Combining ability and testcross performance of drought-tolerant maize inbred lines under stress and non-stress environments in Kenya

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Abstract

Drought and poor soil fertility are among the major abiotic stresses affecting maize productivity in sub-Saharan Africa. Maize breeding efforts at the International Maize and Wheat Improvement Center (CIMMYT) have focused on incorporating drought stress tolerance and nitrogen-use efficiency (NUE) into tropical maize germplasm. The objectives of this study were to estimate the general combining ability (GCA) and specific combining ability (SCA) of selected maize inbred lines under drought stress (DS), low-nitrogen (LN) and optimum moisture and nitrogen (optimum) conditions, and to assess the yield potential and stability of experimental hybrids under these management conditions. Forty-nine experimental three-way cross hybrids, generated from a 7 × 7 line by tester crosses, and six commercial checks were evaluated across 11 optimum, DS and LN sites in Kenya in 2014 using an alpha lattice design with two replicates per entry at each site. DS reduced both grain yield (GY) and plant height (PH), while anthesis–silking interval (ASI) increased under both DS and LN. Hybrids 'L4/T2' and 'L4/T1' were found to be superior and stable, while inbreds 'L4' and 'L6' were good combiners for GY and other secondary traits across sites. Additive variance played a greater role for most traits under the three management conditions, suggesting that further progress in the improvement of these traits should be possible. GY under optimum conditions was positively correlated with GY under both DS and LN conditions, but GY under DS and LN was not correlated. Our results suggest the feasibility for simultaneous improvement in grain yield performance of genotypes under optimum, DS and LN conditions.

Key words: drought tolerance — nitrogen-use efficiency — variance — heritability — stability

Maize production in sub-Saharan Africa (SSA) is constrained by several biotic and abiotic stresses. Maize fields managed by smallholder farmers in this region experience multiple stresses either simultaneously or at different stages of crop growth. Recurrent drought and suboptimal soil fertility are among the major abiotic stresses impacting maize grain yields in SSA (Shiferaw et al. 2011). Climate change is also exacerbating the frequency and/or intensity of drought, further aggravating the challenges smallholder farmers face in SSA. This may lead to greater food insecurity and can place the livelihood of farmers and their families at risk. Poor infrastructure, high cost of irrigation and inadequate capacity to accurately predict rainfall patterns leave maize farmers with limited ability to cope with drought. The inherent poor soil fertility of most African soils, coupled with poor access to inorganic fertilizers due to economic or social constraints, lack of awareness, or poor infrastructure, also contributes significantly to low maize yield in the region (Salami et al. 2010).

Breeding for stress tolerance is advocated as an affordable option to tackle the challenges of yield reduction and crop failure resulting from drought and low soil fertility (Bänziger et al. 2006). The aim of any plant breeding programme is to develop cultivars that are well-adapted to the target environment (s). Virtually, all plant breeding programmes use multi-environment trials (METs) to evaluate newly developed germplasm. With METs, breeders aim at capturing a variety of on-farm conditions by testing genotypes for important traits at multiple locations across several years within the target agroecology of the breeding programme (Hohls 2001, Cooper et al. 2014). However, as some abiotic stresses such as drought are sporadic in nature, the International Maize and Wheat Improvement Center (CIMMYT) uses managed abiotic and biotic stress screening sites to complement METs at its breeding hubs in Africa, Asia and Latin America.

In SSA, an extensive network of managed low-nitrogen and drought stress screening sites are available for routine screening of experimental maize genotypes. Over the past three decades, CIMMYT, in collaboration with the National Agricultural Research Systems (NARS), has made significant progress in developing maize germplasm with tolerance to drought and low-nitrogen stress (Bänziger et al. 2000, 2006, Wegary et al. 2011, Masuka et al. 2012, Weber et al. 2012, Beyene et al. 2013). Improved maize inbred lines have been used to successfully develop and deploy drought-tolerant and nitrogen-use efficient hybrids and synthetics.

Several studies were undertaken to assess the performance of genotypes, and the gene action of traits under optimum-nitrogen and managed low-nitrogen stress or optimum moisture and managed drought stress environments (Bänziger et al. 2006, Derera et al. 2007, Worku et al. 2008, 2012, Weber et al. 2012, Beyene et al. 2013). However, most of these studies considered only one stress at a time. However, under farmers' management conditions in SSA, multiple stresses, particularly drought and low soil nitrogen, occur concurrently or at different times during the same growing season. The need to combine both drought and low-nitrogen tolerance within maize varieties has long been recognized by breeders in SSA. Makumbi et al. (2011) evaluated

diallele crosses of maize inbred lines under optimum moisture and nitrogen, moisture stress and low-nitrogen conditions and identified inbred lines with good GCA. The authors also reported different gene actions in the control of grain yield under different management conditions. Meseka et al. (2006) evaluated drought-tolerant hybrids with different doses of drought-tolerant parents and reported higher yield under low-nitrogen stress in most hybrids involving at least one drought-tolerant parent. Betrán et al. (2003) reported the importance of additive gene effects for grain yield under drought, non-additive under low-nitrogen and both additive and non-additive under optimum moisture and nitrogen conditions. Similarly, Derera et al. (2007) found additive gene action for grain yield under drought, but both additive and non-additive gene actions operate under optimum conditions. Although several studies have been conducted in the past using lines developed through pedigree breeding method, this study will attempt to identify new lines and hybrids that are preforming well under drought and low-nitrogen conditions but also have no yield penalty under optimum conditions. In this study, new lines and testers recently developed in SSA using conventional pedigree breeding, double haploid technology and molecular breeding (Beyene et al. 2013, 2016b) under the framework of the Drought Tolerant Maize for Africa project (DTMA), Water Efficient Maize for Africa (WEMA) and Improved Maize for African Soil (IMAS) were used.

