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Research Article

Genetics of grain yield and its component traits in maize (*Zea mays* L.)

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Abstract
The six essential generations (2 parents, F_1, F_2 and backcrosses) of the cross NAI-137 × 97B developed from two parents distinguishable for grain yield were evaluated to construe the genetics of grain yield and its component quantitative traits during *Kharif,* 2019 at University of Agricultural Sciences, Bangalore, India. The expanse and direction of the additive genetic effects [a], dominance genetic effects [d], magnitudes of additive genetic variance (σ^2_A) and dominance genetic variance (σ^2_D) differed with various traits under study. Additive and ambidirectional dominant effects were involved in controlling most of the traits. Steep magnitudes of additive genetic effects [d] in desirable direction for most of the traits indicated the possibility of retrieving prudent segregants in early segregating generations while exercising pedigree method of handling progenies generated. It was evident from the results obtained that there was dispersion of genes among both the parents for all the traits studied.

Keywords: Additive–dominance model, Epistasis, Genetic gain, Inheritance

INTRODUCTION

Maize is the third most overriding staple cereal food crop of the world. It supports the livelihood of millions of people around the world. Because of its multiple uses, it is truly regarded as 4F crop *i.e.,* Food, Feed, Fuel and Fodder. Hence, it also contributes to the global economy. Grain yield is the most supreme quantitative and complex trait in maize. Its expression is governed by genetic, environmental effects and genotype × environment interaction. The principles and understanding of type of gene action entailed in governing the trait is of help in the choosing the most appropriate breeding procedure for genetic improvement of maize. Generation mean analysis, a biometrical method developed by Mather and Jinks (1982), is an advantageous technique to dictate gene effects for polygenic traits. Its greatest utility lies in the potential to evaluate epistatic gene effects such as additive × additive [i], additive × dominance [j] and dominance × dominance [l] interactions (Singh and Singh, 1992). A rigorous understanding of the genetic mechanisms involved in governing yield and its attributing traits is indispensible to breed improved varieties (Saleem *et al*., 2002; Unay *et al*., 2004). Using the principles of first, second, third and fourth degree statistics, genetics of complex quantitative traits can be deciphered. On account of complementary cancellation of positive and negative additive effects and ambidirectional dominance effects of genes scattered between the parents used in the research programmes, the first degree statistics-based additive and dominance and their digenic interaction effects are likely to be misjudged (Jayasekara and Jinks, 1976; Jinks, 1981). Gene effects that are very low in magnitude (< 1.0), shall be misconstrued when interpreted only based on second degree statistics. Amalgamation of all the degrees statistics of helps in detecting the genetic architecture of traits more precisely (Kearsey and Pooni, 1996). Majority of the researchers seeking to elucidate the genetics of quantitative traits have used either the first or second degree statistics and infrequently both including third and fourth degree statistics as well. Accordingly, the objective of the present study was to interpret the genetics of grain yield and its component traits in maize based on the combination of first, second, third and fourth degree statistics.

MATERIALS AND METHODS

The basic material for the study comprised of the cross NAI-137 × 97B whose parents were varying for grain yield and productivity *per se* traits. The parents were crossed to obtain F_1's during *Kharif,* 2018 to generate F_2 and backcrossed to their respective parents to develop B1 and B2 populations during summer 2018 at the experimental plots of the Department of Genetics and Plant Breeding (GPB), University of Agricultural Sciences (UAS), Bengaluru, India. The two parental genotypes and F_1, F_2, B_1 and B_2 generations derived from the cross constituted the experimental material.The two parental genotypes and their F_1, F_2, B_1 and B_2 generations were planted during *Kharif,* 2019 and were appraised in augmented design. A spacing of 0.6 m and 0.3 m between plants and within a row was maintained, respectively. Proposed agronomic and plant protection practices were followed to raise a healthy crop. Data was documented on 30 plants in parental genotypes and their F_1's (150), on 100 plants in B1 and B2 generations and on 200 plants in F_2 generations for days to tasseling, days to silking, ASI, plant height, ear length, ear circumference, kernel rows/cob, kernels/row, test weight and grain yield.

