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Hybrid Performance and Combining Ability of Quality Protein Maize Inbred Lines under Low-Nitrogen Stress and Non-Stress Conditions in Ethiopia

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በምስራቅና በደቡብ አፍሪካ ሀገሮች የበቆሎን ምርታማነትን ከሚቀንሱ ተግዳሮቶች መካከል ዝቅተኛ የአፈር ለምነት በዋናነት የሚጠቀስ ነው፡፡ ይህ የምርምር ስራ ዝቅተኛ የአፈር ለምነትን (ዝቅተኛ የናይትሮጂን መጠን በአፈር ውስጥ) የመቋቋም ባህሪ እንዲሁም በፕሮቲን መጠናቸው የበለፀጉ የበቆሎ ዘረ-መሎችን በግብአትነት ተጠቅሟል፡፡ ከዘረ መሎቹ የተገኙት ድቃዮች ከወላጆቻቸው በወረሱት ባህሪይ ምክንያት በዝቅተኛ የአፈር ለምነት (የናይትሮጅን መጠን) እንዲሁም በቂ የናይትሮጅን መጠን ባለው አፈር ላይ የምርታማነታቸውን ሁኔታ ለማጥናት ዒላማ አድርጎ ወደ ስራ ተገብቷል፡፡ በጥናቱ ውስጥ 106 በፕሮቲን የበለፀጉ የሙከራ ድቃዮች እንዲሁም በምርት ላይ የሚገኙ አራት ዝርያዎች (ሁለት በፕሮቲን የበለፀጉ ዝርያዎች እንዲሁም ሁለት በፕሮቲን ያልበለፀጉ ዝርያዎች) ለማነፃፀሪያነት አካተን በአምቦና በባኮ ግብርና ምርምር ማዕከላት ውስጥ በሁለት ለም በሆኑ (በቂ የናይትሮጅን መጠን ባላቸው) እንዲሁም በሁለት ለም አፈር ባልሆኑ (በቂ የናይትሮጅን መጠን በሌላቸው) በአጠቃላ በአራት የሙከራ ቦታዎች ላይ ተዘርተው ጥናቱ ተካሂዷል፡፡ በዚህም መሰረት ለጥናቱ አስፈሊጊ የሆኑ መረጃዎች ተሰበሰቡ፡፡ የተሰበሰቡ መረጃዎችን ለማስላት አስፈሊጊ የስታትስቲክስ ፓኬጆችን በመጠቀም እንዲሰሉ ተደርጎ በሙከራ ዝርያዎቹ መካከል የተሰበሰበውን መረጃ ስሌት መንሰዔ በማድረግ የባህሪ ልዩነት እንዳለ ተረጋገጠ፡፡ በመሆኑም የጥናቱን ውጤት መነሻ በማድረግ በጥናቱ ውስጥ ከተካተቱ 106 የሙከራ ድቅዮች 10 በመቶ የሚሆኑት ለማነፃፀሪያ ከምንገለገልበት በፕሮቲን ከበለፀገው ዲቃላ ዝርያ (ZS261) እንዲሁም 79 በመቶ ለማነፃፀሪያ ከምንገለገልበት በፕሮቲን ካልበለፀገው ዲቃላ ዝርያ (SC627) የላቀ ምርት አስገኝተዋል፡፡ እንዲሁም ዘረ-መል ቁጥር (እናት ዝርያ) 3፣6፣8፣16 እና 18 በአፈር ውስጥ ናይትሮጅን እጥረት ባለባቸውና በሌለባቸው አካባቢዎች ከፍተኛ የበቆሎ ምርት መስጠት እንደሚችሉ ታዉቋል፡፡ እንዲሁም ዘረ-መል ቁጥር (እናት ዝርያ) 4 ቀድሞ የማበብ እንዲሁም አጭር ተክለ ቁመና ያለው መሆኑ ተደርሶበታል፡፡ በዚህ ጥናት የተገኙትን በፕሮቲን ይዘታቸው የላቁ እናት ዝርያዎችን እንዲሁም ከፍተኛ ምርት የሚሰጡ ድቃዮችን የአፈር ለምነት ችግር ባለባቸው አካባቢዎች ለሚደረገው ምርምር እንደ ግብዓት መጠቀም እንደሚያስፈልግ ይህ ጥናት ይጠቁማል፡፡

Abstract

Poor soil fertility is among the major abiotic stresses affecting maize productivity in Ethiopia. The objectives of this study were to assess hybrid performance and estimate combining ability of elite QPM inbred lines under optimum and low-Nitrogen (Low-N) stress conditions. One hundred and six testcross hybrids generated from line x tester crosses were evaluated together with four checks under optimum and low-N stress conditions at four locations in Ethiopia during the 2015 cropping season using a 5 x *22 alpha lattice design. Combined analysis of variance showed highly significant variations among the genotypes for grain yield and most other agronomic traits under optimum, low-N stress and across environments.*

Across environments, 10 and 79% of the new QPM hybrids had superior performance over the commercial QPM check (ZS261) and non-QPM check (SC627), respectively. Both general (GCA) and specific (SCA) combining ability mean squares were significant for grain yield and most other agronomic traits under each management and across environments, indicating the importance of both additive and non-additive genetic effects in the inheritance of these traits. However, the proportion of additive gene action was higher than that of non-additive for grain yield and other traits under optimum management and across environments. Combined analysis across environments showed that L3, L6, L8, 16 and L18 were good general combiners for grain yield. L4 exhibited good GCA for reduced days to anthesis and silking, and plant and ear heights. QPM inbred lines and high yielding hybrids identified in this study could be used as potential source germplasm for breeding low soil fertility tolerant varieties.

Introduction

In Ethiopia, maize (*Zea mays* Z.) is one of the most important cereal crops grown by the highest number of house-holds (Tsedeke *et al*., 2015). The average yield of maize in Ethiopia is 3.9 t h^{-1} (CSA, 2018), which is more than the average yield of sub-Saharan Africa (SSA) (1.5- 2.0 t ha^{-1}) (Tsedeke *et al*., 2017) and eastern and southern (1.2 t ha^{-1}) Africa (Setimela *et al*., 2017). In Ethiopia, it contributes about 16.7% of the national caloric intake followed by sorghum (14.1%) and wheat (12.6%) (Guush *et al*., 2011). Nutritionally, however, normal maize is deficient in the two essential amino acids, lysine and tryptophan (Adefris *et al*., 2015; Sarika *et al*., 2018) resulting in protein energy malnutrition and growth failure (Nuss and Tanumihardjo, 2011).

