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Genetic analysis and heterotic grouping of quality protein maize (*Zea mays* L.) inbred lines and derived hybrids under conditions of low soil nitrogen and drought stress

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Abstract Quality Protein Maize (QPM) varieties are rich in lysine and tryptophan, but suffer reduced grain yield (GY) in West and Central Africa (WCA) due to low soil nitrogen (low-N) and intermittent drought stress (DS). Development of stress-tolerant QPM hybrids will enhance sustainable maize production and improve nutritional health in WCA. Knowledge of combining ability, gene action and heterotic grouping of QPM inbred lines are crucial to successful breeding strategies for the development of superior hybrids with enhanced nutritional values. The objectives of this study were to: (i) determine the combining ability for GY and yield-related traits among 13 newly developed QPM inbred lines, and (ii) assign the QPM inbred lines to distinct heterotic groups based on general combining ability effects of multiple traits under low-N and DS conditions. Seventy-eight single cross hybrids were generated through half-diallel mating of 13 QPM inbred lines and evaluated along with three commercial checks for GY and yield-related traits under the low-N and DS conditions. Significant general combining ability (GCA) and specific combining ability effects were obtained for GY and yield-related traits. Both additive and non-additive gene effects were involved in the inheritance of GY and other traits under low-N and DS conditions. However, the additive gene effect for GY was twice as large as non-additive gene effect. Three heterotic groups were each delineated under low-N and DS. Inbred lines, CRIZEQ-44 and CRIZEQ-77 belonging to different heterotic groups were identified as testers for the development of superior hybrids for low-N and DS environments.

Keywords Drought stress · General combining ability · Grain yield · Low soil nitrogen · Quality protein maize · Specific combining ability

Abbreviations

ASI	Anthesis-silking interval
BI	Base index
DAS	Days after sowing
AD	Days to 50% flowering
SD	Days to 50% silking
DS	Drought stress
EA	Ear aspect
EHT	Ear height
GCA	General combining ability
GY	Grain yield

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HGCAMT	Heterotic grouping based on GCA of multiple traits
High-N	High soil nitrogen
Low-N	Low soil nitrogen
MC	Moisture content
EPP	Number of ears per plant
PA	Plant aspect
PHT	Plant height
QPM	Quality protein maize
SCA	Specific combining ability
SG	Stay-green characteristics
WW	Well-watered

Introduction

Maize (*Zea mays* L.) is one of the world's most important cereal crops, serving multiple applications as food, feed and industrial crop. In sub-Saharan Africa (SSA), its cultivation cut across a wide range of agro-ecological zones. Despite its broad adaptation, maize grain yield (GY) in SSA is very low (< 1.8 t/ha) compared to the global average of 5.4 t/ha (FAOSTAT 2020). The low yield can partly be attributed to poor soils (low soil nitrogen) and intermittent droughts occurring during the growing season, which causes significant GY losses.

In SSA, over 300 million people obtain up to 70% of their daily calories from maize-based diets (Martin et al. 2000; Abe et al. 2013). In most households, maize also supplies 17–60% of daily dietary protein requirements (Krivanek et al. 2007). However, the commonly cultivated maize varieties in SSA are nutritionally deficient in two key amino acids, lysine and tryptophan, leading to malnutrition particularly in households that cannot afford animal protein sources or protein food supplements (Prasanna et al. 2001). Quality Protein Maize (QPM) is a maize variety rich in lysine and tryptophan and can supply up to 73% of the human dietary protein requirement compared to 46% from normal endosperm varieties (Prasanna et al. 2001; Krivanek et al. 2007; Twumasi-Afriyie et al. 2016). Therefore, the development and promotion of QPM varieties will help mitigate the incidence of malnutrition-related ailments in SSA.

Nitrogen (N) deficiency (Bellon 2001; Abe et al. 2013) and drought (Meseka et al. 2006; Badu-Apraku et al. 2011; Wang et al. 2019) are two major abiotic stresses that affect the growth and productivity of maize in SSA. Whereas human activities have contributed to the reduction soil fertility in SSA, the incidence of drought has been compounded by global climatic changes, resulting in reduced amounts and poor distribution of rainfall. Studies have shown that maize GY losses due to low soil nitrogen (low-N) and drought stress (DS) vary between 10 and 50% (Wolfe et al. 1988; Meseka et al. 2006; Annor and Badu-Apraku 2016) and 40 and 90% (NeSmith and Ritchie 1992; Bänziger et al. 2006; Annor and Badu-Apraku 2016), respectively. These two stresses can occur simultaneously on farmers' fields and their combined effect could be more severe than the individual effects (Kim and Adetimirin 1997; Wegary et al. 2014). Therefore, the development of QPM varieties with tolerance to low-N and DS is crucial to sustainable food and nutritional security, as well as poverty alleviation among most maize-growing farmers in SSA.

Breeding stress-tolerant hybrids require knowledge of the combining ability (general and specific combining abilities), heterotic grouping and gene actions controlling the inheritance of traits (Dhillon and Pollmer 1978). This important information is limited on the multiple stress tolerant QPM inbred lines held at the maize breeding program of CSIR-Crop Research Institute, Kumasi, Ghana. There is therefore the need to assess the effect of low-N and DS on the combining ability and performance of the QPM inbred lines for GY and other traits. Some studies on combining abilities have been reported by earlier workers, but there is more to achieve in terms of knowledge of gene actions largely responsible for the inheritance of GY among QPM inbred lines under low-N and DS conditions (Annor and Badu-Apraku 2016; Bhadmus et al. 2021; Owusu et al. 2021). Under the DS, reports from previous studies (Wegary et al. 2014; Ofori et al. 2015; Owusu et al. 2021) involving QPM inbred lines revealed significant effects of both GCA and SCA for GY, although GCA effects were greater than the SCA's effects; suggesting that additive gene action largely controlled the inheritance of the GY. Other reports involving QPM inbred lines (Bhatnagar et al. 2004; Njeri et al. 2017) indicated that non-additive gene action was largely responsible for the variations in GY under DS conditions. Under low-N conditions, some studies involving QPM inbred lines (Musila et al. 2010; Obeng-Bio et al. 2019; Oyekale et al. 2020) revealed that additive gene action primarily controlled the inheritance

of GY, whereas Wegary et al. (2014), Bhadmus et al. (2021) and Dosho et al. (2021) reported the superiority of non-additive gene action in the inheritance of GY under low-N condition. In the light of this conflicting information in the literature, further studies are required to unravel the gene action mainly responsible for the inheritance of GY and other traits in QPM inbred lines under low-N and DS conditions.

The study therefore, sought to (i) determine the combining ability for GY and other traits in QPM inbred lines under low-N and DS conditions (ii) examine the nature of the gene action responsible for the inheritance of GY and other traits in QPM under conditions of low-N and DS and (iii) classify the QPM inbred lines into heterotic groups based on GCA effect of multiple traits.

