

DETECTION OF NON ALLELIC INTERACTIONS VIA GENERATIONS MEAN ANALYSIS IN MAIZE

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ABSTRACT

This experiment was conducted at the field of Field Crop Dept. College of Agric / Univ.of Baghdad to evaluate the genetic gene effects to some traits of maize. Six generations P1, P2, F1, F2, BC1 and BC2 for four crosses produced from crossing of genetically different six inbred lines. The six parameters were evaluated in randomized complete block design with four replications. The analysis of variance showed significant differences among generations. Means of F1's were higher than the highest parent for all the traits of all crosses, indicated over dominance gene action. Hybrid vigor and heterosis were positive for most of traits for crosses. Result of scaling test for four criteria A , B, C, and D indicated significant effects of non-allelic interaction controlling genetic variation among six generations for seven traits. The mean effects were highly significant for all traits in all crosses indicated that all traits were quantitatively inherited, also indicated that lines had genetic diversity. Dominance effects were higher than mean and additive effects for all traits and all crosses, indicated the importance role of dominance component of gene action in inheritance traits. There were different type of epistasis interaction effects observed for various traits and crosses. Their values were varied for different trait and crosses. The dominance × dominance interactions were higher than other epistasis interaction effects. We can conclude that the traits in all crosses shown the complex behavior, hence the selection should be delayed after several generations of segregation until reached homozygosity.

Key words: Additive, dominance, epistasis. back cross, gene action.

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الكشف عن التداخلات غير الاليلية من خلال تحليل متوسط الأجيال في الذرة الصفراء.

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المستخلص

نفذت تجربة حقلية في حقل قسم علوم المحاصيل الحقلية - كلية الزراعة - جامعة بغداد، لتقدير التأثيرات الوراثية والتفوقية للجينات التي تحكم توريث بعض صفات الذرة الصفراء. تم التضريب بين ست سلالات مختلفة وراثيا لإنتاج ست أجيال هي P1 و P2 و F1 و F2 و BC1 و BC2. تم تقدير هذه الثوابت باستخدام القطاعات الكاملة المعشاة بأربعة مكررات. أوضح تحليل التباين فروقا معنوية بين الأجيال الستة. كان متوسط الجيل الأول على من أعلى الأبوين لكل الصفات ولكل التضريبات، موضحا فعل التفوق للجين. كانت قوة الهجين والتهجين موجبة لأغلب الصفات للتضريبات المدروسة. أوضحت نتيجة اختبار scaling للمعايير الأربعة A و B و C و D تأثيرات معنوية للتفاعل غير الاليلي الحاكم للتغايرات الوراثية بين الأجيال الستة وللصفات السبع. كان متوسط التأثيرات عالي المعنوية لكل الصفات ولكل التضريبات موضحا أن تلك الصفات كمية، وإن السلالات المستخدمة متغايرة وراثيا. كانت تأثيرات السيادة أعلى من تأثيرات فعل الجين المضيف لكل الصفات ولكل التضريبات، مبينة أهمية دور فعل الجين السيادة في توريث الصفات. تم ملاحظة أشكال مختلفة من التداخلات التفوقية للجينات لمختلف الصفات والتضريبات، وقد اختلفت قيمها بحسب الصفة والتضريب. كان شكل تأثير فعل الجين ا لتفوق من نوع سيادي × سيادي أعلى من بقية تأثيرات التفوقية، لذا يمكن أن نستنتج أن سلوك الصفات في كل التضريبات كان معقدا لذا يجب تأخير الانتخاب إلى ما بعد عدة أجيال من الانعزال كي تصل الآباء إلى درجة عالية من التماثل الوراثي.

كلمات مفتاحية: فعل الجين المضيف، فعل الجين السيادة، التفوق، التهجين الرجعي، الفعل الجيني

INTRODUCTION

Many genetic models have been proposed for the estimation of gene action. Most of these genetic models were developed to estimate relative importance of additive and dominance gene effects. Epistasis gene effects were assumed to be negligible (12). Many of scientists' reports indicated that epistasis gene effects are presented in sufficient magnitude in quantitative traits to impede the assumption of negligible epistatic gene effects (3, 11, 15, 16, and 21). Genetic models permitting the estimation of additive, dominance and epistasis effects have proposed by (1, 5, and 14). These models were based on the factorial model used in the design of experiments, but Anderson and Kempthorne (1) have partitioned the genotypic value into additive, dominance and epistasis gene effects, while Cockerham (5) and Hayman and Mather (14) have partitioned the genetic variance into these components. Genetic mean analysis is a useful technique that provides the estimation of main genetic effects (additive, dominance and their digenic interaction) involved in the expression of quantitative traits (22). The phenotypic expression of traits depends upon the type of gene action: dominance and additive. Many of researchers observed the important role of non-allelic interactions in the inheritance of quantitative traits (4, 9, 17, 23, 25, and 27). Haq, et al. (13) found that generation mean analysis showed the superiority of non-additive gene effects for all studied traits. Significant dominance effects were indicated in all crosses for leaf area and plant height in maize, and these effects were much higher in magnitude than their additive effects. All crosses indicated significant additive \times dominance effects for leaf area. Significant additive \times additive effects were present in some crosses for two traits. Complementary and duplicate gene interactions were seen effective in the inheritance of leaf area. Duplicate gene interactions were observed in controlling plant height in most crosses. Epistasis played a considerable role in controlling leaf area and plant height (19). Result of Wannows et al. showed that the additive \times dominance model was adequate to illustrate the genetic variation and its importance in the inheritance of most

traits. The objectives of this experiment were to estimate the main genetic effects and digenic non-allelic interactions effects controlling some traits in four crosses of maize.

