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Research Article

MODE OF ACTION OF GENES CONTROLLING ANTHESIS-SILKING INTERVAL (ASI) AND GRAIN YIELD AND ITS COMPONENT TRAITS IN MAIZE

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Abstract- Triple test cross analysis was used to detect epistasis for eleven quantitative traits in maize. Analysis of variance for detection of epistasis revealed the presence of epistasis for all traits studied. Additive × additive (*i* type) digenic epistasis was highly significant for the traits such as days to tasseling, days to silking, cob width, kernel rows cob^{-1} and shelling *per cent* except ASI, cob length, kernels row^{-1}, grain yield plot^{-1} and 100 grain weight. Both additive × dominance (*j* type) and dominance × dominance (*l* type) epistasis were significant for all characters. The degree of dominance was less than one for all the traits, indicating the presence of partial dominance in inheritance of all the traits. The correlation coefficient of sums and differences and F-value were found non-significant for all the traits. The magnitude of additive components was higher compared to dominance components for all traits.

Keywords- Maize, Triple Test Cross, Epistasis, Additive Variance, Dominance Variance

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Introduction

Maize is the third most important food grain in the developing world after wheat and rice. Maize known as the 'Queen of Cereals' is an important economic crop with enormous genetic variability and, due to its high yield potential, it is recognized as a major crop that can ensure food security worldwide. The fact that, maize is cultivated in diverse environments indicates its versatility.

Grain yield is the most important trait in maize. Selection based on grain yield *per se*, especially under moisture stress condition has often been ineffective due to low heritability and greater genotype × environment interaction. However, the use of secondary traits of adaptive value whose genetic variability increases under drought is reported to increase selection efficiency [2]. Anthesis-Silking Interval ASI), the difference between days to silking and days to tasseling is a powerful secondary trait in maize that is positively correlated with grain yield under drought stress has a relatively high heritability [18].

Elucidation of genetic components of variance is an important pre-requisite for efficient management of available genetic variability and formulation of systematic breeding programme [17]. Knowledge on the genetic control of ASI, grain yield and its component traits in the working collection is essential in formulating appropriate selection strategy. The choice of most suitable breeding procedure, among the several available, depends to a large extent on the nature of gene action involved in the expression of target traits [4]. The detection, estimation and interpretation of epistasis has progressed much faster at the level of first degree statistics [13] which suffers from a few limitations due to the internal cancellation of genic effects. TTC (Triple Test Cross) analysis [11], provides unambiguous test for the detection of epistasis of epistasis regardless of gene frequencies, degree of inbreeding and linkage relationships. The information obtained through TTC analysis would help to understand the genetic basis and design appropriate breeding strategy for the development of high yielding cultivars in maize. Hence, the present study was undertaken to get an insight into the mode of action of genes underlying expression of ASI, grain yield and its component traits.

Material and Methods

The basic genetic material for the study included two maize inbred lines MAI-349 and BGD-89 which differed for ASI, grain yield and its component traits [Table-1a] and [Table-1b]. These two inbred lines were crossed to produce F_1 during summer 2013 and the F_1 was raised and selfed during *kharif* 2013 to get F_2 seeds. A total of 17 randomly selected F_2 plants from the cross MAI-349×BGD-89, was backcrossed, as male parent to three testers MAI-349 (P_1), BGD-89 (P_2) and their F_1 (MAI-349×BGD-89) in the experimental plots of the Department of Genetics and Plant Breeding (GPB), UAS, GKVK, Bengaluru during 2014 *kharif* to generate 51 TTC progeny families, which consisted of $17L_{1i}$, $17L_{2i}$ and 17L3i progeny families. The 51 TTC progeny families were evaluated in a block containing rows of 3 m length with a spacing of 0.6 m between rows and 0.3 m between plants within a row in experimental plots of the Department of Genetics and Plant Breeding, UAS, GKVK, Bengaluru during *rabi* 2014. Data on eleven quantitative traits (days to tasseling, days to silking, ASI, plant height, cob length, cob width, kernels row^{-1}, kernel rows cob^{-1}, grain yield plant^{-1}, shelling *per cent* and 100 grain weight) were recorded on randomly labelled 30 plants in each of the 51 TTC progenies.

