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GENETIC VARIANCE, CORRELATION AND HERITABILITY FOR GRAIN YIELD IN A MEDIUM-MATURING YELLOW-ENDOSPERM MAIZE POPULATION

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ABSTRACT

Information on the magnitude of additive relative to non-additive variance of a trait in a population helps in deciding the appropriate breeding strategies for improving such trait. Two hundred and fifty-five full-sib families derived from IARTZI-Y Pop DT STR C_0 using North Carolina Design I were evaluated at three environments in 2017 to determine the magnitude of additive variance relative to other components of variance in the population, and to assess relationship between grain yield and other agronomic traits. A 17 × 15 alpha-lattice design with two replications was used in each trial after sub-dividing the males into 17 sets, each containing 15 full-sib families. Data collected were subjected to analysis of variance using appropriate software at $P < 0.05$. Males-within-set and females in male-within-set mean squares were significant ($P < 0.01$) for measured traits. Non-additive variances were larger than additive variances for grain yield and anthesis-silking interval but not for other traits, indicating the predominance of non-additive gene action for inheritance of grain yield in the population. The heritability estimates ranged between 1% for grain yield and 94% for ear height. Grain yield had significant positive genotypic correlations with days to mid-silk ($r_g = 0.75^{**}$) and number of ears per plant ($r_g = 0.26$) but negative with husk cover ($r_g = -14^{*}$), anthesis-silking interval ($r_g = -0.11^{*}$), and ear aspect ($r_g = -22^{**}$). Recurrent selection schemes would be effective for improving yield-related traits while grain yield could be improved through hybrid development or by indirect selection through secondary traits.

Keywords: Additive variance, non-additive variance, full-sib families, genotypic correlation, heritability

INTRODUCTION

Maize (*Zea mays* L.), is the third most important cereal crop in the world after wheat and rice and ranks top in grain yield per unit area of land, and its demand is expected to surpass that of wheat and rice by 2020 (Odiyo *et al*., 2014). The shift will be as a result of a 50% projected increase in global maize demand from 558 million tons in 1995 to 837 million tons by 2020 (Pingali and Pandey, 2001). The production of maize is about one billion tons worldwide, with Africa producing about 78 million tons and West Africa (WA) producing about 19.6 million tons (FAOSTAT, 2015).

Maize provides about 30% of the daily calories for more than 4.5 billion people in developing countries (Oyewo, 2011). It is greatly used as food for human consumption, animal feed and extensively in industrial products (Saleh *et al*., 2002). Maize production and productivity is greatest in the savanna agro-ecological zones compared with other agro-ecologies of the WA due to adequate solar radiation, low night temperatures and low incidence of pest and diseases. However, its production and productivity are still hindered by biotic and abiotic factors, including parasitic weed such as *Striga hermonthica*, recurrent drought, and low soil nitrogen (Badu-Apraku *et al*., 2003).

Due to the aforementioned production constraints, maize breeders in national programmes and international maize research centers have devoted considerable efforts over a decade to developing several inbreds, open-pollinated varieties and hybrids with tolerance to drought and low soil nitrogen, as well as resistance to *Striga* to mitigate the production constraints. Such products emanated from well-adapted and broad-based maize population. Availability of sufficient genetic variability in a population is a key factor that determine the appropriate breeding strategies in any maize improvement programme as well as achieving significant progress from selection. Information on the levels of genetic variability and heritability in a population is crucial for designing appropriate breeding strategies for improving the population for target traits. The magnitude of additive, dominance and epistatic variance in a population helps the breeder to decide whether or not to improve the population for target traits and the breeding schemes to be used for the improvement (Shahi and Singh, 1985). Badu-Apraku *et al* (2007) reported preponderance of dominance variance over additive variance for grain yield, plant and ear heights, and *Striga* damage rating at eight weeks after planting. The authors also reported low heritability for most of the traits measured.

Another important requirement in breeding for improved grain yield is the identification of secondary traits that could be utilized in selecting for improved maize grain yield due to low heritability for grain yield most especially under stressed conditions (Bolanos and Edmeades, 1996). The knowledge of genetic association between grain yield and other important traits is, therefore, crucial for making significant progress from selection. Several workers (Edmeades *et al*., 1993, 1995; Bolanos and Edmeades, 1996; Badu-Apraku *et al*., 2007) reported that number of ears per plant, days to anthesis and silking, and ASI are reliable indirect selection criteria for drought tolerance. Badu-Apraku *et al.* (2012) reported that plant aspect and plant and ear heights are the most reliable traits for simultaneous selection for yield improvement under drought and low soil nitrogen conditions.