The mean values, along with their standard errors of the six generations (P1, P2, F1, F_2, B1 and B2) of the cross was enumerated for all the traits under the study (Fisher, 1950). For biometrical genetic analysis the estimates of means were used. Joint scaling test was used to appraise the adequacy of additive–dominance (A–D) model for inheritance of the traits (Cavalli, 1952) as delineated by Mather and Jinks (1982). The observed and estimated means to determine the goodness of fit of the six generations and the various other parameters *viz.,* the general mean [m], the additive genetic effects [a] and the dominant genetic effects [d] are used as the yardsticks to scrutinize the adequacy of A–D model in the inheritance of the traits under investigation. The weighted least square principle was used to estimate the parameters *viz*., [m], [a] and [d] (Cavalli, 1952; Mather and Jinks, 1982). The adequacy and nonadequacy of A–D model was determined based on the good and lack of fit, respectively. Upon the A–D model being inadequate, estimation and determining the significance of estimate additive [a], dominance [d] and digenic epistatic effects, namely additive×additive [i], additive × dominance [j] and dominance × dominance [l] effects is done using the perfect fit solution and '*t*' test, respectively (Mather and Jinks, 1982). Additive genetic variance [σ^2_A] and dominance genetic variance [σ^2_D] were reckoned using the method defined by Mather and Jinks (1982). The mentioned biometrical genetic analyses were estimated using GENSTAT software v15. Genetics of all the traits under description were interpreted based on the joint contemplation of [a] and [σ^2_A]; [d] and [σ^2_D]; and [d] and [l] (Kearsey and Pooni, 1996).

RESULTS AND DISCUSSION

A combination of enormous of genes with diverse enormity of effects and modes of action (additive, dominance and epistasis) are involved in the inheritance of complex quantitative traits like grain yield and its attributing traits, including a significant noncrossover/ crossover interaction with environment (Kearsey and Pooni, 1996). Recurrence of genes, kinds of genetic material, history of selection and chief mode of pollination shall be used as a function to determine the mode of action of genes and their interaction with environment (Bernardo, 2010, 2014; Acquaah, 2012). Hence, it is pre-requisite to decode modus operandi of genes governing quantitative traits in the genetic material that shall be handled by breeders to advance improved crop cultivars. Conjecturing only additive and dominance effects using simple genetic models mode of action of genes can be unraveled, further cautiously escalating the complexity of the model by inclusion of parameters specifying digenic interactions and genotype × environment interaction (GEI).

Inadequacy of first degree statistics-based simple A–D model was confirmed by significance of joint scaling test observed in the present study (**Table 1**). Inadequacy of A–D model could be imputed due to the complicity of parameters specifying digenic epistasis and/or GEI. The study encompassed only digenic epistasis parameters namely [i], [j] and [l] in the A–D model presupposing the absence of GEI or GEI is of noncrossover type (Mather and Jinks, 1982). Most of the parameters designating epistasis were significant in for most of the traits

Quantitative traits governed by epistatic genes shall be categorized as either largely duplicate or complementary, the contrast being wholly based on the relative signs of [d] and [l] components. Positive estimates of [d] and [l] results in complementary epistasis between dominant increasing alleles, while negative estimates result in complementary epistasis between dominant decreasing alleles. Whereas, positive [d] and negative [l] constitutes the duplicate epistasis between dominant increasing alleles, negative [d] and positive [l] constitutes the duplicate epistasis between dominant decreasing alleles (Kearsey and Pooni, 1996). ASI, plant height and test weight were governed by dominant genes with decreasing effects and duplicate epistasis (**Table 2**), as dominance × dominance type of gene action is non-fixable, it can be said that selection may not be effective in early segregating generation in realizing genetic gains for these traits. With respect to the test weight and grain yield per plant, the magnitude of additive gene effects [d] and dominance × dominance [l] gene interaction was noticed to be positive. This suggested the need to exploit heterosis and or selection of beneficial segregants through pedigree method for the improvement of grain yield per plant. The existence of duplicate type of epistasis accompanied with dominance [h] gene effects in negative direction suggested the need for one or two cycles of biparental mating to dissipate [h] and increase [d] so as to assist in isolating desirable segregants for ASI, plant height and test weight.