The objectives of this study were to estimate the general and specific combining abilities (GCA and SCA) of selected maize inbred lines under drought stress, low-nitrogen and optimum moisture and nitrogen conditions, and to assess yield potential of three-way cross hybrids under these different management conditions.

Materials and Methods

Experimental materials: Seven drought-tolerant inbred lines were used to form testcrosses with seven single-cross testers from the complimentary heterotic group (Table 1). The inbred lines used in this study were selected from a group of elite inbred lines developed from seven tropical biparental crosses. Details on line development were described previously by Beyene et al. (2016a). In brief, the inbred lines were extracted from $F_{2:3}$ lines based on testcross performance across 5–7 optimum and 2–3 drought stress locations. The selected lines were then advanced to $F_{5:6}$ with visual selection at each stage of inbreeding. The top 10% of F_2-derived lines were selected based on phenotypic trait BLUPs of $F_{2:3}$ testcrosses within each population from the combined analysis of the drought stress and well-watered trials for grain yield and agronomic traits. The selected lines from each population were planted in a nursery at Kibos, Kenya. Selections were made within and among families, and selected plants were self-pollinated to form $F_{3:4}$ lines. Selection was based on germination and good stand establishment, plant type, low ear placement, and well-filled ears as well as resistance to grey leaf spot caused by *Cercospora zeae-maydis*; leaf blight caused by *Exerohilium turcicum*; common rust caused by *Puccinia sorghi*; and maize streak virus caused by maize streak *geminivirus*. Selected $F_{3:4}$ plants were planted at Kiboko, Kenya, at a high plant density (80 000 plants/ha), selected visually for low root and stalk lodging as well as low ear placement, and then self-pollinated to form $F_{4:5}$ lines. The above procedure was repeated to form $F_{5:6}$ lines. Seven $F_{5:6}$ lines were selected for this study and crossed with seven single-cross testers from a complimentary heterotic group. The CIMMYT-derived testers are well-adapted to SSA and have proven useful previously in hybrid formation for subtropical and mid-altitude environments. These testers have also been used in many successful commercial hybrids (Beyene et al. 2013).

Experimental design and management: Forty-nine experimental hybrids and six commercial checks were evaluated across 11 location–year combinations in seven well-watered and well-fertilized sites, two managed drought stress sites and two managed low-nitrogen sites in 2013 and 2014 (Table 2). At all sites, the entries were hand-planted in two-row plots, 5 m long each, with 0.75 m spacing between rows and 0.25 m between hills, except at Kiboko where a row length of 4 m with 0.2 m intrarow spacing was used. Two seeds were initially planted per hill and then thinned to one plant per hill at 3 weeks after emergence to

Table 1: Pedigree, descriptions and sources of materials used in this experiment

No	Code	Pedigree	Description
1	L1	([Ent320:92SEW2-77/[DMRESR-W]EarlySel-#I-2-4-B/CML386]-B-22-1 -B-2-#-1-BB-1-B/INTA-F2-192-2-1-1-1-B*9)-B-7-6-1-B	Line
2	L2	(INTA-F2-192-2-1-1-1-B*7-3-B/[INTA-2-1-3/INTA-60-1-2]-X-11-6-3-BBB) F2-192-8-1-B	Line
3	L3	(INTA-F2-192-2-1-1-1-B*7-3-B/MAS[MSR/312]-117-2-2-1-B*4-2-1-B) -B-146-8-1-B	Line
4	L4	([Ent320:92SEW2-77/[DMRESR-W]EarlySel-#I-2-4-B/CML386]-B-11-3 -B-2-#-B*4/[INTA-2-1-3/INTA-60-1-2]-X-11-6-3-BBB)-B-101-6-1-B	Line
5	L5	(ZEWAc1F2-219-4-3-B-1-B*4-3-B/ZEWAc1F2-80-1-1-B-1-B*4-1-B)-B -74-2-2-B	Line
6	L6	([CML390/CML206]-BB-2-4-BBB/LaPostaSeqC7-F71-1-2-1-1-BBB)-B-91-4-3-B	Line
7	L7	[DTP2WC4H255-1-2-2-BB/[[NAW5867/P30-SR]-111-2/[NAW5867/P30 -SR]-25-1]-8-1-1-B-1]-1-2-2-B]-1-1-1-1-BBB-1-B/LaPostaSeqC7-F103-1 -2-1-1-BBB)-B-35-5-2-B	Line
8	T1	CML395/CML444	Tester
9	T2	CML489/CML444	Tester
10	T3	CML312/CML395	Tester
11	T4	CML566/CKDHL0333	Tester
12	T5	CML566/CML569	Tester
13	T6	CKDHL0159/CML569	Tester
14	T7	CML566/CML395	Tester
15	C1	Check 1	Check
16	C2	Check 2	Check
17	C3	Check 3	Check
18	C4	Check 4	Check
19	C5	Check 5	Check
20	C6	Check 6	Check

Table 2: Characterization of trial growing locations, average yield, CV, heritabilities and variances of trials

