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Genetic Studies of Extra Early Maize Genotypes Under Low Nitrogen

G. Amuzu¹, *P. F. Ribeiro², M. D. Asante^{1,2} and J. N. L. Lamptey¹

¹Department of Plant Resources Development, CSIR College of Science and Technology, Fumesua - Kumasi, Ghana

²Council for Scientific and Industrial Research – Crops Research Institute (CSIR-CRI), Fumesua-Kumasi, Ghana

*Corresponding author: prisboat@yahoo.com

Received: 14 April 2023

Accepted: 20 November 2023

Abstract

Nitrogen (N) is a major limiting factor associated with maize production in sub-Saharan Africa. Low N tolerant hybrids can absorb and utilise N from the soil as well as applied fertilisers, making them efficient users of N. This study focused on identifying inbred lines with desirable GCA for grain yield and other agronomic traits under low N, determining the gene action governing grain yield and other agronomic traits under low N and estimating the genotypic variability for grain yield and other agronomic traits among extra early maize hybrids. Ten extra early white endosperm maize inbred lines were crossed to five testers in a line tester mating design to generate fifty (50) single cross hybrids (SCH) which were evaluated under low N (30 kg N ha⁻¹) and optimum N (90 kg N ha⁻¹). The combined analysis of variance (ANOVA) under low and optimum N showed significant mean squares for the environment and hybrids but non-significant hybrid environment interaction mean squares for grain yield (GY) under low N. General combining ability of line and tester as well as specific combining ability showed significant mean squares for GY under both low and optimum N environments. Non-additive gene action governed GY under low and optimum N. GY had moderate genotypic coefficient of variability and high genetic advance as a percentage of mean under low and optimum N. Lines CRIZEEL-W-242 and CRIZEEL-W-261 were the best inbred lines identified under low and optimum N conditions, hence should be used in recurrent selection or other hybridization programmes.

Keywords: Low nitrogen; Line Tester; Combining Ability; Heritability; Genetic Advance.

Études Génétiques de Génotypes de Maïs Extra-précoces Sous Faible Teneurs en Azote

Résumé

L'azote (N) est un facteur limitant majeur associé à la production de maïs en Afrique subsaharienne. Les hybrides tolérants à l'azote peuvent absorber et utiliser l'azote du sol ainsi que les engrais appliqués, ce qui en fait des utilisateurs efficaces de l'azote. Cette étude s'est concentrée sur l'identification de lignées consanguines avec une ACG souhaitable pour le rendement en grains et d'autres caractéristiques agronomiques sous faible azote, sur la détermination de l'action des gènes régissant le rendement en grains et d'autres caractéristiques agronomiques pour le rendement en grains et d'autres caractéristiques agronomiques d'autres caractéristiques agronomiques sous faible azote et sur l'estimation de la variabilité génotypique pour le rendement en grains et d'autres caractéristiques agronomiques parmi les hybrides de maïs extra-précoces.

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Dix lignées consanguines de maïs extra-précoce à endosperme blanc ont été croisées avec cinq testeurs dans un plan d'accouplement ligne-testeur pour générer cinquante (50) hybrides simples croisés (SCH) qui ont été évalués sous faible niveau d'azote (30 kg N ha⁻¹) et sous niveau d'azote optimal (90 kg N ha⁻¹). L'analyse de variance combinée (ANOVA) dans des conditions d'azote faible et optimal a montré des carrés moyens significatifs pour l'environnement et les hybrides, mais des carrés moyens d'interaction hybride-environnement non significatifs pour le rendement en grain (GY) dans des conditions d'azote faible. Les lignées CRIZEEL-W-242 et CRIZEEL-W-261 ont été les meilleures lignées consanguines identifiées dans des conditions d'azote faible et optimal, et devraient donc être utilisées dans des programmes de sélection récurrente ou d'autres programmes d'hybridation.

Mots Clés: Faible teneur en azote; ligne x testeur; capacité de combinaison; héritabilité; avance génétique.

Introduction

Maize (Zea mays) is one of the major cereal crops cultivated and utilised mainly as a staple crop in sub-Saharan Africa (SSA) (Effa et al., 2012; Okweche et al., 2013; Macauley, 2015). It is consumed across SSA and in 2019, the total maize production recorded in Ghana stood at 2.7 million Mt, corresponding to a 45% increase in production (FAO, 2020). An estimated 85% of the total maize produced in Ghana is used for food, with a per capita consumption of 43.8 kg per head. The remaining 15% is used in feed formulation, mainly in the livestock and poultry industries, where it constitutes about 40 - 75% of their ration(Angelucci, 2012; Abdulai et al., 2017). Despite the economic importance of maize and the efforts made by most researchers to improve the qualities of the crop, the key challenging abiotic constraint in SSA, including Ghana, is low soil fertility (Oyekunle & Badu-Apraku, 2014; Ribeiro et al., 2017). For most soils in Ghana, the total N in the upper portions of the soil after years of cultivating tend to be low (Bationo et al., 2018). Ghana has one of the lowest nitrogen (N) application rates of 34 kg N ha⁻¹ in SSA despite efforts to attain a minimum application rate of 50 kg N ha⁻¹ (Henao & Baanante, 2006; Bationo et al., 2018). Nitrogen stress not only retards the growth of plants but also markedly affects the photosynthetic rate per unit area by reducing both leaf size and photosynthetic capacity(Su et al., 2020) and, subsequently, the final grain yield, resulting in a range of 10% - 50% yield loss annually (Logrono & Lothrop, 1996).

Current yields of less than 1.5 t ha⁻¹ in SSA lag behind the global average of 5.75 t ha (Cairns et al., 2013; FAO, 2017). These low yields are attributable to farmers low fertiliser application rates, about 5 - 10 kg N ha⁻¹ compared to the average of 100 kg N ha⁻¹ applied worldwide (Ogunniyan et al., 2019). Furthermore, low production capacity locally worsens the issue at hand. The limited supply and the high cost of fertilisers deter farmers from purchasing these fertilisers (Mosier et al., 2005). In addition, the reduced availability of productive land for agricultural purposes and low fertiliser application rates continue to pose a major threat to maize production in Ghana (Ribeiro et al., 2017).

