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Hybrids performance of doubled haploid lines derived from 10 tropical bi-parental maize populations evaluated in contrasting environments in Kenya

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The doubled haploid (DH) technology enables maize breeders to develop a large number of homozygous lines rapidly and test them in hybrid combinations early in the breeding cycle. The objectives of this study were to evaluate testcross performance of 556 DH lines derived from 10 diverse tropical backcross (BC$_1$) populations, and to estimate variance components and broad-sense heritability under both well-watered and managed drought-stress conditions in Kenya. The 556 DH testcrosses were divided into six trials, with each trial comprising 84 to 126 entries and six commercial checks developed through conventional pedigree method. Trials were evaluated at 3 or 4 well-watered (WW) and two managed drought-stress (WS) sites in 2012 using an alpha lattice design with three replications per environment. Test crosses of the DH lines showed significant differences in grain yield and other agronomic traits. In the combined analysis across the WW locations, the top 10 DH testcrosses from each trial gave 0.6 to 32.7% higher grain yield than the best commercial check. Under managed drought-stress condition, the top 10 DH testcrosses from each trial gave 11.8 to 40.9% more grain yield than the best check. The best DH lines identified in the study could be used in tropical maize breeding programs in Africa for improving grain yield and drought-tolerance. Following evaluation in advanced testing and national performance trials (NPT), a total of 36 hybrids involving DH lines from this study were recommended for commercial cultivation in east and southern Africa.

Key words: Africa, heritability, managed drought-stress, testcrosses.

INTRODUCTION

Maize is among the most important food crops in the world. Together with rice and wheat, maize provides at least 30% of the food calories to more than 4.5 billion people in 94 developing countries (Shiferaw et al., 2011). As compared to other regions, maize yield variability in sub-Saharan African (SSA) countries is extremely high,

even though maize is the most important staple food for over 300 million people in the region. For example, between 2005 and 2008, the average maize yield was estimated at 1.8 tons per hectare (t/ha) as compared to 2.5 t/ha in the Philippines, 3.1 t/ha in Mexico and 3.9 t/ha in Thailand (Smale et al., 2011). Although, several factors could contribute to this low production, drought has been cited as one of the major factors that frequently limits maize production in SSA. Heisey and Edmeades (1999) estimated that 20 to 25% of the global maize production area is affected by drought in any given year.

Breeding maize for drought tolerance has been a major thrust of International Maize and Improvement Center (CIMMYT) and the International Institute for Tropical Agriculture (IITA) to help attain food security in SSA (Monneveux et al., 2006). Since 2007, over 200 drought-tolerant hybrids and improved open-pollinated varieties (OPVs) of maize have been released in several African countries within the framework of the Drought Tolerant Maize for Africa project (DTMA, 2015). Inbred lines with superior breeding values for yield, and tolerance to abiotic stresses have been used as parental lines to develop high-yielding and drought-tolerant hybrids (Dhliwayo et al., 2009; Beyene et al., 2013). Recently, CIMMYT in collaboration with public and private partner, have undertaken substantial marker assisted recurrent selection (MARS) and genomic selection (GS) projects to develop stress-resilient tropical maize germplasm for sub-Saharan Africa (Beyene et al., 2015, 2016).

Doubled haploid (DH) technology is now being increasingly used in maize breeding at CIMMYT to increase breeding efficiency and genetic gains (Prasanna et al., 2012). Improvement of *in vivo* haploid induction by specific pollinators (tropicalized haploid inducers) has made it possible to produce large numbers of DH lines in Africa-adapted source populations. The use of doubled haploids has several advantages over inbred lines developed through inbreeding, as outlined by Geiger and Gordillo (2009): (i) maximum genetic variance between lines for per se and testcross performance from the first generation; (ii) reduced breeding cycle length; (iii) perfect fulfillment of distinctness, uniformity and stability (DUS) criteria for variety protection; (iv) reduced expenses for selfing and maintenance breeding; (v) simplified logistics; and (vi) increased efficiency in marker-assisted selection, gene introgression, and stacking genes in lines. Currently, elite inbred lines developed through both pedigree breeding and DH methods are used by CIMMYT to develop improved maize hybrids in Africa.