Table-1a *Salient features of two maize inbred lines contrasting for ASI, grain yield and its components*

Lines	Days to tasseling	Days to silking	ASI	Grain yield plant^{-1} (g)	Cob length (cm)	Cob width (cm)
BGD-89	**63.13**	**69.63**	**6.50**	42.70	12.02	10.21
MAI-349	**59.41**	**60.38**	0.96	131.30	14.90	11.56

Table-1b *Salient features of two maize inbred lines contrasting for ASI, grain yield and its components*

Lines	Kernel rows	Kernels row^{-1}	100 grain weight (g)	Shelling *per cent*	Plant height (cm)
BGD-89	11.20	19.81	19.11	79.07	156.31
MAI-349	14.67	32.13	32	85.50	177.80

Statistical analysis of data

Test for epistasis

The trait values of individual plants of TTC progenies were used for statistical analysis. The detection of epistasis was investigated according to the method given [11], and is based on genetic model;

$$Lijk = M + Gij + Rk + Eijk$$

Where,

Lijk = Phenotypic value of the cross between tester i and line j in k replication

M = Overall mean of all single

Gij = Genotypic value of cross between tester i and line j

Rk = Effect of kth replication.

Eijk = Error

For the detection of epistasis, the contrast ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) of each of the TTC progeny set was computed, where, L_1 and L_2 are the two parents of the cross and L_3 is the F_1 of these parents. $\bar{L}_{1i}$is the trait mean of the progeny obtained by crossing ith F_2 plant to P_1, $\bar{L}_{2i}$ is the trait mean of the progeny obtained by crossing ith F_2 plant to P_2 and $\bar{L}_{3i}$ is the trait mean of the progeny obtained by crossing an ith F_2 plant to F_1. For detection of epistasis the mean square for deviations L1i + L2i-2L3i was used. The total epistasis was partitioned into three types, *viz*., additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) gene interactions. To detect the direction of dominance, the estimates of additive (D) and dominance (H) genetic components and the correlation coefficient (r) between sums (L_{1i}+L_{2i}) and differences (L_{1i}-L_{2i}) were obtained [9]. The degree of dominance was calculated as $(H/D)^{1/2}$.

Direction of dominance

Direction of dominance can be known by 'F' value [1] where, F is the covariance of sums ($\bar{L}_{1i} + \bar{L}_{2i}$) and differences ($\bar{L}_{1i} - \bar{L}_{2i}$). F measures the sum of the products of the additive effects (d) and dominance (h) genetic effects at the loci controlling the inheritance of target traits. Direction of dominance was inferred from the different combination of estimates of dominance genetic variance (σ^2_d) and 'F'. Significant 'F' and σ^2_d indicate the presence of unidirectional dominance; non-significant 'F' and σ^2_d indicate the presence of ambi-directional dominance and significant σ^2_d and non-significant 'F' indicate bidirectional dominance.

Detection of linkage

Linkage and its phases between the genes controlling quantitative traits was detected following Lavene statistic and interpreted using $\sigma^2_{F_2}$(variance due to F2 population) and σ^2_{L3i}(variance due to progeny obtained by crossing an ith F2 plant to F1) relationships. The equal $\sigma^2_{F_2}$ andσ^2_{L3i} implies absence of linkage, and if $\sigma^2_{F_2}$is greater than σ^2_{L3i}indicate presence of coupling phase and if $\sigma^2_{F_2}$lesser than σ^2_{L3i}indicate the presence of repulsion phase.

The relationship was tested using 'F' test [19, 8]. Also, significance of ($\bar{F}_2$- $\bar{L}_{3i}$) which is tested following 't' test, implies presence of linkage of epistatic genes displaying epistasis controlling quantitative traits [3].