Low N tolerant hybrids can increase maize productivity since they can absorb and utilise N from the soil and from applied fertilisers, thereby making them efficient users of nutrients (Arisede et al., 2020). However, only a few such hybrids have been released in Ghana. Badu-Apraku et al. (2015) indicated that genetic improvement of maize germplasm is the most feasible and sustainable choice for mitigating the negative impacts of abiotic stress conditions such as low N in SSA. Genetic approaches to improve yield at reduced N application rates are crucial since fertiliser use in SSA is low (Ogunniyan et al., 2019). In maize breeding programs, knowledge of the general combining ability (GCA) of inbred lines and specific combining ability (SCA) of hybrid combinations are crucial for successful hybrid development. This provides information on the type of gene action controlling yield and its associated traits under stress conditions (Nasser et al., 2020). Successful studies on gene action (combining abilities) are achieved through popular mating schemes such as diallel, Line Tester and North Carolina Design II (NCD II) (Hallauer et al., 2010; Fasahat et al., 2016).

Determination of genotypic variability through the use of parameters such as genotypic coefficient of variation (GCV), phenotypic coefficient of variation (PCV), heritability and genetic advance are vital in every efficient and effective breeding programme (Arunkumar et al., 2018). GCV and PCV usually determine the variation present in a breeding population (Roychowdhury & Randrianotahina, 2011; Bello et al., 2012). PCV and GCV are useful indices as they also act as measuring tools for effective selection in crop improvement (Bello et al., 2012). Effective selection procedures that significantly influence the improvement of a character can be established through the measure of heritability (Samadia, 2005). Heritability deals with the transmissibility of a character from one generation to the other. Though traits with high narrow sense heritability can quickly be fixed using simple selection methods, it requires genetic advance in order to be of practical importance or be more applicable and helpful in formulating selection procedures (Jaiswal *et al.*, 2019). Estimating heritability also assists breeders in allocating resources necessary to select desired traits effectively and to achieve maximum genetic gain faster with limited resources (Smalley *et al.*, 2004). Genetic advance is a useful indicator of the progress that can be expected due to selection (Reddy *et al.*, 2013).

For newly developed inbred lines, the effect of GCA has been reported to be relatively more significant than the SCA effect in tropical maize germplasm (Dhliwayo et al., 2009; Adebayo et al., 2017). There are also inconsistencies in the combining abilities and genetic variability of low N tolerance among inbred lines developed for hybrid maize development. For instance, in the report of Akinwale et al. (2014), there was a significant role of GCA in the determination of grain yield of maize inbred lines under varying environmental stress, but Oyekunle et al. (2015) reported higher SCA than GCA effect for grain yield when early yellow endosperm maize inbred lines were studied under various stress conditions. Aside the insufficient low N varieties in Ghana, there is limited information on the combining abilities (i.e. general and specific) of newly developed maize inbred lines by the Council for Scientific and Industrial Research (CSIR) -Crops Research Institute (CRI). The objectives of this research were to: identify inbred lines with desirable GCA effect for grain yield and other agronomic traits under low N; assess the gene action governing grain yield and other agronomic traits under low N and; assess the genotypic variability among hybrids for grain yield and other agronomic traits.

Materials and Methods Germplasm and generation of F. hybrids

Ten extra early maturing inbred lines of white endosperm maize were obtained from the CSIR-CRI. These are newly developed inbred lines by the maize breeding programme. Five other inbred lines were used as testers. The ten lines were crossed to the five testers in a line x tester mating design as described by Kempthrone (1957). Each member of the testers was crossed to each member of the lines (i.e. Ti all females; $Ti = i^{th}$ tester) (5 testers x 10 lines), thus giving a total of 50 single cross hybrids (SCH).

Depletion of soil of nitrogen

The experimental sites were depleted of N by cultivating maize at a high population density. The stover (biomass) was entirely removed after each harvest, and soil sampled to a depth of 30 cm for soil total N determination. Nitrogen depletion continued till the residual N reached an acceptable level (<0.2%). The N content was determined using the Kjeldhal method (Bremner & Mulvaney, 1982) at the CSIR - Soil Research Institute (CSIR-SRI), Kwadaso.

Experimental site, field layout and evaluation of single cross hybrids (SCH)

The SCH were evaluated under contrasting environments during the major season of 2022 (April 2022 - August 2022) at three different locations: Fumesua, Kwadaso and Ejura.

The vegetation was cleared using glyphosate herbicide at 200 mL per 15 L of water. Entries, comprising the 50 SCH developed and two commercial hybrids used as checks, were laid in a 413 alpha-lattice designed experiment with three replications. Each plot was two rows and 4 m long. Seeds were sown at a spacing of $0.75 \text{ m} \times 0.40 \text{ m}$ at three seeds per hill and thinned to two plants per hill two

weeks after sowing (WAS).

The experiment comprised low N and optimum N at all locations except Ejura which had only optimum N trial (low N trial was invaded prior to flowering stage and destroyed by cattle). Phosphorus (triple superphosphate) and potassium (muriate of potash) were each applied at 60 kg ha^{\perp} to low and optimum N plots at 2 WAS. The low N treatments received 30 kg N ha⁻¹ while the optimum N treatments received 90 kg N ha⁻¹ applied as urea in two splits: 50% at 2 WAS and the remaining 50% applied at 5 WAS. The low N was selected on the basis of the results from the works of Tetteh et al. (2017) and Wongnaa et al. (2021) who indicated that about 85% of maize farmers in the Ashanti region do not comply with the CSIR-Savanna Agriculture Research Institute (SARI)/CSIR-CRI's recommended fertiliser application rate for maize production by Adu et al. (2014) and thus apply lower than the average recommended rate (90 kg N ha⁻¹). The optimum N application rate employed in this study is in line with the recommendations made by the CSIR-SARI/CRI and AGRA in the work of Adu et al. (2014) stating that, the optimum application rate is selected on the basis of the maturity period and production potential of the maize variety. Since the hybrids developed from this study are extra early and their production potential was not certain, it was advisable to use the optimum/average rate of application of 90 kg N ha⁻¹ and not 120 kg N ha⁻¹ for depleted soil as recommended by the CSIR-SARI /CRI and AGRA in the work of Adu et al. (2014).

Weeds were managed using the postemergence weedicides (120 mL per 16 L of water) as well as the manual method, whilst fall armyworm larvae were also managed when necessary by applying emamectin benzoate at 30 mL per 15 L of water (knapsack).