MATERIALS AND METHODS

Field experiment:

Ten maize inbred lines maize were tested in Iraqi central environments at the field of Field Crop Dept., College of Agric. Univ. of Baghdad. Selfing was done in spring and fall seasons of 2009, and spring of 2010, to maintain and increase homozygosity. The homozygous inbred have been crossed to produced F1 generation. F1's were planted in spring 2011 with their parents to produced BC1 and BC2, also selfing was done for parents to produce F2 generation. Comparative field trial include six population of each cross: P1, P2, F1, F2, BC1 and BC2 has been conducted in fall season 2013, in Randomized Complete Block Design with four replications. Dimensions of plots were 75cm \times 25cm, population density was 53333 plants.ha⁻¹. The calcium super phosphate 45% P₂O₅ with 200 kg.ha⁻¹ were added at soil preparation. Nitrogen fertilizer as urea (46%) was added 3 times, at planting, elongation stage and before anthesis. 8kg. ha⁻¹. of diazenon was applied to protect the maize plant from attack of *Sesamia cretica*. The observation were taken on 20 plants randomly selected from P1, P2, and F1 population, 30 plants of each BC1 and BC2, and 40 plants for F2 population. The data were recorded for plant height, number of leaves, leaf area, number of branches per tassel, number of ears per plant, ear weight and grain yield.

Statistical analyze

Analysis of variance:

Analysis was conducted for individual cross for each trait to estimate the significant differences among different generation. Mean values, standard error of mean, hybrid vigor and heterosis have been calculated as:

$$SE(m) = (Vm)^{1/2}, SE(d) = (Vd)^{1/2}$$

$$SE(h) = (Vh)^{1/2}, SE(i) = (vi)^{1/2}, SE(j) = (Vj)^{1/2}, SE(l) = (Vl)^{1/2}$$

$$\text{Heterosis\%} = (\overline{F1} - \overline{MP}) / \overline{MP}$$

$$\text{Hybrid vigor \%} = (\overline{F1} - \overline{BP}) / \overline{BP}$$

Scaling test:

It was used to estimate the magnitude each of A, B, C, and D, and their variances:

$$A=2\overline{B_1} - \overline{P_1} - \overline{F_1}$$

$$B=2\overline{B_2} - \overline{P_2} - \overline{F_1}$$

$$C=4\overline{F_2} - 2\overline{F_1} - \overline{P_1} - \overline{P_2}$$

$$D=2\overline{F_2} - \overline{B_1} - \overline{B_2}$$

The significant of A, B, pointed to presence of all non-allelic interactions. The significant of C showed to dominance \times dominance (i), the significant of D referred to additive \times additive and (i) gene interaction, significant of C + D pointed to both of (dominance \times dominance) and (additive \times additive) type of interaction. A and B test give evidence about (l), (j) gene interaction, and they affect additive \times dominance (j) interaction, but it has not effect on C and D (Singh and Chaudhary) (26).

c) Six parameters model:

The generation's means analysis were calculated due to Mather and Jinks (22) according to linear model:

$$Y = m + \alpha(d) + \beta(h) + \alpha_2(i) + 2\alpha\beta(j) + \beta_2(l)$$

where: generation mean

$$m = \text{mean effect} = \overline{F_2}$$

$$d = \text{additive effects} = \overline{B_1} - \overline{B_2}$$

$$h = \text{dominance effects} = \overline{F_1} - 4\overline{F_2} - 0.5\overline{P_1} - 0.5\overline{P_2} + 2\overline{B_1} + 2\overline{B_2}$$

$$i = \text{additive} \times \text{additive gen action} = 2\overline{B_1} + 2\overline{B_2} - 4\overline{F_2}$$

$$j = \text{additive} \times \text{dominance gen action} = \overline{B_1} - 0.5\overline{P_1} - \overline{B_2} + 0.5\overline{P_2}$$

$$l = \text{dominance} \times \text{dominance gene action} = \overline{P_2} + \overline{P_1} + 2\overline{F_1} + 4\overline{F_2} - 4\overline{B_1} - 4\overline{B_2}$$

The programmer's software excels 2007 and genestate 2013 and spr-2 were used to analyze the data.