Location	Management	Year	No of Reps	Mean	CV	Entry Variance	Residual variance	Heritability
Embu	Optimum	2014	2	7.77	11.04	0.94	0.65	0.74
Homabay_DT	Managed drought	2014	2	4.43	23.64	0.48	0.89	0.52
KYUC	Optimum	2014	2	5.74	12.02	0.47	0.44	0.68
Kaguru	Optimum	2014	2	7.98	10.89	0.36	0.70	0.51
Kakamega	Optimum	2014	2	9.56	9.59	3.79	0.82	0.90
Kakamega_LN	Managed LN	2014/15	2	2.00	23.98	0.15	0.16	0.65
Kiboko	Optimum	2014	2	7.00	8.48	0.78	0.30	0.84
Kiboko_DT	Managed drought	2014	2	3.01	17.37	0.14	0.22	0.56
Kiboko_LN	Managed LN	2014/15	2	2.67	18.05	0.15	0.17	0.63
Mtwapa	Optimum	2014	2	5.73	13.36	0.31	0.39	0.61
Shikutsa	Optimum	2014	2	7.81	14.09	2.29	1.04	0.81

obtain a final plant population of 53 333 plants ha^{-1}. For managed LN trials, triple super phosphate (46% P$_2$O$_5$) was applied at planting at the rate of 50 kg P$_2$O$_5$ ha^{-1} with no further top dressing. For optimum and DS trials, calcium ammonium nitrate (CAN) fertilizer was used at the rate of 54 kg N ha^{-1} followed by top dressing of urea fertilizer at the rate of 138 kg N ha^{-1} three weeks after planting. Most optimum and LN trials were grown under rain fed conditions except at Kiboko where trials were irrigated as needed to avoid moisture stress. For managed drought trials, irrigation was withheld three weeks before the expected date of flowering to induce drought stress. All trials were kept weed free, and all recommended agronomic practices for the locality were implemented. At harvest, end plants from either end of each row were removed from all LN and DS trials to minimize the border effects.

Data were recorded on grain yield (GY), anthesis date (AD), silking date (SD), number of ears per plant (EPP) and plant height (PH) at all sites and under all management conditions. GY was measured in tons per hectare adjusted to a grain moisture content of 12.5%. Number of days to anthesis was recorded by counting the total number of days from planting to when 50% of plants in a plot started shedding pollen in the primary tassel axis; PH was measured in centimetres from the base of the plant to the first branch of the tassel; EPP per plot was obtained by dividing the total number of ears harvested from a plot by the total number of plants at harvest. ASI was calculated by subtracting the number of days to anthesis from the total number of days to silking. In DS and LN trials, ears harvested from each plot were shelled and weighed to determine GY and grain moisture per cent. In the optimum experiments, ears harvested from each plot were weighed, and subsamples were shelled to determine representative grain moisture. GY was estimated assuming a shelling percentage of 80% and adjusted to 12.5% moisture content.

Data analysis: Individual site and combined analysis across sites was conducted using META-SAS (Vargas et al. 2013). Correlations among optimum, LN and DS environments were determined using combined mean grain yield of each management condition. The 'Line by Tester' procedure embedded in AGD-R (analysis of genetic designs with R, Rodríguez, et al. 2015) software was used to estimate general and specific combining abilities and variance components for all traits with significant entry effects. Correlation analysis was performed with MINITAB 14.2 software (Minitab Inc., State College, PA, USA) while SIGMAPLOT version 10 (Systat Software, Inc., San Jose, CA, USA, www.systatsoftware.com.) was used to create graphs. GGE biplot (Yan 2001) was used to estimate genotype-by-environment interaction and generate 'which-won-where' and 'ranking' graphs.

Results
Analysis of variance and performance of hybrids by management

Combined analysis of variance across environments showed significant (P < 0.01) genotype (G), environment (E), and G × E interaction (GEI) mean squares for GY and all other measured traits under optimum, DS and LN conditions. Entry effect for GY, AD, PH, EPP and ASI was highly significant across optimum, DS and LN sites (data not shown).

Average GY of trials was 7.5 t ha^{-1} under optimum conditions, 3.7 t ha^{-1} under DS and 2.3 t ha^{-1} under LN environments (Table 3). On average, GY under DS and LN management conditions was 49% and 31% of the GY under optimum condition, respectively. LN resulted in delayed male flowering (70.6 days) while DS triggered early flowering (63.1 days) compared to optimum management (67.8 days). ASI was highest under LN (4.3 days) and was lowest under optimum management (0.6 days). Plants were tallest (245 cm) under optimum condition and were shortest (146 cm) under LN condition (Table 3).

From combined analysis by management, hybrids L4/T2 and L4/T1 were consistently high yielding across all three management conditions, suggesting the possibility to identify hybrids that can perform across management conditions. Average GY of the top ten hybrids and the highest yielding hybrid against the average yield of all checks was higher under all management conditions (Table 3). Grain yield of the top 10 hybrids under each management over the mean of commercial checks was 46%, 59% and 61% higher under optimum, DS and LN, respectively.

Genetic variance, heritability and correlation

Genotypic variance for GY was higher than error variance under optimum sites, except at Kaguru and Mtwapa (Table 2). For DS and LN sites, the error variances were slightly greater than entry variances. The average ratio of genotypic to error variance from individual sites was 1.89, 0.59 and 0.91 under optimum, DS and LN, respectively. The higher genotypic variances were translated to higher heritability for GY under optimum sites followed by LN. The highest heritability among optimum sites was recorded in Kakamega (0.90), whereas the lowest was recorded in Kaguru (0.51) with the overall average of 0.73. Average heritability was 0.54 for DS sites and 0.64 for LN sites. For combined data, we observed higher variance components and heritability under optimum than under managed stress sites. Also, the proportion of genotypic variance to both genotype × environment and error variances were higher under optimum than under the managed stress site indicating less effect of genotype × environment interaction and error variances on traits heritability estimated under optimum condition.

Among the top 15 hybrids under each management, optimum and LN had the highest number of hybrids in common (8) followed by DS and LN (6), and optimum and DS (5) (Table 3).