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Entry no	. Testers	Agronomic Characteristics	Source
1	Tester 1	52 DTA, Moderately tolerant under low N	CSIR-CRI
2	Tester 2	52 DTA, Tolerant under low N	CSIR-CRI
3	Tester 3	52 DTA, Moderately tolerant under low N	CSIR-CRI
4	Tester 4	51 DTA, Moderately tolerant under low N	CSIR-CRI
5	Tester 5	51 DTA, Moderately tolerant under low N	CSIR-CRI
	Lines		Source
6	CRIZEEL-W-217	49 DTS Moderately tolerant under low N	CSIR-CRI
7	CRIZEEL-W-219	47 DTS Moderately tolerant under low N	CSIR-CRI
8	CRIZEEL-W-222	46 DTS, low N tolerant	CSIR-CRI
9	CRIZEEL-W-261	49 DTS, low N tolerant	CSIR-CRI
10	CRIZEEL-W-232	50 DTS, Moderately tolerant under low N	CSIR-CRI
11	CRIZEEL-W-236	45 DTS, Moderately tolerant under low N	CSIR-CRI
12	CRIZEEL-W-242	49 DTS, low N tolerant	CSIR-CRI
13	CRIZEEL-W-208	47 DTS, Moderately tolerant under low N	CSIR-CRI
14	CRIZEEL-W-263	47 DTS, Moderately tolerant under low N	CSIR-CRI
15	CRIZEEL-W-257	49 DTS Moderately tolerant under low N	CSIR-CRI

Table 1. List of extra early maturing maize germplasm used to generate hybrids

DTA=Days to Anthesis, DTS=Days to Silking

Table 2. Description	of experiment	tal sites
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Features/location	Fumesua	Kwadaso	Ejura
Coordinates	6°41′ N, 1°28′ W	6°43′ N, 1°36′ W	7°23′N, 1°21′W
AEZ	Deciduous Forest	Deciduous Forest	Forest-savannah transition
Soil type	Ferric acrisol	Ferric acrisol	Ferric lixisol
	(Asuansi series)	(Asuansi series)	(Ejura series)
Altitude (m)	257	254	254
Rainfall pattern	Bimodal	Bimodal	Bimodal
Major season	April to July	April to July	March to August
Minor season	September to November	September to November	September to November

NB: AEZ = Agro-Ecological Zone, N = North, W = West

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Data collection

Data were recorded on days to anthesis (DTA) and silking (DTS), anthesis - silking interval (ASI), chlorophyll content (CC) using the portable CCM-200 plus-opti sciences meter (OptiSciences Inc., Hudson USA), stay green (SG), plant height (PHGT), ear height (EHGT), plant aspect (PASP), ear aspect (EASP), number of ears per plant (EPP) and grain yield (GY). The measurement of all the parameters were carried out according to the method described in the works of Nelimor et al. (2020) and Ribeiro et al. (2020).

Grain yield (GY) for the low N trials was estimated from the shelled grain weight per plot while assuming a moisture content of 15%. On the other hand, GY for the optimum trials was estimated from the field weight while assuming a shelling percentage of 80% and moisture content of 15%. Grain yield was estimated using the formulae from the works of Mageto et al. (2020) and Tandzi & Mutengua (2020).

Statistical analysis

The plot mean values of the 52 entries for grain yield and the other agronomic traits were subjected to analysis of variance (ANOVA). The 50 SCH were further subjected to line tester analysis (Kempthrone, 1957) using R software (R version 4.1.2 (2021-11-01)) where environment and replication served as random effect and genotype as fixed effect. The hybrid component of variation was further partitioned into variations due to tester, line and line tester interaction. The F tests for line, tester and line tester mean squares were computed using the mean squares for their respective interaction with environment. The mean square attributable to line environment and tester environment were tested using the mean square for line tester environment whereas the mean square for line tester environment was tested using the pooled error mean squares. The line and tester main effect served as the GCA-line and GCAtester, respectively, and the line tester effect served as the SCA. The model for the combined analysis of variance is described below

 $Y_{i\,i\,k} = \mu + G_i + E_i + GE_{i\,i} + L_1 + T_m +$ $LT_{lm} + LE_{lj} + TE_{mj} + LTE_{lmj} +$ $R_k: E_j + B_n: R_k: E_j + \varepsilon ijk,$ where:

Yijk = the response variables

 $\mu = \text{grand mean.}$

 G_i = effect of the ith genotype.

- $E_i = \text{effect of the } j^{\text{th}} \text{ environment.}$
- GE_{ii} = effect of the interaction between the ith genotype and the jth environment.
- $L_i = effect of the 1th line.$
- $T_m = \text{effect of } \mathbf{m}^{\text{th}} \text{ tester.}$
- $L_l = effect of the lth line.$
- $T_m = \text{effect of } \mathbf{m}^{\text{th}} \text{ tester.}$
- $LT_{int} = effect of the interaction$ between the 1th line and the mth tester.
- LE_{ii} = effect of the interaction between the jth environment and the lth line.
- TE_{mj} = effect of the interaction between the jth environment and the mth tester.
- LTE_{imj} = effect of the interaction between the 1th line, the mth tester and the jth environment.

 $R_k:E_i =$ effect of replicate nested in environment

 $B_n: R_k: E_j =$ effect of Blocks nested in replicate nested in environment. $\mathcal{E}_{iik} = \text{error term}$

General combining ability (GCA) and

specific combining ability (SCA) were computed for all characters according to the method described by Kempthrone (1957) and Singh & Chaudhary (1985). Broad sense heritability (H²b) and narrow sense heritability (h^2n) were estimated under each of the three environments (i.e. low N, optimum N) using the variance component method. The variance components were obtained from a restricted maximum likelihood (REML) analysis using the "lmerTest" and "lme4" packages (Bates *et al.*, 2015; Kuznetsova *et al.*, 2017) in R software. Heritability was calculated as follows:

$$H^{2}b = \frac{\sigma_{g}^{2}}{\sigma_{g}^{2} + \frac{\sigma_{gxe}^{2}}{e} + \frac{\sigma_{e}^{2}}{r \times e}}$$
$$h^{2}n = \frac{\sigma_{a}^{2}}{\sigma_{g}^{2} + \frac{\sigma_{gxe}^{2}}{e} + \frac{\sigma_{e}^{2}}{r \times e}}$$

Where:

 $H^{2}b = Broad$ sense heritability $h^{2}n = narrow$ sense heritability $\sigma^{2}{}_{g}$ = Variance due to genotype

 σ^2_a = Variance due to additive gene action

σ²gxe= Variance due to genotype × environment interaction

 $\sigma^2_e = Error variance$

e = number of environments and r = number of replications

Heritability in narrow sense was categorized as: low = 0 - 30 %, intermediate (medium) = 30 - 50 % and high = above 50 %; according to Bhateria *et al.* (2006).