In an effort to mitigate malnutrition problem in eastern and southern Africa (ESA), the International Maize and Wheat Improvement Center (CIMMYT) maize breeding program has been working for decades in collaboration with National Agricultural Research partners and has developed high yielding and nutritionally improved QPM inbred lines adapted in the region (Dagne *et al*., 2014; Setimela *et al*., 2017; Njeri *et al*., 2017). The breeding and dissemination efforts of QPM varieties in Africa have been progressing (Atlin *et al*., 2011); as a result of which diverse QPM genotypes adapted to SSA conditions were developed (Badu-Apraku and Lum, 2010; Musila *et al*., 2010). The nutritional impacts of QPM among the children have also been documented (Girma *et al*., 2010). To utilize the potential nutritional benefits of QPM, research on QPM was started in Ethiopia in 1994 (Adefris *et al*., 2015) with introduction and evaluation of open pollinated varieties (OPVs) and pools introduced from CIMMYT (Gudeta *et al*., 2017). Continued QPM breeding efforts in Ethiopia has released eight QPM hybrids and OPVs through introduction and evaluation, and converting adapted elite normal maize genotypes to QPM version.

In SSA, breeding and dissemination of QPM varieties have been targeted towards smallholder farmers who are located in marginal environments, and who cannot manage to pay for fertilizer (Setimela *et al*., 2017). In the sub-region, maize is frequently produced under low soil nitrogen stress conditions (Dagne *et al*., 2011). Low soil nitrogen is an important abiotic factor affecting maize production in some tropical regions (Njeri *et al*., 2017). In addition to recurrent drought, low soil fertility, and diseases, lack of improved varieties also limit yield of maize in the sub-region (Bekele *et al*., 2011; Langyintuo *et al*., 2010). Drought stress and sub-optimal soil nitrogen condition alone can reduce yield up to 80% (Bänziger *et al*., 2006).

To address these constraints in a comprehensive manner, the QPM breeding effort of CIMMYT in ESA has resulted in the development of stress resilient inbred lines well adapted to the region. For effective utilization of these inbred lines, knowledge and understanding of the genetic potentials of the lines in hybrid combinations would be paramount important. Therefore, combining ability analysis of newly identified key abiotic stress resilient elite inbred lines would be helpful for the development of high yielding and nutritionally enhanced QPM cultivars adapted to the target environments. The objectives of this study were: (i) to assess the performance of QPM single cross hybrids that were developed using elite inbred lines and (ii) to estimate GCA and SCA effects of the newly developed elite CIMMYT's QPM inbred lines for grain yield and other agronomic traits under optimum and low nitrogen stress conditions.

Materials and Methods

Germplasm

Twenty-eight medium to late maturing drought and low-nitrogen (low-N) stress tolerant QPM inbred lines (Table 1) were crossed with four QPM testers from two complimentary heterotic groups (two each from heterotic groups A and B). The test crosses were done during the summer cropping season (November 2014 – April 2015) at Harare, Zimbabwe using the line-by-tester design proposed by Kempthorne (1957). The inbred lines used in this study were selected through rigorous phenotypic evaluations in breeding nurseries and light table evaluation for endosperm modification, followed by biochemical analysis of tryptophan and protein content (Table 1). Most of the lines were developed by converting popular normal maize lines through backcross breeding procedure described by Vivek *et al*. (2008), and by recycling elite QPM inbred lines. To introgress maize streak virus (MSV) resistance genes, the elite QPM inbred lines were crossed to MSV donor lines during the processes of conversion and recycling. The testers included in this study are well-adapted to SSA and have previously been proven useful in hybrid formation for tropical and subtropical mid-altitude environments. The commercial checks used represent late maturing QPM (ZS261) and non-QPM (SC627) hybrids widely grown in eastern and southern African regions. In addition, two popular standard checks were included in the trial at each environment: AMH760Q (QPM) and AMH851 at Ambo; BHQPY545 and BH546 at Bako. AMH760Q (QPM) and AMH851 (non-QPM) are three-way cross hybrids released for highland agro-ecologies of Ethiopia and widely adopted by farmers in the highland and transitional highland areas of the country. BHQPY545 is a single cross yellow-grain QPM hybrid released for mid-altitude sub-humid areas of Ethiopia. BH546 is a high yielding and medium maturing non-QPM three-way cross hybrid released for mid-altitude sub-humid areas of the country.

Environments

The field evaluations of 110 entries composed of 106 testcross hybrids (excluding hybrids with insufficient seed quantity), two commercial and two local check varieties were conducted at four environments in Ethiopia at Bako and Ambo in 2015 (May –November) under both low nitrogen stress and optimum nitrogen conditions. Bako lies at 9°06'N latitude, 37°09'E longitude and at an altitude of 1650 masl (meters above sea level). The total precipitation during the growing season was 944 mm, and the mean minimum and maximum temperatures were 12.3 and 29.8◦C, respectively. The soil is reddish brown clay (nitosol). Ambo is located at 8°57'N latitude, 38°07'E longitude at an altitude of 2225 masl. The total precipitation during the growing season at Ambo was 1022 mm, and the mean minimum and maximum temperatures were 10 and 25.0◦C, respectively. The soil at Ambo is heavy vertisol. Bako and Ambo Research Centers represent mid-altitude and highland maize growing mega-environments of the country.

