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Performance and yield stability of maize hybrids in stress-prone environments in eastern Africa☆

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ABSTRACT

Identification and deployment of high-yielding and stress-tolerant maize hybrids adapted to stress-prone agro-ecologies is important for improving the food security and livelihoods of smallholder farmers in eastern Africa. The objectives of this study were to (i) assess the performance of maize hybrids under well-watered and drought stress conditions; (ii) evaluate grain yield stability of 65 intermediate-maturing and 55 early-maturing hybrids in 24 well-watered locations and seven drought stress locations; and (iii) identify representative and/or discriminative testing locations for increasing genetic gains for the target traits. There were significant differences for grain yield among early- and intermediate-maturing hybrids tested under well-watered and drought stress environments. Among the early-maturing hybrids, the top 10 hybrids produced 46.8%–73.9% and 31.2%–42.1% higher mean grain yields than the best commercial check under drought and well-watered conditions, respectively. Among the intermediate-maturing hybrids, the top 10 hybrids produced 25.2%–47.7% and 8.5%–13.5% higher grain yield than commercial checks under drought stress and well-watered conditions, respectively, suggesting improvement in the levels of drought tolerance in both early- and intermediate-maturing hybrids. GGE biplot analysis and a bi-segmented regression linear method identified specific early-maturing and intermediate-maturing hybrids that performed well under both well-watered and drought stress conditions. These hybrids could be recommended for commercial production in eastern Africa. Kakamega in Kenya was found to be the most representative and highly discriminating site among well-watered testing locations, while Kabuku in Tanzania was the least representative of test locations. For testing under drought stress

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conditions, Kiboko in Kenya was identified as the most representative location. This information could be useful for allocating resources and streamlining CIMMYT maize hybrid testing in eastern Africa.

1. Introduction

Maize is the main staple food in eastern Africa, accounting for nearly 50% of total calorie intake in the region [1] and an annual production of 28 million metric tons on 25% of the agricultural area [2]. Both production and productivity of maize need to be increased in this region, owing to rapid population and economic growth [3]. Between 2017 and 2050, the African population is projected to grow by 90%, from the current 1.3 billion to 2.5 billion [4]. The average maize yield in sub-Saharan Africa (SSA) is 1.8 t ha^{-1}, which is lower than in other maize-growing regions in the developing world and below the world average of 4.9 t ha^{-1}. This low productivity is attributed to several factors, including drought, poor soil fertility, insect pests, and diseases.

Drought stress, which causes several changes in morpho-physiological traits and metabolism of plants, is a major constraint to maize production in eastern Africa [5–7]. About 40% of the maize-growing areas in Africa experience occasional drought stress, resulting in yield losses of 10%–25% [8]. Drought stress is also predicted to occur more frequently and severely in future owing to the changing climate [3], impairing agricultural production especially in the tropics and subtropics and particularly in SSA [9,10]. Crop production in SSA is mainly by smallholder farmers who are highly dependent on rainfall for sustaining the crops. Thus, development and deployment of tropical maize varieties with drought tolerance and other relevant agronomic and adaptive traits is key to enhancing the food security and livelihoods of maize farming communities in regions such as eastern Africa.

Breeding for drought tolerance and yield stability is an important objective of maize breeding programs in SSA and a high priority for the CIMMYT Global Maize Program [11]. Inbred lines with superior breeding values for grain yield and tolerance to abiotic stresses are used as base materials for developing high-yielding and drought-tolerant hybrids [11]. Under the Water Efficient Maize for Africa (WEMA) [12,13], and Stress Tolerant Maize for Africa (STMA) projects, CIMMYT has adopted several breeding approaches for developing drought-stress tolerant maize hybrids adapted to SSA. These include pedigree selection, marker-assisted recurrent selection (MARS), and genomic selection (GS) [6]. Over the past decades, CIMMYT has made progress in developing maize germplasm tolerant to drought and low nitrogen [11,14]. Wossen et al. [15] reported that if farmers had not adopted these drought-tolerant (DT) maize cultivars, their yields would have decreased by 13.3%, poverty would have increased by 12.9%, and the probability of seasonal food scarcity would have increased by 84.0%. Yet the seed cost and labor required to grow DT maize cultivars are no different from those for non-DT cultivars [8].

In the process of breeding, newly developed hybrids should be tested in multiple relevant locations for several years to determine their performance and adaptability before commercial release. Genotype-by-environment (GE) interaction may cause inconsistencies in genotype ranking across environments, making the selection of suitable maize hybrids challenging [16,17]. Thus, identifying and interpreting GE interaction is essential for genetic progress [18]. To reduce the negative effects of GE interaction it is important to identify stable genotypes across multiple environments and to characterize the ability of test environments to discriminate genotypes and to represent the target population of environments in each region [19,20].

Several statistical methods are available to analyze GE interaction and genotype stability, including those based on linear regression [21,22], bi-segmented regression [23,24], non-parametric tests [25,26] and linear-bilinear models such as AMMI and GGE biplot [27,28]. Some of these methods are considered as alternatives and others as complementary, and use of more than one method to study GE interaction could increase efficiency [29,30].

The objectives of this study were (i) to evaluate the performance of maize hybrids under well-watered and drought stress conditions in eastern Africa, (ii) to estimate the grain yield stability of 65 intermediate-maturing and 55 early-maturing hybrids across seven drought stress locations and 24 optimum (well-watered) locations, and (iii) to identify the best representative and/or discriminating testing locations for increasing genetic gains for the target traits.

2. Materials and methods

2.1. Germplasm, experimental sites, experimental design, and field evaluations

A total of 55 early-maturing and 65 intermediate-maturing maize hybrids (at stage 4 of testing) were selected for regional trials in this study. CIMMYT regional trials are the last stage of testing in the breeding cycle, and include promising pre-commercial DT maize hybrids along with relevant commercial checks, and the evaluation data are used for the annual hybrid advancement process. The hybrids in these trials were selected based on yield and other agronomic traits from the first, second, and third stages of testing across locations within CIMMYT maize breeding pipelines (Beyene et al., unpublished data). Five commercial checks were included in trials with early-maturing hybrids and seven commercial checks in trials with intermediate-maturing hybrids. The experimental

Table 1 – Description of experimental sites used to evaluate maize hybrids in eastern Africa.