The genotypic coefficient of variation (GCV) and phenotypic coefficient of variation (PCV) were calculated according to Burton (1951), Burton & Devane (1953), and Aravind *et al.* (2019) and then ranked as; low = 0 - 10%, intermediate = 10 - 20% and high = greater than 20% (Sivasubramanian & Madhavamenon, 1973; Abebe *et al.*, 2017).

The expected genetic advance was calculated

as follows;

 $h^2 n =$ narrow sense heritability, $\delta p =$ phenotypic standard deviation,

k = selection differential at 5% selection intensity=2.06.

Genetic advance as percentage of mean (GAM) was calculated by using the method proposed by Robinson *et al.* (1949); Johnson *et al.* (1955); Jilo *et al.* (2018) and classified as: low = less than 10%, intermediate = 10-20%, and high = more than 20% (Johnson *et al.*, 1955; Abebe *et al.*, 2017; Jilo *et al.*, 2018).

Results

Combined analysis of variance

The combined ANOVA under low N indicated significant (p < 0.05) environment, hybrid, and hybrid environment interaction mean squares for all traits except SG and PASP for environments and DTA, CC, EPP, PASP and GY for hybrid environment interaction. The GCA-line, GCA-tester, and SCA showed significant (p < 0.05) mean squares for the measured traits except DTS and DTA for the GCA-tester and SG for SCA. The interaction of GCA-line and GCA-tester with the environment showed significant (p < 0.05) mean squares for the measured traits except DTA, CC, EPP, PASP and GY for GCA-line environment and then CC, SG and EPP for GCA-tester environment. In the case of SCA environment, only ASI and EASP showed significant (p < 0.05) mean squares (Table 3).

Under optimum N, hybrid, environment and hybrid environment interaction showed significant (p < 0.05) mean squares for the measured traits except EPP for the hybrids and CC, EPP and EASP for the hybrid environment interaction. The GCA-line, GCA-tester, and SCA showed significant (p <0.05) mean squares for the measured traits except EPP for GCA-line effect; DTS, DTA and EPP for the GCA-tester effect and finally ASI, CC, EPP and EASP for the SCA effect.

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Source	đ	DTS	DTA	ASI	8	PHGT	EHGT	SG	EPP	PASP	EASP	GY
		(days)	(days)	(days)		(cm)	(cm)	(1-9)		(1-9)	(1-9)	(kg ha ⁻¹)
Hybrid	51	16.1**	11.0^{**}	3.7**	268.9**	797.0**	368.7**	•**6.0	0.03**	3.3**	2.9**	1012990**
Environment (Env)	1	4092.6**	3759.3**	7.1**	7607.2**	68508.0**	25542.7**	0.2	0.49**	2.5	134.7**	13720313**
$Hybrid \times Env$	51	6.5**	3.8	3.3**	94.2	146.0*	96.8**	0.5*	0.02	0.4	1.6**	387386
Env(Rep)	4	30.1**	28.4**	2.5**	553.3**	489.0**	280.6**	2.2**	0.04*	1.4	2.3**	1466701**
$(Env \times Rep)Blk$	72	4.6	3.8	0.4	120.7*	112.0	50.1	0.6**	0.02*	1.3**	0.8	376562
Residuals	132	3.7	2.9	0.7	75.7	87.0	44.8	0.3	0.01	0.7	9.0	334140
Line	6	49.4**	31.4**	12.6**	723.6**	2112.0**	835.4**	1.6**	0.04**	8.6**	7.6**	2131132**
Tester	4	7.7	3.5	6.2**	338.1**	2509.0**	1501.9**	0.9*	0.05**	7.2**	6.6**	1209950**
Environment (Env)	1	3938.6**	3668.0**	4.8**	7858.1**	64025.0**	24908.6**	0.0	0.53**	2.8	126.8**	12293602**
Line \times Tester	36	6.8**	6.0**	1.1^{**}	143.9**	232.0**	132.2**	0.4	0.03**	1.4**	1.4**	720021**
Line \times Env	6	13.6**	3.6	11.1^{**}	45.1	215.0*	122.0**	0.7*	0.02	0.2	4.1**	405992
Tester × Env	4	12.6**	13.0**	5.8**	178.7	549.0**	458.3**	0.2	0.02	2.0*	2.3**	1165093*
Line \times Tester \times Env	36	4.1	2.8	1.1^{**}	94.6	76.0	53.9	0.4	0.01	0.3	1.0*	305056
Env(Rep)	4	29.1**	30.1**	1.3	575.0**	506.0**	258.9**	2.5**	0.04*	1.2	2.2**	1603855**
$(Env \times Rep)Blk$	72	4.2	3.6	0.4	121.3**	104.0	47.4	0.5**	0.02*	1.3**	0.8*	371366
Residuals	124	3.2	2.6	0.6	74.3	88.0	43.5	0.3	0.01	0.7	0.5	342747