Table 1. Estimates of components of generation means and testing the adequacy of Additive- Dominance model in the inheritance of grain yield and its attributing traits in maize

Character	m	$[\hat{d}]$	$[\hat{h}]$	χ^2 statistic	Probability	Adequacy of Additive-Dominance (A-D) model
Days to tasseling	60.23*	4.90*	-9.41*	22.88	0.00	Inadequate
Days to silking	65.15**	6.02	-12.16	37.22	0.00	Inadequate
Anthesis-Silking interval (days)	3.92*	1.12*	-2.74	33.92	0.00	Inadequate
Plant height (cm)	199.22*	-34.24	-39.90	36.28	0.00	Inadequate
Ear length (cm)	16.55*	-1.02	6.31	61.82	0.00	Inadequate
Ear circumference (cm)	12.07*	-1.68*	23.84*	309.93	0.00	Inadequate
Kernel rows / cob	13.56**	-2.64*	4.22	48.36	0.00	Inadequate
Kernels / row	20.98*	-5.20	5.27*	53.64	0.00	Inadequate
Test weight (g)	23.56**	2.38*	-7.32	18.57	0.00	Inadequate
Grain yield per plant (g)	152.30*	-18.26	-46.75*	117.43	0.00	Inadequate

* Significant P @ 0.05 ** Significant P @ 0.01

Table 2. Estimates of main genetic and digenic-epistatic effects for which Additive-Dominance model was inadequate in the inheritance of grain yield and its attributing traits in maize

Traits	m	$[\hat{d}]$	$[\hat{h}]$	$[\hat{i}]$	$[\hat{j}]$	$[\hat{l}]$	Type of digenic epistasis
Days to tasseling	60.31*	-0.12	30.92	-12.24	10.05*	21.51**	Complementary epistasis genes with dominant increasing effect
Days to silking	63.26*	-1.75*	40.28*	-14.16	15.54	28.12	Complementary epistasis genes with dominant increasing effect
Anthesis-Silking interval (days)	4.94*	-1.62*	-9.35	-1.92*	5.49*	6.61**	Duplicate epistasis genes with dominant decreasing effect
Plant height (cm)	185.50	-4.07	-15.23*	-34.08*	-60.33	11.33*	Duplicate epistasis genes with dominant decreasing effect
Ear length (cm)	12.09**	3.15**	23.53	7.76*	-8.34**	-17.22	Duplicate epistasis genes with dominant increasing effect
Ear circumference (cm)	11.31*	0.87	69.69*	27.24	-5.11	-45.83*	Duplicate epistasis genes with dominant increasing effect
Kernel rows / cob	12.98	-0.01*	14.37*	4.64	-5.18**	-10.15	Duplicate epistasis genes with dominant increasing effect
Kernels / row	24.59**	-0.75	4.28	5.36**	-8.90	0.99*	Complementary epistasis genes with dominant increasing effect
Test weight (g)	30.66	4.11	-21.08	-1.00*	-3.46*	13.75	Duplicate epistasis genes with dominant decreasing effect
Grain yield per plant (g)	142.45*	1.02	85.63*	18.20	30.00**	96.85**	Complementary epistasis genes with dominant increasing effect

* Significant P @ 0.05 ** Significant P @ 0.01

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The estimates of σ^2_A were higher than the [d] for days to tasseling, days to silking, plant height, ear length, kernel rows / cob, kernels / row and grain yield per plant. Both additive gene effects and dominance gene effects (**Table 3**) were noticed in second degree statistics, unlike first degree statistics. A significantly lower magnitude of additive genetic effect [d] coupled with small and non significant additive genetic variance (σ^2_A) was discerned to be paramount in the expression of days to tasseling, ASI, ear circumference, kernel rows/cob and test weight. Significantly lower magnitude of additive genetic effects [d] coupled with significant additive genetic variance (σ^2_A) were observed to be important in the expression of ASI.

The dispersion of increasing and decreasing alleles controlling these traits between parents could be presumed because of the evidence of significant additive genetic effects [d] of lower magnitude coupled with substantial additive genetic variance (σ^2_A). Often this results in mutual cancellation of effects of increasing and decreasing alleles (Mather and Jinks, 1982). Significant higher estimates of additive genetic effects [d] coupled with minor non-significant additive genetic variance and or massive additive genetic variance (σ^2_A) suggested that effect of individual gene controlling trait are very small. A significant association of additive effect genes was observed to be involved in the inheritance of days to tasseling, days to silking, ASI and grain yield per plant as evident by a higher magnitude of additive genetic effects and their variances. As these traits were under the influence of additive gene effects, which are fixable, simple selection may be worthwhile in refining these traits.