Where,

$\bar{F}_2$is the mean of F_2 population

$\bar{L}_{3i}$ismean of the progeny obtained by crossing an ith F_2 plant to F_1

Results and Discussion

Test for epistasis

The analysis of variance for detection of epistasis in the inheritance of traits [Table-2a] and [Table-2b], revealed that mean squares due to total epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$) was highly significant for all the characters. Additive × additive (*i* type) digenic epistasis was highly significant for the traits such as days to tasseling, days to silking, cob width, kernel rows cob^{-1}, and shelling *per cent* except ASI, cob length, kernels row^{-1}, grain yield plot^{-1} and 100 grain weight which suggested effectiveness of selection in early segregating generation for the improvement of the characters [17,16,7]. Both additive × dominance (*j* type) and dominance × dominance (*l* type) of epistasis were significant for all characters indicating that epistasis cannot be ignored in genetic models designed to estimate components of genotypic variances and also emphasized the inadequacy of additive-dominance model and the importance of epistasis in the inheritance of the characters. The magnitude of additive components were higher compared to dominance components for days to tasseling, days to silking, ASI, plant height, kernel rows cob^{-1}, shelling *per cent* and kernels row^{-1} indicating that the fixable components of epistasis were more important than non-fixable in the inheritance of most of the traits [10,17,9,14,15].

Table-2a *Analysis of variance for detection of epistasis for eleven quantitative traits in maize*

Source	Degrees of freedom	Mean sum of squares					
		Days to tasseling	Days to silking	ASI (Days)	Plant height (cm)	Cob length (cm)	Cob width (cm)
Total epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$)	17	4.12**	2.91**	0.95**	84.6**	1.29**	0.16**
Additive × Additive (*i* type) of epistasis	1	10.3**	6.96**	0.32	320.66**	0.003	0.0004
Additive × Dominance + Dominance × Dominance (*j* and *l* type) of epistasis	16	3.73**	2.66**	0.99**	69.84**	1.37**	0.17**
Within progeny	1479	0.27	0.33	0.2	8.36	0.16	0.02

*Significance at P = 0.05, **Significance at P =0.01

Table-2b *Analysis of variance for detection of epistasis for eleven quantitative traits in maize*

Source	Degrees of freedom	Mean sum of squares				
		Kernels row^{-1}	Kernel rows cob^{-1}	Grain yield plant^{-1} (g)	Shelling *per cent*	100 grain weight (g)
Total epistasis ($\bar{L}_{1i} + \bar{L}_{2i} - 2\bar{L}_{3i}$)	17	6.17**	0.82**	196.63**	5.22**	5.56**
Additive × Additive (*i*type) of epistasis	1	0.12	2.28**	0.66	10.27**	0.43
Additive × Dominance + Dominance × Dominance (*j* and *l* type) of epistasis	16	6.55**	0.73**	208.88**	4.90**	5.88**
Within progeny	1479	1.14	0.09	30.54	0.74	0.61

*Significant at P = 0.05, **Significant at P =0.01

Estimation of additive and dominance components of genotypic variation

The analysis of variance of sums ($\bar{L}_{1i} + \bar{L}_{2i}$) and differences ($\bar{L}_{1i} - \bar{L}_{2i}$) [Table-3a] and [Table-3b], was used to estimate the additive and dominance components of genotypic variation, in the presence of epistasis. Mean squares attributable to 'sums' were found significant for all the traits studied, indicating the presence of additive genetic variance (σ^2_A)for all the traits investigated. Significance of mean squares attributable to differences ($\bar{L}_{1i} - \bar{L}_{2i}$) indicated prevalence ofdominance genetic variance (σ^2_D) for all the traits. In the presence of epistasis, estimates of σ^2_A are affected by digenic interactions (additive × additive and additive × dominance) at the loci for which the parents of TTC progeny families differ.