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Source	Df	DTS	DTA	ASI	Ŋ	PHGT	EHGT	SG	EPP	PASP	EASP	GY
		(days)	(days)	(days)		(cm)	(cm)	(1-9)		(1-9)	(1-9)	(kg ha ⁻¹)
Hybrid	51	19.6**	18.6**	2.9**	326.4**	1442.4**	561.1**	1.3**	0.05	2.2**	1.6**	3064024**
Environment (Env)	2	1661.4**	2943.3**	188.7**	18056.4**	18482.5**	11761.1**	3.1**	0.18*	5.7**	4.7**	31600091**
$Hybrid \times Env$	102	4.7**	4.4*	2.7**	7.7	207.2*	78.2*	0.7*	0.04	1.0^{**}	0.7	749419*
Env(Rep)	9	21.4**	29.2**	1.8**	493.9**	1371.0**	633.1**	2.2**	0.10*	4.6**	1.4*	6380351**
$(Env \times Rep)Blk$	108	4.7**	4.7**	9.0	87.5	174.3	6.99	0.5	0.04	9.0	9.0	793041*
Residuals	198	3.1	3.0	9.0	80.8	144.7	53.2	0.5	0.04	9.0	9.0	539830
Line	6	61.2**	59.3**	8.8**	1105.6**	3588.9**	1285.5**	3.5**	0.07	5.5**	4.9**	6095803**
Tester	4	3.1	4.7	6.8**	522.6**	4869.5**	2028.3**	1.5*	0.01	1.6*	2.5**	2772400**
Environment (Env)	2	1576.4**	2845.1**	191.5**	16923.2**	17064.9**	11217.5**	2.9**	0.18*	5.9**	4.8**	29662390**
Line \times Tester	36	6.8**	7.0**	0.8	119.5	536.4**	243.5**	0.7*	90.0	1.5**	0.7	2059177**
$Line \times Env$	18	6.9**	5.1	7.7**	118.0	169.9	74.1	1.3^{**}	0.03	1.9**	1.2**	725880
Tester $\times Env$	00	8.9**	8.3**	3.5**	113.2	460.4**	131.8**	0.9	0.02	2.0**	1.1	1889152**
$Line \times Tester \times Env$	72	3.5	3.9	1.1^{**}	64.3	184.2	68.6*	0.5	0.04	0.7	0.5	661130
Env(Rep)	9	19.8**	26.4**	2.0**	496.6**	1434.3**	599.7**	2.6*	0.12*	4.7**	1.4*	6243772**
$(Env \times Rep)Blk$	108	4.4*	4.6**	9.0	85.5	161.7	59.2	0.5	0.04	9.0	9.0	807712**
Residuals	186	3.2	3.1	0.6	83.0	141.0	49.8	0.5	0.04	9.0	9.0	528542

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The interaction of GCA-line, GCA-tester and SCA with the environment showed significant (p < 0.05) mean squares for the measured traits except DTA, CC, PHGT, EHGT, EPP and GY for GCA-line environment and then CC, SG, EPP, and EASP for GCA-tester environment. In the case of SCA environment, only ASI and EHGT showed significant (p < 0.01) mean squares (Table 4).

Specific combining ability (SCA) effect of hybrids.

Under low N, none of the cross combinations had a desirable SCA effect for GY. Even though the cross between CRIZEEL-W-261 and Tester 5 was the only combination that had a significant SCA effect it had a negative SCA value (Table 7). Cross combinations CRIZEEL-W-232 Tester 1 and CRIZEEL-W-232 Tester 4 under optimum conditions had significant positive SCA effects (p < 0.01) for GY (Table 8).

Gene action governing grain yield and other agronomic traits

Under low N, most of the traits had higher proportions of GCA than SCA except for EPP (60.58% SCA) and GY (51.90% SCA) which had higher proportion of SCA than GCA. For GY, GCA-line and GCA-tester accounted for about 38.41 % and 9.69%, respectively, of the total gene action. Also, SG characteristic which had a higher proportion of GCA (53.78%), had GCA-line and GCA-tester separately, contributing 43.41% and 10.37%, respectively (Fig. 1). Under optimum N, EPP (74.80%), and GY (52.92%) were the only traits that had higher proportions of SCA than GCA. The proportion of GCA-line and GCAtester for GY under optimum conditions was 39.16% and 7.92%, respectively, of the total GCA effect (Fig. 2)

Genotypic variability

The hybrids generated from the line tester

mating design had different degrees of variability. Under low N, PCV ranged from low (2.80%) for DTA to high (38.59%) for ASI. GCV also ranged from low (2.31%) for DTA to high (20.26%) for PASP. Broad sense heritability ranged from low (12.39%) for ASI to high (80.67%) for PHGT while narrow sense heritability ranged from low (12.39%) for ASI to high (63.77%) for PHGT. The genetic advance as a percentage of the mean (GAM) also ranged from low (3.78 %) for DTS to high (35.51%) for PASP. GY, EHGT, EASP and CC all had high GAM (Table 9).

Under optimum N, PCV ranged from low (2.79%) for DTS to high (25.16%) for ASI. GCV also ranged from low (2.40%) for DTS to intermediate (19.47%) for GY. Broad sense heritability ranged from low (11.31%) for ASI to high (87.94%) for EHGT while narrow sense heritability ranged from low (11.31%) for ASI to high (64.29%) for PHGT. GAM also ranged from low (4.26%) for DTS to high (34.35%) for GY. EHGT, CC and PASP all had high GAM (Table 10)..

Discussion

Combined analysis of variance

The significant hybrid mean squares observed for traits such as ASI, SG, EPP, GY, EASP and PASP under low N implies the hybrids evaluated in this research showed significant differences and expressed varying degrees of tolerance under low N, which could be attributed to the genetic make-up of the lines and testers used. This is in accordance with the findings from the work of Badu-Apraku et al. (2011), who further indicated that these traits have a strong correlation with genotype performance under stress conditions such as low N, and that these traits are very vital in maize improvement under stress conditions. Lima et al. (2022) also indicated that ASI is very important and directly influences GY. The significant line, tester and line tester effect recorded in this study for traits such as