RESULT AND DISCUSSION**Generations mean, Hybrid****Vigor and Heterosis:**

The means, standard error, hybrid vigor and heterosis of the six generations with four crosses for seven traits are presented in Table 1. Mean's of F₁'s was higher than the highest parent, indicated over or partial dominance, respectively for plant height. Hybrid vigor for three crosses (1, 2, and 3) were positive toward increase plant height, cross 4, was negative toward decrease plant height. All means of F₁ for leaves number were higher than the other generation, indicated over dominance gene

effects. As well as, transgressive segregation was also observation in the F₂ generation. Similar results were obtained by Sharokhi et al. (25). Hybrid vigor and heterosis of all crosses are positive towards increase leaves number were, highest one for cross 2. Means of F₁'s were higher than the highest parent for leaves area indicated over dominance gene action, highest one for cross 1 and 4. Transgressive segregation was also observed in F₂ generation. BC₁ and BC₂ were higher than parents for cross 2 and 3, but in cross 4 only BC₁ was higher than two parents. Hybrid vigor for three crosses (1, 2 and 4) was positive towards increased leaf area, while in cross 3, hybrid vigor and heterosis was negative towards decreased leaf area. Similar result was obtained by Iqbal et al (19). Tassel branches number for F₁ were higher than other generations, indicated over dominance gene effects. F₂ mean was higher than p₂ and BC₂ only. BC₁ was higher than p₂, F₂ and BC₂ for cross 1. In cross 2 for generation F₁, F₂, BC₁ and BC₂ were higher than P₂, indicated that the over dominance gene effects was occurred, in addition to the transgressive segregation was observed in the F₂ generation. Cross 3 with also, four generation were higher than P₁ and P₂, and transgressive segregation was also observed in mean of F₂ generation, moreover BC₁ was higher than all generations, due to parent 1 which gave high mean close to the mean of F₁, F₂ and BC₂, which in turn was similar to F₁ and F₂. As well as cross 4. Hybrid vigor and heterosis of all crosses were positive towards increase the number of tassel branches. The mean values of F₁'s generation for ears number of four crosses were higher than other generations, indicated over dominance gene action controlling this trait, also transgressive was observed for F₂ generation for cross 1, 2, and 3. Mean of BC₂ was higher than mean of P₂ for cross 1, while means of BC₁ and BC₂ for crosses 2 and 3 were higher than their parents. Mean of BC₁ for cross 4 was lower than P₁, therefore mean of BC₂ was the closed mean of P₂. Hybrid vigor and heterosis for cross 1 and 2 were positive and higher, While for cross 3 and 4 were positive too, but lower than cross 1 and 2, which indicated that the effect was towards increased number of ears per plant. Means of

F1 generations for two crosses 1 and 3 were higher than other generations for ears weight of maize, indicated over dominance effects were controlled the trait, as well as transgressive segregation observed for F2 generations. Mean of F1 for cross 4 higher than other generations except BC1 which was higher over all generation even F1 mean. Mean of F1 generations for cross 2 was higher than other generations except BC2 which gave higher value than all generations except BC2 which gave higher value than all other generation even F1 mean. Hybrid vigor and heterosis had high values and positive, indicated that were parents more homozygous and unrelated. F1's means for grain yield were higher than other generations for all crosses except cross 3, where BC2 was higher than all due to increase of ear weight. The highest value of F1's means indicated that over dominance effect controlled the trait, also, the transgressive observed in F2 means for the same generation. Hybrid vigor and heterosis were high and positive for all generations of four crosses, indicated that parents were more homozygous and unrelated. High value of hybrid vigor and heterosis indicate that non-additive gene action affects these traits. Similar results were reported by (1, 9).

Scaling Test:

Results of scaling test for four criteria A, B, C, and D, indicated significant effects of non-allelic interaction controlling genetic variation among six generations for seven traits (Table 2). The significant of any one of these scales indicate the presence of non-allelic interaction. Type (i) of gene interaction (additive \times additive) test by D. Type (l) of gene action (dominance \times dominance) indicated by C. The significant of C + D related to (i) type of gene interaction (additive \times additive) and (l) was (dominance \times dominance). There were no effect of (j) (additive \times dominance) type of gene interaction on C and D, but it affects A and B. A and B tests gave index for i, j and l types of gene interaction. Values of A, B, C, and D scaling test were significant for plant height for cross 1. Cross 2, just A and C were significant, while cross 3 only D was not significant. Cross 4 only B significant. When the values of any one of A, B, C, and D were

not significant that mean the absence of non-allelic interaction and the additive – dominance model was sufficient to illustrate the genetic variation, and it is important in the inheritance of trait in these crosses. Similar results reported by (4, 20). Values of A and B for number of leaves were significant, but C and D were not significant in cross 1 and 3, only D was significant for cross 2, other were not significant, while all parameters were not significant. Three parameters A, B and C were highly significant for number of branches per tassel in cross 1, cross 2 and 3, A, B, were highly significant, but C and D not significant. Cross 4, A highly significant and D was significant; B and C were not significant. A and B were significant for leaf area of maize in cross 1 and 3, in cross 2 only B was significant. A, B, and C were significant in cross 4. Number of ears per plant showed that parameters A, B, and C were significant, but D not significant in cross 1, while in cross 2 and 4 there are A and B were significant. All parameters in cross 3 were not significant. A, B, and C in cross 1 and 3 for ear weight were significant, while D not significant. All highly significant in cross 4. Also A, B, and C in cross 1 and 3 for grain yield were significant, in cross 2, only B was significant, cross 4, A and B were highly significant, and significant for D and not significant for C.