Table-3a *Analysis of variance for detection and estimation of additive (D) and dominance (H) components of genetic variance for eleven quantitative traits in maize*

Source	Degrees of freedom	Mean sum of squares					
		Days to tasseling	Days to silking	ASI (Days)	Plant height (cm)	Cob length (cm)	Cob width (cm)
Sums ($\bar{L}_{1i} + \bar{L}_{2i}$)	16	6.72**	8.06**	1.48**	246.63**	1.55**	0.50**
Difference ($\bar{L}_{1i} - \bar{L}_{2i}$)	16	2.65**	2.14**	0.67**	108.61**	0.43*	0.10**
Within progeny	986	0.28	0.32	0.19	8.51	0.14	0.026

*Significance at P = 0.05, **Significance at P =0.01

Table-3b *Analysis of variance for detection and estimation of additive (D) and dominance (H) components of genetic variance for eleven quantitative traits in maize*

Source	Degrees of freedom	Mean sum of squares				
		Kernels row^{-1}	Kernel rows cob^{-1}	Grain yield plant^{1} (g)	Shelling *per cent*	100 grain weight (g)
Sums ($\bar{L}_{1i} + \bar{L}_{2i}$)	16	19.12**	0.96**	589.01**	10.61**	13.53**
Difference ($\bar{L}_{1i} - \bar{L}_{2i}$)	16	3.75**	0.50**	130.53**	10.00**	2.36**
Within progeny	986	1.06	0.09	31.20	0.80	0.58

*Significance at P = 0.05, **Significance at P =0.01

The estimates of σ^2_D are influenced by only the dominant genes for which L_1 and L_2 differ. Significant mean squares due to sums ($\bar{L}_{1i} + \bar{L}_{2i}$) and differences ($\bar{L}_{1i} - \bar{L}_{2i}$) for the traits indicated importance of both additive and dominance components of genetic variance in the inheritance of all the characters [10, 17, 9]. The estimate of additive genetic component (D) was highly significant for all characters [Table-3a] and [Table-3b]. The estimate of dominance genetic component (H) was significant for all traits except for cob width. The magnitudes of additive components were higher compared to dominance components for all traits. Therefore, reliance should mainly be placed on mass selection or inter–population selection or progeny selection or family selection in order to congregate superior genes for the improvement of aforesaid characters. The degree of dominance $(H/D)^{½}$ was less than one for all the traits, indicating the presence of partial dominance in inheritance of all the traits. Further, the correlation coefficient of sums and differences and F-value were found non-significant for all the traits [Table-4a] and [Table-4b] suggesting equal distribution of positive and negative genes among the parents.

Significance of dominance component of genetic variance (H) for all the traits studied indicate any type of selection scheme would fail to achieve higher expression of studied traits; however, a hybrid programme in general is expected to be most effective for exploitation of these traits [16]. Reciprocal recurrent selection [5] is expected to be the most effective breeding method for the improvement of the characters, which are under the influence of dominant gene action.

Direction of dominance

The estimate of 'F' was non-significant while σ^2_d was significant for all the traits [Table-3a] and [Table-3b], indicating bi-directional dominance in the inheritance of the studied traits. Further, both increasing and decreasing alleles were dominant and recessive to the same extent as revealed from significant 'σ^2_d' and non-significant 'F' value [15].

Table-4a *Estimates of additive and dominance components, degree of dominance $(H/D)^{1/2}$, correlation coefficient (sums and differences) and direction of dominance (F), for eleven quantitative traits in TTC progenies of maize*

Genetic parameters	Days to tasseling	Days to silking	ASI (Days)	Plant height (cm)	Cob length (cm)	Cob width (cm)
D	25.77**	30.96**	5.14**	352.47**	5.60**	1.92**
H	9.46**	7.27**	1.91*	400.38**	1.15*	0.30
$(H/D)^{1/2}$	0.60	0.48	0.60	0.64	0.45	0.39
F	-0.08	-11.04	7.97	-53.16	2.88	0.78
r (Sums/difference)	0.001	0.16	-0.49	0.02	-0.21	-0.21

*Significance at P = 0.05 **Significance at P =0.01

Table-4b *Estimates of additive and dominance components, degree of dominance $(H/D)^{1/2}$, correlation coefficient (sums and differences) and direction of dominance (F), for eleven quantitative traits in TTC progenies of maize*