Various studies have provided useful information on the performance of DH based hybrids in maize. Bordes et al. (2007) found that maize lines generated through DH were as good as those produced by single-seed descent (SSD) methods. Seitz (2005) compared testcross performance of DH lines with conventionally derived lines, and found similar variation. Wilde et al. (2010) reported that mean testcross performance of the three DH-line groups developed from three European landraces yielded 22 to 26% lower than that of present elite flint lines. However, Beyene et al. (2011) evaluated 70 DH based hybrids derived from tropical adapted backcross populations and reported that the top 10 DH hybrid produced 19.6 to 29.4% higher grain yield than the best commercial check. In another study, Beyene et al. (2013) further reported that the mean grain yield of the top 15 DH testcrosses was 1.3 to 2.2 t/ha higher than the mean of the commercial checks used in the study.

The Water Efficient Maize for Africa (WEMA) project is a public-private collaboration involving the African Agricultural Technology Foundation (AATF), Monsanto Company, the International Maize and Wheat Improvement Center (CIMMYT) and the National Agricultural Research Systems of Kenya, Mozambique, South Africa, Tanzania and Uganda. One of the components of the WEMA project is to effectively utilize DH technology to accelerate product development. Through the WEMA project, CIMMYT developed DH lines from several drought tolerant source populations (Beyene et al., 2013). The objectives of the present study were to evaluate testcross performance of 556 DH lines derived from 10 tropical backcross (BC_1) populations, and to estimate variance components and broad-sense heritability under both well-watered and managed drought-stress conditions.

MATERIALS AND METHODS

Genetic materials

DH lines were derived from BC_1F_1 of 10 tropical maize backcross populations (Table 1) by means of *in vivo* haploid induction at the Monsanto Company facility in Mexico, under the WEMA collaboration. The 10 source populations were obtained by crossing four drought tolerant (DT) donor lines with four recurrent parents (CML539, CML395, CML444 and CML488). Three of the DT donor lines were extracted from La Posta Seq C7, a drought-tolerant population developed at CIMMYT-Mexico through recurrent selection among full sib/S_1 families (Edmeades et al., 1999). The fourth donor parent was developed from M37W, a temperate high yielding line. The recurrent parents are elite Africa-adapted lines with good combining ability (Beyene et al., 2013). From each of the 10 source populations, 250 BC_1F_1 seeds were submitted for DH induction. A total of 895 DH lines were received from Monsanto. The DH lines were grown at the Kenya Agriculture and Livestock Research Organization (KALRO) Research Center at Kiboko, Kenya, during the 2009-2010 short rains season (October to January). Based on the results of *per se* evaluation (germination and good stand establishment, plant type, low ear placement, and well-filled ears) the best 686 DH lines were selected for testcross formation. Of these, 556 DH testcrosses were subsequently constituted and evaluated in yield trials (Table 1), representing 77% utilization of the original DH lines generated. Some of the testcrosses formed (19%) were not evaluated because of inadequate seed for field evaluation.

Testcross formation

Two nurseries were planted at KALRO-Kiboko Experimental Farm to form the three-way cross hybrids for yield testing. Each

Table 1. Details of the DH lines generated and evaluated from different tropical backcross source populations evaluated in the study.

Source population	Pedigree of the backcross population	DH lines generated	DH lines discarded based on *per se* evaluation (%)	DH lines used in testcross formation	DH lines evaluated in multi-location trials
1	La Posta Seq C7-F96-1-2-1-1-B-B-B/CML444//CML444	124	20	99	84
2	La Posta Seq C7-F96-1-2-1-1-B-B-B/CML488//CML488	47	26	35	32
3	La Posta Seq C7-F71-1-2-1-2-B-B-B/CML312SR //CML312SR	124	46	67	43
4	La Posta Seq C7-F71-1-2-1-2-B-B-B/CML395//CML395	181	18	149	126
5	La Posta Seq C7-F71-1-2-1-2-B-B-B/CML444//CML444	133	22	104	96
6	La Posta Seq C7-F71-1-2-1-2-B-B-B/CML488//CML488	48	27	35	33
7	CML395/[M37W/ZM607#bF37sr-2-3sr-6-2-X]-8-2-X-1-BB-B-xP84c1 F27-4-3-3-B-1-B] F29-1-2-2 x [KILIMA ST94A]-30/MSV-03-101-08-B-B-1xP84c1 F27-4-1-4-B-3-B] F2-1-2-1-1-1-B x CML486]-1-1/CML395	70	20	56	44
8	CML395/La Posta Seq C7-F102-1-3-1-2-B-B-B/CML395	19	26	14	12
9	CML488/La Posta Seq C7-F102-1-3-1-2-B-B-B/CML488	41	34	27	1
10	La Posta Seq C7-F96-1-2-1-1-B-B-B/CML395//CML395	108	7	100	85