Maize breeders at the Institute for Agricultural Research (IAR) Samaru, recently developed a medium-maturing yellow-endosperm maize population (IARTZI-Y Pop DT STR C_0), which is tolerant to drought and resistant to *S. hermonthica.* The population was developed from diallel crosses involving elite maize germplasm available in the Institute and those obtained from the International Institute of Tropical Agriculture (IITA). Drought tolerance and *Striga* resistance genes were incorporated into the population by crossing drought-and *Striga* resistant maize inbred lines to the F_1 population followed by backcrossing to the recurrent parent. Hybridization and selection were used in the development of the population. Information on the levels of genetic variability and narrow-sense heritability in the population, IARTZI-Y Pop DT STR C_0 is completely lacking. It is, therefore, desirable to assess the levels of genetic variability and heritability in the population so as to help design appropriate breeding strategies for improving the population for grain yield and other desirable traits. The objectives of the study were to (i) determine the magnitude of additive variance relative to other components of phenotypic variance, and (ii) assess the phenotypic and genotypic relationships between grain yield and yield-related traits.

MATERIALS AND METHODS

Two hundred and fifty-five full-sib families were generated from the drought-tolerant and *Striga* resistant medium-maturing yellow-endosperm maize population, IARTZI-Y Pop DT STR C_0 using the North Carolina Design I mating scheme (Hallauer and Miranda, 1988) by crossing each of 51 randomly selected non-inbred (S_0) male plants to five randomly selected (S_0) female plants at Samaru research farm during the 2016/2017 dry season. The 255 full-sib families were evaluated at Zaria (northern Guinea savanna, 11°11'N, 7°38'E, 640 m asl, 1200 mm annual rainfall), Minjibir (Sudan savanna 12°00' N, 8°22' E, 580 m asl, 800 mm annual rainfall) and Batsari (northern Guinea savanna, 12°45' N, 7°49' E, 605 m asl, 1300 mm annual rainfall) during the growing season of 2017. A 17 × 15 alpha-lattice design with two replications was used in each trial after sub-dividing the males into 17 sets, each containing 15 full-sib families. Sets and full-sib families within each set were allocated randomly to the blocks. Experimental unit consisted of single-row 4-m-long plots, with inter- and intra-row spacing of 0.75 m and 0.40 m, respectively. Three seeds were planted per hill, and the resulting maize plants were thinned to two plants per stand about two weeks after emergence to give a final plant population density of 66,666 plants ha^{-1}. A compound fertilizer, NPK 15-15-15, was applied at rate of 60 kg NPK ha^{-1} two weeks after planting (WAP). An additional 60 kg N ha^{-1} was applied in form of urea at five WAP using urea. The trials were kept weed-free by applying 5 l ha^{-1} each of a mixture of paraquat as a foliar contact herbicide and atrazine as a pre-emergence herbicide. In addition, manual weeding was done, as necessary, to keep the trials weed-free.

Observations were made from each plot on: days to 50% anthesis and days to mid-silk were recorded as the number of days from planting to when 50% of plants had shed pollen and had emerged silks, respectively. Anthesis-silking interval was computed as difference between number of days to mid-silk and days to 50% anthesis. Plant and ear heights were measured as the distance from the base of the plant to the flag leaf and from the base to the node bearing the upper ear respectively. Plant aspect was scored on a scale of 1 to 5, where 1 = true to type with desirable plant height, ear size, low ear placement, excellent husk cover, resistance to foliar diseases and lodging and 5 = plants with severally stunted growth, small ears, susceptible to foliar diseases and lodging. Ear aspect was scored on a scale 1 to 5, where 1= clean, uniform, and large ears and 5= rotten, variable and small ears. Husk cover was rated on a scale of 1 to 5, where 1= husks tightly arranged and extended beyond the ear tip and 5= very loosely arranged husk with ear tip exposed. Numbers of ears per plant was calculated as number of ears harvested divided by the number of plants at harvest. Ears harvested from each plot were shelled to determine percent moisture and grain weight. Grain yield adjusted to 150 g kg^{-1} moisture content was computed from grain weight.