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INBRED LINES	GY	ASI	S	DTA	DTS	EASP	EHGT	EPP	PASP	PHGT	SG
	(kg ha ^{.1})	(days)		(days)	(days)	(1-9)	(cm)		(1-9)	(cm)	(1-9)
Lines	GCAI										
CRIZEEL-W-217	-95.65	0.43*	4.34	0.82	1.26**	-0.16	2.18	-0.02	-0.02	6.04*	0.07
CRIZEEL-W-219	52.55	-0.83**	-7.69**	-0.51	-1.34**	-0.33	5.78**	0.01	0.18	8.41**	0.04
CRIZEEL-W-222	-140.78	0.67**	1.56	-0.61	90.06	0.30	-5.76**	-0.04	0.78**	-6.51**	0.01
CRIZEEL-W-261	390.02**	-0.17	5.95**	-0.78	-0.94*	-0.73**	-2.31	0.04	-0.92**	-1.57	-0.56**
CRIZEEL-W-232	-481.89**	-0.50**	2.64	1.92**	1.42**	0.37	-8.03**	-0.08*	0.65*	-12.33**	-0.03
CRIZEEL-W-236	-82.05	0.37*	-1.55	-1.18**	-0.81	-0.16	-5.05**	-0.03	0.08	-7.37**	0.11
CRIZEEL-W-242	445.37**	0.23	3.35	0.52	0.76	-0.33	7.95**	0.02	-0.78**	8.91**	-0.09
CRIZEEL-W-208	72.43	-0.80**	-8.29**	-0.04	-0.84	-0.13	0.52	0.02	0.12	-0.58	-0.06
CRIZEEL-W-263	-71.46	-0.47*	2.29	-1.11	-1.58**	0.07	0.21	0.02	0.08	-7.05**	0.27
CRIZEEL-W-257	-88.52	1.07**	-2.60	*96.0	2.02**	1.10^{**}	4.50**	0.04	-0.18	12.07**	0.24
SE	151.16	0.19	2.23	0.42	0.46	0.19	1.70	0.03	0.22	2.42	0.14
Testers	GCAt										
Tester 1	99.66	0.43**	-2.65	0.04	0.47	0.20	4.54**	-0.02	0.07	5.40**	0.06
Tester 2	-134.52	0.07	0.42	0.223	0.29	0.003	-1.33	-0.02	0.53**	-2.65	0.09
Tester 3	41.70	-0.22	1.31	0.04	-0.18	-0.20	-6.14**	-0.01	-0.30*	-7.58**	0.11
Tester 4	156.07	0.12	-2.11	-0.41	-0.29	0.42**	5.9**	0.05*	-0.32*	**86.7	-0.09
Tester 5	-162.91	-0.40**	3.03	0.11	-0.29	-0.43**	-2.76*	-0.01	0.02	-3.14	-0.16
SE	106.89	0.14	1.57	0.29	0.33	0.13	1.20	0.02	0.15	1.71	0.10

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INBRED LINES	GY	ASI	8	DTA	DTS	EASP	EHGT	EPP	PASP	PHGT	SG
	(kg ha ^{.1})	(days)		(days)	(days)	(1-9)	(cm)		(1-9)	(cm)	(1-9)
Lines	GCAI										
CRIZEEL-W-217	-217.22	0.46*	2.95	0.76	1.22**	-0.20	2.11	-0.001	0.11	5.41	-0.12
CRIZEEL-W-219	70.54	-0.52**	-9.45**	-0.30	-0.82	-0.14	6.00**	0.006	0.04	8.13**	0.37*
CRIZEEL-W-222	39.34	0.50**	-1.65	-1.02*	-0.51	0.24	-3.62*	-0.072	0.40*	-3.01	0.28
CRIZEEL-W-261	401.03*	0.04	7.71**	-0.19	-0.16	-0.58**	-3.78*	0.053	-0.71**	-0.89	-0.58**
CRIZEEL-W-232	-715.97**	-0.65**	-0.61	2.61**	1.95**	0.55**	-8.35**	-0.034	0.22	-16.49**	0.19
CRIZEEL-W-236	84.27	0.08	0.76	*66:0-	-0.91	-0.11	-5.67**	-0.048	0.15	-8.09**	-0.01
CRIZEEL-W-242	516.67**	0.24	4.38	0.14	0.38	-0.29	8.27**	0.017	-0.51**	9.57**	-0.14
CRIZEEL-W-208	-283.47	-0.39*	-5.64*	-1.02*	-1.40**	0.11	0.72	0.028	0.26	0.32	0.22
CRIZEEL-W-263	-204.63	-0.30	2.74	-0.79	-1.09*	60.0	0.02	0.024	60:0	-6.72*	-0.14
CRIZEEL-W-257	309.44	0.55**	-1.19	0.81	1.35**	0.33	4.30*	0.027	-0.05	11.76**	-0.07
SE	187.71	0.19	2.35	0.45	0.46	0.19	1.82	0.05	0.20	3.07	0.18
Testers	GCAt										
Tester 1	63.64	0.424**	-2.24	-0.28	0.14	-0.16	3.81**	0.003	0.11	4.26*	-0.15
Tester 2	-23.86	-0.18	1.25	-0.04	-0.21	0.03	0.56	-0.009	0.03	0.19	0.16
Tester 3	165.95	-0.13	2.27	-0.06	-0.19	-0.11	-4.47**	0.004	-0.20	-5.95**	-0.11
Tester 4	84.08	0.12	-2.95	0.03	0.15	0.26	5.31**	0.017	-0.06	9.74**	0.03
Tester 5	-289.81*	-0.24	1.67	0.35	0.11	-0.02	-5.21**	-0.014	0.12	-8.23**	0.07
SE	132.73	0.13	1.66	0.32	0.32	0.14	1.29	0.04	0.14	2.16	0.12

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	Tester 1	Tester 2	Tester 3	Tester 4	Tester 5	
CRIZEEL-W-217	-444.55	4.81	348.42	44.71	46.61	-
CRIZEEL-W-219	-382.20	-25.94	357.38	85.64	-34.88	
CRIZEEL-W-222	28.83	-215.60	252.61	-166.08	100.24	
CRIZEEL-W-261	638.61	-0.69	-117.45	278.36	-798.82*	
CRIZEEL-W-232	513.27	-152.22	-368.63	415.03	-407.45	
CRIZEEL-W-236	115.95	-224.78	-78.88	28.65	159.05	
CRIZEEL-W-242	50.65	544.87	-228.16	-324.10	-43.27	
CRIZEEL-W-208	-448.04	-111.69	-51.53	130.90	480.36	
CRIZEEL-W-263	-310.94	-27.40	76.72	37.81	223.82	
CRIZEEL-W-257	238.43	208.65	-190.49	-530.92	274.34	
SE	338.01	338.01	338.01	338.01	338.01	

 Table 7. Specific combining ability effects for grain yield of extra early maturing maize

 hybrids under low nitrogen

Significance codes: p<0.001 = *** p<0.01 = ** p<0.05 = *.