Genetic Components:

The Table 3 illustrates the genetic variation components according to six parameters model. The estimate of six parameters includes effects of mean (m) for F2, effect of additive gene action (d), dominance effects (h), additive \times additive interaction (i), additive \times dominance (j), and dominance \times dominance (l). The mean effects were highly significant for all trait in all crosses, indicated that all studies traits are quantitatively inherited, and pointed that lines were genetic diversity.

Plant height

Additive effects for this trait were highly significant and positive; except for cross 3 it was negative. However three of crosses exhibit significant additive gene effects which indicated that additive genetic variation was present in plant height. It was very small in magnitude relative to parameter m in all crosses. The relative magnitudes of the

estimates suggests that additive gene effects made only a minor contribution to the inheritance of plant height in these inbreds. The positive or negative sign of additive (d) effects and additive \times dominance (dh) depends upon the parents P1 or P2. For example, in cross 1 (F101301 \times Rustico), if F101301 is considered as P1 and Rustico as P2, the estimate of parameters d was positive, so, if Rustico is considered as P1 and F101301 as P2 the estimate of parameters d was negative. Nevertheless, the sign of (dh) was be changed correspondingly in most cases, but the sign of the other parameters would be unaffected. If the inbred had been used as P1 in each cross, and it performed better, most of estimates would have been positive for (d) and (dh) (6,11). Dominance effects were highly significant in two crosses only 1 and 2 not significant in 3 and 4. It was positive in cross 2 and 3, negative in 1 and 4. It was more than m only in cross 2. The values of dominance effects were higher than additive effects in all crosses for this trait, indicated the importance role of dominance components of gene action in inheritance trait. As well as, the additive and dominance effects, epistatic component have also contributed to the genetic variations for plant height. Cross 1 and 2 exhibited highly significant difference in additive \times additive (d \times d) interaction, while cross 3 and 4 were not significant. The value of (d \times d) for cross 1 was negative and close to the mean value, but for cross 2 was positive and higher than mean. The additive \times dominance (d \times h) interaction for this trait was highly significant in three crosses, 1, 2, and 4, just significant in cross 3, all of them were positive, but less than mean (m). The dominance \times dominance (h \times h) interaction was highly significant in cross 1 and 2, but significant in 3 and not significant in cross 4. In general, (h \times h) was higher than m in cross 1, negative and higher than m in cross 2, and positive and less than m in cross 3, and 4. Cross 1 and 2 were significant in three types of epistasis. Cross 3 significant in two types (d \times h) and (h \times h). Cross 4 was significant only in type (d \times h). If we take the absolute values of epistatic gene effects relative to the mean effects it can be noted that the absolute magnitude of epistatic gene effects was larger than the mean

effects, the additive effects and dominance effects in cross 1, 2 and 3 was less than mean effects. However, the (h \times h), (d \times d) and (h) gene effects were relatively more importance than (d \times h) and (d) gene effects in cross 1 and 2. The sign of estimate (l) was opposite to that of (h), indicated duplicate epistasis. Thus crossing among lines to produce hybrid was more efficient than selection. Similar results reported by other researchers (9,18,27). As well as, there were significant additive effects and (d \times d) which point to the contributed of the additive gene action in inherited the trait in cross 2. If the two gene effects (Additive and non-additive) gene effects were found, the favorable methods used to breeding was reciprocal recurrent selection, which was more efficient than recurrent selection for general combining ability which depend on the dominance effects, and more efficient than recurrent selection for specific combining ability, due to its dependence on additive effects. The sign with estimates of (i), (j) and (l) indicate the direction in which the gene effect influences the mean of the population (22).

Number of leaves

Data from Table 3 showed that the mean effects were highly significant in all crosses indicated that the trait was quantitatively inherited. Additive and dominance effects were not significant for all crosses. The additive \times additive and dominance \times dominance were significant in cross 1 and two only, additive \times additive was significant for cross 3 and 4, all types of epistasis were not significant.

Leaves area

The mean effects were highly significant for all crosses. This means the trait was quantitatively inherited (Table 3). The additive effects (d) were significant for cross 1, highly significant for cross 4, and not significant for cross 2 and 3. The not significant effect may be due to the large error variance (8). Dominance effect were negative and highly significant for cross 1, Positive and highly significant for cross 4, not significant for cross 2 and 3, however, it is larger than additive, indicated important role of dominance gene action in inheritance the leaf area. Similar results obtained by others (9,18,25). There are

different types of epistasis interaction were found in leaf area for these crosses. Cross 1 and 4 were positive and highly significant, but cross 2 and 3, were not significant for additive \times additive effects. Additive \times dominance effects were positive and significant, positive and highly significant for cross 1 and 4, not significant for cross 2 and 3. Dominance \times dominance were positive highly significant for cross 1, not significant for 2, 3 and 4. For this trait the value of additive gene effects was small in magnitude relative to the mean value for cross 1, and less than dominance and three types of epistasis, indicated that the dominance gene action controlled this trait.