Materials and methods

Genetic materials

The genetic materials used for this study consisted of 13 QPM inbred lines [CRIZEQ-77 (P-77), CRIZEQ-55 (P-55), CRIZEQ-54 (P-54), CRIZEQ-49 (P-49), CRIZEQ-46 (P-46), CRIZEQ-45 (P-45), CRIZEQ-44 (P-44), CRIZEQ-42 (P-42), CRIZEQ-40 (P-40), CRIZEQ-25 (P-25), CRIZEQ-24 (P-24), CRIZEQ-14 (P-14) and CRIZEQ-5 (P-5)] sourced from the Maize Breeding Programme at the Crops Research Institute, Fumesua, Ghana. The lines were crossed in half-diallel to generate 78 single-cross hybrids which were evaluated along with three commercial checks (Enibi, Etubi and Mamaba genotypes). The three checks were selected based on their enhanced levels of tryptophan and lysine, and GY stability across low-N and DS conditions (Twumasi-Afriyie et al. 2016).

Evaluation of genetic materials for yield and yield-related characters

Three independent trials, in terms of management conditions, were used to assess the performance of the genetic materials. All trials were arranged using a 9×9 alpha-lattice design and replicated three times. Plots comprised two rows that were 3 m long, with 0.75 m inter-row and 0.40 m intra-row spacing. Three seeds were sown per hill and later thinned to two seedlings per stand after two weeks of emergence to achieve a plant population of about 66,667 per hectare. Pre-emergence weed control was done using a herbicide composed of metolachlor, mesotrione and terbuthylazine as active ingredients at 4 L/ha.

In the first trial, the 78 single-cross hybrids and three standard checks were evaluated over two rainy seasons (June–September) from 2019 to 2020 at two locations, Branam (Lat. 007° 54'N, Long. 002° 01'W, 160 masl) and Fumesua (Lat. 06° 41'N, Long. 01° 28'W) under low-N (30 kg N/ha) and high-N (90 kg N/ha) conditions. The trial fields had previously been depleted of N through repeated growing and complete removal of residues of maize during harvest for three consecutive years. Soil samples were collected at a depth of 0–20 cm for the determination of N, P and K levels using the Kjeldahl method as described by Bremer and Mulvaney (1982). The laboratory analysis was performed at the Analytical Services Division of CSIR-Soil Research Institute, Kwadaso/Kumasi, Ghana in May 2019. Results of the soil analyses (Table 1) showed that the experimental

Table 1 Pre-cropping soil analysis for N, P and K

	Soil samples						
	A1	A3	A4	B1	B2	B3	B4
Fumesua							
N (g/kg)	0.08	0.07	0.04	0.07	0.06	0.13	0.07
P (mg/kg)	847.66	571.68	510.57	364.69	739.24	448.47	193.19
K (cmol/kg)	0.54	0.20	0.12	0.08	0.05	0.29	0.20
Branam							
N (g/kg)	0.14	0.07	0.06	0.09	0.04	0.07	0.04
P (mg/kg)	802.32	637.26	711.83	636.67	711.43	621.09	714.19
K (cmol/kg)	0.20	0.08	0.04	0.03	0.02	0.06	0.06

A1-A4, and B1-B4 represent the number of soil samples taken from trial evaluation for low-N and high-N conditions, respectively

fields were ideal for screening maize genotypes for tolerance to low-N (Page et al., 1982; Landon 2014). Based on the results of the soil analyses, nitrogen fertilizer was applied to bring the total available N of the low-N block to 30 kg/ha at two weeks after sowing (WAS). Also, 60 kg/ha each of single superphosphate (P_2O_5) and muriate of potash (K_2O) were applied at two WAS. Timely insect pest management, especially against fall armyworm was done as and when necessary, by spraying emamectin benzoate at the rate of 0.30 L/ha. Post-emergence weed management was done as and when necessary, using manual weeding and selective herbicide spraying using dicamba (1.0 L/ha). As a control, the genetic materials were evaluated under high-N condition within the same period and location in adjacent blocks, about 10 m away from the low-N trial. Based on pre-cropping soil test values, fertilizers were applied at a rate of 60 kg N/ha, 60 kg P/ha and 60 kg K/ha at two WAS and later top-dressed with an additional 30 kg N/ha at four WAS to bring the total available N to 90 kg N/ha. Apart from the different N fertilizer application rates, management of both low-N and high-N trials was the same.

The 78 single-cross hybrids along with three commercial checks were also evaluated over two dry seasons (2018/2019; 2019/2020) at the research field of the Crops Research Institute, Fumesua (Lat. 06° 41'N and Long. 01° 28'W, 280 masl) under managed DS and well-watered (WW) conditions. The trials were conducted during the last fortnight of November so that the flowering and grain filling stages of the DS trial occurred in mid-January when the incidence of rainfall was negligible, thus predisposing the plants to DS at reproductive stage. Pre-emergence weed control was done by spraying a combination of terbuthylazine, mesotrione and S-metolachlor at a rate of 4 L/ha. The plants were watered using an overhead sprinkler irrigation system at a flow rate that supplied 17 mm of water to the plants each week for the first 25 days after sowing (DAS). The supply of irrigation water was thereafter withdrawn to ensure that the plants depended on retained soil moisture for their growth and development. Moisture was maintained at 100% field capacity during the first 25 days only. Thereafter, the plants were predisposed to severe drought at reproductive stage when irrigation was fully withdrawn. On the other hand, the WW block continued to receive irrigation water, thus maintaining 100% field capacity until physiological maturity. For both DS and WW trials, NPK 15–15-15 compound fertilizer was applied at a rate of 60 kg N/ha, 60 kg P/ha and 60 kg K/ha at two WAS and later top-dressed with additional 30 kg N/ha at four WAS. Post-emergence weed control was done by spraying a combination of dicamba and topramezone at a rate of 0.30 L/ha. Attack by fall armyworm (FAW) was controlled by spraying emamectin benzoate and acetamiprid at a rate of 0.30 L/ha.

Data collection

Under each condition, data were recorded on days to 50% anthesis (AD) as the number of days from the sowing date to the date when half of the plants in a plot shed pollen, days to 50% silking (SD) as the number of days from sowing date to date when half of the plants in a plot have emerged silks, and anthesis-silking interval (ASI) as the difference between SD and AD. Measurement of plant height (PHT) in centimeters, was done from soil level to the first tassel branch of five competitive plants at physiological maturity (Badu-Apraku et al. 2011). Also, ear height (EHT) in centimeters, was measured from soil level to the upper ear insertion node of five competitive plants and the average values were recorded (Badu-Apraku et al. 2011). Data was recorded for plant aspect (PA) on a score of 1 to 9 based on uniformity in plant and ear heights, lodging characteristics, reaction to pests and diseases, etc., where 1 = excellent and, 9 = poor (Badu-Apraku et al. 2011). Also, ear aspect (EA) was rated on a scale of 1 to 9, where 1 = excellent and 9 = poor phenotypic appearance of ears harvested. The number of ears per plant (EPP) was estimated as the ratio of the number of harvested ears to plant stand count at harvest (Owusu et al. 2021). Stay-green characteristics (SG) for trials under low-N and DS conditions were rated at 70 days after sowing on a scale of 1 to 9, where 1 = all the leaves of plants remaining green and 9 = all the leaves of plants dead in appearance (Obeng-Bio et al. 2019). All harvested ears of each plot were shelled and weighed and the grain moisture content (MC) was determined. Estimation of grain yield (kg/ ha) at 15% MC was done as:

$$Grain\ yield\ (kg/ha) = \frac{GW(100 - MC)}{85} \times \frac{(10000)}{(3.4 \times 0.75 \times 2)} \quad (1)$$

where *GW* is the grain weight in kilograms of all ears harvested and *MC* is the grain moisture content after shelling (Owusu et al. 2021).