Table 3: Performance of top 15 yielding hybrids and commercial checks under each of the three management conditions. Entries common under the three management conditions are in boldface and underlined while those common under drought and low N are underlined

Entry	GY Opt	AD Opt	ASI Opt	PH Opt	Entry	GY DS	AD DS	ASI DS	PH DS	Entry	GY LN	AD LN	ASI LN	PH LN
L6/T4	8.8	67.1	0.1	254.6	L4/T4	5.0	62.0	1.0	231.6	L6/T1	3.2	70.5	1.8	158.8
L2/T1	8.8	67.4	1.6	265.2	**L4/T2**	4.7	62.2	0.5	228.2	L2/T5	2.9	71.4	5.3	151.3
L6/T1	8.7	67.5	0.2	263.8	L7/T1	4.6	66.2	0.8	240.9	**L4/T2**	2.9	69.6	4.0	149.5
L6/T6	8.6	68.2	−1.1	257.6	**L4/T1**	4.6	62.8	1.5	240.8	L5/T3	2.9	68.7	5.1	141.7
L2/T4	8.5	68.6	1.4	257.7	L5/T4	4.5	62.7	0.3	212.4	L6/T6	2.8	70.2	4.8	150.7
L4/T1	8.5	66.9	0.9	257.4	L3/T2	4.2	62.4	1.3	216.8	L4/T3	2.7	69.4	4.5	158.5
L6/T5	8.5	67.5	0.0	259.4	L7/T5	4.2	66.1	1.0	227.9	L6/T2	2.7	71.2	2.7	151.0
L7/T5	8.5	71.1	0.1	250.2	L3/T5	4.2	64.0	0.8	202.6	L2/T3	2.6	71.4	1.7	143.9
L2/T3	8.4	67.2	2.1	267.1	L3/T6	4.2	62.0	2.3	212.2	L2/T7	2.6	69.2	7.9	157.0
L2/T6	8.4	67.6	1.4	255.2	L6/T3	4.2	63.4	0.8	229.0	**L4/T1**	2.6	71.4	6.8	148.9
L6/T7	8.4	67.3	−0.1	257.6	L2/T7	4.1	64.3	2.3	239.8	L6/T3	2.6	70.1	4.5	147.1
L4/T6	8.3	67.1	−0.1	251.0	L2/T4	4.1	63.4	2.0	249.1	L2/T6	2.6	72.3	3.8	149.5
L2/T5	8.2	68.0	2.4	259.2	L5/T7	4.1	63.0	1.0	211.3	L4/T7	2.6	69.8	5.0	150.8
L4/T2	8.2	67.0	−0.5	247.7	L4/T6	4.1	62.9	1.3	235.3		2.6	70.4	3.5	155.5
L2/T7	8.0	67.7	2.5	253.5	L6/T2	4.1	62.4	0.3	220.1		2.6	69.7	3.6	143.9
Check 1	8.2	71.9	0.1	244.5	50.0	3.4	62.2	2.5	221.3	50.0	2.1	73.3	4.8	153.0
Check 2	7.7	70.1	0.4	239.4	51.0	4.0	64.9	1.3	219.9	51.0	1.6	72.1	5.7	131.2
Check 3	5.3	67.1	1.6	243.3	52.0	1.8	64.7	4.3	201.6	52.0	2.2	75.0	2.8	164.5
Check 4	3.5	67.9	2.6	232.0	53.0	1.8	60.9	4.0	225.7	53.0	1.3	69.1	4.0	151.2
Check 5	5.6	68.3	1.9	249.7	54.0	2.4	63.7	3.5	232.5	54.0	1.7	73.9	4.0	148.4
Check 6	5.1	67.7	1.0	242.7	55.0	3.3	63.7	2.3	229.2	55.0	1.6	70.3	3.0	133.5
Grand Mean	7.5	67.8	0.6	245.2		3.7	63.1	1.6	225.0		2.3	70.6	4.3	145.9
Number of reps	2	2	2	2		2	2	2	2		2	2	2	2
Number of locations	7	7	7	7		2	2	2	2		2	2	2	2
Location Variance	3.64	82.7	0.53	1350.3		0.57	10.8	0.04	176.09		0	53.42	4.28	0
Entry Variance	0.83	2.03	0.46	123.69		0.1	0.97	0.02	112.92		0.02	2.39	0.42	50.78
Loc_ × _Entry_Variance	0.48	0.65	0.43	13.21		0.21	0.96	0.99	22.8		0.12	0.93	0.71	14.82
Residual Variance	0.61	1.41	1.28	67.49		0.54	1.7	1.44	65.55		0.17	1.37	2.88	100.28
LSD	0.97	1.28	1.09	7.75		1.54	2.78	2.62	16.03		0.95	2.64	3.03	17.54
CV	6.57	0.96	86.55	1.61		20.66	2.2	81.92	3.55		20.35	1.87	35.01	5.99
Heritability	0.88	0.91	0.75	0.95		0.3	0.52	0.03	0.8		0.19	0.75	0.28	0.61
The top 10 hybrids	8.59					4.42					2.81			
The Best hybrid	8.84					4.97					3.17			
Checks	5.89					2.78					1.74			
The Best check	8.17					4.02					2.15			
Yield Improvement														
Top ten hybrids over checks	46%					59%					61%			
Top ten over the best check	5%					10%					31%			
The best hybrid over checks	50%					79%					82%			
The best hybrid over the best check	8%					24%					47%			

GY, grain yield; AD, Anthesis date; PH, Plant height; ASI, Anthesis–silking interval; Opt, optimum; DS, Drought stress; LN, Low nitrogen.

Grain yield showed higher correlation between optimum and LN ($r = 0.64$; $P = 0.00$; $n = 55$), followed by optimum and DS ($r = 0.55$; $P = 0.00$; $n = 55$) and LN and DS ($r = 0.30$, $P = 0.03$; $n = 55$) (data not shown).