Number of Branches per Tassel

Table 3 indicates that all means of crosses were highly significant, thus the trait quantitatively inherited. Additive gene action was not significant in crosses 1 and 2, but it was positive and highly significant for crosses 3 and 4. Dominance effects were not significant in crosses 1 and 2 also, positive and significant in cross 3, positive and highly significant in cross 4. The value of dominance for cross 3 and 4 were higher than the mean of populations which indicates major contribution of dominance gene effects to the variation in these crosses. Addition to dominance and additive effects, was different types of epistasis were found. The type Additive \times Additive effects were not significant for all crosses. The type additive \times dominance interaction gene effects was negative and significant in cross 1, positive significant in cross 2, positive highly significant in cross 4, and not significant in cross 3. The type dominance \times dominance was positive and highly significant in cross 1, negative and highly significant in cross 2 and 3, and not significant in cross 4. The additive sign for (l) and (h) in cross 3 indicated a duplicate epistasis. The values of epistasis for all crosses were higher than the mean of populations which indicate the importance of its effect in controlling this trait.

Number of ears per plant : The mean effects were highly significant for all crosses which meant the trait was quantitatively inherited. The additive effects (d) were positive and highly significant for cross 4 only, and not

significant in others, this may be attributed to the large error variance (8). Dominance effects were positive and significant only in cross 3. In spite of non significant, its values were higher than additive effects, which indicates that the trait was under controlling dominance gene effects. Although it was less than the means of populations. There were different types of epistasis interaction effects for crosses. The additive \times additive interactions were negative and significant in cross 1 only. The additive \times dominance interactions were negative and highly significant in cross 4 only. Dominance \times dominance interaction were positive and highly significant for two crosses 1 and 4 only. In general, its more than additive and additive \times additive gene action indicated that the trait under dominance gene action.

Ear Weight : The data in Table 3 indicated that the mean effects were highly significant of all crosses, thus the trait was quantitatively inherited. The additive effects were negative and highly significant in two crosses 2 and 3, but it was positive and highly significant in cross 4, but cross 1 was not significant. All these additive values for all crosses were less than the means. Dominance effects were positive and highly significant for three crosses 2, 3, and 4, significant in cross 1. All values of dominance effects for all crosses were higher than mean and values of additive effects indicated that the ear weight of maize were controlled by dominance gene effects. There were different types of epistasis interaction effects for all crosses. Additive \times additive effects were positive and highly significant for three crosses 2, 3, 4; and not significant in cross 1. Dominance \times dominance effects were positive and highly significant in cross 1, but it was negative and highly significant in crosses 2, 3, and 4. All these effects were higher than all other parameters indicated that the ear weight was controlled by dominance gene action. The same sign of Dominance \times dominance and dominance effects indicated the presence of complimentary type of gene action in this trait. (10,19, 20) found similar results.

Grain Yield : As was shown in Table 3, all mean of grain yield of maize for all crosses were highly significant indicated that was the trait is quantitatively inherited. The additive

gene effects were not significant in cross 1, may be due to the large error variance. Negative and highly significant differences in cross 2 and 3, and positive and highly significant in cross 4. All values of additive were less than the mean. Dominance gene effects for grain yield were positive and highly significant for all crosses, and their values were higher than additive values, and values of mean, indicated that dominance gene effects were controlling grain yield. Hence the selection cannot be use unless the parents reached homozygosis in later generations. There were different types of epistasis interaction effects present for this traits for these crosses. The Additive \times additive effects were positive and highly significant in two crosses, 2 and 3, but it was not significant in other two crosses 1 and 4. Additive \times dominance interaction effects were not significant in cross 1, negative and highly significant in cross 2 and 3, positive and highly significant in cross 4. Dominance \times dominance interaction effects were positive and highly significant in cross 1, and negative highly significant in other three crosses. The

sign of three estimate types of epistasis (I, j, and l) indicated that the direction of the gene effects influencing the mean of generations (22). The opposite sign of estimates (l) to the (h) in cross 2, 3, and 4 indicated the duplicate epistasis. Generally, this type of epistasis was impedes the improvement via selection, for this, the higher magnitude of dominance and (l) type of interaction effects cannot be expected. So, the selection must be used after the population reached homozygosis after many generations of selection. However, the same sign of (l) with (h) indicated presence of complimentary type of gene action for trait, for that the trait can be improved by crossing to exploit the heterosis.

Conclusion

We can conclude that the traits in all crosses of maize have shown a complex genetic behavior, and the additive and dominance components could be exploited in later generations of segregation populations in maize after reached homozygous. The selection in the early generation may not play a important role for the improvement of these traits.

Table 1. Generation means , standard error(SE), hybrid vigor and hetrosis for seven traits of four maize crosses.