Site name	Country	Longitude and latitude	Elevation (m·a.s.l.)	Early maturity		Intermediate maturity	
				WW	DS	WW	DS
ADC Nai	Kenya	n/a	n/a	X	–	X	–
Boit	Kenya	n/a	n/a	–	X	X	–
Chepkanga	Kenya	0°35′N, 35°21′E	2170	X	–	–	–
Embu	Kenya	0°30′S, 37°28′E	1500	X	X	X	X
Isinya	Kenya	1°40′S, 36°51′E	1640	X	–	X	–
Kabuku	Kenya	1°09′S, 36°40′E	2155	X	–	X	–
Kabula	Kenya	0°47′N, 34°50′E	1331	–	X	X	–
Kaguru	Kenya	0°05′S, 37°40′E	1480	X	–	X	–
Kakamega	Kenya	0°17′N, 34°46′E	1585	X	–	X	–
Kibire	Kenya	n/a	n/a	–	–	X	–
Kiboko	Kenya	2°13′S, 37°44′E	975	X	X	X	X
Kirinyaga	Kenya	0°34′S, 37°19′E	1297	X	–	X	–
Kitale	Kenya	0°59′N, 35°01′E	1900	–	–	X	–
Kochalia	Kenya	0°37′N, 34°21′E	1238	X	–	X	–
Marima	Kenya	0°16′N, 37°40′E	1404	–	–	–	X
Mbeere	Kenya	0°44′S, 37°34′E	1048	X	–	X	–
Mtwapa	Kenya	4°21′S, 39°13′E	30	X	–	X	–
Naivasha	Kenya	0°41′S, 36°23′E	1904	X	–	X	–
Ol-Eldowns	Kenya	n/a	n/a	X	–	X	–
Wambugu	Kenya	0°27′S, 36°59′E	1756	X	–	X	–
Ilonga	Tanzania	9°04′S, 36°51′E	506	X	–	X	–
Mlangarini	Tanzania	3°26′S, 36° 46′E	1269	X	–	–	X
Abii	Uganda	3°05′N, 30°57′E	1147	–	X	–	X
Bulindi	Uganda	1°29′N, 31°26′E	1276	X	–	X	–
Ngetta	Uganda	2°16′N, 32°27′E	1082	X	–	X	–
Serere	Uganda	1°30′N, 33°27′E	1085	–	X	–	X

n/a, data not available. X, trial was planted. In locations where a trial was planted under both well-watered (WW) and drought stress (DS) conditions, the DS trials were conducted outside of the rainy season with supplemental irrigation. –, trial was not planted.

hybrids and commercial checks were evaluated in 23–24 well-watered (WW) and 6–7 drought stress (DS) locations, depending on maturity, in Kenya, Uganda, and Tanzania in 2017 (Table 1). The experimental design was an alpha lattice with two replications. Trials with a mean grain yield of <3 t ha^{-1} were treated as DS trials, while those with mean grain yield of >3 t ha^{-1} were considered WW trials [31]. Entries were planted in two-row plots, 5 m long, with 0.75 m spacing between rows and 0.25 m between hills. Two seeds per hill were initially planted and then thinned to one plant per hill at three weeks after emergence for a final plant population density of 53,333 plants ha^{-1}. Fertilizers were applied at the rate of 60 kg N and 60 kg P_2O_5 ha^{-1} as recommended for the area. Nitrogen was applied twice: at planting and 6 weeks after emergence. Fields were kept free of weeds by hand weeding.

Grain yield (GY), anthesis date (AD), plant height (PH), gray leaf spot (GLS, caused by *Cercospora zeae-maydis*) and northern corn leaf blight or Turcicum leaf blight (NCLB/TLB, caused by *Exserohilum turcicum*) were recorded. PH was measured in cm as the distance from the base of the plant to the height of the first tassel branch. AD was determined as the number of days from sowing until 50% of plants shed pollen. GLS and NCLB were measured on a 1–5 scale, where 1 was highly resistant (with no symptoms) and 5 was highly susceptible. GY was calculated from ear weight based on an average shelling percentage of 80%, adjusted to 12.5% moisture content, and converted to t ha^{-1}.

2.2. Data analysis

Best linear unbiased estimates (BLUEs) for grain yield across locations for each trial and each trait were generated using the following linear mixed model [32]:

$$Y_{ijrk} = \mu + L_j + R_r(L_j) + B_k[R_r(L_j)] + G_i + GL_{ij} + \varepsilon_{ijrk}$$

where Y_{ijrk} is the grain yield of genotype i at location j in replicate r within block k; μ is the general mean; L_j is the fixed effect of location j; $R_r(L_j)$ is the fixed effect of replicate r within location j; $B_k[R_r(L_j)]$ is the random effect of incomplete block k within replicate r and location j, assumed to be independently and identically normally distributed with mean zero and variance $\sigma^2_{B(RL)}$; G_i is the fixed effect of genotype i; GL_{ij} is the fixed effect of genotype × location interaction; and ε_{ijrk} is the random residual error, assumed independently and identically normally distributed with mean zero and variance σ^2_ε.

Variance components and heritability across locations were estimated. Broad-sense heritability (H^2) was estimated based on entry means as follows:

$$H^2 = \frac{\sigma^2_g}{\sigma^2_g + \frac{\sigma^2_{gl}}{l} + \frac{\sigma^2_\varepsilon}{lr}}$$

where σ^2_g is genotype variance, σ^2_{gl} is genotype × location interaction variance, and σ^2_ε is the error variance for l locations and r replicates of the genotypes at each site.

The BLUEs for each location were generated and used for GGE biplot analyses with META-R software [33].

The GY stability of the hybrids and the suitability of the test environments for selecting these hybrids were assessed using the multivariate method GGE biplot based on the following model [28]:

$$Y_{ij} - \overline{Y}_j = \lambda_1 \xi_{i1} \eta_{1j} + \lambda_2 \xi_{i2} \eta_{2j} + \varepsilon_{ij}$$

where Y_{ij} is the mean grain yield of genotype i in environment j; $\overline{Y}_j$ is the mean grain yield of environment j; λ_1 and λ_2 are the singular values of the first and second principal components, PC1 and PC2, respectively; ξ_{i1} and ξ_{i2} are the scores of genotype i for PC1 and PC2, respectively; η_{1j} and η_{2j} are the scores of environment j for PC1 and PC2, respectively; and ε_{ij} is the error associated with the model [28].

GGE biplot analyses were performed for each management regime (Early WW, Early DS, Intermediate WW, and Intermediate DS) and hybrid maturity (all early-maturing trials and all intermediate-maturing trials) separately. These analyses were performed with the GGE Biplots [34] and ggplot2 [35] packages of R 3.4.3 [36].