backcross-derived DH line was crossed to one elite single-cross hybrid tester (CML312 × CML442 or CML395 × CML444) from an opposite heterotic group. Testcrosses were produced during the 2011 dry season (September to January). The testers used were widely used in hybrid formation for subtropical and mid-altitude environments, and are parents of several successful commercial maize hybrids in SSA (Beyene et al., 2013). The DH lines were used as the female parent, while the single-cross testers were used as pollinators. Each female was planted in five rows of 5 m length while the males were planted in two rows of 5 m length at two different times (-5 and 0 days) to achieve synchronization of flowering. Plots were overplanted and thinned to one seed per hill with a spacing of 0.75 x 0.25 m. Fertilizers were applied at the rate of 60 kg N and 60 kg P_2O_5 per ha at planting. Nitrogen was given in two split applications: at planting and at six weeks after emergence. At flowering, all the ears of female plants were covered with shoot bags. Pollen was collected and bulked from the male plants when 20% of the males started to shed pollen. Female plants that were free of diseases and other defects were pollinated to make maximum number of crosses within a plot. Seeds were harvested and bulked within each female row plot for use in the testcross evaluations.

Evaluation of testcrosses across well-watered and drought-stressed locations

The 556 DH testcrosses were divided into six trials, with each trial containing from 84 to 126 DH testcrosses and six commercial checks. Testcrosses were evaluated in 3-4 well-watered (WW) sites and two water-stressed (WS) sites in 2012 using alpha lattice designs with three replications. At WS sites, irrigation was withdrawn about two weeks before flowering and the trials did not receive any irrigation through harvest. In the well-watered experiments, supplemental irrigation was given as required to avoid moisture stress. At all locations, each entry was planted in two-row plots of 5 m long with rows spaced at 0.75 m between rows and 0.25 or 0.30 m between hills. Two seeds per hill were initially planted then thinned to one plant per hill 3 weeks after emergence to obtain a final plant population density of 53,333 plants per hectare. Fertilizers were applied at the rate of 60 kg N and 60 kg P_2O_5 per ha as recommended for the area. Nitrogen was given in two split-applications: at planting and six weeks after emergence. Hand-weeding was employed to effect proper weed control.

For each plot, a number of traits were recorded: days to silking, as the number of days from planting to when 50% of the plants had emerged silks, and days to anthesis, when 50% had shed pollen. Anthesis-silking interval was computed as the difference between days to silking and anthesis. Plant height was measured as the distance from the base of the plant to the height of the first tassel branch and ear height as the distance from the base to the node bearing the upper ear. In drought-stressed condition, ears were harvested from each plot and shelled to determine grain yield per hectare. In the well-watered experiments, harvested ears of each plot were weighed and the grain yield was estimated based on 800 g grain kg^{-1} ear weight and adjusted to 125 g kg^{-1} moisture content.

Data analysis

Analysis of variance (ANOVA) for all the recorded traits was done separately for each location, and combined across locations

Table 2. Performance of DH testcrosses evaluated under well-watered (WW) and water-stressed (WS) locations in Kenya.

Trial	Source Population	Number of WW locations	Number of WS locations	Mean GY under WW (t/ha)	Mean GY under WS (t/ha)	Mean AD under WW (days)	Mean AD under WS (days)	Mean PH under WW (cm)	Mean PH under WS (cm)	Heritability for GY under WW (WS)	Heritability for AD under WW (WS)	Heritability for PH under WW (WS)
1	Pop1	4	2	5.57	2.96	75.07	75.46	244.29	210.0	0.76(0.21)	0.84(0.78)	0.4(0.0)
2	Pop2 and 3	4	2	6.10	2.48	73.73	73.79	225.83	205.27	0.67(.039)	0.91(0.73)	0.75(0.75)
3	Pop4	4	2	5.71	2.69	76.94	74.79	223.16	215.11	0.62(0.29)	0.78(0.68)	0.18(0.76)
4	Pop5	3	2	5.82	2.94	77.66	76.72	223.20	202.47	0.75(0.51)	0.81(0.59)	0.35(0.45)
5	Pop6,7,8,9	4	2	5.57	3.05	74.67	74.14	230.42	214.43	0.80(0.38)	0.90(0.81)	0.83(0.84)
6	Pop10	4	2	5.79	2.16	73.98	73.60	233.03	197.17	0.82(0.51)	0.87(0.71)	0.75(0.67)