Experimental design and field management

The trial was laid out in a 5 x 22 alpha lattice design (Patterson and Williams, 1976) with two replicates at each environment. Entries were hand-planted in single row plots of 4.8 m length at Bako and 4.25 m length at Ambo. The spacings used were 0.75 m between rows at both locations, while 0.25 m distance was used between hills at Ambo and 0.3 m at Bako. Initially, two seeds were planted per hill and later thinned to one plant to achieve the desired plant densities of 53,333 and 44, 444 plants ha^{-1} at Ambo and Bako, respectively. Optimum nitrogen conditions were maintained by applying the recommended nitrogen rates for the respective locations, managed by crop rotation and residue incorporation. For the optimum management trials 92 kg ha^{-1} nitrogen was applied in two splits, half at planting and the rest at 37 days after emergence at Bako, while 100 kg ha^{-1} nitrogen was applied in two splits, half at planting and the rest at 37 days after planting at Ambo. In both optimum and low N trials a recommended rate of 69 kg ha^{-1} phosphate (P_2O_5) was applied at planting at both locations. Low N trials were planted on N-depleted plots and received no N fertilizer both at Bako and Ambo. Low N stress conditions were achieved by continuous planting of maize for a minimum of five years without applying N fertilizer and removal of crop residues as well. All other agronomic management practices were applied following the research recommendations of the respective locations.

Table 1. Names, pedigrees and protein quality profiles of 28 medium to late maturing QPM inbred lines and four testers used for the study

Parent	Name	Pedigree (Source: CIMMYT-Harare)	Prot†	Trp‡	QI§
			________	%	______________
Line					
L1	TL156579	([NIP25-100-1-1-B-1-B*5/[GQL5/[GQL5/CML202]F2-3sx]-11-1-3-2-B*4]- 3/CML395IR)-BBB(IR)-1-B-B-B-B	9.54	0.07	0.73
L2	TL156580	([NIP25-100-1-1-B-1-B*5/[GQL5/[GQL5/CML202]F2-3sx]-11-1-3-2-B*4]-3/CML395IR)-BBB-1-2-1-B-B-B-B	11.05	0.06	0.54
L3	TL156583	(CML312IR/[[[CLQRCWQ83/CML312SR//CML312SR]/CML312SR]-26-B/(CLQRCWQ50/CML312SR)-2-2-1-BB]-BB)F2-B-7-2-2-B-B-B-B	11.64	0.09	0.74
L4	TL156584	([CML389/GQL5]-B-22-1-1-1-B*5/[CML205/CML176]-B-2-1-1-2-B*5)-B-1-1-2-1-B-B-B	9.63	0.08	0.83
L5	TL156587	[[CML202/CML144]F2-1-1-3-B-1-B*6/CZL066]-B*5-3-B-B-B-B	10.34	0.08	0.79
L6	TL156593	(([CML511*/[CML390//[CML390/GQL5]-B-3sx]-B-1-1-2-BBB]-3/CML390IR)-B)F2-B-6-1-1-1-B-B-B	10.58	0.08	0.76
L7	TL156594	([CML205/CML176]-B-2-1-1-2-B*5/CML511//CML511)-1-1-1-1-1-B-B-B	10.61	0.09	0.85
L8	VL05118	CML159-B	11.76	0.07	0.58
L9	TL101711	[CML159/[CML159/[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-BB]F2-3sx]-8-1-1-BBB-4-B-B-B	11.01	0.07	0.68
L10	TL156602	(CZL083/[[CLQRCWQ83/CML312SR//CML312SR]/CML312SR]-26-BB-1-B)F2-19-1-1-2-B-B-B	11.66	0.08	0.70
L11	TL102715	[CML202/CML144]F2-1-1-3-B-1-B*5-1-1-B-B	9.40	0.08	0.82
L12	TL116956	[[CML202/CML144]F2-1-1-3-B-1-B*6/CML442]-B*5-4-B-B-B	9.65	0.07	0.71
L13	TL156603	[[CML202/CML144]F2-1-1-3-B-1-B*6/CZL066]-B*5-2-B-B-B	10.98	0.08	0.74
L14	TL156606	(CML489/[CML202/CML144]F2-1-1-3-B-1-B*6)-B-14-2-2-2-B-B-B	10.61	0.08	0.75
L15	TL135470	([NAW5867/P49SR(S2#)//NAW5867]F#-48-2-2-B*5/([CML144/[CML144/CML395]F2-8sx]-1-2-3-2-B*4-1-B/[INTA-2-1-3/INTA-60-1-2]-X-11-6-3-BB)F2)-B-B-34-2-B	10.44	0.07	0.62
L16	TL147070	(CML197/(CML197/[(CLQRCWQ50/CML312SR)-2-2-1-BB/CML197]-BB)F2)-B-B-44-2-B	10.44	0.07	0.66
L17	TL156607	(CML197/(CML197/(CLQRCWQ50/CML312SR)-2-2-1-BBB)F2)-B-B-6-4-B	11.90	0.10	0.84
L18	TL147078	(CML197/(CML197/(CLQRCWQ50/CML312SR)-2-2-1-BBB)F2)-B-B-36-2-B	11.91	0.11	0.95
L19	TL147129	(CML395/(CML395/CML511)F2)-B-B-11-1-B	12.15	0.11	0.88
L20	TL155810	(CML395/(CML395/[NAW5867/P49SR(S2#)//NAW5867]F#-48-2-2-B*4)F2)-B-B-17-2-B	10.33	0.08	0.78
L21	TL147114	(CML395/(CML395/S99TLWQ-B-8-1-B*4-1-B)F2)-B-B-20-2-B	12.06	0.10	0.84
L22	TL156595	[(CLQRCWQ50/CML312SR)-2-2-1-BB/[CML390//[CML390/GQL5]-B-10sx]-B-6-1-BBB]-B*5-2-B-B-B-B	11.04	0.10	0.87
L23	TL156596	((CLQRCWQ50/CML312SR)-2-2-1-BBB/[CML390//[CML390/GQL5]-B-10sx]-B-6-1-BBB)-B-18-1-2-2-B-B-B	10.44	0.08	0.77
L24	VL06373	(CLQRCWQ01/CML312SR)-4-2-1-BB-1-B-B-B	11.35	0.07	0.62
L25	TL156598	([CML390//[CML390/GQL5]-B-3sx]-B-1-1-2-BBB/[CML202/CML144]F2-1-1-3-B-1-B*6//[CML390//[CML390/GQL5]-B-3sx]-B-1-1-2-B)-1-4-3-2-2-B-B	10.74	0.08	0.74
L26	TL156610	([CML181/[CML181/[MSRXPOOL9]C1F2-174-1(OSU31ss)-1-7(I)-X-X-1-B]F2-2sx]-1-3-3-1-BB-2-1/CML181-2-1)-47-B-6-2-2-1-B-B-B	10.60	0.09	0.85
L27	TL156611	([CML181/[CML181/[MSRXPOOL9]C1F2-174-1(OSU31ss)-1-7(I)-X-X-1-B]F2-2sx]-1-3-3-1-BB-2-1/CML181-2-1)-47-B-6-2-3-2-B-B-B	9.72	0.07	0.72
L28	VL05117	CML144-B	11.94	0.09	0.75
Inbred tester					
T1	TL156587	[[CML202/CML144]F2-1-1-3-B-1-B*6/CZL066]-B*5-3-B-B-B-B	10.34	0.08	0.79