The GY stability of the hybrids was assessed following Cruz et al. [24]. These analyses were performed for only the trials grouped by hybrid maturity and using means instead of BLUEs. Cruz et al. [24] presented a bi-segmented regression linear method based on the following model:

$$Y_{ij} = \beta_{0i} + \beta_{1i} I_j + \beta_{2i} T(I_j) + \sigma_{ij} + \varepsilon_{ij}$$

where Y_{ij} is the average grain yield of genotype i in location j; I_j is the environmental index; $T(I_j) = 0$ if $I_j < 0$, $T(I_j) = I_j - I_+$ if $I_j > 0$, where I_+ is the mean of the positive I_j indexes; β_{0i} is the general mean of genotype i; β_{1i} is the coefficient of the linear regression associated with I_j; β_{2i} is the coefficient of linear regression associated with $T(I_j)$; σ_{ij} is the deviation of the linear regression; and ε_{ij} is the experimental error. These analyses were performed using Genes software [37].

3. Results

The combined analysis of variance across WW and DS environments showed highly significant differences among genotypes for GY, PH, AD, GLS, and NCLB. The proportion of genotype to GE variance was higher for WW than for DS, indicating that GE interaction was greater under drought stress than under optimum-moisture conditions. Genotypic variance for GY for early- and intermediate-maturing hybrid trials was 137%–150% higher under WW than under DS conditions. Broad-sense heritability estimates for GY were slightly higher under WW (0.92 for both maturity groups) than under DS (0.73–0.75) conditions (Table 2).

3.1. Hybrid performance

In the early-maturing hybrids evaluated across 23 WW locations (hereafter referred to as Early WW), GY ranged from 4.13 (E53, commercial check) to 7.01 t ha^{-1} (E11, experimental hybrid). In the Early WW, the top 10 hybrids produced a mean grain yield of 6.67 t ha^{-1}, representing an addition of 2.04 t ha^{-1} compared to the mean of commercial checks, and 1.74 t ha^{-1} compared to the best commercial check (E55 with 4.93 t ha^{-1}). The top 10 hybrids on average showed 10 cm increase in PH compared to the mean of the commercial checks. However, there was no difference between the top 10 hybrids and the commercial checks in AD and in their responses to the two main foliar diseases, GLS and NCLB (Table 3).

In combined analyses across seven drought stress locations (hereafter referred to as Early DS), mean GY ranged from as low as 1.75 (E51, commercial check) to as high as 4.31 t ha^{-1} (E14, experimental hybrid). Among early-maturing hybrids, the top 10 hybrids produced 46.8%–73.9% higher mean GY than the best commercial check under drought stress. In Early DS, the mean

Table 2 – Estimation of variance components and heritability for grain yield (GY), plant height (PH), days to anthesis (AD), gray leaf spot (GLS) and northern corn leaf blight (NCLB) in early- and intermediate-maturity trials under WW and DS conditions.

Statistics	Well-watered conditions (Early WW)					Drought stress conditions (Early DS)				
	GY	PH	AD	GLS	NCLB	GY	PH	AD	GLS	NCLB
Early-maturity trials										
Broad-sense heritability	0.92	0.97	0.93	0.00	0.32	0.75	0.91	0.88	0.50	0.64
Genotype variance	0.55	204.36	2.65	0.00	0.02	0.22	222.35	3.52	0.03	0.08
Genotype × location variance	0.50	41.89	2.05	0.14	0.18	0.21	0.00	1.36	0.05	0.09
Residual variance	1.21	161.95	2.45	0.12	0.20	0.59	168.73	4.03	0.10	0.17
LSD	0.63	7.05	1.17	0.31	0.33	0.79	13.96	2.04	0.35	0.50
CV	18.61	5.67	2.32	17.48	18.79	24.22	5.87	2.91	24.32	16.18
Intermediate maturity trials										
Broad-sense heritability	0.92	0.96	0.95	0.31	0.66	0.73	0.79	0.87	0.13	0.47
Genotype variance	0.45	124.27	3.41	0.01	0.03	0.19	141.60	2.43	0.01	0.03
Genotype × location variance	0.35	28.49	1.74	0.08	0.06	0.16	0.00	0.71	0.04	0.00
Residual variance	1.04	180.49	3.41	0.13	0.12	0.53	219.94	3.07	0.07	0.15
LSD	0.57	6.34	0.90	0.31	0.18	0.78	18.35	1.80	0.38	0.43
CV	16.99	5.78	2.58	17.45	17.53	26.49	7.26	2.48	22.16	16.94

Table 3 – Grain yield (GY), plant height (PH), days to anthesis (AD), gray leaf spot (GLS), and northern corn leaf blight (NCLB) trait values of the top 10 hybrids relative to commercial checks in early-maturity trials (Early WW and Early DS).

Hybrids (top 10)	No.	Well-watered conditions (Early WW)					Hybrids (top 10)	No.	Drought stress conditions (Early DS)				
		GY (t ha^{-1})	PH (cm)	AD (days)	GLS (1–5 score)	NCLB (1–5 score)			GY (t ha^{-1})	PH (cm)	AD (days)	GLS (1–5 score)	NCLB (1–5 score)
CKDHH170002	E11	7.01	237	67.9	2.02	2.15	CKDHH170028	E14	4.31	236	69.5	0.99	2.39
CKDHH170048	E23	6.85	239	67.7	1.98	2.75	CKDHH170148	E35	4.04	237	69.9	1.30	2.81
CKDHH170028	E14	6.84	239	67.8	1.97	2.55	WM5126	E2	4.00	189	67.7	1.07	2.43
CKDHH170029	E15	6.82	250	68.2	2.00	2.46	WM5312	E8	3.86	210	68.5	1.33	2.12
WM5126	E2	6.67	200	65.9	2.05	2.15	CKDHH170150	E37	3.85	242	69.6	1.14	2.63
CKDH160004	E41	6.53	235	68.0	1.98	2.21	WM5307	E4	3.68	212	70.9	1.10	2.13
CKDHH170075	E31	6.51	238	66.9	2.03	2.30	CKDHH170149	E36	3.68	225	70.8	1.42	2.44
CKDHH170027	E13	6.50	235	67.7	1.99	2.47	CKDHH170146	E33	3.68	238	69.8	1.03	2.45
WM5307	E4	6.48	211	69.2	1.82	2.21	CKDHH170029	E15	3.65	244	70.0	1.04	2.38
CKDHH170071	E27	6.47	248	69.4	1.96	2.66	CKDHH170145	E32	3.64	235	70.9	1.13	2.80
Mean of top 10 hybrids		6.67	233.30	67.86	1.98	2.39	Mean of top 10 hybrids		3.84	226.84	69.76	1.15	2.46
Checks							Checks						
Local check	E55	4.96	231	69.1	1.87	2.24	Local check	E55	3.31	232	71.8	1.14	1.80
Duma 43	E52	4.93	228	64.3	2.17	2.20	Duma 43	E52	2.52	232	65.8	1.18	2.44
PAN4M-19	E54	4.84	209	66.2	2.14	2.71	PAN4M-19	E54	2.48	205	66.8	1.55	2.82
DH04	E51	4.29	222	68.4	2.10	2.49	DK 8031	E53	2.04	228	69.8	0.99	2.12
DK 8031	E53	4.13	221	67.2	2.09	2.29	DH04	E51	1.75	225	69.8	1.21	3.19
Mean of checks		4.63	222.23	67.04	2.07	2.39	Mean of checks		2.42	224.63	68.80	1.21	2.47
Overall trial mean		5.90	224.37	67.52	2.01	2.40	Overall trial mean		3.18	221.24	68.95	1.27	2.54