Genetic parameters	Kernels row^{-1}	Kernel rows cob^{-1}	Grain yield plant^{1} (g)	Shelling *per cent*	100 grain weight (g)
D	72.23**	3.49**	223.14**	51.78**	39.26**
H	10.78**	1.65*	397.19**	7.10**	36.80**
$(H/D)^{1/2}$	0.38	0.68	0.42	0.37	0.96
F	20.93	2.99	193.08	-8.81	55.61
r (Sums /difference)	-0.15	-0.26	-0.04	0.09	-0.33

*Significance at P = 0.05 **Significance at P =0.01

Detection of linkage between loci controlling quantitative traits

The genes controlling plant height, cob width, kernel rows cob^{-1}, grain yield^{-1} and shelling *per cent* were unlinked as indicated by non-significance of Lavene's statistic. On the other hand, genes controlling, days to tasseling, days to silking, ASI, cob length, kernels row^{-1} and 100 grain weight were found linked in coupling phase [Table-5]. Non-significance of ($\bar{F}_2$- $\bar{L}_{3i}$)implied absence of linkage between interacting genes controlling all the traits [Table-6].

Table-5 *Test of linkage and its phase between genes controlling eleven quantitative traits in maize as per Levene test*

Traits	$\sigma^2_{F_2}$	$\sigma^2_{L_{3i}}$	Levene Statistic	Prob.	State of Linkage
Plant height (cm)	179.56	127.69	0.29	0.59	Absent
Days to tasseling	10.75	2.04	7.06	0.01	Predominantly coupling phase
Days to silking	11.49	2.95	10.55	0.001	Predominantly coupling phase
ASI (Days)	6.45	1.58	5.00	0.03	Predominantly coupling phase
Cob length (cm)	4.97	0.72	6.89	0.01	Predominantly coupling phase
Cob width (cm)	1.46	0.32	3.48	0.06	Absent
Kernels row^{-1}	58.36	8.35	5.62	0.02	Predominantly coupling phase
Kernel rows cob^{-1}	6.70	0.84	2.69	0.10	Absent
Grain yield plant^{1} (g)	1310.44	219.04	3.14	0.08	Absent
Shelling *per cent*	66.91	4.88	0.96	0.33	Absent
100 grain weight (g)	20.16	4.41	4.28	0.04	Predominantly coupling phase

*Significance at P = 0.05 **Significance at P =0.01

Table-6 *Test of linkage and its phase between genes controlling for eleven quantitative traits in maize as per 't' test*

Traits	$\bar{F}_2$	$\bar{L}_{3i}$	Two sample 't'statistic	State of linkage
Plant height (cm)	200.67	203.62	-0.059	No linkage between interacting genes
Days to tasseling	76.87	74.97	0.16	No linkage between interacting genes
Days to silking	79.35	77.42	0.15	No linkage between interacting genes
ASI (Days)	2.47	2.45	0.002	No linkage between interacting genes
Cob length (cm)	15.91	16.51	-0.07	No linkage between interacting genes
cob width (cm)	11.90	11.67	0.05	No linkage between interacting genes
Kernels row^{-1}	27.94	28.35	-0.01	No linkage between interacting genes
Kernel rows cob^{-1}	13.64	13.95	-0.03	No linkage between interacting genes
Grain yield plant^{1} (g)	85.92	83.55	0.02	No linkage between interacting genes
Shelling *per cent*	80.45	82.01	-0.05	No linkage between interacting genes
100 grain weight (g)	21.18	22.56	-0.08	No linkage between interacting genes

Linkage between desirable characters enhances the effectiveness of selection, whereas linkage between desirable and undesirable genes hinders the progress of selection. Thus, in the present study-coupling phase of linkage between genes controlling ASI suggested the effectiveness of selection for ASI in segregating generations.

Conclusion

Epistasis played a significant role in the inheritance of all the characters. The preponderance of additive component for expression of grain yield and other traits indicated the amenability of these traits for improvement through simple selection procedure. Significance of dominance component of genetic variance indicated lesser effectiveness of simple selection to achieve genetic gain for all the traits investigated. Reciprocal recurrent selection (RSS) is expected to be the most effective breeding method for the improvement of the characters, which are under the influence of dominant gene action.

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Author Contribution

The present reported work is a part of PhD thesis research

Conflict of Interest: None declared

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