T2	VL05552	CML491	10.53	0.08	0.76
T3	TL148289	[WWO1408-1-1-2-B*4-#/[CML202/CML144]F2-1-1-3-B-1-B*6]-B*4-4-1-B-B-B	10.41	0.09	0.85
T4	TL149662	[[[CZL083/CML509]F2-1/[GQL5/[GQL5/[MSRXPOOL9]C1F2-205-1(OSU23i)-5-3-X-X-1-BB]F2-4sx]-11-3-1-1-B*4]-9-B-1-BBB-1-B-B-B	10.92	0.10	0.93
Mean			10.80	0.08	0.76

[†] *Prot, Protein contents (%) in whole grain*

[‡] *Trp, Tryptophan contents (%) in whole grain*

[§] *QI, quality index (calculated as the ratio of tryptophan to protein concentration in whole grain)*

Field measurements

Field measurements were taken from well-bordered plants by excluding the border plants of each row. Days to anthesis (DA) and silking (DS) were recorded as the number of days from planting to 50% pollen shed and silk emergence, respectively. Anthesis silking interval (ASI) was calculated by subtracting DA from DS (ASI = DS-DA). Plant height (PH) and ear height (EH) were measured in cm from the base of the plant to the insertion of the first tassel branch, and insertion of the upper most ear, respectively. Average of ten randomly sampled plants were used to record PH and EH for each plot. Number of ears per plant (EPP) was obtained by dividing the total number of ears (a cob with at least one fully developed kernel is considered as an ear) by the respective number of plants harvested from each plot. The total grain weight from all the ears of each experimental unit was used to calculate grain yield in t ha^{-1} after adjusting to 12.5% moisture content.

Statistical analysis

Analysis of variance (ANOVA) per environment was conducted with the PROC MIXED procedure in SAS computer package (SAS Institute, 2002) considering genotypes as fixed and replications and blocks within replications as random effects. Combined analysis of variance was performed using entry means adjusted for block effects for traits that showed significant entry mean squares in individual environment analyses, and confirming homogeneity of error variances through Bartlett's test. Combined analysis across environments was done using PROC GLM in SAS computer package (SAS Institute, 2002) using a RANDOM statement with TEST option. For combined analysis 108 genotypes (excluding the two popular standard checks varying along the two locations) were used. Mean squares for hybrids and environments were tested against the mean squares for hybrid x environment as error term, whereas hybrid x environment mean squares were tested against pooled error mean squares.

The total variations among QPM hybrids were partitioned into lines (L), testers (T) and line x tester (L x T) sources of variations. The main effects of line (L) and tester (T) represent the GCA effects while the line x tester (L x T) interaction represents SCA effects (Hallauer and Miranda, 1988). Test of significance for line, tester, and line x tester mean squares were computed using the mean squares for their respective interaction with environment. Mean squares attributable to line x environment, tester x environment and line x tester x environment were tested using the pooled error mean squares. GCA and SCA effects and their respective standard errors were determined for all measured traits across environments using SAS computer package (SAS Institute, 2002). GCA effects of lines and testers were obtained based on their respective performances in hybrid combinations with all possible testers and lines, respectively. The relative contribution of GCA (additive) and SCA (non-additive) sum squares to the variation among hybrids for each trait was computed as percentage of the sum of squares for the crosses across environments using the method proposed by Kang (1994).

Results and Discussion

Analysis of variance

Analysis of variance for each environment revealed significant variations for grain yield and most other agronomic treats measured (data not shown). Combined analysis of variance across optimum (Table 2), low N stress (Table 3) and across (Table 4) environments showed significant ($P \leq 0.01$) genotype and hybrids mean squares for grain yield and all other measured traits, indicating the presence of high genetic variability among the genotypes and single-cross QPM hybrids studied. The presence of genetic variability increases the possibility of selecting better performing hybrids under each environment and across the management conditions for the targeted traits. In line with this study, variations among QPM hybrids for grain yield and related agronomic traits evaluated under different environments and management conditions were previously reported by other investigators (Njeri *et al*., 2017; Setimela *et al*., 2017; Owusu *et al*., 2017).

The highly significant genotype x environment and hybrid x environment interaction mean squares observed for grain yield across optimum and across environments suggested that the QPM genotypes and testcross hybrids evaluated in this study responded differently across the testing environments, which indicated the need for wide testing of QPM genotypes across varying environmental conditions to identify the best performing and stable hybrids that can be released for commercial production. Significant hybrid x environment interaction in QPM genotypes under contrasting management and environmental condition has previously been reported by various investigators (Musila *et al*., 2010; Dagne *et al*., 2011; Dagne *et al*., 2014; Badu-apraku *et al*., 2016; Njeri *et al*., 2017). However, across low N stress conditions, non-significant genotype and hybrid x environment interactions were observed for grain yield signifying the consistent performances of QPM hybrids across low N conditions.