Crosses	Generations	Plant height(cm)	Leaf No.	Leaf area (m ²)	Tassel branches No.	Ear No.	Ears weight (gm)	Grain yield(gm)
1) Rustico×FI013 01	P1	111.57±1.28	10.17±0.35	0.363 ±0.003	13.94 ±0.21	1.00 ±0.00	98.35 ±3.66	84.59 ±0.76
	P2	139.22±1.88	9.50±0.32	0.358 ±0.004	6.98 ±0.14	1.05 ±0.05	125.58 ±3.18	88.75 ± 0.53
	F1	150.85±1.43	12.18±0.43	0.457 ±0.009	14.94 ±0.21	1.87±0.08	281.15 ±0.46	219.63 ±4.55
	F2	150.60±3.62	11.50±0.91	0.451 ±0.035	8.95 ±0.73	1.19±0.11	110.53 ±9.52	69.94 ±6.76
	BC1	116.81±2.63	9.19±0.76	0.318 ±0.02	9.32 ±0.41	1.00±0.00	89.76 ±4.81	54.39 ±5.55
	BC2	112.09±1.04	9.42±0.67	0.256 ±0.015	7.76 ±0.78	1.17±0.10	93.28 ±3.38	65.09 ±1.90
	Hybrid vigor%	8.35	19.85	26.08	26.02	78.57	123.88	147.49
	Heterosis%	21.3	23.97	26.78	42.94	82.44	151.11	153.4
	P1	110.34±1.06	8.75±0.25	0.272±0.005	7.73± 0.36	1.00±0.00	74.54±1.62	53.81± 0.90
	P2	114.83±0.83	8.85±0.11	0.274±0.006	9.67±0.41	1.00±0.00	71.51±0.55	63.45± 0.99
2) AntignaoHi3× Nostred	F1	122.06±0.98	10.92±0.26	0.327±0.007	11.89± 0.16	1.89±0.07	152.96±2.21	108.27±3.16
	F2	94.50±2.63	10.00±0.91	0.303±0.027	12.75± 1.75	1.18±0.19	84.63±6.13	72.65± 6.15
	BC1	125.59±1.61	9.78±0.55	0.352±0.027±	16.51±1.38	1.17±0.10	102.42±4.34	75.17± 3.08
	BC2	119.63±2.33	10.38±0.29	0.351±0.016	13.63±1.05	1.25±0.08	155.37±2.65	104.66±2.10
	Hybrid vigor%	6.29	23.42	19.08	53.82	89.03	105.21	70.64
	Heterosis%	8.42	24.12	19.64	62.00	89.05	109.45	84.67
	P1	115.05 ±1.22	9.84 ±0.17	0.393 ±0.008	13.51 ±0.17	1.08 ±0.05	63.42 ±0.79	44.59 ±0.87
	P2	139.72 ±0.98	9.50 ±0.50	0.359 ±0.005	6.97 ± 0.14	1.20 ±0.04	125.58 ±1.01	88.75 ±0.53
	F1	142.53 ±1.47	11.20 ±0.27	0.371 ±0.004	13.75 ±0.25	1.50 ± 0.00	167.19 ±1.22	144.21 ±2.33
	F2	121.46 ±6.61	11.51 ±0.68	0.399 ±0.044	13.77 ±1.64	1.25 ±0.10	162.61 ±6.49	90.68 ±6.10
3) Lo1391×Rustic 0	BC1	118.64 ±1.87	11.19 ±0.28	0.433 ±0.016	19.65 ±1.25	1.37 ±0.05	129.26 ±0.59	106.09 ±4.23
	BC2	120.95 ± 4.30	11.51 ±0.23	0.399 ±0.017	13.77 ±0.59	1.33 ±0.06	250.81 ±5.77	160.87 ±3.78
	Hybrid vigor%	2.01	13.82	- 5.59	1.78	25.00	33.13	62.49
	Heterosis%	11.88	15.82	-1.33	34.28	31.58	76.92	116.30
	P1	123.25 ±0.63	10.13 ±0.13	0.371 ±0.007	7.63 ±0.47	1.26 ±0.10	100.19 ±1.45	59.58 ±1.21
	P2	139.47 ±0.60	9.50 ±0.32	0.359 ±0.005	6.97 ±0.14	1.20 ±0.04	125.58 ±1.01	88.75 ±0.53
	F1	137.01 ±1.34	11.26 ±0.25	0.453 ±0.007	22.71 ±0.64	1.39 ±0.04	163.99 ±2.54	112.45 ±1.13
	F2	130.25 ±14.89	10.38 ±0.89	0.349 ±0.016	14.25 ±1.70	0.98 ±0.34	109.75 ±5.63	91.65 ±3.77
	BC1	125.0 ±3.54	10.38 ±0.55	0.443 ±0.015	18.52 ±0.85	1.00 ±0.00	174.37 ±5.89	104.24 ±2.70
	BC2	117.67 ±2.47	10.37 ±0.55	0.349 ±0.006	14.25 ±0.85	1.21 ±0.01	109.75 ±3.54	91.65 ±1.88
4) Rusticocangin× Rustico	Hybrid vigor%	-1.76	11.15	22.10	197.64	10.31	30.59	26.70
	Heterosis%	4.30	3.16	24.11	211.09	13.01	45.27	51.61

Table 2. Scaling tests for seven traits of four crosses of maize.