Line by tester analysis

The total variation due to genotypes was partitioned into lines, testers and line by tester (Table 4). Genotype effect was significant ($P \leq 0.05$) for all traits under all management conditions except GY and EPP under DS. Line and tester mean squares were significant for all traits under the three management conditions except EPP of line under DS, EPP of tester under optimum, and GY and ASI of testers under DS and LN conditions. Line × tester mean square was significant for most traits under optimum except EPP and PH, but line × tester mean square was not significant for all traits under DS and LN, except AD under LN (Table 4). Genotype × site, line × site and tester x site interactions were significant for most traits while line-by-tester-by-site interaction was significant only for AD under optimum and for ASI under LN condition (Table 4). The proportion of additive variance relative to the total variance was consistently higher for GY, PH and ASI under all management conditions (Fig. 1). The proportion of both variance components was equal for EPP under optimum, but dominance variance contributed more than 80% of the total variance for EPP under DS. Whereas additive variance was important in the control of AD under optimum and DS conditions, dominance variance was more important in the control of AD under LN conditions (Fig. 1).

General combining ability

The contribution of lines and testers to crosses was not consistent across traits and management conditions, with a few exceptions (Table 5). Among the lines, L4 and L6 had positive GCA for GY under all management conditions while L2 had positive GCA for GY under both optimum and low N conditions. Among the testers, T1 had small but positive GCA for GY under all management conditions while T4 and T6 had positive GCA effect for GY under optimum and DS conditions. Among all parental lines, L4 and L6 manifested desirable GCA effect for GY and most secondary traits under the three management conditions. The correlation between GCA effects of GY from optimum and LN was positive and significant ($r = 0.62$, $P = 0.02$; data not shown), but there was no significant correlation between the GCA effects of optimum and DS, and LN and DS ($P > 0.05$). Among secondary traits, the relation of GCA estimates among the three management conditions was positive and significant ($r > 0.65$, $P < 0.01$) for AD and ASI.

Specific combining ability

The SCA effects of some cross-combinations for grain yield and management conditions are summarized in Fig. 2. L7/T5, L4/T2, L3/T6 and L6/T1 were ranked among the best specific combiners with highest SCA estimates in all the three management conditions. In contrast, L1/T1, L2/T2, L5/T5, L6/T5 and L7/T7 ranked among the worst cross-combinations for GY with negative SCA effect under all management conditions. Some other cross-combinations were good under optimum and DS, DS and LN or optimum and LN (Fig. 2). Significant positive relationship between mean GY and SCA estimates under optimum ($r = 0.40$; $P = 0.01$; $n = 55$), DS ($r = 0.64$; $P = 0.00$;

Table 4: Analysis of variance of crosses for grain yield and other secondary traits under optimum, drought and low-nitrogen environments in Kenya

Source	Optimum						DS						LN			
	DF	GY	AD	EPP	PH	ASI	DF	GY	AD	EPP	PH	ASI	GY	AD	PH	ASI
SITE	6	65.04+	2904.72+	0.19+	28384.22+	47.13+	1	22.61+	358.61+	0.18+	2877.43+	4.00	5.55+	2613.29+	12.67	468.41+
REP(SITE)	7	2.72+	3.04*	0.02**	128.8*	1.23+	2	1.11	5.79+	0.01+	907.97+	5.55+	0.21	4.05+	893.34+	13.49*
GENOTYPES	48	4.75+	24.63+	0.01**	1682.76+	7.59+	48	0.68	6.71+	0.01	497.84+	2.34+	0.33*	9.98+	284.3+	6.46*
LINE	6	27.13+	165.41+	0.03+	11348.78+	39.56+	6	1.45*	33.59+	0.00	3128.93+	9.32+	1.26+	42.9+	880.18+	30.4+
TESTER	6	2.86+	15.46+	0.01	1487.1+	7.15+	6	1.05	7.77+	0.03*	352.88+	1.07	0.17	7.66+	387.99**	2.72
LINE:TESTER	36	1.22+	2.7+	0.01	100.33	2.33**	36	0.45	1.95	0.01	84.32	1.39	0.21	4.76+	167.17	3.09
SITE:GENOTYPES	288	1.22+	2.38+	0.01	90.45*	1.79**	48	0.93*	3.43***	0.01	93.09	2.95*	0.34**	2.73**	119.38	4.98
SITE:LINE	36	4.98+	5.21+	0.01	183.08+	3.84+	6	3.98+	11.13+	0.01	158.97*	8.01+	0.63**	1.54	265.82*	7.83+
SITE:TESTER	36	0.86	2.87+	0.01*	102.79	2.65+	6	0.38	6.46+	0.01	201.47**	2.60	0.24	7.78+	73.87	4.25
SITE:LINE:TESTER	216	0.68	1.83*	0.01	73.62	1.31	36	0.54	1.74	0.01	62.87	2.16+	0.29	2.22	103.96	4.62
Residuals	196	0.61	1.38	0.01	72.26	1.3	56	0.52	1.63	0.01	67.22	1.30	0.18	1.47	119.29	3.19

DS, drought stress; LN, low nitrogen; GY, grain yield; AD, anthesis date; EPP, ear per plant; PH, plant height; ASI, Anthesis–silking interval.
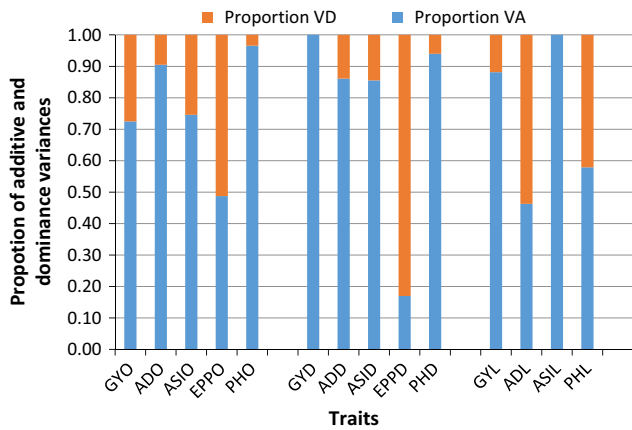*Significant at P = 0.05; **Significant at P = 0.01; +Significant at P < 0.01.