Table 2. Combined analysis of variance and means for grain yield and other agronomic traits evaluated at Bako and Ambo under optimum nitrogen conditions in 2015

Sources of variation	df	GY	AD	DS	PH	EH	EPP
Environments (E)	1	131.5**	58867.2**	62978.6**	11523.7**	1789.0**	2.00**
Replication (Rep)	1	13.47**	134.48**	138.41**	2347.50**	729.59**	0.17**
Block (Rep x E)	84	1.39**	12.36**	19.99**	348.74**	274.14**	0.02
Genotype (G)	107	4.76**	19.41**	21.03**	675.88**	597.95**	0.10**
G x E	107	1.59**	7.74	11.77	169.30*	176.089	0.05**
Hybrid (H)	105	4.41**	16.97**	18.53**	627.61**	555.70**	0.10**
GCA_{Line}	27	10.09**	39.40**	35.86*	1267.30**	1104.03**	0.25**
$\text{GCA}_{\text{Tester}}$	3	1.84	41.75**	41.78	2060.68	2839.70*	0.13
SCA	75	2.48**	7.91	11.36	340.00**	266.94**	0.04
H x E	105	1.59**	7.66	11.65	171.01*	178.31	0.05 **
GCA_{Line} x E	27	1.08*	10.84	18.75**	141.28	238.11*	0.05**
$\text{GCA}_{\text{Tester}}$ x E	3	18.38**	1.06	13.03	559.21**	292.32	0.29**
SCA x E	75	0.91*	7.29	9.2	147.17	148.4	0.03**
Error	126	0.60	7.51	9.58	120.24	142.27	0.02
%SS GCA		59.9	66.72	56.21	61.3	65.69	71.08
%SS SCA		40.1	33.28	43.79	38.7	34.31	28.92
Mean		5.7	89.47	90.4	256.97	144.28	1.17
Minimum		1.7	81.25	82.25	189.75	93.5	0.81
Maximum		7.5	97.75	98	290.5	173	1.68
SE (m)		0.6	1.94	2.19	7.75	8.43	0.10
CV (%)		14	3.02	3.42	4.27	8.27	11.99

* Significant at the $P < 0.05$ level of probability; ** Significant at the $P < 0.01$ level of probability
GY, grain yield; AD, days to anthesis; DS, days to silking; PH, plant height; EH, ear height; EPP, ears per plant; GCA, general combining ability; SCA, specific combining ability; SE, standard error

Table 3. Combined analysis of variance and means for grain yield and other agronomic traits evaluated at Bako and Ambo under low-N stress environments in 2015

Sources of variation	df	GY	AD	DS	PH	EH
Environments (E)	1	286.1**	20156.7**	20015.0**	226413.1**	174378.4**
Replication (Rep)	1	0.61	6.81	15.60	9844.70**	4553.08**
Block (Rep x E)	84	1.03	12.64	16.38*	462.61**	236.58**
Genotype (G)	107	2.80**	30.830**	32.89**	673.84**	240.83**
G x E	107	0.96	12.87	12.63	178.60	72.63
Hybrid (H)	105	2.70**	26.85**	29.07**	657.08**	238.02**
GCA_{Line}	27	4.68**	53.98**	49.84**	1107.37**	440.61**
$\text{GCA}_{\text{Tester}}$	3	8.80	50.34	75.82	3703.99	1085.31
SCA	75	1.88**	16.15*	19.72**	374.00**	126.35**
H x E	105	0.92	12.95	12.58	178.66	69.07
GCA_{Line} x E	27	1.09	16.85*	16.91	154.48	98.33*
$\text{GCA}_{\text{Tester}}$ x E	3	3.93 **	43.53**	21.99	1435.35**	140.57
SCA x E	75	0.75 **	9.69	10.82	131.89	57.32
Error	126	0.87	10.38	11.44	151.35	58.88
%SS GCA		51.98	57.05	51.54	59.44	60.63
%SS SCA		48.02	42.95	48.46	40.56	37.92
Mean		3.88	90.96	92.7	214.02	113.37
Minimum		1.20	82.50	85	141.00	87.75
Maximum		6.22	104.75	105.5	241.75	137
SE (m)		0.66	2.28	2.39	8.70	5.43
CV (%)		23.97	3.54	3.65	5.75	6.77

* Significant at the $P < 0.05$ level of probability; ** Significant at the $P < 0.01$ level of probability
GY, grain yield; AD, days to anthesis; DS, days to silking; PH, plant height; EH, ear height; GCA, general combining ability; SCA, specific combining ability; SE, standard error

Hybrid mean performances

Across optimum management, grain yield ranged from 1.7 to 7.5 t ha^{-1} with an average of 5.7 t ha^{-1} (Table 2). About 70% and 21% of the testcross hybrids had superior grain yield to ZS261 and the trial mean, respectively. The top five high yielding QPM hybrids under optimum management conditions were H57 (L16 x T2), H56 (L16 x T1), H29 (L8 x T3), H20 (L20 x T2) and H60 (L17 x T1) with grain yield ranging from 7.2 to 7.5 t ha^{-1} (Table 5). Across low-N stress conditions, mean grain yield ranged from 1.2 to 6.22 t ha^{-1} with a mean of 3.88 t ha^{-1}. About 32, 82 and 57% of the hybrids were superior to SC627, ZS261 and the trial mean, respectively. Hybrids H11 (L3 x T3), H87 (L24 x T1), H40 (L12 x T1), H21 (L6 x T3) and H2 (L1 x T2) were the top five QPM hybrids in order listed, with grain yields ranging from 5.30 to 6.22 t ha^{-1} (Table 5). Across managements conditions and environments, grain yield ranged from 1.7 to 6.5 t ha^{-1} with a mean of 4.8 t ha^{-1}; and 10, 79 and 56% of the QPM hybrids were superior to SC627, ZS261 and the trial mean. The top high-yielding hybrids across environments were hybrids H87 (L14 x T1), H40 (L12 x T1), H11 (L3 x T3), H57 (L16 x T2) and H29 (L8 x T3) with grain yields ranging from 6.2 to 6.5 t ha^{-1} (Table 5). This study identified experimental QPM hybrids with superior grain yield performance than both QPM and non-QPM commercial check hybrids, suggesting the existence of effective genetic gains in QPM breeding. Similarly, Setimela *et al*. (2017) reported superior performance of QPM experimental hybrids under contrasting environments than check varieties used. Yield gains in SSA have been mainly attributed to increased stress tolerance, especially to random drought and poor soil fertility (Setimela *et al*., 2017).