Analysis of variance (ANOVA) was performed on plot means basis of the traits measured across sites using PROC GLM with random option in SAS (SAS Institute, 2002). In the ANOVA, genotypes, replication and block (set) were considered random effects, while location was considered as fixed effect. Variance component attributable to male and female within males and their interaction with environment were computed using expected mean squares. The additive genetic variance (σ^2_a) and dominance variance (σ^2_d) were estimated from the mean squares of the ANOVA as follows:

$\sigma^2_a = 4\sigma^2_m$ (inbreeding coefficient, F = 0 for non-inbred plants)

$\sigma^2_d = 4\sigma^2_{f/m} - 4\sigma^2_m$

where σ^2_m is variance due to male and $\sigma^2_{f/m}$ is variance due to female within male. The standard error of the variance estimates and narrow-sense heritability estimates were computed as described by Hallauer *et al.* (2010)). Genotypic and phenotypic correlation coefficients among agronomic traits and their standard error were computed with the REML method (Holland, 2006) using the MIXED (i.e. the effects of locations was considered as fixed effects, while genotype, replication and genotype x environment interaction were considered as random effects) using SAS (SAS Institute, 2002).

RESULTS

Combined analysis of variance for grain yield and other agronomic traits of the 255 full-sib families across locations showed that environment and set mean squares were highly significant ($P < 0.01$) for all measured traits (Table 1).

Table 1. Mean squares for grain yield and agronomic traits of full-sib families developed from IARTZI-Y Pop DT STR Co evaluated at Zaria, Minjibir and Batsari in 2017.

Source	df	Grain yield	Days to anthesis	Days to silking	ASI	Plant height	Ear height	Ear aspect	EPP	Husk cover	Plant aspect
Environment, E	2	487929562**	5455.6**	3658.9**	199.4**	46062.8**	31045.5**	158.3**	3.7**	86.8**	75.1**
Set	16	5553055**	132.6**	120.3**	1.3**	9090.6**	1126.3**	3.8**	0.1**	0.3**	2.0**
E × Set	32	5454023**	100.8**	97.8**	0.7	10273.4**	573.3**	2.8**	0.1	0.2**	2.2**
Rep (E × Set)	51	1717080*	160.0**	147.6**	0.9**	661.1**	137.4	1.2**	0.0	0.3**	0.3**
Male (Set)	34	3807978**	30.3**	28.0**	1.5**	9428.1**	1075.9**	1.5**	0.1**	0.3**	1.0**
Female (Set × Male)	204	3672186**	9.5**	8.9**	1.4**	7561.2**	497.0**	1.3**	0.1**	0.2**	0.8**
E × Male (Set)	68	2507448**	14.1**	12.7**	0.7	6436.8**	232.2**	1.1**	0.1	0.2**	0.7**
E × Female (Set × Male)	408	2678970**	3.9	3.8	0.6	6873.6**	183.2**	1.0**	0.1**	0.2**	0.6**
Error	714	1257467	3.9	3.5	0.6	193.5	116.1	0.4	0.1	0.1	0.1

*, ** Mean squares significant at P< 0.05 and P < 0.01 levels, respectively.
ASI, anthesis-silking interval and EPP, number of ears per plant

Similarly, environment × set interaction mean squares were significant for all measured traits except anthesis-silking interval and number of ears per plant. Males-within-set and females in male-within-set mean squares were significant ($P < 0.01$) for all measured traits. The interactions of males-within-set with environment were significant for all measured traits except anthesis-silking interval and number of ear per plant. On the other hand, the interactions of females in males-within-set with environment were significant for grain yield, plant and ear heights, plant and ear aspects, husk cover and number of ears per plant. The mean grain yield of the full-sib families varied from 1,330 to 5,900 kg ha^{-1} with an average of 3,569 kg ha^{-1} (Table 2).

Table 2. Mean and their standard error, minimum and maximum for grain yield and agronomic traits of full-sib families developed from IARTZI-Y Pop DT STR Co evaluated at Zaria, Minjibir and Batsari in 2017.