Data analyses

Data collected on EPP, PA, EA and SG were transformed using log transformation method as $\log(x+1)$ where x represents the raw count or scored data. The data for all measured traits were then subjected to the Bartlett's test for homogeneity of variances (Snedecor and Cochran 1989). Results of the homogeneity tests across environments (condition-year-location) for grain yield showed no significant differences, and thus combined analysis of variance (ANOVA) was separately performed across each condition-year-location combinations for all the measured traits using the PROC GLM procedure in SAS (SAS version 9.4, SAS Institute 2017). The research conditions, genotype × environment interactions, and replications were considered random factors, while the entries (genotypes) were considered fixed. The estimated values for repeatability (R) of traits were determined as:

$$Repeatability\ (R) = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e}{re}} \quad (2)$$

where σ_g^2 is a variance of additive gene effect (Hallauer et al. 2010), σ_{ge}^2 is the variance of genotype × environment interaction, r is the number of replications,e is the number of research conditions, and σ_e is the variance of experimental error.

The general combining ability (GCA) of the parents and specific combining ability (SCA) of the crosses, as well as environmental effects for each research condition were determined following Griffing's method 4, model 1 (Griffing 1956), using the DIALLEL-SAS program (Zhang et al. 2005) in SAS software (version 9.4, SAS Institute 2017). The statistical linear model used for the combining ability analysis for each condition was as follows:

$$Y_{ijk} = \mu + E_e + g_i + g_j + S_{ij} + gE_{eg} + sE_{es} + \varepsilon_{ijk} \quad (3)$$

where Y_{ijk} is the observed performance for a trait of the combination between the parents i and j in the k^{th} environment, μ is the grand mean, $g_i + g_j$ are the GCA effects, S_{ij} is the SCA effect, gE_{eg} is the interaction between GCA and the environment (E), sE_{es} is the interaction between SCA and the environment and ε_{ijk} is error associated with the ij^{th} cross evaluated in the k^{th} replication and E_e environment (Hallauer and Miranda, 2010). Significant effects of GCA and SCA were compared using *t-test* statistics. The relative contributions of GCA and SCA effects of traits were determined based on Baker's ratio (Baker 1978) as:

$$Baker's\ ratio = \frac{2MSgca}{2MSgca + MSsca} \quad (4)$$

where *MSgca* and *MSsca* are mean square estimates of GCA and SCA effects of traits, respectively.

The contributions of GCA and SCA variances were calculated as the percentage of the GCA components to the total genetic variance based on the sum of squares (Baker 1978).

Heterotic grouping based on the GCA effects of multiple traits (HGCAMT) was used to classify the 13 QPM inbreds into heterotic groups. The significant effects of GCA on a trait for the inbreds were standardized and subjected to Ward's minimum variance cluster analysis (SAS Institute 2017). Identification of testers was based on criteria described by Pswarayi and Vivek (2008), that inbred testers must (i) have a high and positive GCA effect for the GY (ii) be assigned to a heterotic group, and (iii) manifest a reasonable from the GY. Similarly, hybrid testers were identified based on the assumption that (i) the inbred lines must show high and positive GCA effects for the GY, (ii) the inbred lines must be assigned to the same heterotic group, and (iii) the single-cross hybrid must be high yielding.

Results

Variability of traits among entries

Under low-N stress conditions, significant ($p \leq 0.05$) environment, genotype, and genotype × environment interaction effects were obtained for the GY and some traits (Table 2). A significant environment effect was obtained for GY and other traits except for EA, while the genotypic effect was significant for the GY and other traits, except ASI, EHT, SG and EPP. Genotype × environment interaction effect was significant for the GY and other traits, except for the EPP. Significant GCA and SCA effects were obtained for the GY and all traits, although GCA effect was twice as large as SCA effect. Significant GCA × environment interaction effects were obtained for GY and other traits, except AD, SD, ASI and PA. Also,

Table 2 Mean squares for grain yield and other selected yield traits of quality protein maize singe-cross hybrids were evaluated under low-N and high-N conditions

Sources of variation	Df	GY (kg/ ha)	AD	SD (days)	ASI	PHT (cm)	EHT	PA (1–9 rating)	EA	SG	EPP
Low-N condition											
Environment (Env.)	3	53,374,970.9***	7.19**	127.21***	73.92***	108,991.8***	47,000.2***	74.72***	0.48	35.56***	1.715***
Replication (Env.)	8	1,528,234.6***	3.29***	3.58***	0.77***	1188.6***	806.4***	2.16***	13.82***	4.32***	0.030***
Genotypes (G)	77	2,043,058.3***	6.07***	8.74***	0.89	500.8*	136.4	2.50***	2.05*	1.28	0.023
G×Env	231	953,526.1***	15.91**	2.92***	0.77***	305.6***	99.1***	1.22***	1.23***	1.12***	0.019
GCA	12	3,542,622.4***	4.25***	24.16***	2.07***	1406.0***	285.5***	2.80***	5.49***	3.78***	0.027*
SCA	65	1,766,215.7***	1.27***	5.89***	0.67***	333.7***	108.8***	2.45***	1.42***	0.82**	0.023**
GCA×Env	36	1,388,534.4***	0.75	1.36	0.32	239.9*	160.6***	0.67	3.62***	2.24***	0.030*
SCA×Env	195	873,216.9***	1.37***	3.21***	0.86	317.7***	87.8***	1.32***	0.79	0.92***	0.017
Residual	520	224,099.7	0.76	1.05	0.34	116.9	42.0	0.63	0.70	0.47	0.015
Repeatability		0.572	0.689	0.605	0.090	0.34	0.40	0.637	0.347	0.231	0.129
High-N condition											
Environment (Env.)	3	64,381,860.5***	20.94***	35.01***	1.80**	586.70*	68.46	1.80	44.31***	–	0.494***
Replication (Env.)	8	70,049,903.5***	3.49***	5.41***	0.85***	2917.90***	1557.48***	4.84***	0.76***	–	0.018*
Genotypes (G)	77	7,571,910.5***	2.04***	2.19***	0.34	684.12***	136.75***	1.17*	0.41	–	0.013**
G×Env	231	2,721,611.9***	0.87***	0.88***	0.30	48.89	9.72	0.71*	0.39	–	0.008*
GCA	12	16,048,738.4***	6.97***	7.32***	0.44*	1778.97***	217.35***	1.93***	0.75*	–	0.022***
SCA	65	6,006,957.7***	1.13***	1.24***	0.32	481.99***	121.87***	1.03***	0.35	–	0.012***
GCA×Env	36	3,348,073.9***	1.29***	1.30***	0.25	39.97	8.45	1.27**	0.51	–	0.007
SCA×Env	195	2,605,957.4***	0.80***	0.81***	0.31	50.53	9.96	0.61	0.36	–	0.008*
Residual	520	667,675.4	0.29	0.32	0.24	89.39	35.78	0.52	0.34	–	0.005
Repeatability		0.882	0.957	0.940	0.619	0.878	0.942	0.901	0.853		0.657