ASI, CC, EPP and GY implies that selection of genotypes for these traits will be promising since the genotypes had differences in their combining ability. This finding agrees with Ribeiro et al. (2020), who reported significant mean squares for GY, ASI and EPP but disagreed with Amegbor et al. (2022), who reported non-significant mean squares for ASI and EPP. The non-significance of line environment and line tester environment mean squares for GY, CC and EPP implies the gene effects for these traits were stable and thus, selecting an inbred line in any of the conditions would not come with an extra cost. This could be attributed to the stage of inbreeding (S6) in the lines used. This finding agrees with Ajala et al. (2020), who indicated non-significant line tester environment effect for GY but contradicts the findings of Ribeiro et al. (2020), who reported significant line

tester environment mean squares for GY.

Combining ability of inbred lines

Inbred lines CRIZEEL-W-261 and CRIZEEL-W-242 was promising under low N since both recorded desirable GCA effect for GY. Furthermore, when used as female parents in hybridization or current selection programme, these two inbred lines would readily pass on favourable genes controlling GY to their offspring. More so, the advantage of a desirable GCA effect for SG, EASP and CC shown by inbred line CRIZEEL-W-261 suggested its high probability of transmitting genes governing these traits to its progenies in a breeding programme. SG is an important agronomic trait that allows plants to maintain their photosynthetic activity and improve the grain-filling process even under stress (Borrell et al., 2014; Zhang et al., 2019). In

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х	Tester 1	Tester 2	Tester 3	Tester 4	Tester 5
CRIZEEL-W-217	-623.59	204.37	179.31	142.00	97.91
CRIZEEL-W-219	-693.39	-112.59	436.43	-268.27	637.81
CRIZEEL-W-222	-47.76	-81.96	79.05	24.36	26.31
CRIZEEL-W-261	340.85	311.60	-384.83	187.5824	-455.21
CRIZEEL-W-232	1039.98*	-311.89	-1028.53*	1117.49*	-817.05
CRIZEEL-W-236	-278.42	-26.47	72.36	128.31	104.22
CRIZEEL-W-242	-107.37	266.38	171.43	-546.25	215.81
CRIZEEL-W-208	139.048	-379.38	345.84	218.25	-323.76
CRIZEEL-W-263	10.20	32.03	-60.37	-390.73	408.87
CRIZEEL-W-257	220.45	97.91	189.30	-612.75	105.08
SE	419.74	419.74	419.74	419.74	419.74

 Table 8. Specific combining ability effects for grain yield of extra early maturing maize hybrids under optimum nitrogen.

Fsignificance codes: p < 0.001 = *** p < 0.01 = ** p < 0.05 = *.

addition to yield improvement and tolerance against abiotic stress, SG also confers a greater number of grain per ear, enhanced resistance to stem lodging (Luche et al., 2015; Adeyanju et al., 2016) and increased tolerance to diseases and pests (Howard & Smart, 1993). The desirable GCA for GY recorded by inbred line CRIZEEL-W-261 under low and optimum N could be associated with its desirable GCA for most of the traits proposed by Banziger et al. (1997), Banziger et al. (2000), and Badu-Apraku et al. (2011) (i.e. SG, EASP and PASP) for indirect selection and improvement in GY. This further indicates that CRIZEEL-W-261 will be a good source of genes for maize GY improvement.

Gene action

The significant proportions of GCA-line, GCA-tester and SCA variations observed under low N and optimum N suggested both additive and non-additive gene actions played a role in the expression of the traits studied in this research. Under both low and optimum N, the eminence of SCA in the expression of GY and EPP suggest these two traits were under the influence of non-additive gene action and that early generation testing would not be effective. Unsurprisingly, both GY and EPP were under the influence of non-additive gene action because EPP determines the degree of barrenness of a genotype under stress and has direct effect on GY (Badu-Apraku et al., 2011). The eminence of non-additive gene

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Figure 1. Gene Action for Grain Yield and Other Agronomic Traits Under Low N; DTS = days to silking, DTA = days to anthesis, ASI = anthesis-silking interval, CC = chlorophyll content, PASP = plant aspect, EASP = ear aspect, PHGT = plant height, EHGT = ear height, EPP = ears per plant, SG = stay green, GY = grain yield, GCAl & GCAt = general combining ability of line and tester parents respectively.

action for grain yield under low N in this research is consistent with the report of previous works by Betran *et al.* (2003), Meseka *et al.* (2006), and Mafouasson (2014) who also reported the eminence of nonadditive gene action for GY under low N. The additive (GCA) variance under low and optimum N had the effect of GCA-line being more pronounced than the effect of GCAtester, implying the action of maternal effect in these traits.

Although the preponderance of non-additive gene action for GY under optimum N is consistent with the findings by Wegary *et al.* (2014), who also showed that non-additive gene action in GY were more pronounced under low and optimum N, these findings contradict the results of Mafouasson (2014), Ifie et al. (2015), Obeng-Bio et al. (2019), and Amegbor et al. (2022), all of whom reported additive gene action for GY under optimum N. This contradiction may have resulted from the amount of genes controlling GY in the various germplasms. Again, the significance and eminence of non-additive gene action governing EPP under low N contradicts the findings of Ifie et al. (2015) and Obeng-Bio et al. (2019), who reported additive gene action for EPP under low N. The significance of GCA-line mean squares, coupled with the higher proportion of GCA-line than GCAtester in controlling SG implies SG is probably influenced by maternal effect. Hence, female lines with desirable GCA for SG would improve GY.

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Genotypic variability

The high PCV and moderate GCV observed for GY, ASI, PASP and EASP under low and optimum N suggests that there is adequate variation within the population to enable improvement under low N. Thus, a good selection or genetic gain could be made from the population used in this study. This finding is consistent with the results from the work of Tesfaye et al. (2021), who also reported a moderate GCV among hybrids developed using the same mating design (i.e. line tester). The low difference in magnitude between the GCV and PCV for GY, CC and PASP further supports the claim that, the genotypes used were stable in terms of the performance of these traits. However, the high difference between PCV and GCV observed for ASI implies that the environments greatly influenced this trait and, subsequently, the success of pollination and seed set. These findings contradict the findings of Ige *et al.* (2019) who reported high GCV coupled with low difference between GCV and PCV for GY and ASI under similar contrasting environments. The low GCV and PCV for DTS and DTA under low and optimum N conditions, imply little variation for the two traits. This is very evident from the fact that, all the inbred lines used were in the same maturity group (extra early maturity group).