Variable	Mean ± S.E.	Minimum	Maximum
Grain yield, kg ha^{-1}	3568.6 ± 43.12	1330	5900
Days to anthesis	58.5 ± 0.12	54.6	62.8
Days to silking	62.1 ± 0.11	57.86	65.7
ASI	3.6 ± 0.03	1.917	5.98
Plant height, cm	149.1 ± 1.57	108.1	190.1
Ear height, cm	71.0 ± 0.42	30.9	95.5
Husk cover (1-5) †	1.6 ± 0.01	1.12	2.191
Plant aspect (1-5) ‡	2.6 ± 0.02	1.594	3.625
Ear aspects (1-5) ¶	3.1 ± 0.03	1.651	4.885
EPP	0.9 ± 0.01	0.514	1.305

ASI, anthesis-silking interval; EPP, number of ears per plant; S.E. = standard error

†ASI, Anthesis-silking interval;

† Husk cover (scale 1-5), where 1= husk tightly arranged and extended beyond the ear tip and 5 = ear tips exposed.

‡Plant aspect (scale 1-5), where 1 = excellent plant type and 5 = poor plant type.

¶Ear aspect (scale 1-5), where 1 = clean, uniform, large, and well-filled ears and 5 = ears with undesirable features.

The mean plant height varied from 108.1 cm to 190.1 cm with an average of 149.1 cm. Wide range of values were also observed for other measured traits. All measured traits had negative dominance variance and were therefore equated to zero except grain yield and anthesis-silking interval. In contrast, all measured traits had positive additive and environment variance (Table 3).

Table 3. Variance components and heritability estimates of grain yield and agronomic traits among Design I progenies from IARTZI-Y Pop DT STR C_0 evaluated at Zaria, Minjibir and Batsari in 2017.

	σ^2_e	σ^2_a ± S.E	σ^2_d ± S.E	σ^2_{ae}	σ^2_{de}	σ^2_p	h^2, % ± S.E
Grain yield	41915.567	40975.20 ± 416748.2692	621168.8 ± 562148.76	0.00†	2911614.80	3615674.37	0.01 ±4.364
Days to anthesis	0.129	41.92 ± 0.011	0.0 ± 0.01	4.10	0.00	46.15	0.91 ± 0.000
Days to silking	0.118	40.72 ± 4.395	0.0 ± 6.08	3.56	0.00	44.40	0.92 ± 0.411
ASI	0.018	0.12 ± 0.517	0.4 ± 0.78	0.03	0.01	0.61	0.20 ± 7.893
Plant height	6.450	9215.19 ± 7126.953	0.0 ± 11518.18	0.00	13534.96	22756.60	0.40 ± 2.810
Ear height	3.870	2119.78 ± 6.796	0.0 ± 9.38	19.60	114.59	2257.85	0.94 ± 0.012
Husk cover	0.002	0.67 ± 0.213	0.0 ± 0.35	0.00	0.24	0.91	0.74 ±1.246
Ear aspects	0.014	0.97 ± 0.117	0.0 ± 0.19	0.02	1.18	2.18	0.45 ± 0.422
Plant aspect	0.005	0.86 ± 0.821	0.0 ± 1.26	0.02	0.95	1.84	0.47 ± 3.427
EPP	0.002	0.16 ± 0.093	0.0 ± 0.15	0.00	0.05	0.22	0.76 ± 2.152

σ^2_e = environment variance; σ^2_{ae} = additive × environment interaction variance; σ^2_{de} = dominance × environment interaction variance; σ^2_d = dominance variance; σ^2_a = additive variance; ASI, anthesis-silking interval; EPP, number of ears per plant; S.E. = standard error.

† Negative variance equated to zero.

The mean plant height varied from 108.1 cm to 190.1 cm with an average of 149.1 cm. Wide range of values were also observed for other measured traits. All measured traits had negative dominance variance and were therefore equated to zero except grain yield and anthesis-silking interval. In contrast, all measured traits had positive additive and environment variance (Table 3). All measured traits had positive additive × environment variance except grain yield, plant height, husk cover, and number of ear per plant. Only days to 50% anthesis and mid-silk had negative dominance × environment variance while other traits had positive dominance × environment interactions. In the case of grain yield and anthesis-silking interval where additive and dominance variances were positive, dominance variances were larger than additive variances. The heritability estimates ranged from 0.01 for grain yield to 0.94 for ear height. Grain yield and anthesis-silking interval had low heritability estimates whereas plant height, plant and ear aspect had moderately high heritability estimates. Days to anthesis and mid-silk, ear height, husk cover, and number of ears per plant had high heritability estimates ranging between 0.74 and 0.94.