Table 4. Combined analysis of variance and means for grain yield and agronomic traits of maize hybrids evaluated across optimal and low N stress environments at Bako and Ambo, 2015

Sources of variation	df	GY	AD	DS	PH	EH	df	ASI	EPP
Environments (E)	3	344.3**	26515.6**	28047.1**	203272.3**	123775.3**	2	95.3**	1.23**
Replication (Rep)	4	7.04**	70.65**	77.01**	6096.10**	2641.33**	3	3.00	0.24**
Block (Rep x E)	168	1.21**	12.50**	18.16**	405.68**	255.36**	126	1.63	0.03
Genotype (G)	107	6.07**	39.37**	40.01**	1106.20**	634.90**	107	3.35**	0.12**
G x E	321	1.20**	9.57	11.56	172.61*	131.40**	214	1.82	0.04*
Hybrid (H)	105	6.06**	33.23**	34.32**	1083.86**	616.70**	105	3.42**	0.12**
GCA $_{Line}$	27	12.99**	79.14**	69.78**	2146.46**	1298.36**	27	4.95*	0.28**
GCA$_{Tester}$	3	7.95	78.21*	109.60**	5398.71**	3658.33**	3	18.71	0.15
SCA	75	3.49**	14.90**	18.54**	528.73**	249.64**	75	2.26**	0.06**
H x E	315	1.19**	9.5	11.47	172.28*	130.88*	210	1.82	0.04*
GCA $_{Line}$ x E	81	1.25**	11.73	15.20*	154.33	183.88**	54	2.51	0.04*
GCA $_{Tester}$ x E	9	8.30**	19.33*	14.78	757.95**	213.74*	6	5.19*	0.15**
SCA x E	225	0.78	8.24	9.91	148.76	108.65	150	1.34	0.03
Error	252	0.75	8.94	10.51	135.79	100.58	189	1.88	0.03
%SS GCA		58.86	67.98	61.41	65.16	71.09		52.8	64.6
%SS SCA		41.14	32.02	38.59	34.84	28.91		47.2	35.4
Mean		4.78	90.22	91.55	235.51	128.82		1.32	1.15
Minimum		1.7	82.75	84.38	165.38	93.38		-1	0.84
Maximum		6.47	98	99.63	259.13	152.88		4.17	1.67
SE (m)		0.43	1.5	1.62	5.83	5.01		0.79	0.1
CV (%)		18.12	3.31	3.54	4.95	7.78		5.43	15.08

* Significant at the $P < 0.05$ level of probability; ** Significant at the $P < 0.01$ level of probability, GY, grain yield; AD, days to anthesis; DS, days to silking; PH, plant height; EH, ear height; ASI, anthesis-silking interval; EPP, ears per plant; GCA, general combining ability; SCA, specific combining ability; SE, standard error

The QPM hybrids showed better performance under optimum conditions than low N environments. Compared to optimum management, low N stress conditions reduced grain yield and plant height by 32 and 17%, respectively. The downward effect of low N on grain yield and other traits observed in this study agrees with previous studies in QPM (Wegary *et al*., 2011; Wegary *et al*., 2014; Njeri *et al*., 2017) and non-QPM germplasm (Berhanu *et al*., 2017; Mageto *et al*., 2017; Makumbi *et al*., 2018). Different stress conditions such as low N have different effects on crop growth (Bänziger *et al*., 2006). However, in this study, some QPM hybrids such as H87, H40, H11, H57 and H29 with high grain yield performance across optimum and low N environments were identified. These results suggested the feasibility of developing hybrids with wide adaptation which corroborates with the finding of previous studies (Berhanu *et al*., 2017; Setimela *et al*., 2017; Makumbi *et al*., 2018).

Table 5. Mean grain yield and other traits of 25 top-yielding testcross quality protein maize hybrids and commercial checks evaluated under optimum and low N stress conditions at Ambo and Bako

Hybrid	Crosses	Grain yield (t ha^{-1})			Agronomic traits					
		OPT	Low N	Across	AD	DS	ASI	PH	EH	EPP
H87	L24 x T1	7.0	5.9	6.5	93.3	87.3	0.2	237.3	141.5	1.2
H40	L12 x T1	7.0	5.9	6.5	88.3	93.8	1.7	252.1	140.3	1.1
H11	L3 x T3	6.5	6.2	6.4	88.4	84.4	0.3	245.1	128.5	1.2
H57	L16 x T2	7.5	5.0	6.3	90.8	92.1	2.0	247.9	132.0	1.4
H29	L8 x T3	7.3	5.2	6.2	86.5	91.8	0.5	244.3	131.1	1.1
H2	L1 x T2	7.1	5.3	6.2	90.0	92.0	2.3	240.1	114.5	1.1
H21	L6 x T3	7.0	5.3	6.1	86.8	90.5	0.5	246.0	133.5	1.0
H27	L8 x T1	7.1	5.1	6.1	87.4	92.9	0.3	243.0	134.8	1.1
H56	L16 x T1	7.3	4.8	6.1	90.3	89.5	1.8	253.3	152.9	1.3
H60	L17 x T1	7.2	4.8	6.0	88.1	90.4	1.5	234.1	139.9	1.4
H66	L18 x T3	6.8	5.1	5.9	88.0	92.8	1.2	245.8	135.5	1.0
H20	L6 x T2	7.2	4.6	5.9	89.1	90.0	1.5	244.4	118.1	1.1
H64	L18 x T1	7.1	4.7	5.9	89.8	91.0	1.0	248.9	151.5	1.1
H94	L25 x T4	7.1	4.7	5.9	97.8	86.6	0.5	231.0	117.5	1.3
H9	L3 x T1	6.7	5.1	5.9	89.5	89.4	-0.2	228.6	130.5	1.7
H3	L1 x T3	6.4	5.1	5.8	87.5	88.4	1.2	235.9	117.3	1.0
H93	L25 x T3	6.2	5.2	5.7	86.6	90.3	-0.3	246.6	125.6	1.1
H19	L6 x T1	6.6	4.8	5.7	88.0	93.0	2.2	239.8	129.3	1.1
H89	L24 x T3	6.5	4.8	5.7	91.0	96.9	0.7	236.0	126.1	1.0
H10	L3 x T2	6.7	4.6	5.7	89.4	91.3	1.8	241.3	126.4	1.3
H41	L12 x T2	6.7	4.6	5.7	89.9	89.9	4.2	257.3	142.1	1.0
H45	L13 x T2	6.7	4.5	5.6	90.8	99.6	1.7	232.4	127.8	1.3
H75	L21 x T1	6.9	4.2	5.6	90.8	93.3	0.8	252.4	150.4	1.4
H16	L5 x T2	5.8	5.3	5.5	92.6	87.3	0.7	237.9	142.1	1.2
H65	L18 x T2	6.7	4.4	5.5	90.5	91.0	2.7	234.0	122.8	1.2
	Mean	5.7	3.9	4.8	90.2	91.5	1.3	235.5	128.8	1.1
	LSD $_{(0.05)}$	1.1	1.3	0.9	2.9	3.2	1.6	11.5	9.8	0.2
H107	SC627	7.5	4.3	5.9	82.8	95.0	1.7	249.3	132.5	1.1
H108	ZS261	5.3	3.1	4.2	83.4	85.3	1.3	220.8	108.9	1.0