Crosses	Traits	A	B	C	D
1) Rustico×FI01301	Plant height(cm)	-28.81± 5.59**	-65.89±3.16**	49.91±14.94**	72.31±15. 54**
	No. of leaves	-3.96±1.62*	-2.85±1.44*	1.96±3.78 ^{n.s}	5.77±4.17 ^{n.s}
	Leaf area (m ²)	-0.18±0.04**	-0.30±0.032**	0.17±0.14 ^{n.s}	0.33±0.22 ^{n.s}
	No. branches/tassel	-11.23±0.87**	-6.39±1.59**	-15.99±2.98**	0.82±3.49 ^{n.s}
	No. ears/plant	-0.88±0.08**	-0.58±0.23*	-1.05±0.46*	0.23±0.48 ^{n.s}
	Ear weight (gm)	-199.97±10.29**	-220±7.49**	-344.10±38.40**	+38.02±42.86 ^{n.s}
	Grain yield (gm)	-195.42±12.04**	-178.18±5.96**	-332.82±28.54**	-20.39±29. 47 ^{n.s}
2) AntignaoHi39× Nostred	Plant height(cm)	18.79±3.55**	2.36±4.83 ^{n.s}	-91.30±10.79**	-5.79±11.84 ^{v.s}
	No. of leaves	-0.09±.116 ^{n.s}	0.97±0.66 ^{n.s}	0.56±3.69 ^{n.s}	10.73±3.85**
	Leaf area (m ²)	0.10±0.06 ^{n.s}	0.10±0.03**	0.01±0.23 ^{n.s}	0.09±0.23 ^{n.s}
	No. branches/tassel	13.40±2.79**	5.68±2.15**	9.81±7.02 ^{n.s}	-4.64±7.84 ^{n.s}
	No. ears/plant	-0.55±0.21**	-0.38±0.18*	-1.03±0.76 ^{n.s}	-0.05±0.79 ^{n.s}
	Ear weight (gm)	-22.67±9.11*	86.27±5.77**	-113.45±24.97**	23.22±27.46 ^{n.s}
	Grain yield (gm)	-11.75±6.97 ^{n.s}	37.59±5.34**	-43.19±25.43 ^{n.s}	28.04±27.53 ^{n.s}
3) Lo1391 ×Rustico	Plant height(cm)	-20.30±4.20**	-40.34±8.78**	-54.00±26.67*	-3.32±28.62 ^{n.s}
	No. of leaves	1.34±0.64*	2.32±0.63**	4.31±2.79 ^{n.s}	0.33±2. 81 ^{n.s}
	Leaf area (m ²)	0.10±0.033**	0.07±0.034*	0.10±0.18 ^{n.s}	0.036±0.18 ^{n.s}
	No. branches/tassel	12.05±2.52**	6.82±1.23**	7.11±6.59 ^{n.s}	-5.88±6. 56 ^{n.s}
	No. ears/plant	0.18±0.11 ^{n.s}	-0.03±0.13 ^{n.s}	-0.27±0.42 ^{n.s}	-0.21±0.58 ^{n.s}
	Ear weight (gm)	27.91±1.88**	208.85±11.65**	127.05±26.10**	-54.84±28.05 ^{n.s}
	Grain yield (gm)	23.39±8.81**	88.78±7.92**	-59.03±24.87*	-85.51±27.30 ^{n.s}
4) Rusticocangini×Rus tico	Plant height(cm)	-10.26±7.23 ^{n.s}	-41.15±5.16**	-15.74±59.62 ^{n.s}	17.84 ±66.59 ^{n.s}
	No. of leaves	-0.63±1.14 ^{n.s}	-0.10±1.18 ^{n.s}	-0.64±3.64 ^{n.s}	0001±3.93 ^{n.s}
	Leaf area (m ²)	0.062±0.033*	-0.11±0.015**	-0.23±0.066**	-0.0931±0.072 ^{n.s}
	No. branches/tassel	6.70±1.87**	-1.19±1.83 ^{n.s}	-3.03±6.64 ^{n.s}	-4.27±7.63*
	No. ears/plant	-0.64±0.111**	-0.17±0.061**	-1.33±1.38 ^{n.s}	-0.255±1. 35 ^{n.s}
	Ear weight (gm)	84.56±12.16**	-70.07±7.59**	-114.75±23.16**	-64.67±26.25**
	Grain yield (gm)	36.45±5.61**	-17.91±3.96**	-6.65±15.29 ^{n.s}	34.96±16.90*

Table 3. Estimates of generation means parameters ,mean (m) ,Additive (d),dominance(h), Additive × Additive(i), Additive× dominance(j) ominance× dominance(l) for seven traits of four maize crosses.