grain yield of the top 10 hybrids was 3.84 t ha^{-1}, representing an increase of 1.42 t ha^{-1} over the mean of checks (increase of 59%) and 1.32 t ha^{-1} (52.4%) over the best check (E52). The hybrids did not show significant differences in other traits (Table 3).

In the intermediate-maturing hybrids evaluated across 24 WW locations (hereafter referred to as Intermediate WW), the mean GY of the top 10 hybrids was 6.70 t ha^{-1}, representing an increase of 0.7 t ha^{-1} over the overall mean of the trial and

Table 4 – Grain yield (GY), plant height (PH), days to anthesis (AD), gray leaf spot (GLS) and northern corn leaf blight (NCLB) trait values of the top 10 hybrids relative to commercial checks in intermediate-maturity trials (Intermediate WW and Intermediate DS).

Hybrids (top 10)	No.	Well-watered conditions (Intermediate WW)					Hybrids (top 10)	No.	Drought stress conditions (Intermediate DS)				
		GY (t ha^{-1})	PH (cm)	AD (days)	GLS (1–5 score)	NCLB (1–5 score)			GY (t ha^{-1})	PH (cm)	AD (days)	GLS (1–5 score)	NCLB (1–5 score)
CKH160125	I53	6.82	236	74.7	2.24	1.79	WM5330	I2	3.81	197	70.8	2.24	1.75
CKH160101	I49	6.80	245	73.8	2.19	1.82	CKDHH170059	I41	3.74	229	69.2	0.99	2.06
CKDHH170018	I21	6.79	243	71.1	1.95	2.04	CKDHH170018	I21	3.74	220	69.5	1.26	2.42
CKDHH170021	I23	6.73	233	71.3	1.90	2.02	CKDHH170032	I27	3.55	210	68.4	1.12	2.22
CKDHH170054	I38	6.71	243	71.7	1.78	2.09	WM5404	I7	3.50	178	68.8	1.51	2.15
CKDHH170013	I18	6.70	230	71.0	1.91	2.04	WM5460	I4	3.45	200	68.8	1.37	2.46
CKDHH170049	I35	6.69	244	70.9	2.00	1.66	WM5310	I10	3.43	195	69.5	1.01	2.47
WM5497	I3	6.66	218	71.1	2.40	2.39	CKDHH170011	I17	3.34	203	70.3	0.99	2.48
CKDHH170059	I41	6.57	255	70.5	2.00	1.90	WM5465	I1	3.28	193	68.1	1.37	2.18
CKDHH170008	I15	6.52	240	72.8	2.07	2.11	WM5497	I3	3.23	194	70.6	1.38	2.34
Mean of top 10 hybrids		6.70	238.86	71.89	2.04	1.99	Mean of top 10 hybrids		3.51	202.03	69.42	1.33	2.25
Checks							Checks						
WE3106	I60	6.61	243	72.8	1.92	1.97	WE3106	I60	3.05	223	72.2	1.13	2.49
WE1101	I59	6.34	231	70.6	2.15	1.87	WH505	I63	3.02	224	72.0	1.12	2.20
CKH10717	I61	6.28	230	72.3	2.13	1.79	WE1101	I59	2.78	198	70.0	1.12	1.75
P30G19	I64	6.01	240	70.6	1.97	1.61	P30G19	I64	2.70	219	69.5	1.00	2.43
WH505	I63	5.98	245	73.6	1.85	1.86	CKH10717	I61	2.61	199	71.2	1.36	2.30
Local check	I65	5.60	238	72.5	2.10	2.08	Local check	I65	2.03	199	73.1	1.00	2.01
H516	I62	5.15	251	73.5	2.13	1.92	H516	I62	1.86	223	72.8	1.13	2.24
Mean of checks		6.00	239.85	72.28	2.03	1.87	Mean of checks		2.58	212.29	71.55	1.12	2.20
Overall trial mean		6.02	232.63	71.55	2.05	1.99	Overall trial mean		2.75	204.39	70.80	1.18	2.26

checks (Table 4). In combination across six DS locations (hereafter, Intermediate DS), the top 10 hybrids produced a mean of 3.51 t ha^{-1}, which was 0.76 t ha^{-1} higher than the overall mean and 0.93 t ha^{-1} (36%) higher than the mean of checks. Among the intermediate-maturing hybrids, the top 10 hybrids produced 8.5%–13.5% higher yield than the commercial checks under WW conditions, while the top 10 hybrids under DS yielded 25.2%–47.7% more than the commercial checks.

3.2. Suitability of locations for selecting hybrids according to the GGE biplot method

Fig. 1 shows the discriminativeness and representativeness of testing locations according to the GGE biplot method for the early- and intermediate-maturing hybrids evaluated under WW and DS locations (Early WW, Early DS, Intermediate WW, and Intermediate DS). The first two components in these