OPT, optimum management, Low N, low nitrogen stress, AD, anthesis date; DS, days to silking; ASI, anthesis-silking interval; PH, plant height; EH, ear height; EPP, ears per plant; SC627, commercial non-QPM check; ZS261, commercial QPM check

Combining ability analysis

Significant mean squares of GCA (mostly line GCA) and SCA observed across optimum (Table 2), low N stress (Table 3) and across (Table 4) environments for grain yield and most other traits indicated the presence of both additive and non-additive gene action in the inheritance of grain yield and other measured agronomic traits. Baker (1978) stated that the significance of GCA and SCA is an indication for the importance of both additive and non-additive gene effects for the inheritance of the traits being studied. As a result, it would be essential to consider both components by evaluating parents for GCA followed by testing the resulting hybrids in target environments (Makumbi *et al*., 2011). However, across optimum and across environments, the proportion of GCA sum of squares were larger than SCA sum of squares, indicating that additive gene action was predominantly responsible for the inheritance of grain yield under these environmental conditions. Previous studies also indicated the preponderance of additive gene action under optimum environmental conditions in QPM (Dagne *et al*., 2014; Gudeta *et al*., 2015; Njeri *et al*., 2017) and non-QPM (Mageto *et al*., 2017) under stress and non-stress conditions. On the other hand, Oyekunle and Badu-Apraku (2014) reported a sizeable contribution of additive and non-additive gene effects for grain yield under stress conditions.

Significant line GCA x E and tester GCA x E interaction mean squares observed for few traits across optimum, low-N stress, and across environments indicating that there was variations in the GCA effects of the lines and testers under different environments used in this study, which indicates the need to select lines for specific adaptation (Makumbi *et al*., 2011). Extensive testing of inbred lines in multiple stress environments over seasons and/or years, therefore, is necessary to identify the best lines with consistent performance across the different environments for hybrid development (Mageto *et al*., 2017; Njeri *et al*., 2017). Significant GCA x E interaction have been previously reported in QPM hybrids tested across environments for grain yield and agronomic traits (Makumbi *et al*., 2011; Dagne *et al*., 2014; Gudeta *et al*., 2015; Demissew *et al*., 2016b). In contrast, SCA x E were not significant for almost all traits under optimum management, low-N stress and across environments, indicating the stability of SCA variance of lines x testers across the test environments. Similar findings were previously reported for QPM germplasms across environments (Musila *et al*., 2010; Dagne *et al*., 2014; Gudeta *et al*., 2015).

In the current study, there was larger contribution of GCA sum of squares compared to SCA sum of squares for grain yield and most other agronomic traits under optimal (Table 2) and across environments (Table 4). This result suggested that inheritance of grain and some agronomic traits in these QPM inbred lines is largely controlled by additive genetic effects under optimal and across environments. These results corroborated the findings from other studies (Makumbi *et al*. 2011; Njeri *et al*; 2017; Mageto *et al*., 2017) in which the importance of additive over non-additive genetic effects for grain yield under optimal and across stress and non-stress conditions was reported. In this study, however, comparable magnitudes of GCA and SCA sum of squares were observed for grain yield across low N stress environments (52 vs. 48%). This result suggested that both additive and non-additive gene actions were important for inheritance of grain yield under low N stress conditions. In such scenario, breeding progress should exploit both components by evaluating parents for GCA followed by testing the resulting hybrids in target environments (Makumbi *et al*., 2011; Demissew *et al*., 2016a).

Estimates of combining ability effects

The estimate of GCA effects of a parent is an important indicator of its potential for generating superior breeding genotypes (Hallauer *et al*., 2010). Inbred line L8 across optimum, L3 across low N stress and L3, L6, L8, L16 and L18 across environments (Table 6) showed significant ($P \leq 0.01$) and positive GCA effects for grain yield. Only L8 showed consistently positive and significant GCA effects for grain yield under optimum, low N and across environments. This suggested that this inbred line had the potential for use in QPM breeding programs that target development of hybrids suitable for optimum and low N conditions. L8 that showed consistently positive GCA effects for grain yield across a range of environments is, therefore, a candidate for use in QPM inbred line recycling program. Across stress and nonstress environments, inbred lines L3, L6, L8, L16 and L18 were the best general combiners for grain yield, indicating that these lines contributed to increased grain yield in their crosses under all conditions. Early-maturing maize genotypes are important, as they escape terminal drought in areas with short rainy seasons. Inbred lines that were good general combiners for both early anthesis and silking across stress and non-stress environments were inbred lines L4, L6, L8, L10 and L22 and tester T3. Inbred lines L2 and L4 across stress and non-stress environments significantly reduced plant stature and hence are desirable, as shorter plants are less prone to lodging (Dagne *et al*., 2014; Demissew *et al*., 2016a). When selecting for a high yielding genotype, maintaining a balance between higher yield and shorter stature is critical. This study identified hybrids with desirable SCA effects for grain yield and other traits across stress and non-stress environments. Few QPM inbred lines, namely, L3, L26 and L27 had highly significant and positive GCA effects for number of ears per plant across environments, indicating good potential for breeding for low N stress conditions in which increased number of ears per plant are important for higher yield (Njeri *et al*., 2017).