Crosses	Traits	M(mean)	[d](additive)	[h]dominance	[i] additive× additive(d×d)	[j]additive× dominance (d×h)	[l]dominance× dominance (h×h)	type of epistats
1) Rustico×FI01301	Plant height(cm)	150.60± 3.62**	4.72±2.83 ^{ns}	-119.16±15.65**	-144.61± 15.55**	18.54±3.04**	239.31±18.73**	Duplicate
	No. of leaves	11.50±0.91**	-0.22±1.02 ^{ns}	-6.41±4.21 ^{ns}	-8.77±4.17*	-0.56±1.04 ^{ns}	15.58±5.56*	Duplicate
	Leaf area (m ²)	0.452±0.036**	0.062±0.026*	-0.56±0.15*	0.66±0.15*	0.059±0.03*	1.14±0.17*	
	No. branches/tassel	8.95±0.74**	1.57±0.88 ^{ns}	2.35±3.44 ^{ns}	-1.63±3.43 ^{ns}	-2.42±0.89*	19.25±4.62**	Complementary
	No. ears/plant	1.19±0.11**	-0.18±0.10 ^{ns}	0.45±0.49 ^{ns}	-0.40±0.48*	-0.15±0.11 ^{ns}	1.85±0.62**	
	Ear weight (gm)	110.33±9.52**	-3.52±5.88 ^{ns}	93.16±39.94*	-76.03±39.87 ^{ns}	10.10±6.36	496.16±45.04**	Complementary
	Grain yield (gm)	69.94±6.76**	-10.71±5.87 ^{ns}	92.17±29.83**	-40.78±29.47 ^{ns}	8.62±5.89 ^{ns}	414.38±36.97**	
2) AntignaoHi39× Nostred	Plant height(cm)	94.50±2.63**	5.97±2.84**	121.92±12.01**	112.45±11.95**	8.22±2.91**	-133.59±15.65**	Duplicate
	No. of leaves	10.00±0.91**	-0.59±0.62 ^{ns}	2.44±3.87 ^{ns}	0.33±3.85**	-0.54±0.64 ^{ns}	-1.21±0.45 ^{ns}	
	Leaf area (m ²)	0.30±0.06**	0.001±0.032 ^{ns}	0.25±0.24 ^{ns}	0.19±0.24 ^{ns}	0.001±0.032 ^{ns}	-0.39±0.26 ^{ns}	Duplicate
	No. branches/tassel	12.75±1.75**	2.89±1.74 ^{ns}	12.48±7.82 ^{ns}	9.28±7.81 ^{ns}	3.86±1.76*	-28.36±9.88**	
	No. ears/plant	1.19± 0.19**	-0.083±0.13 ^{ns}	0.98±0.79 ^{ns}	0.09±0.79 ^{ns}	-0.08±0.13 ^{ns}	0.84±0.92 ^{ns}	Duplicate
	Ear weight (gm)	84.63±6.12**	-52.96±5.09**	256.98±26.65**	177.05±26.53**	-54.47±5.16**	-240.64±32.21**	
	Grain yield (gm)	72.65±6.15**	-29.49±3.72**	118.68±25.89**	69.04±25.69**	-24.67±3.78**	-94.88±29.46**	
3) Lo1391 ×Rustico	Plant height(cm)	121.46±6.61**	-2.32±4.69 ^{ns}	8.50±28.12 ^{ns}	-6.64±28.07 ^{ns}	10.02± 4.75*	67.27±32.60*	Duplicate
	No. of leaves	11.51±0.68**	-0.33±0.36 ^{ns}	0.88±2.83 ^{ns}	-0.65±2.81 ^{ns}	-0.49±0.40 ^{ns}	-3.03±3.15 ^{ns}	
	Leaf area (m ²)	0.399± 0.04**	0.033±0.023 ^{ns}	0.063±0.18 ^{ns}	0.068±0.18 ^{ns}	0.02± 0.02 ^{ns}	-0.23±0.20 ^{ns}	Duplicate
	No. branches/tassel	13.77±1.64**	5.88±1.39**	15.27±7.13*	11.75±7.12 ^{ns}	2.61±1.39 ^{ns}	-30.62±8.61**	
	No. ears/plant	1.25±0.10**	0.038±0.08 ^{ns}	0.79±0.45*	0.42±0.46 ^{ns}	0.10 ±0.08 ^{ns}	-0.58±0.53 ^{ns}	Duplicate
	Ear weight (gm)	162.61±6.49**	-121.55±5.81**	182.39±28.45**	109.71±28.43**	-90±5.80**	-346.45±34.94**	
	Grain yield (gm)	90.69±6.10**	-54.78±5.67**	248.73±27.01**	171.20±26.91**	-32.69±5.69**	-283.38±33.64**	
4)Rusticocangin i×Rustico	Plant height(cm)	130.25±14.89**	7.33±4.31 ^{ns}	-30.02±60.2 ^{ns}	-35.66±60.18 ^{ns}	15.44±4.34**	87.07±62.08 ^{ns}	Duplicate
	No. of leaves	10.37±0.89**	0.000±0.78 ^{ns}	1.45±3.93 ^{ns}	0.00±3.92 ^{ns}	-0.31±0.80 ^{ns}	0.64±4.81 ^{ns}	
	Leaf area (m ²)	0.34±0.016**	0.094±0.074**	0.275±0.07**	0.187±0.07**	0.09±0.017**	-0.14±0.095 ^{ns}	Duplicate
	No. branches/tassel	14.25± 1.70**	4.27±1.20**	23.95±7.25**	8.54±7.22 ^{ns}	3.94±1.23**	-14.06±8.45 ^{ns}	
	No. ears/plant	0.97±0.34**	0.208±0.01**	0.67±1.37 ^{ns}	0.51±1.36 ^{ns}	-0.23±0.06**	0.29±1.37**	Duplicate
	Ear weight (gm)	109.75±5.63**	64.62±6.88**	180.34±26.54**	129.24±26.4**	77.31±6.94**	-143.72±35.97**	
	Grain yield (gm)	91.65±3.77**	12.59±3.29**	63.48±16.51**	25.19±3.34 ^{ns}	27.18±3.34**	-43.73±20.19**	

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