GY Grain yield; *SD* Silking date; *AD* Anthesis date; *ASI* Anthesis-silking interval, *EHT* Ear height, *PHT* Plant height; *EA* Ear aspect; *PA* plant aspect, *EPP* number of ears per plant; *SG* Stay-green characteristics

*, **, and ***significant at 5, 1 and 0.1% probability levels, respectively

SCA × environment interaction effect was significant for GY and some traits, but not ASI, EA and EPP. The repeatability estimates ranged from 9.0% for ASI to 63.7% for PA (Table 2).

Under high-N conditions, a significant environment effect was obtained for the GY and other yield characters, except EHT, and PA, while the genotype effect was significant for the GY and other traits except for ASI and EA. A significant genotype × environment interaction effect was obtained for GY and other traits, except for the ASI, PHT, EHT, EA and SG (Table 2). The General combining ability effect was significant for GY and all measured traits, while a significant SCA effect was obtained for GY and other traits, except ASI, EA and SG. The significant GCA effect for GY and other traits was twice as large as SCA effect. Significant GCA × environment interaction effect was obtained for GY and other traits, except for the ASI, PHT, EHT, EA and EPP, while SCA × environment interaction effect was obtained for GY and other traits, except ASI, PHT, EHT, PA, EA and SG. The repeatability estimates ranged from 61.9% for ASI to 95.7% for AD (Table 2).

A significant environment effect was obtained for GY and other traits under DS condition, while the genotypic effect was significant for GY and other traits, except for AD, SD, ASI and PHT. Genotype × environment interaction effect was significant for GY and other traits, except PA and EPP. Significant GCA and SCA effects were obtained for GY and other traits except for EPP. Also, the significant GCA effect for GY and other traits was twice as large as SCA effect. A significant GCA × environment interaction effect was obtained for GY and other traits, except ASI, PA, and EPP. SCA × environment interaction effect was significant for GY and other traits, except PA, EA, SG and EPP. Repeatability estimates ranged from 16.2% for SD to 87.3% for PA (Table 3).

Under WW conditions, a significant environmental effect was obtained for GY and other traits, except ASI, PHT, EHT, and PA, while the genotypic effect was significant for GY and other traits except for EA. A significant genotype × environment interaction effect was obtained for GY and other traits, except PHT and EHT. Partitioning the genotypic effect into its components revealed significant GCA and SCA effects for GY and other traits, except the SCA effect for EA. The GCA effect was twice as large as the SCA effect, except for AD and PA. Significant GCA and SCA × environment interaction effect was obtained for GY and other traits, except PHT, and EHT. Repeatability estimates ranged from 17.2% for ASI to 93.8% for PHT (Table 3).

Relative contributions of additive and non-additive gene effects

The GCA and SCA effects obtained for GY and other traits indicated that both additive and non-additive gene actions were involved in the inheritance of those traits under low-N and DS conditions. In this study, the proportion of additive gene action obtained for GY was greater under optimal (84.4%) than under low-N (80.00%), DS (69.85%) and across low-N and DS conditions (74.93%) (Table 4). In general, the additive gene effect was largely responsible for the inheritance of GY and other measured traits under low-N and DS (Fig. 1). Under low-N, additive gene action was more important in the inheritance of GY and other traits, ranging from 69.57% for PA to 90.21% for SG (Fig. 1). Under the DS condition, the proportion of additive gene effect was greater than the non-additive gene effect for GY and all measured traits ranging from 58.58% (PA) to 90.23% (EA) (Fig. 1). Across low-N and DS conditions, the proportion of additive gene effect for GY and other traits was greater than the non-additive gene effect. The proportion of additive gene effect ranged from 64.08% for PA to 89.37% for EA across low-N and DS conditions (Fig. 1). Additive gene effect contributed 74.93% of the total genetic variance in GY across low-N and DS conditions. Under optimal conditions, additive gene effect of GY and other yield traits were greater than non-additive gene action, ranging from 67.08% (AD) to 91.77% (SD) (Fig. 1). Also, the additive gene effect contributed 84.40% of the total genetic variance in GY (Fig. 1).

General combining ability effect of inbred lines

A significant GCA effect for GY and other yield traits was obtained for inbred lines under low-N and DS conditions. Under the low-N condition, a significant positive GCA effect of GY was obtained for inbred lines CRIZEQ-49, CRIZEQ-77, CRIZEQ-42 and CRIZEQ-44 while a significant positive GCA effect

Table 3 Mean squares for grain yield and other selected yield traits of quality protein maize singe-cross hybrids were evaluated under drought stress and well-watered conditions

Sources of variation	Df	GY (kg/ ha)	AD (days)	SD	ASI	PHT (cm)	EHT	PA (1–9 rating)	EA	SG	EPP
Drought stress condition											
Environment (Env.)	1	8,617,993.7***	313.44***	450.17***	12.34***	168,500.3***	27,724.6***	4.33**	1120.03**	148.92***	0.409**
Replication (Env.)	4	106,585.0***	5.96***	5.83***	0.90***	1136.7***	708.4***	0.57*	11.80**	0.32***	0.260***
Genotypes (G)	77	2,014,378.4***	3.70	4.21	0.69	451.9	170.1**	3.78***	3.14**	1.98***	0.052*
G × Env	77	933,106.1***	8.82***	4.48***	0.62***	395.9***	95.3***	0.47	1.24*	0.30*	0.038
GCA	12	2,276,957.3***	2.86***	7.81***	1.68***	1404.8***	418.9***	2.80***	9.28**	3.68***	0.046
SCA	65	1,965,902.3***	3.24***	3.88***	0.54**	369.7***	124.3***	3.96***	2.01**	1.67***	0.059
GCA × Env	12	825,007.1***	7.10***	7.74***	0.48	657.6***	137.1**	0.60	2.44**	0.56**	0.052
SCA × Env	65	953,062.9***	2.53***	3.88***	0.65***	347.6***	87.5**	0.45	1.02	0.26	0.036
Residual	260	285,425	0.96	1.08	0.34	170.29	50.06	0.45	0.87	0.35	0.05
Repeatability		0.576	0.295	0.162	0.186	0.432	0.477	0.873	0.576	0.769	0.188
Well-watered conditions											
Environment (Env.)	1	46,600,226.0**	77.95**	82.93**	0.08	69.2	1.7	0.42	147.80**	–	0.647**
Replication (Env.)	4	6,951,604.4**	9.11**	11.10**	0.39**	2831.9**	1813.1**	7.01**	5.47**	–	0.005**
Genotypes (G)	77	7,177,054.7**	5.10*	5.78**	0.56**	896.8**	228.0**	2.30**	0.65	–	0.014*
G × Env	77	2,626,067.5**	15.36**	4.09**	0.70**	13.4	7.8	1.27**	0.64*	–	0.009**
GCA	12	15,339,084.5**	3.21**	23.03**	1.12**	2111.6**	287.7**	3.78**	1.55**	–	0.029**
SCA	65	5,670,218.4**	3.15**	4.13**	0.51**	672.5**	216.9**	2.03**	0.48	–	0.012**
GCA × Env	12	2,653,646.5**	3.73**	5.40**	0.61*	12.8	3.5	2.18**	0.84*	–	0.011*
SCA × Env	65	2,620,976.0**	3.04**	3.85**	0.71**	13.5	8.6	1.10**	0.6	–	0.009**
Residual	260	495,870	0.40	0.51	0.29	73.1	35.5	0.61	0.48	–	0.005
Repeatability		0.660	0.414	0.447	0.172	0.938	0.892	0.466	0.501	–	0.235