GY= Grain yield; PH = plant height; AD = anthesis date.

within well-watered and water-stressed environments using PROC MIXED procedure from SAS version 9.2 (SAS, 2009). Genotypes were considered as fixed effects, and replications and blocks within replications as random effects. For the combined analysis, variances were partitioned into relevant sources of variation to test for differences among genotypes and the presence of G × E interaction. Broad-sense heritability was calculated as the proportion of genetic variance over the total phenotypic variance. Heritability estimates refer to entry means across environments and replicates. Comparisons were made to compare the performance of all DH testcrosses and the top 10 DH testcrosses versus the best commercial check and the mean of commercial check within well-watered and water-stressed locations.

RESULTS

Analysis of variance

Results of the ANOVA combined across locations under water-stressed and well-watered conditions showed significant genotypic and genotype-by-environment interaction (GEI) mean squares (p < 0.01) for grain yield, anthesis date and plant height. Genotypic mean squares were significant (p < 0.01) for all traits under water-stressed and

well-watered conditions (data not shown).

Mean DH testcross performance under well-watered conditions

Mean grain yield averaged across WW locations varied from 5.57 (Trial 1) to 6.10 t ha^{-1} (Trial 2) with an overall mean of 5.76 t ha^{-1} (Table 2). The top 10 DH testcrosses in each trial were either similar (e.g. Trial 2) or gave 17.5 to 32.7% higher grain yield than the best commercial check; but they all performed better (28.1 to 54.8%) than the mean of the commercial checks (Table 3). The 10 highest yielding DH testcrosses in each trial showed a difference of -1.2 to 3.8 days to flowering as compared to the best commercial check and up to 4.4 days delay in anthesis as compared to the mean of the commercial checks (Table 3). For plant height, the mean of the of 10 highest yielding DH testcrosses from four trials (Trials 1, 3, 4 and 5) were 0.6 to 18 cm higher than the mean plant height of the best commercial check. In Trial 2, the 10 highest-yielding DH testcrosses were 14.3 cm shorter than the best commercial check. The 10 highest yielding DH

testcross hybrids from each trial were 2.6 to 15.7 cm taller than the mean of commercial checks (Table 3).

Mean DH testcross performance across drought-stressed locations

Based on the results of the combined analysis across two managed drought-stressed locations, there were significant differences in the average values for grain yield, anthesis date and plant height among DH testcrosses in all the six trials (data not shown). The grain yield of all DH testcrosses for the trials ranged from 2.16 (Trial 6) to 3.05 t ha^{-1} (Trial 5), with a mean of 2.75 t ha^{-1} (Table 2). The mean grain yield of all DH testcrosses in each trial was 19 to 50% higher than the mean of the commercial checks in all trials, except Trial 3. The top 10 DH testcrosses from each trial gave 11.8 to 40.9% more grain yield that the mean of the best check and 33.3 to 90% more grain yield than the mean of commercial checks (Table 3). There was no significant difference in flowering dates among the DH testcrosses, with the top 10 DH testcrosses and

Table 3. Means of test crosses from all DH lines, the top 10 DH lines, mean of commercial checks and the best check of six trials developed from 10 tropical backcross. Three traits, grain yield (GY, t ha^{-1}), anthesis days (AD, days) and plant height (PH, cm) were evaluated in water-stress and well-watered sites.

