plant Height and Certain Component Attributes of Yield. *Can. J. Plant Sci.*, **42:** 349-358.

10. Gamble, E. E. 1962c. Gene Effects in Corn *Zea mays* L. III. Relative Stability of the Gene Effects in Different Environments. *Can. J. Plant Sci.*, **42:** 626-634.

11. Guei, R. G. and Wassom, C. E. 1992. Inheritance of Some Drought Adaptive Traits in Maize: 1. Interrelationships between Yield, Flowering, and Ears per Plant. *Maydica*, **37:** 157-167.

12. Hallauer, A. R. 1990. Methods Used in Developing Maize Inbreds. *Maydica*, **35:** 1-16.

13. Hallauer, A. R. and Miranda Fo, J. B. 1988. *Quantitative Genetics in Maize Breeding*. 2nd edition. Iowa State University Press, Ames, IA.

14. Hinze, L. L., and Lamkey, K. R. 2003. Absence of Epistasis for Grain Yield in Elite Maize Hybrids. *Crop Sci.*, **43:** 46-56.

15. Kearsey, M. J., and Jinks, J. L. 1968. A General Method of Detecting Additive, Dominance, and Epistatic Variation for Metrical Traits. I. *Theory Heredity* **23:** 403-409.

16. Ketata, H., Smith, E. L., Edwards, L. H. and McNew, R.W. 1976. Detection of Epistasis, Additive, and Dominance Variation in Winter Wheat (*Triticum aestivum* L. em Thell.). *Crop Sci.*, **16:** 1-4.

17. Lamkey, K. R., Schnicker, B. J. and Melchinger, A. E. 1995. Epistasis in an Elite Maize Hybrid and Choice of Generation for Inbred Line Development. *Crop Sci.*, **35:** 1272-1281.

18. Malvar, R. A., Ordas, A. Revilla, P. and Cartea, M. E. 1996. Estimates of Genetic Variances in Two Spanish Populations of Maize. *Crop Sci.*, **36:** 291-295.

19. Martin, J. M., and Hallauer, A. R. 1976. Relation between Heterozygosis and Yield for

20. Four Types of Maize Inbred Lines. *Egypt. J. Genet. Cytol.* **5:** 119-135.

21. Mather, K. and Jinks, J. L. 1982. *Introduction to Biometrical Genetics*. 3rd editoion. Chapman and Hall Ltd., London.

22. Melchinger, A. E., Schmidt, W., and Geiger, H. H. 1988. Comparisons of Test Crosses Produced from F₂ and First Backcross Populations in Maize. *Crop Sci.*, **28:** 743-749.

23. Moll, R. H. and Stuber, C. W. 1971. Comparisons of Response to Alternative Selection Procedures Initiated with Two Populations of Maize (*Zea mays* L.) *Crop Sci.,* **11:** 706-711

24. Moreno-Gonzalez, J., and Dudley, J. W. 1981. Epistasis in Related and Unrelated Maize Hybrids Determined by Three Methods. *Crop Sci.*, **21:** 644-652.

25. Robinson, H. F., Comstock, R. E. and Harvey, P. H. 1955. Genetic Variances in Open-pollinated Varieties of Corn. *Genetics* **40:** 45-60.

26. Russel, W. A. 1972. Registration of B70 and B73 Parental Line of Maize. *Crop Sci.*, **12:** 721.

27. Shonnard G. C., and Gepts, P. 1994. Genetics of Heat Tolerance during Reproductive Development in Common Bean. *Crop Sci.*, **34:** 1168–1175.

28. Silva, J. C., and Hallauer, A. R. 1975. Estimation of Epistatic Variance in Iowa Stiff Stalk Synthetic Maize. *J. Hered.*, **66:** 290-296.

29. Stuber, C. W., and Moll, R. H. 1969. Epistasis in Maize (*Zea mays* L.). I. F₁ Hybrids and Their S₁ Progeny. *Crop Sci.*, **9:** 124-127.

30. Templeton, A. R. 2000. Epistasis and Complex Traits. In: "*Epistasis and the Evolutionary Process.*" (Eds.) J. B. Wolf *et al.* Oxford University Press, New York. PP. 41-57.

31. Upadhyaya, H. D., and Nigam, S. N. 1998. Epistasis for Vegetative and Reproductive Traits in Peanut. *Crop Sci.*, **38:** 44-49.

32. Warner, J. N. 1952. A Method for Estimating Heritability. *Agron. J.*, **44:** 427-430.

33. Warnock, D. F., Davis, D. W. and Gingera, G. R. 1998. Inheritance of Ear Resistance to European Corn Borer in 'Apache' Sweet Corn. *Crop Sci.*, **38:** 1451-1457.

34. Weir, B. S., and Cockerham, C. C. 1977. Two-locus Theory in Quantitative Genetics. In: "*Proceedings. of the International Conference on Quantitative Genetics.*" (Eds.) Pollak, E., Kempthorne, O., and Bailey, T.

B. Iowa State University Press, Ames. PP. 247-269.

34. Wolf, D. P., and Hallauer, A. R. 1977. Triple Test Cross Analysis to Detect Epistasis in Maize. *Crop Sci.*, **37:** 763-770.

35. Wright, S. 1968. *Evolution and Genetic of Population. Volume I. Genetic and Biometric Foundation*. University of Chicago Press, Chicago. pp. 371-420.

36. Zuber, M. S. 1973. Registration of 20 maize Parental Lines. *Crop Sci.*, **13:** 779-780.

تجزیه و تحلیل میانگین نسل‌ها برای تخمین پارامترهای ژنتیکی صفات مختلف در دو تلاقی اینبرد لاین‌های ذرت در سه تراکم کاشت

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چکیده

انتخاب موثرترین روش به‌نژادی به دانش کافی از نظام ژنتیکی کنترل کننده صفت بستگی دارد. هدف این بررسی تعیین پارامترهای ژنتیکی برای عملکرد دانه و صفات وابسته از جمله برخی از اجزاء عملکرد در سه تراکم کاشت بود. بدین منظور از تجزیه میانگین نسلهای P_1، P_2، F_1، F_2، BC_1 و BC_2 درتلاقیهای اینبرد لاین B73 با Mo17 و K74/1 استفاده شد. تجزیه واریانس نشان داد که اثر متقابل تراکم کاشت و نسل به ژنوتیپ و نوع صفت وابسته است. تجزیه میانگین نسلها نشان داد که آثار افزایشی و غالبیت ژنها برای همه صفات مورد بررسی اهمیت دارند، ولی اثر غالبیت بارزتر بود. اثر متقابل غیر آللی بر نمود تمام صفات در هر دو تلاقی و سه تراکم کاشت اثر داشت و این اثر در تلاقیها و تراکمها متفاوت بود. اثر متقابل تراکم کاشت با اپیستازی شدیدتر از اثر متقابل آن با آثار جمع‌پذیری و غالبیت بود.