Fig. 1: Proportional contributions of additive and dominance genetic variances for GY and other secondary traits under optimum (O), drought (D) and low N (L) management conditions. [Colour figure can be viewed at wileyonlinelibrary.com]

n = 55) and LN (*r* = 0.59; P = 0.00; n = 55) was observed (Table 6). Mean GY under optimum was not related to SCA under DS or LN. Also, the SCA estimates under the three

management conditions (P > 0.05) for GY were not correlated (Table 6).

Genotype-by-environment interaction and stability of hybrids

The genotype-by-environment interaction was plotted using mean grain yields, at each site (Fig. 3). The GGE biplot divided all environments into two major mega-environments, each with a winning genotype. The first group predominately encompassed optimum environments, except Homabay (DS), with entry 47 (L7/T5) as a winner genotype. The second cluster was mainly formed with stress environments, except Kakamega and Shikutsa, with entries 36 (L6/T1) and 39 (L6/T4) as winning genotypes. Genotypes 53, 54 (commercial check) and 55 (local check) were the losers in all the environments, highlighting the superior performance of the experimental hybrids for GY over three popular commercial hybrids grown by farmers in those areas. To identify high yielding and stable genotypes, all the genotypes were ranked relative to the 'ideal genotype' based on their mean GY and stability across environments (Fig. 4). The centre of the concentric circles represents the position of the 'ideal genotype'.

Table 5: GCA estimates of lines and testers for grain yield and other traits under optimum, drought and low-nitrogen management conditions

Genotype	Optimum					DS					LN			
	GY	AD	EPP	PH	ASI	GY	AD	EPP	PH	ASI	GY	AD	PH	ASI
L1	−0.48	−1.05	−0.02	−5.25	0.07	−0.20	−0.90	0.01	−2.52	0.04	−0.13	−1.63	2.24	0.15
L2	0.59	−0.10	−0.02	12.82	1.22*	−0.32	0.37	−0.02	15.75	1.18	0.13	0.07	4.45	2.08
L3	−0.57	−0.08	0.01	−10.32	0.14	0.21	−0.19	−0.01	−12.28	0.25	−0.37	1.10	−3.89	0.15
L4	0.47	−0.52	0.00	7.30	−0.39	0.48	−0.42	0.01	6.70	−0.39	0.15	−0.52	4.59	−0.49
L5	−0.46	−1.07	0.00	−19.15	−0.33	−0.15	−0.87	0.01	−16.86	−0.29	0.10	−1.62	−10.08	−0.03
L6	0.71	−0.17	0.01	11.36	−0.80	0.06	−0.39	−0.01	3.82	−0.39	0.23	1.01	5.77	−1.24
L7	−0.28	3.46*	0.02	2.70	0.08	−0.05	2.46*	0.00	5.33	−0.39	−0.12	1.64	−3.25	−0.60
GCASE	0.49	1.20	0.02	9.96	0.59	0.21	1.01	0.01	9.79	0.53	0.20	1.15	5.19	0.96
T1	0.09	0.26	−0.01	5.50	0.11	0.01	−0.02	0.02	4.28	0.32	0.02	1.05	6.03	−0.57
T2	−0.33*	−0.64	0.00	−7.03	−0.42	0.12	−0.63	0.02	−5.67	−0.11	−0.08	−0.23	−5.41	0.26
T3	−0.18	−0.64	0.00	4.52	0.29	−0.26	−0.31	−0.06	2.48	0.21	0.19	−0.42	3.94	0.36
T4	0.08	0.32	0.01	−2.51	−0.17	0.31	−0.37	0.02	0.76	−0.04	−0.07	0.28	1.00	−0.14
T5	0.18	0.33	−0.01	0.38	0.12	−0.34	1.15	0.01	−5.37	−0.21	−0.06	−0.04	−1.59	−0.14
T6	0.15	0.08	0.01	0.28	−0.21	0.07	−0.12	−0.01	0.88	−0.14	−0.01	−0.74	−1.43	0.08
T7	−0.01	0.35	0.00	−1.70	0.27	0.11	0.36	0.01	2.58	−0.04	−0.01	0.15	−2.70	0.15
GCASE	0.16	0.37	0.01	3.61	0.25	0.18	0.49	0.03	3.29	0.18	0.07	0.48	3.45	0.29

GY, grain yield; AD, anthesis date; EPP, number of ears per plant; PH, plant height; ASI, anthesis–silking interval.
*Significant at P = 0.05; **Significant at P = 0.01; +Significant at P < 0.01.
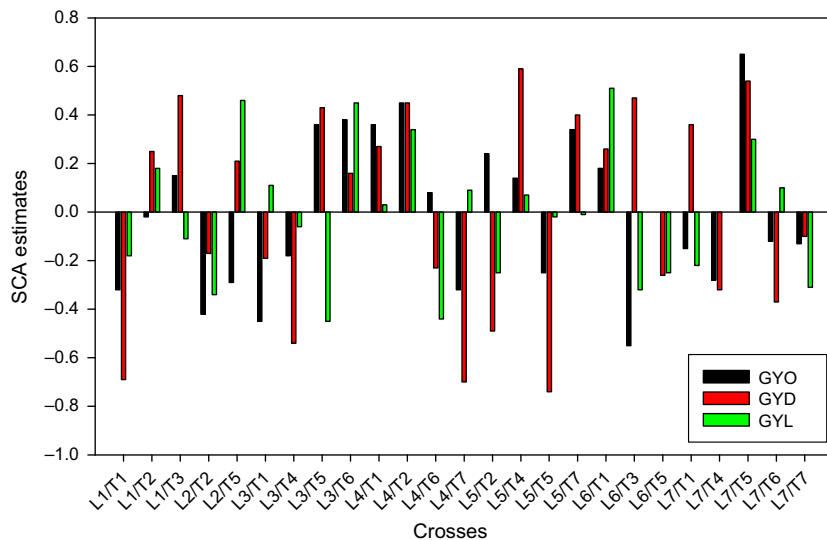

Fig. 2: Specific combining ability estimates of some cross-combinations for grain yield under optimum (GYO), drought (GYD) and low N (GYL) management conditions. [Colour figure can be viewed at wileyonlinelibrary.com]

Genotypes 47 (L7/T5), 50 (commercial check), 22 (L4/T1) and 23 (L4/T2) appeared to be high yielding and the most stable genotypes.