The estimates of [h] and dominance genetic variance (σ^2_D) were significant and non-significant, respectively for days to tasseling, ear circumference and kernels / row, suggesting there is no presence of dominance in the inheritance of these traits) **(Table 4**. While, non-significant estimates of dominance genetic effect [h] and non-significant estimate of dominance genetic

Table 3. Estimates of components of genotypic variance for grain yield and its attributing traits in maize

Character	Components of genotypic variance		
	Additive genetic variance	Dominance genetic variance	Degrees of dominance
Days to tasseling	9.61	-1.49	-1.38
Days to silking	10.43	1.65	-1.42
Anthesis-Silking interval	1.11*	0.07	-1.56
Plant height	-34.19	28.93*	1.07
Ear length	3.06**	-0.39	-2.48
Ear circumference	-3.36	0.28	-3.76
Kernel rows / cob	2.15	0.32	-1.26
Kernels / row	7.29*	1.14	-1.00
Test weight	-11.47	1.13	-1.75
Grain yield per plant	555.56	-75.88**	1.60

* Significant P @ 0.05 ** Significant P @ 0.01

Table 4. Estimates of additive genetic effects and their variances (σ^2_A) and dominant genetic effects and their variances (σ^2_D) in the inheritance of grain yield and its attributing traits in maize

Traits	[d]	(σ^2_A)	[h]	(σ^2_D)	$\square^2_D / \sigma^2_A$
Days to tasseling	4.90*	9.61	-9.41*	-1.49	-0.15
Days to silking	6.02	10.43	-12.16	1.65	0.15
Anthesis-Silking interval	1.12*	1.11*	-2.74	0.07	0.06
Plant height	-34.24	-34.19	-39.90	28.93*	-0.84
Ear length	-1.02	3.06**	6.31	-0.39	-0.12
Ear circumference	-1.68*	-3.36	23.84*	0.28	-0.08
Kernel rows / cob	-2.64*	2.15	4.22	0.32	0.14
Kernels / row	-5.20	7.29*	5.27*	1.14	0.15
Test weight	2.38*	-11.47	-7.32	1.13	-0.09
Grain yield per plant	-18.26	555.56	-46.75*	-75.88**	-0.13

* Significant P @ 0.05 ** Significant P @ 0.01

variance (σ^2_D) was observed for days to silking, ASI, ear length, kernel rows / cob and test weight. Whereas, significant negative dominance genetic effect [h] and dominance genetic variance (σ^2_D) was observed for grain yield plant. It encouraged the association of ambi-directional dominance in the inheritance of these traits. A steep dominance genetic effects [h] and large dominance genetic variance (σ^2_D) indicated the participation of dominance gene action in the inheritance of ear circumference, kernel rows / cob and kernels / row. The results are in agreement with that of the study by Devi (2020) and on quality protein maize by Agrawal and Singh (2014).

Positive platykurtic distribution of F_2 population propounded the implication of enormous number of genes disposing complementary epistasis with decreasing effects in the expression of days to tasseling, days to silking and ear circumference. Expected genetic gain is steady with mild selection while, speedy with vigorous selection for the improvement of these traits.

Negative platykurtic distribution of F_2 indicated the implication of substantial number of genes with duplicate epistasis coupled with increasing effects in the expression of plant height, ear length, kernel rows/cob, kernels/row, test weight, grain yield per plant. Anticipated genetic gain is fleeting with modest selection while, steady with intense selection in magnifying the degree of this trait.

Therefore, statistics based on first, second, third and fourth degree genetics revealed that additive genetic effects and dominance × dominance digenic epistasis especially duplicate digenic epistasis and complimentary epistasis were predominantly entailed in the transmission of almost all yield and its attributing traits. Elevated degree of additive genetic effects [d] in preferable direction for most of the traits revealed the likelihood of capturing desirable segregants in early segregating generations while exercising pedigree breeding method to handle progenies generated from the cross NAI-137 × 97B. Exploitation of $\sigma 2^A$ in populations subjected to one or a few rounds of intermating by inbreds shall be helpful in increasing genetic gains for target traits steeply.

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