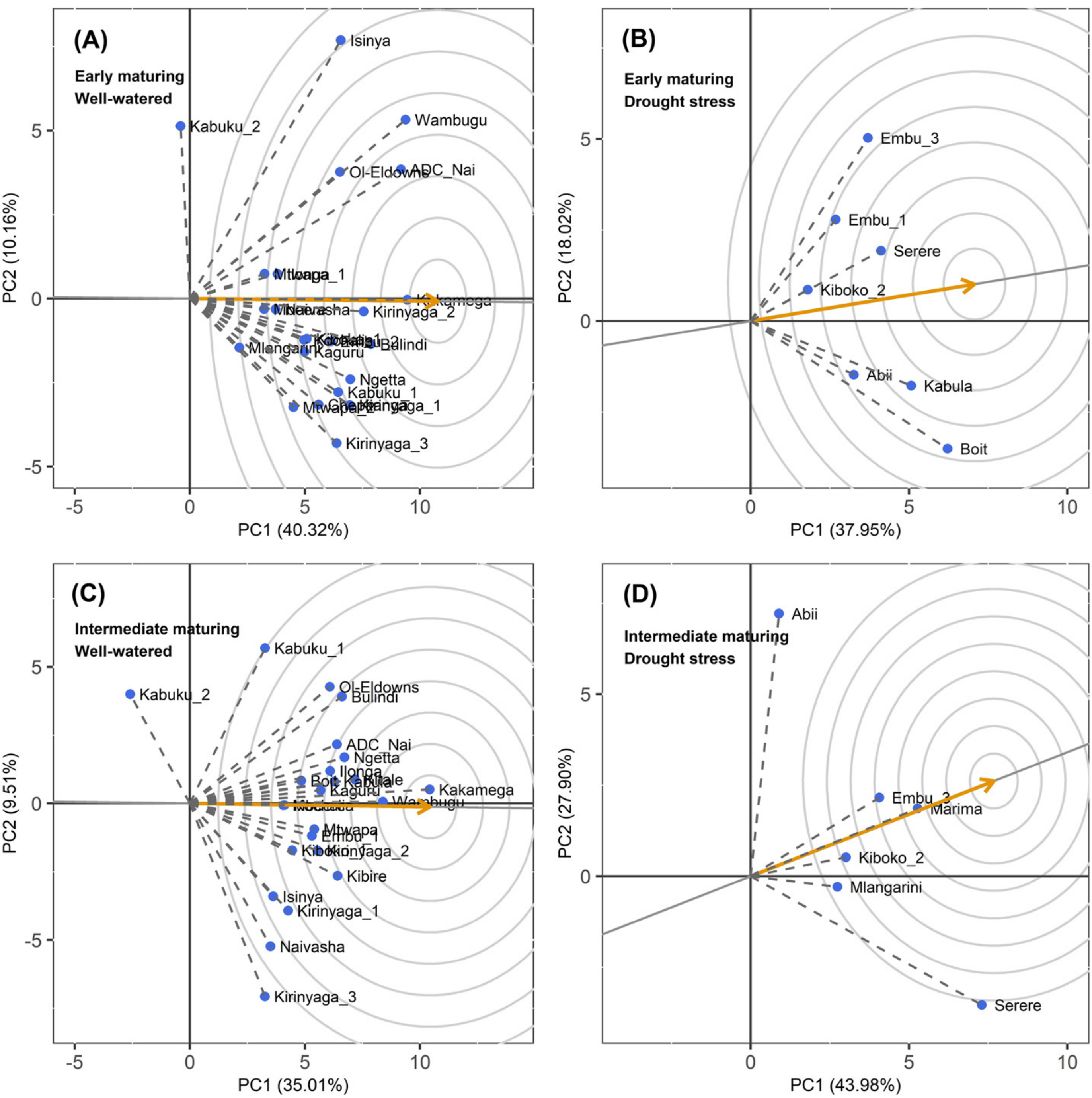

Fig. 1 – Discriminativeness and representativeness of test environments according to the GGE biplot method for maize trials in eastern Africa. (A) Early-maturity hybrids in well-watered conditions. (B) Early-maturity hybrids in drought stress conditions. (C) Intermediate-maturity hybrids in well-watered conditions. (D) Intermediate-maturity hybrids in drought stress conditions.

biplots accounted for between 44.52% and 71.88% of total variation, depending on the trial.

In the Early WW trial, Wambugu, Isinya, ADC Nai, and Kakamega locations show longer vectors than other locations, indicating that they were the most informative locations for genetic differentiation of the hybrids. The least discriminatory locations were Mlangarini, Mbeere, Naivasha, and Mtwapa, as they show short environment vectors (Fig. 1A). Kakamega and Kirinyaga 2 were the most representative locations, as they show smaller angles with the Average-Environment Axis (AEA; Fig. 1A). Overall, Kakamega, Kirinyaga 2, and Bulindi were the ideal testing locations for evaluating hybrids, as they show long environmental vectors (informativeness) and small angle with AEA (representativeness). In contrast, Kabuku 2 was the least suitable environment for selecting hybrids, given that it shows a large angle with AEA (indicating less representativeness).

In the Early DS trials, Embu 3, Boit, and Kabula were the most informative locations, as they show long environmental vectors, and Serere and Kiboko 2 were the most representative as they show small angles with AEA (Fig. 1B). In this trial, Serere and Kabula were closest to the ideal location to assess the hybrids, as they show longer environmental vectors (indicating informativeness) and small angle with AEA (indicating representativeness). The suitability for selecting hybrids in the other locations was similar.

In the Intermediate WW trial, the most informative locations were Kakamega, Wambugu, Kirinyaga 3, Bulindi, and Ol-Eldowns, as they show long environmental vectors. The most representative locations were Wambugu, Kochalia, Mbeere, and Kakamega, as they show very small angles with AEA (Fig. 1C). In this trial, Wambugu and Kakamega were the ideal locations for evaluating the hybrids for high yield potential under well-watered conditions, because they show very high discriminatory ability (long environmental vectors) and representativeness (low angle with AEA). In contrast, Kabuku 2, Kabuku 1, and Kirinyaga 3 were the least suitable for selecting hybrids in this trial, as they show very low representativeness.

In the Intermediate DS trials, the most informative locations were Serere and Abii (Fig. 1D). In this trial, Marima was the best location for assessing the hybrids for tolerance to drought stress because it showed good discriminativeness and high representativeness. Abii and Serere were the least suitable for selecting hybrids because they showed very low representativeness. Considering all WW trials, Kakamega was the best location for selecting maize hybrids for yield owing to its both high discriminativeness and high representativeness in Early WW and Intermediate WW trials. In these trials, Kabuku 2 showed very low representativeness.

3.3. Stability of hybrids according to the GGE biplot method

Fig. 2 shows that high variation was found in mean GY and stability across environments. The GGE biplot shows that 60% of the early maturing hybrids displayed above-average performance across WW locations (Fig. 2A). Hybrids E23, E15, and E12 were closest to the ideal genotype in the Early WW trial (Fig. 2A). Although E11 was very high-yielding (7.01 t ha^{-1}; Table 2), its behavior was very unstable (located far from 0 for principal component 2). Thus, it was far from the ideal genotype. Although E12 (with a yield of 6.39 t ha^{-1}) was not ranked among the 10 highest-yielding hybrids (6.47–7.01 t ha^{-1}), it had grain yield similar to those of the 10 highest-yielding hybrids and showed very high stability (close to 0 for principal component 2). All commercial checks (E51, E52, E53, E54, and E55) showed negative PC1 scores, implying that these hybrids had below-average performance across WW locations.