Discussion

Performance of hybrids, genetic variance and heritability

Compared to optimum management, DS and LN reduced GY by 50% and 69%, increased ASI by 149% and 573%, and decreased PH by 1% and 40%, respectively. The effect of DS and LN on GY and secondary traits observed in our study was in agreement with previous studies (Ribaut et al. 1996, Banziger et al. 1999, Betrán et al. 2003, Meseka et al. 2006, Pswarayi and Vivek 2007, Worku et al. 2007, 2008, 2012, Makumbi et al. 2011, Wegary et al. 2011, Hansey et al. 2012, Beyene et al. 2013). However, the effect of the two stresses on ASI was very high in our study. Menkir et al. (2006) reported relatively higher increase (144%) in ASI due to moisture stress relative to optimum condition in drought-tolerant germplasm adapted to West Africa. The high yield reduction under stress environments could be partly explained by the wider ASI under stress, as ASI typically has a high negative correlation with GY under stress conditions (Westgate 1997, Beyene et al. 2013). Drought stress before or at flowering delays silk elongation but has little or no effect on pollen shed (Westgate 1997, Beyene et al. 2013). For this reason, indirect selection to minimize ASI has been an effective approach for selecting genotypes with improved synchronization of male and female flowering under stress. In addition to yield reduction, stress also reduced genetic variance for GY and other secondary traits and increased error and GEI variances leading to relatively lower heritability estimates under DS and LN conditions.

Table 6: Correlation between specific combining ability (SCA) effects of grain yield under different management and their relation with mean grain yield

	SCAGYO	SCAGYD	SCAGYL
SCAGYD	−0.01 (0.93)		
SCAGYL	0.14 (0.33)	0.16 (0.27)	
Mean GYO	0.40 (0.01)	0.03 (0.85)	0.06 (0.70)
Mean GYD	0.05 (0.73)	0.64 (0.00)	0.10 (0.48)
Mean GYL	0.08 (0.60)	0.09 (0.53)	0.59 (0.00)

SCA, specific combining ability; GYO, grain yield under optimum; GYD, grain yield under drought; GYL, grain yield under low N.
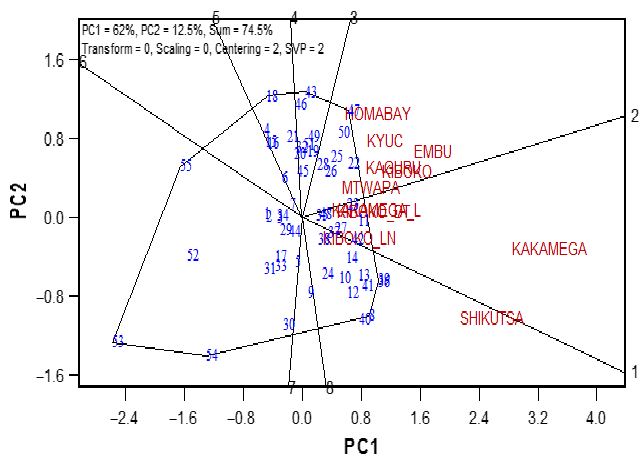

Fig. 3: Which-won-where view of the GGE biplot for all genotypes tested across seven optimum, two DS and two LN sites in Kenya. [Colour figure can be viewed at wileyonlinelibrary.com]
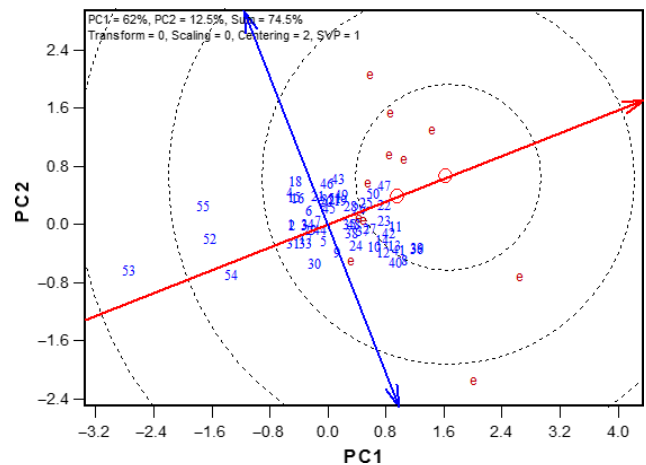

Fig. 4: The ranking of genotypes relative to 'the ideal genotype' based on mean and stability. [Colour figure can be viewed at wileyonlinelibrary.com]

The average GY of the top ten experimental hybrids was higher than the best check under all management conditions indicating that most of the experimental hybrids were superior for drought and low-nitrogen stress tolerance and had greater stability than the commercial checks. Duvick (1996) and Duvic and Cassman (1999) reported better tolerance to drought and LN stresses in new varieties compared to older varieties released in different eras in the USA. CIMMYT and other partners in eastern and southern Africa have been working to improve tropical maize germplasm for both DS and LN for the last three decades (Bänziger et al. 2000, Makumbi et al. 2011, Worku et al. 2012), and these findings confirm the progress made through this effort. Knowledge of the correlation of a trait between different management conditions can be used to make decisions regarding indirect selection in breeding for stress tolerance and can ultimately be useful for designing a breeding strategy. The magnitude of correlation we observed for GYs between optimum and DS, and between optimum and LN was relatively higher than those reported by Ribaut et al.(1996) and Weber et al.(2012). The use of recent germplasm in our study, which have been simultaneously selected for optimum and multiple stress tolerance through several cycles of selection, might have contributed to this observation.