GY Grain yield; *SD* Silking date; *AD* Anthesis date; *ASI* Anthesis-silking interval; *EHT* Ear height; *PHT* Plant height; *EA* Ear aspect; *PA* plant aspect; *EPP* number of ears per plant; *SG* Stay-green

*, **, and *** = significant at 5, 1 and 0.1% probability levels, respectively

Table 4 General combining ability effect for grain yield and selected yield traits for QPM inbred lines evaluated under low-N and drought stress conditions

Inbred	GY (kg/ha)				AD	SD	ASI	PHT	EHT	PA	EA	SG	EPP
	LN	DS	ACR	OPT	ACR	ACR	ACR	ACR	ACR	ACR	ACR	ACR	ACR
CRIZEQ-5	−384.54**	−216.70**	−300.62**	−1052.27***	−0.18**	−0.02	0.16**	−7.73***	−5.08***	0.23***	0.57**	0.28**	−0.029*
CRIZEQ-14	−53.45	159.31**	52.93*	145.21	−0.11	−0.20**	−0.10**	−0.58	−1.21**	0.04	−0.12*	0.00	−0.041***
CRIZEQ-24	−202.00**	−56.96	−129.48**	−431.74***	0.15**	0.17**	0.02	4.49***	3.45***	−0.07	0.22**	−0.37**	0.008
CRIZEQ-25	−14.19	−143.20**	−78.70*	334.79***	0.38***	0.50***	0.12**	1.64*	0.15	−0.03	0.02	0.05	−0.007
CRIZEQ-40	−115.01*	−145.35**	−130.18**	−195.80*	−0.65***	−0.84***	−0.2	−4.40***	−1.71***	0.24***	0.26**	0.31**	−0.010
CRIZEQ-42	91.71*	−150.68**	−29.48	251.76**	0.32***	0.25***	−0.07	1.52*	−1.11**	−0.03	0.28**	−0.08*	0.021
CRIZEQ-44	303.06**	196.77**	249.92**	449.82***	−0.49***	−0.75***	−0.26**	−4.39***	−1.96***	−0.18***	−0.40**	0.15**	0.015
CRIZEQ-45	−112.39*	−112.19*	−112.29**	−29.09	0.82***	0.81***	−0.01	−0.79	1.02*	0.05	−0.28**	−0.12**	−0.005
CRIZEQ-46	−67.63	84.16	8.26	7.62	0.28***	0.05	−0.23**	5.18***	2.25***	−0.04	−0.30**	0.09*	−0.016
CRIZEQ-49	229.18**	146.04**	187.61**	238.93**	−0.02	0.14*	0.17**	5.22***	1.62***	−0.14**	−0.41**	0.24**	0.026*
CRIZEQ-54	−99.59*	−164.12**	−131.85**	−156.86*	−0.34***	−0.30***	0.04	−1.07	1.67***	0.29***	−0.09	0.02	0.003
CRIZEQ-55	−78.26	−6.19	−42.22	−491.36***	−0.18**	−0.08	0.10**	−4.62***	0.54	0.11*	0.46**	−0.25**	0.028*
CRIZEQ-77	503.11**	409.12**	456.11**	928.99***	0.01	0.26***	0.25**	5.53***	0.37	−0.46***	−0.22**	−0.31**	0.005

GY Grain yield; *SD* Silking date; *AD* Anthesis; *ASI* Anthesis-silking interval; *EHT* Ear height; *PHT* Plant height; *EA* Ear aspect; *PA* plant aspect; *EPP* number of ears per plant; *SG* Stay-green characteristics; *LN* Low-N; *DS* Drought stress; OPT Averaged across high-N and well-watered; *ACR* Averaged across low-N and drought stress

*, **, and *** = significant at 5, 1 and 0.1% probability levels, respectively

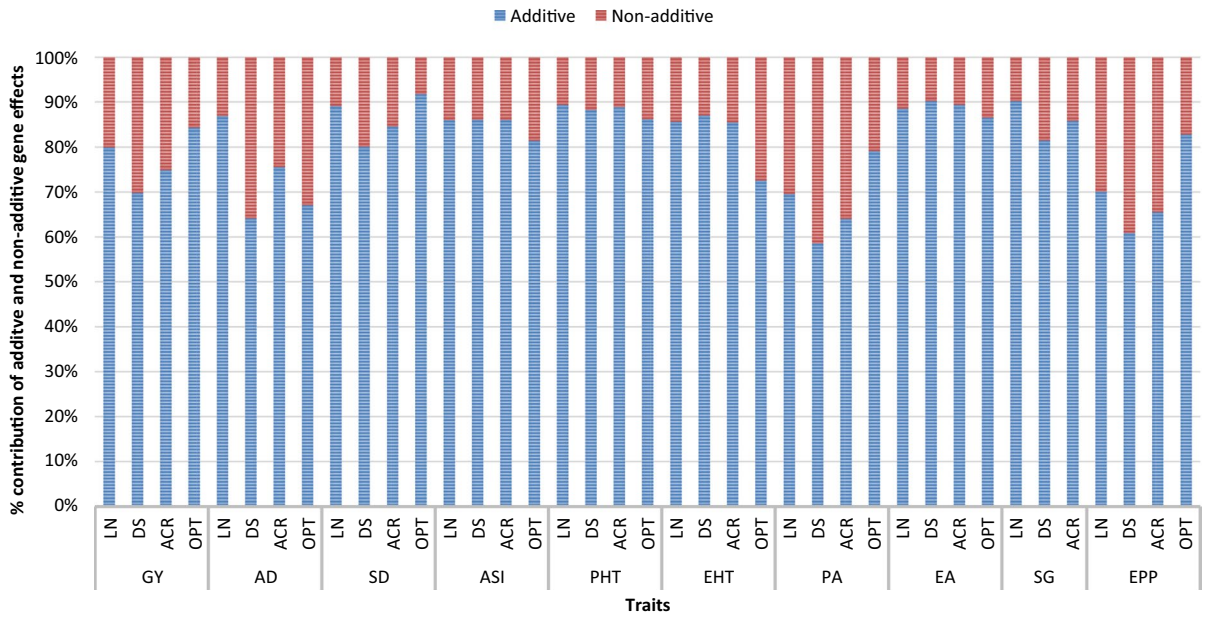

Fig. 1 The proportion of additive (lower bar) and non-additive (upper bar) gene actions to the total genetic variance for grain yield and other yield traits of QPM single-cross hybrids was evaluated under low-N, drought stress and optimal conditions. Grain yield (GY), Silking date (SD), Anthesis date (AD), Anthesis-silking interval (ASI), Ear height (EHT), Plant height (PHT), Ear aspect (EA), plant aspect (PA), number of ears per plant (EPP), Stay-green characteristics (SG), Low soil nitrogen (Low-N), Drought stress (DS), Across high-N and well-watered (OPT), Across low-N and drought stress (ACR)