In the Early DS trial, E4, E37, and E2 were closest to the ideal genotype (Fig. 2B). These hybrids were also among the top 10 performing hybrids for grain yield under DS conditions (Table 2). Hybrids E51, E52, E53, and E54 (commercial checks) had negative PC1 scores, implying that these hybrids had below-average performance across DS locations.

In the Intermediate WW trial, the GGE biplot identified I8, I35, and I15 to be close to the ideal genotypes (Fig. 2C). The three hybrids were also among the top-performing hybrids across the 24 WW locations (Table 4). Two of the commercial checks (I62 and I65) had negative PC1 scores, suggesting below-average performance across the 24 WW locations. In the Intermediate DS trial, the closest hybrids to the ideal genotype were I41, I21, I7, I10, and I4 (Fig. 2D). All the five hybrids were also among the best-performing for GY across DS locations. Four of the commercial hybrids (I61, I62, I64 and I65) were below-average performers, as they had negative PC1 scores.

3.4. Stability of hybrids according to the Cruz et al. [24] method

According to the bi-segmented regression method, there were 12 favorable locations in early-maturity trials (I_+; locations where the mean yield was higher than the overall mean yield), all of which were WW (data not shown). Also, there were 18 unfavorable locations (I-; locations where the mean yield was lower than the overall mean yield), of which 11 were WW and seven were in DS conditions.

In the early-maturity trials, the best hybrids were E2 and E14 (Table 5). The hybrid E14 showed high mean yields in both unfavorable and favorable locations, good adaptability to unfavorable locations ($\beta_1 = 1$), excellent adaptability to favorable locations ($\beta_1 + \beta_2 > 1$), and high stability ($\sigma^2_{di} = 0$). Hybrid E2 showed a high mean yield in both unfavorable and favorable locations, good adaptability in both unfavorable ($\beta_1 = 1$) and favorable locations ($\beta_1 + \beta_2 = 1$), and high stability ($\sigma^2_{di} = 0$). In contrast, hybrids E11 and E15 produced high mean yield but were unstable.

In the intermediate-maturity trials, there were 14 favorable locations, all of which were WW (data not shown). Also, there were 16 unfavorable locations, of which 10 were WW and six were DS. In these trials, the best genotypes were I21, I35, and I41, showing high mean yield in both unfavorable and favorable locations, good adaptability in both unfavorable ($\beta_1 = 1$) and favorable locations ($\beta_1 + \beta_2 = 1$), and high stability ($\sigma^2_{di} = 0$). Hybrid I47, identified by the GGE biplot method as one of the best hybrids, showed good values of adaptability ($\beta_1 = 1$ and $\beta_1 + \beta_2 > 1$) and stability ($\sigma^2_{di} = 0$) according to the Cruz et al. method (data not shown), but its yield (5.73 t ha^{-1}) was not very high. For this reason, it was not listed as one of the best by this method.

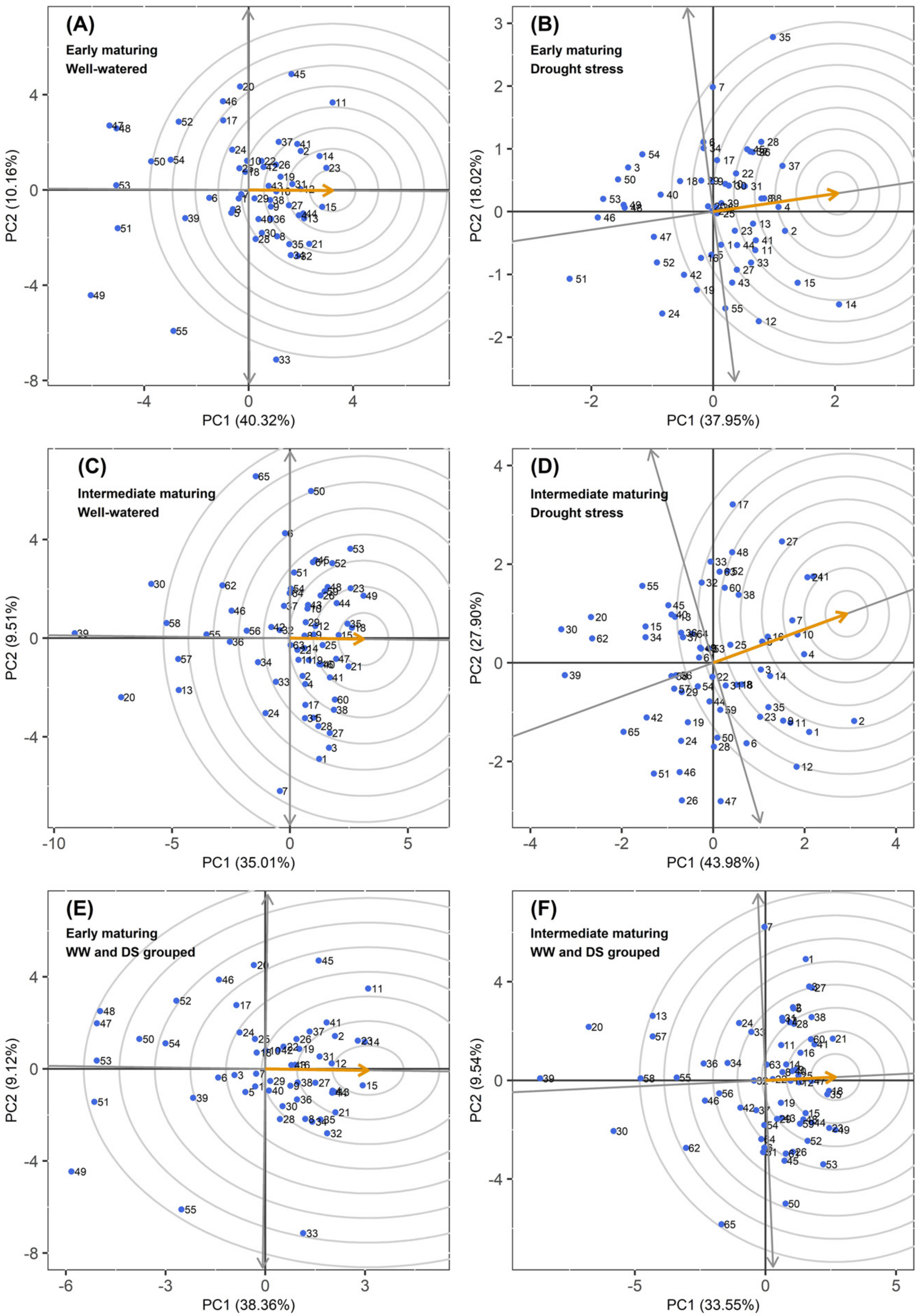
(A)
Early maturing
Well-watered
PC1 (40.32%)
PC2 (10.16%)
(B)
Early maturing
Drought stress
PC1 (37.95%)
PC2 (18.02%)
(C)
Intermediate maturing
Well-watered
PC1 (35.01%)
PC2 (9.51%)
(D)
Intermediate maturing
Drought stress
PC1 (43.98%)
PC2 (27.90%)
(E)
Early maturing
WW and DS grouped
PC1 (38.36%)
PC2 (9.12%)
(F)
Intermediate maturing
WW and DS grouped
PC1 (33.55%)
PC2 (9.54%)