High GY under optimum and improved yield under stress conditions combined with stable performance across sites, and acceptable secondary traits under stress conditions are considered high-priority criteria for selecting genotypes that perform best across optimum and stress environments. In this regard, hybrids, L4/T2 and L4/T1 were the best experimental hybrids with high mean yield and most stable performance across environments. These hybrids perhaps have combined water and nitrogen-use efficiency possibly due to the contribution of favourable genes with additive effects by both parents and/or as a result of heterosis (Makumbi et al. 2011). The two parents of L4/T1 and one parent of L4/T2 had positive GCA effects, and their single crosses testers had positive SCA effects for GY under all management conditions. The fixation of favourable alleles in parental lines of the hybrids that performed well across stress environments might have contributed to superior performance of hybrids. Improvement of these lines was achieved through selection for favourable alleles of secondary traits such as ASI in addition to selecting them for good GCA for GY under optimum, managed and random stress environments in early generation test cross evaluations.

Combining ability effects

Knowledge of the amount of additive and dominance variance components is important for setting breeding strategy to improve a target trait. The proportional contribution of additive and dominance variances showed greater importance of additive variance for GY and all secondary traits under all management conditions, except for EPP under optimum and DS, and for AD under LN. Our results are in agreement with previous studies (Betrán et al. 2003, Derera et al. 2007, Makumbi et al. 2011, Adebayo et al. 2014) that reported a higher role of additive variance for GY and other secondary traits. In contrast, Oyekunle and Badu-Apraku (2014) reported a sizeable contribution of non-additive variance for GY under DS, suggesting the importance of selection for drought tolerance to develop hybrids with enhanced stress tolerance. Traits controlled by additive genetic effects can be improved through selection during inbred line development and through recurrent selection scheme. Selection of lines during different stages of selfing for GCA under optimum and DS environments might have contributed to higher additive variance under all environments. Previously, it had been shown that genotypes with improved performance under DS showed improved performance under LN condition, which could be due to contribution of favourable stress-tolerant alleles by parents. But under both optimum and LN conditions, the contribution of dominance variance was significant and breeding programmes should exploit both components by evaluating parents for GCA followed by testing the resulting hybrids in target environments (Makumbi et al. 2011) as the genetic basis of GCA and SCA effects is different (Qi et al. 2013).

The GCA effects of line-by-environment interaction were significant for GY across optimum, DS and LN environments, but GCA effects of testers were not. The GCA effects for GY were not consistent across optimum, DS and LN environments, which indicates the need to select lines for specific adaptation (Makumbi et al. 2011). The single-cross testers, however, were less affected by environment as opposed to the inbred lines. Among secondary traits, AD was consistently affected by environment under all management conditions, but the ranking of genotypes for plant height was consistent across environments under all management conditions.

Inbred lines with desirable GCA effects for GY and other agronomic and secondary traits could be used in (i) recurrent selection programmes; (ii) as parents to form synthetic varieties; (iii) for recycling of inbred lines; and (iv) as testers for evaluating newly developed inbred lines (Makumbi et al. 2011). In this case, the desirable GCA values of Lines L4 and L6 for GY and other secondary traits across the three management conditions make them the best candidate inbred testers for evaluating new inbred lines under optimum, DS and LN conditions. More testers were found to be good under optimum and DS condition than optimum and LN and across all environments likely due to the fact that these testers were developed from long-term drought-tolerant breeding pipelines. This may reflect the stronger relative focus of the CIMMYT Africa breeding programmes on drought tolerance compared with LN tolerance. Results of the current study demonstrate that it is possible to identify good lines and testers that can be used across management conditions. The prediction of GCA under stress conditions based on GCA under optimum condition is not advisable due to the observed weak relationship between optimum GCA and DS GCA. Several combinations manifested positive or negative SCA effects across optimum, DS and LN conditions for grain yield, indicating the possibility of identifying specific hybrids that can perform well under the three management conditions. This suggests the feasibility of developing varieties which can tolerate multiple stresses. SCA between parental lines can be used as a predictor of GY within the same management condition (Betrán et al. 2003). Conversely, SCA estimates among management conditions were not related despite the positive relationship of mean GY among the different management conditions probably due to the preponderance of additive genetic variance in the control of grain yield.

Conclusions

The current study used lines and hybrids recently developed in SSA and identified hybrids having higher grain yield than the best check under drought, low-nitrogen and optimum conditions. Commercialization of the outstanding hybrids identified in the present study (e.g. L4/T2 and L4/T1) with high mean yield and stable performance across management conditions would contribute to the productivity and yield stability for small farmers' fields in SSA. The high correlation observed in our study between grain yields under optimum and managed drought stress, and under optimum and low-nitrogen condition may be partly due to the use of recent lines that have been simultaneously selected for optimum and multiple stress tolerance through several cycles of selection. We have identified two new lines (L4 and L6), that have high general combining ability effects for grain yield and other secondary traits across the three management conditions, and can be nominated as candidate inbred testers for evaluating new inbred lines under optimum, managed drought stress and low-nitrogen conditions. Results of the current study demonstrate that it is possible to identify good lines and testers that can be used across management conditions and may also reflect the stronger focus of the CIMMYT Africa breeding programmes in developing multiple stress-tolerant lines and hybrids without yield penalty under optimum condition.

Conflict of interest

The authors have no conflict of interest.

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