Parameter	GY	AD	PH	GY	AD	PH
	Water-stress			Well-watered		
Trial 1						
All DH TC	3.0	75.6	210.3	5.6	75.2	244.9
Top 10DH TC	3.7	73.3	213.2	6.5	76.1	249.0
Best check	3.1	71.3	198.4	4.9	76.4	244.7
Mean of the checks	2.4	72.7	205.3	4.2	72.2	234.0
Trial 2						
All DH TC	2.5	73.9	204.9	6.1	73.8	225.6
Top 10 DH TC	3.3	74.0	208.1	7.3	75.1	231.7
Best check	2.9	75.3	225.4	7.3	76.3	246.0
Mean of the checks	2.0	72.9	209.3	5.7	72.7	229.1
Trial 3						
All DH TC	2.7	74.9	215.3	5.8	77.0	223.6
Top 10 DH TC	3.6	74.1	221.3	6.6	77.0	228.8
Best check	2.9	73.0	218.7	5.1	74.3	210.8
Mean of the checks	2.7	74.9	215.3	4.6	74.6	213.1
Trial 4						
All DH TC	3.0	76.7	202.9	5.9	77.8	223.4
Top 10DH TC	3.8	76.9	205.8	6.8	78.6	223.2
Best check	3.4	73.3	207.6	5.4	74.8	222.6
Mean of the checks	2.0	74.4	195.2	4.4	74.2	219.7
Trial 5						
All DH TC	3.1	74.1	214.7	5.6	74.8	230.7
Top 10 DH TC	3.9	73.3	219.3	6.7	75.8	239.7
Best check	3.4	73.2	219.3	5.7	75.1	230.1
Mean of the checks	2.6	74.2	209.0	4.5	73.1	225.1
Trial 6						
All DH TC	2.2	73.6	195.4	5.9	74.1	233.2
Top 10 DH TC	3.1	73.5	201.2	6.9	74.2	240.7
Best check	2.2	72.6	197.6	5.5	74.9	226.8
Mean of the checks	1.8	73.4	190.2	4.6	72.6	229.0

commercial checks showing maximum difference of 3.6 days among the different groups. With respect to plant height, the top 10 DH testcrosses were 2.6 to 14.8 cm taller than the highest-yielding commercial check in three of the trials (Trials 1, 3 and 6) and 1.8 to 17.3 cm shorter than the highest yielding check in Trials 2 and 4. In Trial 5, there was no difference in plant height between the 10 highest-yielding DH testcrosses and the highest-yielding commercial check (Table 3).

Variance components and broad-sense heritability under drought-stressed and well-watered conditions

Broad-sense heritability estimates for grain yield in individual trials ranged from 0.62 to 0.82 under well-watered conditions and 0.21 to 0.51 under drought stressed condition (Table 2). In the combined analysis, as expected, the heritability (H) of grain yield was lower under WS relative to WW (Table 2). The heritability

Table 4. Location, entry, location × entry, and residual variance components for three traits (grain yield, anthesis days and plant height) combined across water stress (WS) and well-watered (WW) locations in each of the six trials evaluated in 2012.

Variance component	Grain yield (t/ha)	Anthesis day (days)	Plant height (cm)	Grain yield (t/ha)	Anthesis day (days)	Plant height (cm)
		WS			WW	
Trial 1						
Location	1.03	6.92	151.27	1.39	51.16	1414.58
Entry	0.04	1.64	0	0.28	1.62	21.82
Loc × Entry	0.06	0.49	0	0.07	0.35	23.39
Residual	0.66	1.26	434.24	0.84	2.54	324.73
Trial 2						
Location	0.78	9.17	22.25	0.61	35.28	301.85
Entry	0.10	2.18	36.56	0.33	2.40	40.31
Loc × Entry	0.00	0.73	5.40	0.29	0.18	5.01
Residual	0.89	2.72	57.37	1.06	2.39	149.71
Trial 3						
Location	0.02	17.74	97.26	0.84	24.90	209.12
Entry	0.06	1.43	45.26	0.17	1.43	53.14
Loc × Entry	0.10	0.49	2.36	0.12	0.22	0.00
Residual	0.65	2.64	79.98	0.93	4.26	2182.51
Trial 4						
Location	0.06	22.72	366.97	0.49	48.23	603.91
Entry	0.14	0.98	14.60	0.31	1.61	7.12
Loc × Entry	0.08	0.70	4.25	0.01	0.14	4.67
Residual	0.56	2.02	94.30	0.87	3.09	106.68
Trial 5						
Location	0.00	13.99	2.48	0.51	19.58	515.55
Entry	0.07	1.27	54.65	0.36	1.66	73.06
Loc × Entry	0.01	0.14	3.20	0.09	0.09	21.21
Residual	0.67	1.42	52.87	0.80	2.06	72.50
Trial 6						
Location	0.35	12.26	0.00	0.16	29.89	520.53
Entry	0.12	1.53	44.69	0.47	1.62	62.39
Loc × Entry	0.06	0.62	32.86	0.08	0.30	33.17
Residual	0.51	1.93	44.54	1.02	2.11	156.36