The low to moderate narrow-sense heritability recorded for majority of the traits under low N except for PHGT, EHGT and PASP suggests that additive gene action played little role in the expression of these traits. The low, narrow sense heritability recorded by GY and EPP supports the earlier findings that non-additive gene action controlled these traits under low N in this study. The relatively higher narrow-sense



Figure 2. Gene Action for Grain Yield and Other Agronomic Traits Under Optimum N; DTS = days to silking, DTA = days to anthesis, ASI = anthesis-silking interval, CC = chlorophyll content, PASP = plant aspect, EASP = ear aspect, PHGT = plant height, EHGT = ear height, EPP = ears per plant, SG = stay green, GY = grain yield, GCAl & GCAt = general combining ability of line and tester parents respectively.

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heritability recorded for a number of the traits under optimum N to that under low N conditions supports the fact that the low N environments had a slightly greater influence on the heritability of these traits, which could be due to the extent of low N stress imposed. This finding agrees with the results of Ige *et al.* (2019), who also reported a low heritability for GY under low N.

The character with high heritability should be accompanied by high genetic advance to arrive at a more reliable conclusion (Arunkumar *et al.*, 2018). Jilo *et al.* (2018), had previously suggested the simultaneous consideration of heritability estimates and GA because high heritability may not always be associated with high GA. The high GAM recorded for GY under both low and optimum N condition shows that GY will respond to selection. This is further supported by the fact that other traits such as CC, EASP and PASP also had high GAM, which may have indirectly improved the GY of maize under low N. This agrees with the findings from the work of Ige et al. (2019), who also reported high GAM for GY under low N. Although a high GAM was recorded for GY, the low narrow sense heritability implies that nonadditive gene action governed GY. As such, heterosis breeding would be most appropriate for GY in this population.

Traits	Population	Ra	nge	PCV	GCV	H²b	h²n	GA	GAM
	Mean	Min	Max	(%)	(%)	(%)	(%)		(%)
ASI	2.08	0.67	3.67	38.59	13.58	12.39	12.39	0.21	9.85
CC	33.51	16.77	46.22	20.36	16.35	64.49	45.31	9.06	27.05
DTA	49.32	46.83	53.17	2.80	2.31	68.02	43.91	1.93	3.92
DTS	51.41	48.83	55.33	3.15	2.40	58.22	42.25	1.94	3.78
EASP	3.12	1.83	5.17	23.13	15.46	44.67	31.78	0.66	21.29
EHGT	59.75	34.93	73.97	13.83	11.87	73.66	54.56	12.54	20.99
EPP	0.89	0.65	1.05	8.31	5.76	48.07	14.31	0.07	8.23
GY	1653.26	630.73	2816.02	25.52	19.75	59.88	25.39	520.47	31.48
PASP	3.17	1.67	4.83	23.81	20.26	72.41	56.03	1.12	35.51
PHGT	137.73	102.40	154.30	8.57	7.70	80.67	63.77	19.62	14.24
SG	2.98	1.83	3.67	11.46	6.76	34.83	31.00	0.25	8.22

Table 9. Genotypic variability parameters of extra early maize hybrids under low nitrogen.

DTS = Days to Silking, DTA = Days to Anthesis, ASI = Anthesis-Silking Interval (days), CC = Chlorophyll Content, PASP = Plant Aspect (1-9), EASP = Ear Aspect (1-9), PHGT = Plant Height (cm), EHGT = Ear Height (cm), EPP = Ears per Plant, SG = Stay Green Characteristics (1-9), GY = Grain Yield (kgha⁻¹)

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Conclusion

CRIZEEL-W-242 and CRIZEEL-W-261 had desirable GCA effect for GY under low N, with CRIZEEL-W-261 being a good genotype for other traits such as SG, CC, EASP and PASP. None of the hybrids had desirable SCA effect for GY under low N in this study. Non-additive gene action controlled GY and EPP under low and optimum N. In contrast, additive gene action controlled the other agronomic traits under low and optimum N. Moderate GCV was observed for GY under low and optimum N whereas high GAM was observed for traits such as GY, EASP, PASP and CC, which assures good genetic gain or improvement from selection. The study provided relevant information on the selected newly developed inbred lines by CSIR-CRI.

Conflict of interest.

The authors declare there are no conflicts of interest.

Table 10.	Genotypic	variability	parameters	of extra	early	maize	hybrids	under	optimum
			nitr	ogen					

					8				
Traits	Population	Ra	inge	PCV	GCV	H²b	h²n	GA	GAM
	Mean	Min	Max	(%)	(%)	(%)	(%)		(%)
ASI	2.28	1.22	3.78	25.16	8.46	11.31	11.31	0.13	5.86
CC	44.49	31.12	58.69	14.16	12.22	74.53	63.47	9.67	21.73
DTA	48.01	45.78	52.67	2.91	2.51	74.39	58.82	2.14	4.45
DTS	50.30	47.56	54.44	2.79	2.40	74.05	58.06	2.14	4.26
EASP	2.91	2.00	4.00	15.00	11.44	58.09	49.38	0.52	17.96
EHGT	57.46	35.96	69.89	14.56	13.66	87.94	60.20	15.16	26.39
EPP	0.86	0.59	1.31	9.04	4.85	28.74	6.29	0.05	5.35
GY	2525.94	769.34	3446.21	22.73	19.47	73.35	26.92	867.55	34.35
PASP	2.80	1.67	4.22	18.25	13.70	56.34	23.95	0.59	21.18
PHGT	130.02	90.49	150.47	10.19	9.49	86.76	64.29	23.68	18.22
SG	2.27	1.33	3.11	17.05	11.83	48.11	33.11	0.38	16.90

DTS = Days to Silking, DTA = Days to Anthesis, ASI = Anthesis-Silking Interval (days), CC = Chlorophyll Content, PASP = Plant Aspect (1-9), EASP = Ear Aspect (1-9), PHGT = Plant Height (cm), EHGT = Ear Height (cm), EPP = Ears per Plant, SG = Stay Green Characteristics (1-9), GY = Grain Yield (kgha⁻¹)

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Ethical standards

Not applicable.

Funding

This work was done with funding from Accelerating Genetic Gains for Maize and Wheat for improved livelihood, through Bill and Melinda Gates foundation.

Acknowledgements

The authors express profound gratitude to accelerating genetic gains for maize and wheat for improved livelihood (AGG project); Mr. Joseph Mensah and the staff of CSIR-CRI.

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