This study also identified hybrids with desirable SCA effects for grain yield and other traits across stress and non-stress environments. The SCA effects of L13 x T2 across optimum, L14 x T4 and L24 x T1 across low N stress and L13 x T2 across environments for grain yield were significant ($P \leq 0.01$) and positive. Across optimum environments, the SCA effects of hybrids L13 x T1, L28 x T2 were significant ($P \leq 0.01$) and negative for plant height, whereas the SCA effect of L3 x T1, L17 x T1, L24 x T4 and L25 x T4 were significant ($P \leq 0.01$) and positive for number of ears per plant (data not shown).

Table 6. General combining ability (GCA) effects of 28 quality protein maize inbred lines and four testers for grain yield and agronomic traits evaluated across optimum and low nitrogen environments in Ethiopia during the 2015 cropping season

Line	Grain yield (t ha^{-1})			AD	DS	PH	EH	ASI	EPP
	OPT	Low-N	Across						
L1	0.85	0.61	0.72	-1.13	-1.17	-6.56	-12.29**	0.1	-0.11
L2	-1.64**	-0.92**	-1.29**	1.4	1.27	-14.78*	-11.89**	0.1	-0.17*
L3	0.84	1.17**	1.00*	-1.88	-2.45*	1.91	-0.82	-0.53	0.21**
L4	-1.47**	-0.52	-1.00*	-3.56**	-4.17**	-17.03**	-17.19**	-0.93*	-0.1
L5	-0.57	0.21	-0.18	2.19*	1.58	-6.82	10.48**	-0.65	0.02
L6	1.27*	0.7	0.98*	-2.72*	-2.55*	4.16	-4.48	0.39	-0.08
L7	0.52	-0.38	0.07	2.56*	2.58*	13.13**	13.65**	-0.03	0.13
L8	1.40**	0.83*	1.11*	-2.47*	-2.84**	5.85	-2.27	-0.49	-0.05
L9	-1.48**	-0.88*	-1.16**	2.86**	2.79**	-5.07	1.65	0.18	-0.1
L10	0.68	0.51	0.59	-2.14*	-2.63*	15.22**	9.67**	-0.38	0.07
L11	-2.12**	-1.47**	-1.80**	2.09*	2.02	-11.12	0.11	-0.15	-0.16*
L12	0.84	0.75	0.79	-1.22	-0.2	14.85*	4.77	1.05**	-0.12
L13	-1.10*	-0.42	-0.73	2.84**	2.42*	-22.93**	-6.23	-0.24	-0.06
L14	-1.01	-0.88*	-0.94*	0.81	0.89	-8.43	-7.07	0.01	0.00
L15	-0.27	-0.13	-0.2	-3.32**	-1.83	-8.28	-7.45	1.76**	-0.09
L16	1.27*	0.62	0.94*	-0.82	-0.3	16.63**	12.21**	0.68	0.12
L17	0.27	0.100	0.18	-0.88	-0.42	-3.06	-1.17	0.55	-0.03
L18	1.20*	0.82	1.01*	-0.93	-0.63	7.35	7.6	0.29	-0.04
L19	0.18	-0.02	0.07	1.12	1.86	3.59	2.21	-0.2	-0.16*
L20	-0.46	-0.39	-0.40	1.55	1.42	8.57	7.18	0.24	-0.05
L21	0.42	-0.4	0.01	1.56	1.3	14.94**	8.65*	-0.4	0.07
L22	0.04	0.28	0.16	-2.04*	-2.95**	3.1	1.71	-0.99**	-0.04
L23	0.59	0.24	0.41	-2.72**	-2.52*	5.82	-7.95	-0.4	0.01
L24	0.03	0.44	0.23	2.37*	2.33*	-5.75	-1.51	0.14	-0.01
L25	0.75	0.89*	0.81	-0.04	-0.92	2.47	-7.08	-0.99**	0.04
L26	0.11	-0.4	-0.15	-0.16	0.2	-2.15	5.3	0.3	0.26**
L27	0	-0.34	-0.18	0.65	1.05	9.16	10.68**	0.35	0.33**
L28	-1.19*	-0.89*	-1.04*	3.06**	2.45*	-14.65*	-5.76	-0.24	0.05
SE (gi)	0.52	0.41	0.43	1.00	1.02	5.71	4.31	0.37	0.07
Tester									
T1	0.19	0.17	0.19	0.33	0.1	-3.81*	6.04**	-0.27	0.04
T2	-0.03	0.16	0.06	0.96**	1.20**	2.22	-2.97*	0.41	0.01
T3	0.06	0.22	0.14	-0.96**	-1.35**	6.82**	1.85	-0.52	-0.04
T4	-0.22	-0.56	-0.39	-0.29	0.12	-6.01**	-4.74**	0.39	-0.01
SE (gj)	0.17	0.14	0.14	0.33	0.34	1.9	1.44	0.29	0.02

* Significant at the $P < 0.05$ level of probability; ** Significant at the $P < 0.01$ level of probability

AD, days to anthesis; DS, days to silking; PH, plant height; EH, ear height; ASI, anthesis-silking interval; EPP, ears per plant; SE (gi) = Standard error of the GCA of inbred lines; SE (gj) = Standard error of the GCA of testers

Conclusions

The current study revealed the presence of considerable variations in grain yield and other agronomic traits among QPM testcross hybrids under optimum nitrogen and low-N environments in Ethiopia. Across environments, inbred lines L3, L6, L8, L16 and L18 were good combiners for grain yield. Inbred lines L4, L8 and L22 had desirable GCA effects for both days to anthesis and silking. Inbred lines L2 and L4 exhibited desirable GCA effects for reducing plant and ear heights. Inbred lines L3, L26 and L27 had desirable GCA effects for number of ears per plant. Across environments, QPM testcross hybrids L24 x T1, L12 x T1, L3 x T3 and L16 x T2 were the best hybrids yielded 6.5, 6.5, 6.4 and 6.4 t ha^{-1} respectively. The QPM inbred lines and hybrids identified in this study are potential candidates for further use in QPM breeding programs for generating commercial products Across environments, additive gene action was more important than nonadditive gene action for the inheritance of grain yield and other related traits, and these traits can be improved through recurrent selection by accumulating desirable genes. Generally, the present study confirmed the possibility of breeding QPM hybrids that thrives well across optimum and low-N conditions .

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