of GY was obtained for inbred lines CRIZEQ-44, CRIZEQ-14, CRIZEQ-77 and CRIZEQ-49 under DS condition (Table 4). The inbred lines CRIZEQ-49, CRIZEQ-44 and CRIZEQ-77 manifested significant positive GCA effects for GY, while a significant negative GCA effect was obtained for CRIZEQ-25, CRIZEQ-24, CRIZEQ-5, CRIZEQ-45, CRIZEQ-40 and CRIZEQ-54 across DS and low-N conditions. Also, the inbred lines CRIZEQ-42, CRIZEQ-25, CRIZEQ-77, CRIZEQ-49 and CRIZEQ-44 manifested significant positive GCA effect for GY across the optimal conditions. However, a significant negative GCA effect for GY was obtained for CRIZEQ-55, CRIZEQ-24, CRIZEQ-54, CRIZEQ-40 and CRIZEQ-5.

The results obtained for other yield related traits revealed a significant negative GCA effect of AD for inbred lines CRIZEQ-5, CRIZEQ-40, CRIZEQ-44, CRIZEQ-54 and CRIZEQ-55 across low-N and DS conditions. A significant positive GCA effect for SD was obtained for inbred lines CRIZEQ-14, CRIZEQ-40, CRIZEQ-44 and CRIZEQ-54, while a significant negative GCA effect for ASI was manifested by inbred lines CRIZEQ-14, CRIZEQ-44 and CRIZEQ-46. Also, a significant negative GCA effect for PHT and EHT was obtained for inbred lines CRIZEQ-5, CRIZEQ-14, CRIZEQ-40, CRIZEQ-42 and CRIZEQ-44. Inbred lines CRIZEQ-44, CRIZEQ-49 and CRIZEQ-77 manifested a significant negative GCA effect for PA, while inbred lines CRIZEQ-5, CRIZEQ-40, CRIZEQ-54 and CRIZEQ-55 had significant positive GCA effect. Significant GCA effect for EA was obtained for inbred lines CRIZEQ-5, CRIZEQ-24, CRIZEQ-40, CRIZEQ-42, and CRIZEQ-55, while inbred lines CRIZEQ-14, CRIZEQ-44, CRIZEQ-45, CRIZEQ-46, CRIZEQ-49 and CRIZEQ-77 manifested significant negative GCA effect for EA. Inbred lines CRIZEQ-24, CRIZEQ-45, CRIZEQ-55 and CRIZEQ-77 had a significant negative GCA effect for SG, while a significant positive GCA effect was obtained for inbred lines CRIZEQ-5, CRIZEQ-40, CRIZEQ-44, CRIZEQ-46, and CRIZEQ-49. A significant positive GCA effect for EPP was obtained for inbred lines CRIZEQ-49 and CRIZEQ-55 (Table 4).

Heterotic grouping of inbred lines

Classification of the inbreds into heterotic groups was based on HGCAMT and illustrated with a dendrogram. Under the low-N condition, the inbred lines were classified into three heterotic groups at a 40.0% level of dissimilarity ($r^2 = 0.4$). Inbred lines CRIZEQ-5, CRIZEQ-40, and CRIZEQ-44 were assigned to heterotic group I. Heterotic group II comprised eight inbred lines, CRIZEQ-14, CRIZEQ-46, CRIZEQ-54, CRIZEQ-24, CRIZEQ-25, CRIZEQ-42, CRIZEQ-45, and CRIZEQ-55, while two inbred lines CRIZEQ-49 and CRIZEQ-77 were classified into heterotic group III (Fig. 2).

Under DS conditions, the inbred lines were assigned to three heterotic groups at a 40.0% dissimilarity level. Heterotic group I comprised four inbred lines; namely, CRIZEQ-5, CRIZEQ-40; CRIZEQ-54 and CRIZEQ-55. Five inbred lines; namely, CRIZEQ-14, CRIZEQ-46, CRIZEQ-49, CRIZEQ-44, and CRIZEQ-77 were assigned to heterotic group II, while CRIZEQ-24, CRIZE-25, CRIZEQ-42 and CRIZEQ-45 were also assigned to heterotic group III. Based on criteria proposed by Pswarayi and Vivek (2008), CRIZEQ-14, CRIZEQ-49, CRIZEQ-44 and CRIZEQ-77 were identified as testers belonging to heterotic group II (Figs. 3, 4).

Averaged across low-N and DS conditions, the inbred lines were assigned to two heterotic groups at a 30.0% ($r^2 = 0.3$) dissimilarity level. Heterotic group I comprised six inbred lines; namely, CRIZEQ-5, CRIZEQ-14, CRIZEQ-54, CRIZEQ-55 and CRIZEQ-44, while inbred lines CRIZEQ-24, CRIZEQ-25, CRIZEQ-42, CRIZEQ-45, CRIZEQ-46, CRIZEQ-49 and CRIZEQ-77 were also assigned to heterotic group II.

Discussion

The development of QPM hybrids that are tolerant to DS and can efficiently use the meager amounts of nitrogen that farmers apply, is an important strategy to reduce food insecurity and malnutrition in WCA. In this study, 78 single-cross hybrids derived from half-diallel mating of 13 QPM inbred lines were evaluated under low-N, high-N, DS and WW conditions. The significant environment effect obtained for GY and other yield traits, underscored the distinctiveness of each condition and thus, the need to extensively test the hybrids across multiple conditions of similar effects to ascertain yield stability. The significant genotype effect for GY and other traits indicated the presence of large genetic variability in the hybrids, which is desirable to facilitate accelerated gains from selection for those traits under each and across stress conditions. The significant genotype × environment effect for GY and other yield traits under each and across stress conditions indicated the varying responses of the hybrids to the different conditions. This result is consistent with the findings of Betrán et al. (2003), Machida et al. (2010), Obeng-Bio et al. (2020) under