estimates for anthesis date were slightly higher in the well-watered than under water-stressed condition. The heritability estimates for plant height varied with populations. In some populations (Trials 2 and 5), the estimates were similar under well-watered and water-stressed conditions. In two other populations (Trials 1 and 6), the estimates were higher under well-watered than under water-stressed condition, while the reverse was the case in Trials 3 and 5.

For most populations, the proportion of genotype to GE variance components was higher for WW than for WS, indicating that GE interaction was less important under optimum-moisture than under drought-stressed conditions (Table 4). Variance of genotypes for grain yield was 56 to 83% larger in the well-watered condition than in drought stressed condition in all trials except Trial 5. For anthesis date, variance of genotypes was 28 to 88% larger in the WW condition than in the WS condition in all trials.

Table 5. Entry code of the top 10 DH derived hybrids and their grain yield (GY) (t ha^{-1}) in water-stress and well-watered sites for each of the six trials evaluated in 2012.

Water-stress		Well-watered		Water-stress		Well-watered	
Entry	GY	Entry	GY	Entry	GY	Entry	GY
Trial 1				Trial 2			
47	4.4	85	6.8	*42*	3.8	39	7.6
3	3.9	1	6.6	25	3.7	43	7.5
29	3.8	39	6.5	69	3.6	73	7.4
54	3.8	64	6.5	9	3.6	52	7.4
11	3.7	50	6.5	58	3.2	35	7.3
70	3.5	*76*	6.4	74	3.2	*42*	7.3
15	3.5	41	6.4	*59*	3.2	34	7.2
26	3.4	78	6.4	3	3.1	49	7.0
77	3.4	72	6.4	64	3.1	*59*	6.9
76	3.4	36	6.3	46	3.0	30	6.9
Trial 3				Trial 4			
90	4.0	86	6.8	35	4.1	38	6.9
50	3.8	98	6.7	65	4.1	75	6.9
46	3.7	34	6.7	*64*	3.9	68	6.8
29	3.6	52	6.7	30	3.8	93	6.8
92	3.5	*90*	6.6	20	3.8	89	6.8
95	3.5	42	6.6	2	3.7	*3*	6.8
59	3.5	16	6.5	*3*	3.6	91	6.8
77	3.5	*46*	6.5	27	3.6	*64*	6.7
61	3.4	3	6.5	56	3.6	16	6.7
94	3.4	23	6.5	54	3.6	5	6.7
Trial 5				Trial 6			
50	4.0	66	7.0	40	3.4	17	7.3
43	4.0	96	7.0	16	3.3	18	7.1
81	4.0	12	6.8	39	3.2	58	7.1
39	4.0	70	6.8	68	3.2	55	7.0
35	3.9	63	6.7	46	3.1	5	6.9
53	3.9	89	6.6	37	3.0	32	6.8
95	3.9	36	6.6	84	2.9	14	6.7
19	3.7	46	6.6	62	2.9	*57*	6.7
49	3.7	78	6.4	*57*	2.9	45	6.6
18	3.6	3	6.4	35	2.8	22	6.6

Bold faces shows hybrids were performed on the top 10 under drought and optimum environments.

DH testcrosses that performed well under both well-watered and water-stressed locations

DH testcrosses that performed well under well-watered and water-stressed conditions were of considerable interest because these combine drought tolerance and yield potential. Of particular interest were Entry 76 (Trial 1), 42 and 59 (Trial 2), 90 and 46 (Trial 3), 64 and 3 (Trial 4) and 57 (Trial 6) which ranked amongst the top 10 under WW and WS locations (Table 5).