Table 4. Genotypic correlation coefficients (upper diagonal) and phenotypic correlation coefficients (lower diagonal) between grain yield and agronomic traits of full-sib families developed from IARTZI-Y Pop DT STR Co evaluated at Zaria, Minjibir and Batsari in 2017.

Traits	Days to anthesis	Days to silking	Plant height	Ear height	Husk cover	Plant aspect	Ear aspect	ASI	EPP	Grain yield
Days to anthesis		-0.20**	0.94**	0.03	-0.01	0.26**	0.25**	0.36**	-0.38**	-0.05
Days to mid-silk	-0.22**		0.48**	0.44**	-0.12*	-0.59**	-0.78**	0.22**	0.25**	0.75**
Plant height	0.93**	0.15*		0.10*	0.64**	-0.36**	-1.00**	-1.00**	0.10*	0.01
Ear height	-0.03	-0.01	0.34**		-0.03	-0.33**	-0.80**	-0.70**	-0.08	0.05
Husk cover	-0.12*	-0.14*	0.27**	0.19*		0.31**	0.22**	-0.11*	-0.10*	-0.14*
Plant aspect	-0.12*	-0.12*	-0.09	0.04	0.26**		0.26**	0.82**	-0.04	0.07
Ear aspect	0.26**	0.26**	-0.17*	-0.43**	0.14*	0.37**		0.34**	-0.17*	-0.22**
ASI	0.26**	0.25**	-0.22**	-0.42**	0.03	0.66**	0.45**		-0.05	-0.11*
EPP	-0.30**	0.05	0.03	-0.01	0.01	-0.05	-0.08	-0.24**		0.26**
Grain yield	-0.02	-0.03	-0.01	0.05	-0.05	-0.06	-0.15*	-0.01	0.35**	

*, ** Significant difference at P< 0.05 and P < 0.01 levels, respectively.
ASI, anthesis-silking interval
EPP, number of ears per plant

Grain yield had significant positive genotypic correlations with days to mid-silk ($r_g = 0.75$**) and number of ear per plant ($r_g = 0.26$**) but negative with husk cover ($r_g = -0.14$*), anthesis-silking interval ($r_g = -0.11$*) and ear aspect ($r_g = -0.22$**) (Table 4). In contrast, there was no phenotypic correlation between grain yield and any other trait except number of ear per plant ($r_p = 0.35$**) and ear aspect ($r_p = -0.15$*). Days to mid-silk had negative genotypic and phenotypic correlations with days to anthesis ($r_g = -0.20$**, $r_p = -0.22$**). Similarly, anthesis-silking interval had significant positive genotypic and phenotypic correlations with plant aspect ($r_g = 0.82$**, $r_p = 0.66$**) but negative with ear height ($r_g = -0.70$**, $r_p = -0.42$**). Plant height had significant positive genotypic and phenotypic correlations with ear height ($r_g = 0.10$*, $r_p = 0.34$**) and husk cover ($r_g = 0.64$**, $r_p = 0.27$**). Similarly, plant aspect had significant positive genotypic and phenotypic correlations with ear aspect ($r_g = 0.26$**, $r_p = 0.37$**).

DISCUSSION

Genetic variability is a key attribute of a population that would allow tremendous progress from selection. The presence of significant differences among environments for all measured traits suggests uniqueness of the three locations that were used in evaluating the performance of the full-sib families. The significant mean squares observed for set for all measured traits indicates that differences existed among the sets of the full-sib families, implying that partitioning of the full-sib families into sets is effective in reducing the experimental error. The presence of significant mean squares observed for environment × set for all measured traits except anthesis-silking interval and number of ear per plant suggests differential ranking of the set of full-sib families in the different environments. This demonstrates the influence of the different environments on the performance of the sets of full-sib families. The significant males-within-set and female in male-within-set for all measured traits indicates the presence of genetic differences among the males-within-set and female in male-within-set. This implies that there are adequate genetic variability among the males-within-set and female in male-within-set for the measured traits and the possibility of making significant progress in the population by accumulating the favourable alleles inherent in the population through selection. The significant interaction between male-within-set and environments for all measured traits except anthesis-silking interval and number of ear per plant indicated that the expression of the traits among male-within-set would be different in varying test environments. On the other hand, the lack of significant interaction between females in males-within-set and environments for days to anthesis and mid-silk, and anthesis-silking interval indicated that the expression of the traits would be consistent in varying test environments.