Table 5 – Parameters of adaptability and stability, according to a bi-segmented regression method, of the 10 highest-ranking maize hybrids (top 10) in terms of yield in all early-maturity trials and in all intermediate-maturity trials.

Hybrids (top 10)	No.	Mean GY (t ha^{-1})			β_1	$\beta_1 + \beta_2$	σ^2_{di}	R^2 (%)
		Overall	*I*-	I_+				
Early maturity								
CKDHH170028	E14	6.21	5.03	7.99	1.03^{ns}	1.94*	1.03^{ns}	88.94
CKDHH170002	E11	6.12	4.59	8.41	1.29*	1.99*	2.26*	83.91
WM5126	E2	6.08	4.92	7.83	0.99^{ns}	1.40^{ns}	1.90^{ns}	77.71
CKDHH170029	E15	6.08	4.90	7.84	1.11^{ns}	0.95^{ns}	2.81*	72.37
CKDHH170048	E23	6.00	4.57	8.16	1.24*	1.05^{ns}	1.56^{ns}	85.42
CKDH160004	E41	5.84	4.42	7.99	1.17^{ns}	1.53^{ns}	2.09^{ns}	81.28
CKDHH170148	E35	5.84	4.55	7.78	0.98^{ns}	0.03*	3.95*	57.03
WM5307	E4	5.84	4.42	7.96	1.16^{ns}	1.18^{ns}	2.39*	77.72
CKDHH170145	E32	5.83	4.65	7.59	0.99^{ns}	0.63^{ns}	1.36^{ns}	80.54
CKDHH170075	E31	5.80	4.61	7.58	1.04^{ns}	0.99^{ns}	1.64^{ns}	79.99
Intermediate maturity								
CKH160125	I53	6.14	4.62	7.88	1.16^{ns}	1.25^{ns}	2.42*	81.82
CKDHH170018	I21	6.03	5.01	7.19	0.82^{ns}	1.25^{ns}	1.78^{ns}	78.69
CKDHH170049	I35	5.98	4.69	7.47	0.98^{ns}	1.02^{ns}	1.68^{ns}	81.83
CKDHH170059	I41	5.98	4.71	7.42	0.92^{ns}	1.31^{ns}	1.25^{ns}	86.32
CKH160101	I49	5.97	4.40	7.78	1.22*	1.13^{ns}	2.73*	80.61
CKDHH170054	I38	5.93	4.55	7.49	1.03^{ns}	0.84^{ns}	2.09^{ns}	78.75
CKDHH170013	I18	5.89	4.13	7.91	1.21*	1.22^{ns}	1.68^{ns}	87.21
WE3106	I60	5.88	4.65	7.29	0.99^{ns}	1.19^{ns}	1.90^{ns}	81.32
WM5497	I3	5.86	4.40	7.53	1.02^{ns}	1.11^{ns}	2.54*	76.72
CKDHH170021	I23	5.86	4.49	7.42	1.02^{ns}	1.27^{ns}	1.48^{ns}	85.92

I-, mean of the unfavorable locations for each hybrid; I_+, mean of the favorable locations for each hybrid; *, significant difference of one for β_1 and $\beta_1 + \beta_2$ and of zero for σ^2_{di} by *t*-test at $P < 0.05$. ^{ns}, not significant by the same tests.

4. Discussion

Identification of high yielding and stable performance of maize hybrids in multi-environment trials is crucial for success of commercial hybrids in the stress-prone agro-ecologies of eastern Africa. The average GY of the top 10 hybrids was higher than those of all commercial checks in all trials. Among the early-maturing hybrids, the top 10 hybrids produced 46.8%–73.9% and 31.2%–42.1% higher mean GY than the best commercial check under DS and WW conditions, respectively. Among the intermediate-maturing hybrids, the top 10 hybrids produced 25.2%–47.7% and 8.5%–13.5% higher grain yields than the best commercial check under DS and WW conditions, respectively. These results are consistent with previous results in studies [7,38,39] conducted to develop DT maize varieties suitable for eastern Africa.

The means of the top 10 experimental hybrids across DS locations were respectively 3.84 and 3.51 t ha^{-1} among early- and intermediate-maturing hybrid trials. Although most of the data were obtained from researcher-managed trials, these yields were high for eastern Africa, where the mean grain yield under farmer management conditions is only 1.75 t ha^{-1} [2]. In our study, DS reduced yield by 46% in early-maturing and by 54% in intermediate-maturing hybrids. These results are within the ranges of 58%–76% decrease previously reported in maize by Beyene et al. [38] and Cairns et al. [40], but much higher than the 11% decrease reported by Sserumaga et al. [39], under DS conditions.

The wide variation in grain yield decrease under drought stress could be attributed to varying levels of drought tolerance in the experimental hybrids, the crop growth stage at which drought stress occurred, and the severity and duration of the drought stress [10,11]. Edmeades et al. [41] reported that the phenotypic correlation between elite hybrid yields under drought stress versus under WW conditions declined when yield reductions reached 50%. They suggested that drought stress-adaptive mechanisms were not expressed until yields had been reduced by 30%–50% under stress compared to WW conditions. In our study, mean grain yields of early-maturing and intermediate-maturing trials under DS were reduced to 46%–56% of mean yields of hybrids under WW conditions, in the same range of yield reduction indicated by Edmeades et al. Thus, the top 10 hybrids identified in the present study may carry some adaptive traits

Fig. 2 – Ranking of hybrids relative to the ideal hybrid based on their mean and stability according to the GGE biplot method for maize trials in eastern Africa. (A) Early-maturity hybrids in well-watered (WW) conditions. (B) Early-maturity hybrids in drought stress (DS) conditions. (C) Intermediate-maturity hybrids in WW conditions. (D) Intermediate-maturity hybrids in DS conditions. (E) Early-maturity hybrids in all locations (WW and DS conditions). (F) Intermediate-maturity hybrids in all locations (WW and DS conditions).

for drought tolerance and some or all of their parental lines might be used in maize breeding programs in eastern Africa as sources of drought tolerance.