DISCUSSION

The main objective of the study was to assess the performance of DH lines developed from the tropical BC1 populations under drought-stressed and well-watered environments and to identify elite new inbred lines for use

in high-performing maize cultivars for the African farmers. Significance of genotypic mean squares for all measured traits indicates that good progress can be made in selecting for improved grain yield under both drought and well-watered environments. Significant variation for GY under drought observed in this study was an indicator of expression of differential levels of tolerance to drought in tropical maize hybrids. Beyene et al. (2013) and Derera et al. (2008) also reported differential responses of tropical maize hybrids to drought stress.

Evaluations of maize varieties in multiple environments reveal a range of adaptation and specific fitness for diverse environments (Setimela et al., 2007; Beyene et al., 2013). In the present study, hybrids performing well under drought-stressed and well-watered environments were identified in 5 out of 6 trials. Superior lines were identified from all the 10 populations, suggesting that the donor parents used in developing the DH lines are excellent sources of germplasm for combining ability with sub-Saharan adapted germplasm. Similarly, Beyene et al. (2013) evaluated 50 hybrids across drought-stress and well-watered locations in Kenya, Uganda and Tanzania, identifying hybrids that performed well across optimum-moisture and drought-stressed locations. Results of this study are in agreement with those of Betran et al. (2003) who reported that lines with different selection history produced high-yielding hybrids under contrasting environments, indicating favorable allele combinations between inbred lines selected under well-watered and water-stressed conditions.

The average grain yield of the top 10 experimental hybrids in each trial was higher than the best check under well-watered and managed drought stress conditions, indicating that most of the DH testcrosses hybrids were superior as compared to the commercial checks. Duvick and Cassman (1999) reported better tolerance to drought and low nitrogen stresses in new varieties as 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 drought stress and low nitrogen tolerance for the last three decades (Bänziger et al., 2000; Makumbi et al., 2011; Worku et al., 2012). Edmeades et al. (2006) reported that the phenotypic correlation between elite hybrid yields under managed drought stress versus well-watered conditions declined as stress intensified, with yield reduction reaching 50%. They suggested that stress adaptive mechanisms were not exposed until yields were reduced by 30 to 50% under stress. In this study, average mean yields of testcrosses in each trial under drought stress represented 37 to 55% of the average yield of hybrids under well-watered conditions which fall within the range of 30 to 50% yield reduction suggested by Edmeades et al. (2006). Therefore, the top 10 DH testcrosses identified in the present study from each population might have adaptive traits for drought tolerance and have the potential to be utilized in breeding for drought tolerance in SSA.

This study demonstrates the use of DH technology in deriving elite lines combining drought-tolerance and elite performance for yield potential and adaptive traits in SSA. The DH lines developed from the tropical-adapted BC populations appeared to possess favorable genes for improving grain yield under stress and non-stress conditions. Such DH lines increase the speed and efficiency to introduce new and improved stress-resilient hybrids in the market, as some of the DH-derived hybrids showed significantly better performance as compared to the best commercials checks in eastern Africa, developed through pedigree breeding. To enable development of DH lines in Africa-adapted maize genetic backgrounds, CIMMYT established a maize DH facility at KALRO-Kiboko research station in Kenya. Since the inception of this facility in September 2013, more than 61, 456 DH lines have been developed.

Based on extensive multi-location field testing (following the present study) for their per se performance under abiotic and biotic stresses and performance in hybrid combinations (data not shown), five of the DH lines identified from the present study have been released as CIMMYT maize lines (CMLs). These are CML566, CML567, CML568, CML569 and CML570, as international public goods. All the five CMLs are of intermediate maturity, white-grained, and adapted to mid-altitude tropical mega-environments of sub-Saharan Africa. The lines are resistant to major foliar diseases of maize in Africa, such as gray leaf spot (GLS), caused by *Cercospora zeaemaydis*, Northern corn or Turcicum leaf blight caused by *Exerohilium turcicum*, common rust caused by *Puccinia sorghi* and maize streak virus caused by maize streak *geminivirus*. In addition, CIMMYT and its partners have released 32 DH-based hybrids in Kenya, Uganda, Tanzania and South Africa between 2012 and 2015 which perform well under optimum drought and low nitrogen stress conditions.

CONFLICTS OF INTERESTS

The authors have not declared any conflict of interests.

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