Assessment of the magnitude of additive relative to other variance components is crucial in designing the most appropriate and effective breeding approach for improving a population for traits of interest. The preponderance of additive genetic variance relative to dominance and epistatic variances in a population is desirable for making significant progress from selection. The preponderance of dominance variances relative to additive variances for grain yield and anthesis-silking interval, indicates that grain yield and anthesis-silking interval were controlled by non-additive gene action, implying that significant progress would not be made in improving the population for grain yield and anthesis-silking interval through selection but the suitable breeding method for improving grain yield in the population is through hybrid development or indirect selection through secondary traits. This result is in agreement with the findings of Badu-Apraku *et al*. (2007) who reported preponderance of dominance variance over additive variance for grain yield. However, there is preponderance of additive variance in the population for days to 50% anthesis, mid-silk, plant and ear heights, husk cover, plant and ear aspects and number of ear per plant, suggesting that significant progress would be made in improving the population for the traits through recurrent selection scheme. This result is in disagreement with the findings of Badu-Apraku *et al*. (2007) who reported preponderance of dominance variance over additive variance for plant and ear heights. The implication of the results of the present study suggests that indirect selection scheme could be utilized in improving grain yield in the population through the use of secondary traits in the selection. This result is in agreement with the findings of Mhike *et al*. (2011) who suggested the use of indirect selection and selection indices to determine the underlying genetic merits of the traits with low heritability. Alternatively, breeding scheme that capitalizes on dominance gene action, such as half-sib family selection involving testcross progenies could be employed for the improvement of grain yield and anthesis-silking interval. The low heritability observed for grain yield and anthesis-silking interval was a reflection of the preponderance of non-additive gene controlling the traits in the population. The moderate–to-large additive genetic variance and narrow-sense heritability (> 40%) and wide range of values observed for all measured traits except grain yield and ASI indicated that substantial genetic variability existed in the population, IARTZI-Y Pop DT STR C_0 to ensure good progress from selection.

The negative variance component which is equated to zero obtained for some traits could be due to the influence of the conditions under which the full-sib families were evaluated. For example, the genetic material was actually developed for drought and *Striga* resistance but the evaluation was carried out under different growing conditions. Badu-Apraku *et al*. (2007) reported that negative additive and non-additive variances could be due to due to sampling error during progenies development, experimental design, data collection procedures, experimental problem and statistical analysis for the computation of variance components.

Information on the relationship among traits is of paramount importance in designing effective breeding scheme for crop improvement. Grain yield is usually the primary trait of interest while other traits could be regarded as secondary traits. Secondary traits such as those with significant correlation with grain yield and high heritability are valuable in indirect selection for improvement of grain yield. The presence of significant positive genotypic correlations between grain yield and number of ear per plant and days to mid-silk indicated that the higher the number of ears per plant and maturity period the higher the grain yield. The positive genotypic and phenotypic correlations observed between plant and ear heights and between plant and ear aspects indicate that one of the traits could be used in selecting for other. This is advantageous in terms of reducing the cost and time of measuring the pairs of the traits. It is worth noting that genotypic correlations for most of the measured traits were higher than the phenotypic correlations. This result indicated that the environment has little or no influence on the traits and thus, making the parameter estimates more reliable for predicting future progress from selection in the population under study. This results is in agreement with the findings of Badu-Apraku *et al*. (2007) who reported that genotypic correlations were higher than the phenotypic correlations.

In conclusion, there was considerable genetic variability in the yellow-endosperm maize population with moderately-to- high narrow-sense heritability for all measured traits except grain yield and ASI. The additive genetic variance was larger than dominance variance for all measured traits except grain yield and anthesis-silking interval. Grain yield had significant positive genotypic correlations with days to mid-silk, and number of ear per plant but negative with husk cover. Recurrent selection schemes that capitalize on additive gene action would be effective for improving yield-related traits while hybridization would be effective for improving grain yield in the maize population.

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