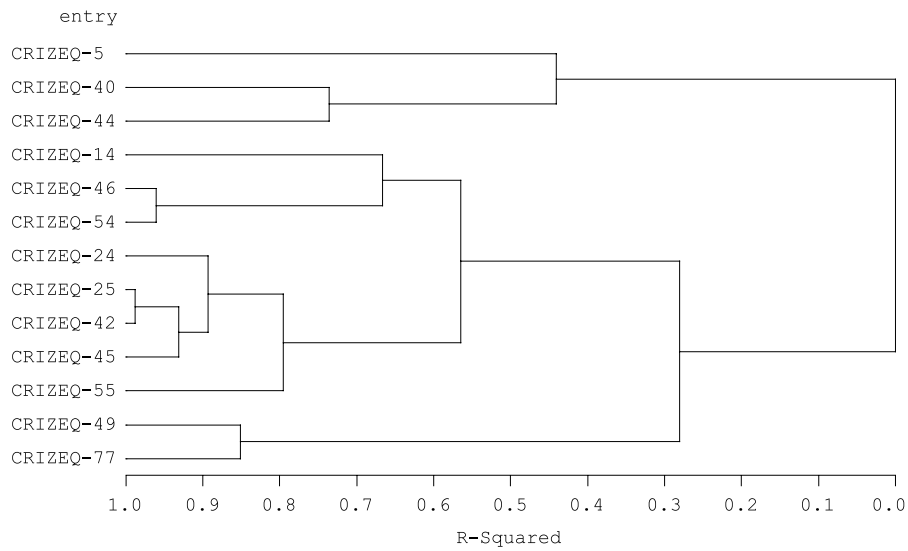

Fig. 2 Classification of inbred lines into heterotic groups based on general combining ability effect of multiple traits (HGCAMT) under low-N conditions

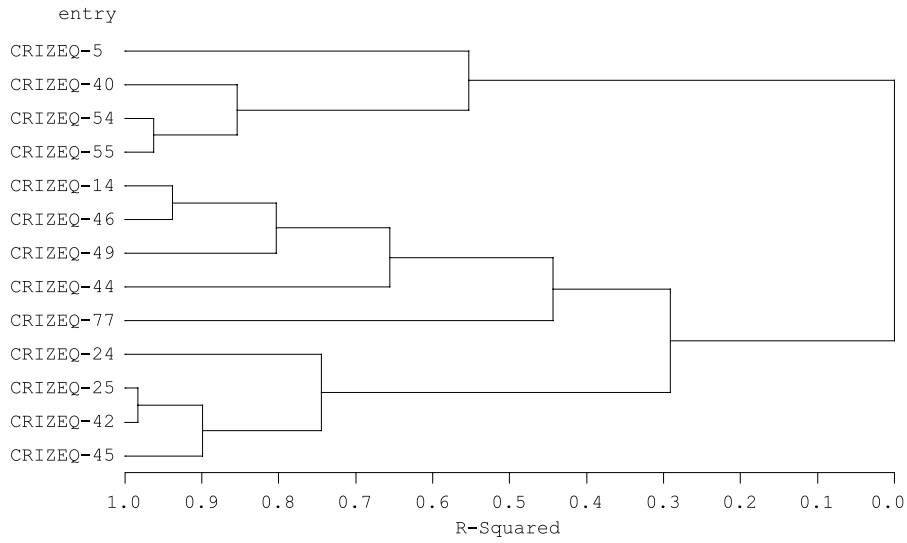

Fig. 3 Classification of inbred lines into heterotic groups based on general combining ability effect of multiple traits under drought stress conditions

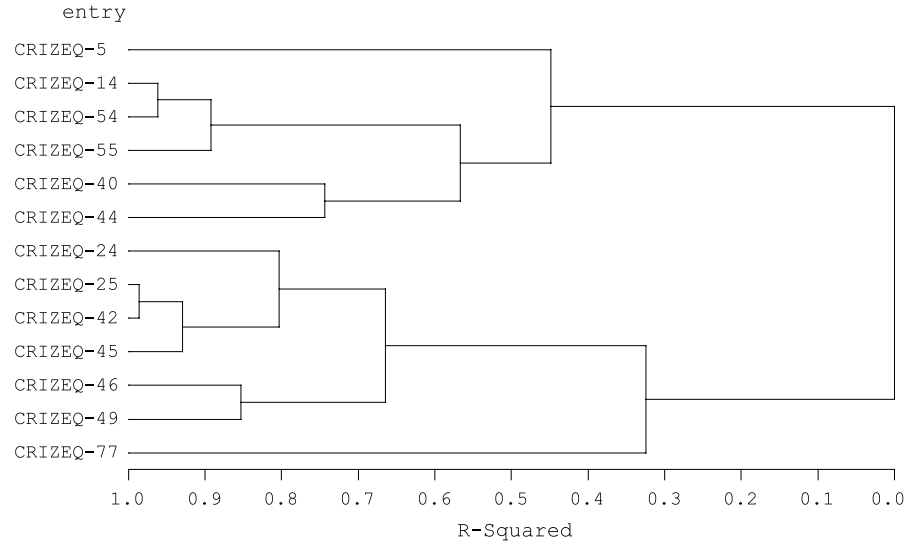

Fig. 4 Classification of inbred lines into heterotic groups based on general combining ability effect of multiple traits across low-N and drought stress conditions

low-N and high-N conditions, and Musila et al. (2010), Njeri et al. (2017), Bhadmus et al. (2021) and Owusu et al. (2021) under DS and WW conditions.

Partitioning the genotypic effect into components of GCA and SCA revealed a significant effect for GY and other yield traits under low-N and high-N conditions. This result indicated that both additive and non-additive gene actions contributed to the inheritance of those traits, although additive gene action was largely involved. This result agrees with the findings of Musila et al. (2010), Wegary et al. (2014), Annor and Badu-Apraku (2016), Abu et al. (2021), and Bhadmus et al. (2021). In contrast, this result disagrees with the findings of Betrán et al. (2003) and Machida et al. (2010) who reported a preponderance of non-additive gene action in the inheritance of GY for QPM inbred lines under low-N conditions. The preponderance of additive gene action over the non-additive, as well as the inherent genetic variability among the QPM inbred lines suggested that selection based on the GCA effect alone could be effective for developing superior hybrids (Baker 1978). The significant GCA and SCA × environment interaction effect for GY and other yield traits underscored the existence of genetic variations among the QPM inbred lines used for the present study. The present result agrees

with the findings of Betrán et al. (2003), Musila et al. (2010), Njeri et al. (2017) who reported significant GCA × environment interaction effect for GY under low-N and high-N conditions. Also, the present result is consistent with the findings of Oyekale et al. (2020) who reported a significant SCA × environment interaction effect for GY among QPM inbred lines under high-N conditions. The non-significant GCA and SCA × environment interaction effects for yield-related traits such as AD, SD, ASI and PA indicated that the performance of the QPM inbred lines based on these traits was consistent under low-N conditions. This result agrees with the findings of Oyekale et al. (2020) who reported a non-significant GCA and SCA × environment interaction effect of GY for QPM inbred lines under low-N conditions. Also, the non-significant SCA × environment effect of ASI and EA under high-N conditions was consistent with the findings of Oyekale et al. (2020) for QPM inbred lines evaluated under high-N conditions.