The mean GYs for early- and intermediate-maturing hybrids were similar under WW but different under DS conditions. The mean GY in the Intermediate DS trial was 2.57 t ha^{-1}, lower than that in the Early DS trial (3.18 t ha^{-1}) indicating that intermediate-maturity hybrids were more adversely affected by drought stress.

Heritabilities of GY in early- and intermediate-maturing hybrids were lower in DS than in WW conditions (Tables 2, 3). These results are consistent with those reported from previous studies in maize [7,39]. The lower heritability of GY in our drought stress trials indicates that secondary traits (minimum anthesis-silking interval (ASI)) with higher heritability can improve selection response [42].

In a maize breeding program, most efforts are spent on evaluating inbred lines by crossing them to a tester and extensively evaluating them in replicated multi-location trials. It is, therefore, important to identify differences in discriminativeness and representativeness among test environments. In the WW trials, the best and worst locations for selecting the hybrids were similar between early-and intermediate-maturity hybrids. For WW locations, Kakamega was the best location and Kabuku the least suitable. However, considering all DS trials, the best locations were highly dependent on the hybrid maturity. For example, Serere was one of the best locations in the Early DS trial but one of the poorest in the Intermediate DS trial (Fig. 1). Most of the highly informative locations (Embu 3 in Early DS and Abii and Serere in Intermediate DS) were also the least representative. This result demonstrates the difficulty in selecting the best locations for drought screening trials. Similar observations led CIMMYT to develop the concept of managed drought stress testing in SSA [43].

In this study, the GGE biplot clearly identified hybrids adapted to WW, to DS, and to both conditions. For example, hybrid E12 (early maturing), and hybrid I15 (intermediate maturing) were high-yielding and well-adapted in WW locations, while hybrid E37 (early maturing) and hybrid I7 (intermediate maturing) were high-yielding and stable in DS locations. High mean yields and stability under DS conditions are important selection criterion for ensuring good harvests in eastern Africa [5,44,45].

Crop production in SSA is mostly rain-dependent, and grain production is vulnerable to the fluctuation of rainfall amount, distribution, and duration. It is accordingly important to develop hybrids that can withstand DS throughout the growing season but especially during flowering stage, but that suffer no yield penalty under optimum moisture conditions. Maize hybrids with these characteristics would contribute to greater food security and reduced risk to farming communities in drought-prone agro-ecologies of SSA. According to the GGE biplot, some hybrids with these characteristics were found in combined trial analyses (Fig. 1E, F). They include the early-maturity hybrid E14 and the intermediate-maturity hybrid I35.

A bi-segmented regression method can be used for identifying suitable genotypes in studies with both WW and DS conditions. This method can identify hybrids that are stable and well-adapted simultaneously to WW and DS conditions. This ideal and stable genotype should have high β_0 (high mean yield), σ^2_{di} = 0, (high stability), $\beta_1 < 1$ (adaptability to unfavorable environments) and $\beta_1 + \beta_2 > 1$ (adaptability to favorable environments) [24,29]. Genotypes close to the ideal genotype were found, and included, in early-maturity trials, E14, which showed high overall yield (6.21 t ha^{-1}), high stability (σ^2_{di} = 0), high responsiveness in favorable conditions ($\beta_1 + \beta_2 > 1$), and medium responsiveness in unfavorable conditions ($\beta_1 = 1$). The bi-segmented regression method makes it more laborious than the GGE biplot method to identify the best genotypes owing to its large number of parameters, but allows for more details in the genotype analysis. For this reason, the Cruz et al. [24] method, unlike the GGE biplot, allowed the observation that the early maturing hybrid E2 is a good genotype for a wide range of environments. This is because it showed high yield, high stability, and responsive in both unfavorable and favorable conditions (β_1 and $\beta_1 + \beta_2 = 1$). Although E2 was not classified by the GGE biplot as one of the best genotypes, it was reasonably close to the ideal genotype in the biplot (the center of the concentric circle in the plot in Fig. 2E).

The genotypes E12 and I47 were well classified by the GGE biplot method into early and intermediate maturities, respectively, though they did not appear in the top 10 highest-yielding hybrids and had not performed well in DS trials. They were classified by the GGE biplot in combined analyses because there were more WW locations than DS locations. For this reason, the WW locations had more influence on the choice. Although these genotypes were stable, they were not assigned to the best genotypes by the Cruz et al. method, owing to their low yields.

The use of complementary statistics to study the stability of genotypes can increase confidence in the selection process in plant breeding [30]. Silva et al. [46] reported a low correlation between a bi-segmented regression method and AMMI, a multivariate method that is like the GGE biplot method. However, a bi-segmented regression method and the GGE biplot offer different advantages. A bi-segmented regression method has adaptability parameters (β_1 and $\beta_1 + \beta_2$) to assess genotype responsiveness to environmental differences. The GGE biplot method considers only the relevant variation sources in the GE interaction study, namely genotype (G) and GE interaction, and assesses simultaneously the genotypes (mean and stability) and the test environments (discriminativeness and representativeness) [20]. For this reason, the GGE biplot and a bi-segmented regression method can be considered complementary methods. In the present study, using both methods it was possible to identify confidently the early-maturity hybrids E14 (CKDHH170028), E2 (WM5126), and E23 (CKDHH170048) and the intermediate-maturity hybrids I35 (CKDHH170049), I18 (CKDHH170013), I21 (CKDHH170018), and I41 (CKDHH170059) as being well adapted to both WW and DS conditions.

5. Conclusions

We have identified the early-maturity hybrids E14 (CKDHH170028), E2 (WM5126), and E23 (CKDHH170048) and the intermediate-maturity hybrids I35 (CKDHH170049), I18 (CKDHH170013), I21 (CKDHH170018), and I41 (CKDHH170059) as being well adapted to both well-watered and drought stress conditions. They can be recommended for commercial production in diverse agro-ecologies of eastern Africa. We have also identified discriminative and representative testing locations that will facilitate allocating resources and streamlining the CIMMYT maize hybrid testing program in eastern Africa.

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