The high repeatability of GY, AD, SD and PA under low-N, and GY and all yield-related traits under high-N suggested a possibility of achieving accelerated genetic gain from selection based on these traits. This result is consistent with the findings of Bhadmus et al. (2021). The low repeatability of ASI, PHT, EHT, EA, SG and EPP under low-N conditions suggested that direct selection for improved performance based on these traits alone would not be effective.

Under DS conditions, the significant GCA and SCA effects for GY and other yield traits suggested that both additive and non-additive gene effects were important in the inheritance of those traits, although additive gene action was largely involved. The result suggested selection for improved performance based on the GCA effect alone would be effective (Baker 1978). Also, the result suggests that the development of superior hybrids could be achieved through a crossing of inbred lines with positive GCA effect for GY. The present result is consistent with the findings of Betrán et al. (2003), Wegary et al. (2014), Owusu et al. (2021). Contrarily, Machida et al. (2010), Annor and Badu-Apraku (2016), and Njeri et al. (2017) reported that non-additive gene action largely contributed to the inheritance of GY under DS conditions. The significant GCA and SCA × environment interaction effect obtained for GY and other traits indicated that the performance of the hybrids was not consistent, and thus, suggested the need to extensively test the hybrids for years before possible release and commercialization. This result is consistent with the findings of Owusu et al. (2021) for QPM inbred lines under DS conditions.

Under WW conditions, the significant GCA and SCA effects for GY and yield traits indicated that both additive and non-additive gene actions controlled the inheritance of those traits. The preponderance of GCA sum of squares over SCA in the inheritance of GY and other traits suggested that additive gene action largely controlled the inheritance of GY and other yield traits under WW conditions. This result further suggested that the development of superior hybrids could be achieved through early generation testing based on the GCA effect. This result is consistent with the findings of Njeri et al. (2017) and Owusu et al. (2021) who reported that additive gene action was more important in the inheritance of GY and other traits among QPM inbred lines under WW conditions. The significant GCA and SCA × environment interaction effect for GY and other traits indicated that GCA and SCA effects for those traits of the parental lines and their derived hybrids were influenced by the test condition. In contrast, the non-significant GCA and SCA effects for PHT and EHT indicated that the performance of the parental lines and their derived hybrids were consistent under WW conditions. This result agrees with the findings of Musila et al. (2010), Wegary et al. (2014) and Owusu et al. (2021) for QPM inbred lines under WW conditions. In this study, the magnitude of the GCA × environment interaction effect for GY and other traits was consistently lower than the respective GCA effect of these traits, suggesting that the interaction effect may be of lower effect compared to the main effect, to influence the identification of top and bottom performing inbred lines based on GCA effect. The moderate to high repeatability for GY and other yield traits under DS and WW conditions suggested the reliability of these traits for improved selection. This result agrees with the findings of Owusu et al. (2021).

The significant effect of both GCA and SCA sum of squares for GY and other yield traits indicated the contributions of additive and non-additive gene actions to the inheritance of these traits under each and across stress conditions. In this study, more than 50% of the total genetic variability in GY and other yield traits was attributed to additive gene action, except AD, PA and EPP under DS, and PA across

stress conditions where non-additive gene action was largely responsible for the inheritance of these traits. This result underscored the general knowledge in the literature that additive gene action is more important in the inheritance of GY than non-additive gene (Fan et al. 2004; Musila et al. 2010). Information on the GCA effect of inbred lines in a diallel is an important indicator of the potential of the lines for generating outstanding hybrids. In this study, the significant positive GCA effect for some of the parental lines under each and across stress conditions suggested the existence of genetic variability of the inbred lines for GY and other yield traits. Three inbred lines, CRIZEQ-44, CRIZEQ-49, and CRIZEQ-77 consistently manifested significant GCA effects for GY under each and across stress conditions. This result indicated that these inbred lines were the best general combiners for GY under each condition, suggesting that these inbred lines could be useful in crosses for developing outstanding hybrids under all conditions. A similar finding was reported by Musila et al. (2010) and Wegary et al. (2014) for QPM inbred lines under DS, low-N, high-N and WW conditions. Inbred lines manifesting significant negative GCA effect for AD, SD and ASI, suggested a possibility of transferring the desirable attributes for proper anthesis-silking synchrony in their hybrids. In this study, inbred lines CRIZEQ-14 and CRIZEQ-44 with desirable GCA effects for GY were also good general combiners for early AD and SD, as well as reduced ASI under each and across conditions. The development of early-maturing hybrids is very crucial for farmers in most parts of WCA experiencing short rainfall durations during their cropping seasons. Inbred lines, CRIZEQ-49 and CRIZEQ-55 with a significant positive GCA effect for EPP indicated that this desirable trait could be transferred to their progenies for the increased number of ears per plant, as an indicator for high GY performance. Inbred lines CRIZEQ-24, CRIZEQ-42, CRIZEQ-45, CRIZEQ-55 and CRIZEQ-77 had significant negative GCA effect for SG, suggesting that these inbred lines could be useful in breeding for delayed leaf senescence. Inbred lines CRIZEQ-5, CRIZEQ-40, CRIZEQ-44 and CRIZEQ-55 were good general combiners for reduced plant height, which is desirable as shorter plants are less prone to lodging.

Based on the HGCAMT grouping method, the 13 QPM inbred lines were classified into three main heterotic groups under low-N and DS conditions. Under the low-N condition, inbred lines CRIZEQ-49 and CRIZEQ-77 were testers that could be exploited for developing superior hybrids in cross combinations. Interestingly, crosses of inbred lines from the different heterotic groups manifested higher heterosis under each and across stress conditions, suggesting the effectiveness of the grouping method. Thus, inbred lines classified into different heterotic groups could be useful for the development of stress-tolerant QPM hybrids with improved yield performance under low-N, DS and across stress conditions (Terron et al. 1997).

Conclusion

This study revealed the existence of genetic variability among the QPM inbred lines for GY and yield-related traits under low-N and DS conditions, which could be exploited for the development of superior hybrids. Significant GCA and SCA effects were obtained for GY and some traits under each and across conditions, an indication that both additive and non-additive gene effects were involved in the inheritance of GY and other traits. However, the additive gene effect was largely responsible for the inheritance of the traits. Inbred lines P7 (CRIZEQ-44), P10 (CRIZEQ-49) and P13 (CRIZEQ-77) manifested a significant positive GCA effect for GY under low-N and DS conditions. Interestingly, these inbred lines were involved in crosses that produced outstanding and most stable hybrid CRIZEQ-24 × CRIZEQ-77 under low-N and DS, and CRIZEQ-44 × CRIZEQ-77 under high-N and WW conditions. Inbred lines CRIZEQ-44 and CRIZEQ-77 were found in different heterotic groups as testers under low-N and DS conditions, that could be exploited for the development of stress-tolerant QPM hybrids.

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Declarations

Conflict of interest The study was undertaken without any private or commercial financial engagements that could be declared a conflict of interest.

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