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Combining ability and heterosis of elite drought-tolerant maize inbred lines evaluated in diverse environments of lowland tropics

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Abstract Estimates of combining abilities and heterosis of inbred lines are imperative for selection of suitable parents of maize hybrids. This study examined the combining ability of 24 drought-tolerant maize inbred lines, 12 each from International Centre for Maize and Wheat Improvement (CIMMYT) and International Institute of Tropical Agriculture (IITA). The lines were allotted into six groups each comprising four lines. The four lines in one group were used as females and crossed to the four lines in another group as males in six different sets using a North Carolina Design II mating scheme to generate 96 hybrids. The hybrids were evaluated together with four checks across six environments in the rainforest and savannah agro-ecologies of Nigeria between 2011 and 2012. The parental inbred lines were also evaluated in separate trial in each location. Significant hybrids × environment interaction was observed for grain yield and other measured traits. GCA effects accounted for 83.3% of the variation for grain yield at Bagauda, 78.1% at Saminaka, and 77.7% at Ikenne. GCA also contributed 91.1 and 80.0% to the variation observed for plant height and ear aspect, respectively, across the environments. Significant SCA × environment interaction detected for grain yield suggests that hybrids were not stable across test environments. Prediction of grain yield in hybrids using midparent values resulted in a R^2 value of 0.13. Midparent heterosis for grain yield varied from 80 to 411%, with the top 36 hybrids recording >200%. Four CIMMYT (EXL02, EXL06, EXL04 and EXL16) and three IITA (ADL33, ADL41, and ADL32) inbred lines had positive and significant GCA effects for grain yield across environments. The novel alleles present in the CIMMYT lines will improve the adapted IITA germplasm in a new population for extracting new set of more productive inbred lines for developing adapted high yielding drought-tolerant maize hybrids.

Keywords CIMMYT · General combining ability · IITA · Maize breeding · Mid-parent heterosis · Specific combining ability

Introduction

Maize (*Zea mays* L.) has enormous potential for achieving self-sufficiency in food production in sub-

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Saharan Africa (SSA) (Abalu 2001). Irrespective of the suitability of Africa's Guinea Savannas as high maize production environments due to availability of abundant radiation, the crop is still limited by a myriad of biotic and abiotic stress factors like drought, and low soil nitrogen as well as poor adaptation of exotic germplasm to host environments, and vulnerability to diseases and pests (Badu-Apraku et al. 2010). Hybrid and per se inbred performance can be substantially affected by variation in these environmental factors. Contrasting environments are created in SSA by insufficient and erratic precipitation and infertile soils, varying temperatures as well as cultural practices, all acting in concert (Abdulai et al. 2007; Badu-Apraku et al. 2011). Maize breeders invest expertise, time and huge resources into developing superior genotypes that are high-yielding and well adapted to the different agro-ecologies where specific stress factors are prevalent (Bello and Olaoye 2009). They also look into exotic germplasm for novel alleles that can be introgressed into locally available materials to confer tolerance and/or resistance against various biotic and abiotic stresses (Giauffret et al. 2000; Dhliwayo et al. 2009) that undermine agronomic performance.

Genetic materials, mostly elite inbred lines, are being exchanged among breeders at CIMMYT and IITA for the purpose of accessing novel genes for maize yield improvement (Dhliwayo et al. 2009) in a target environment. Adoption of CIMMYT germplasm in other maize breeding programs across SSA will be more profitable when basic information about their combining ability is generated (Han et al. 1991). IITA maize breeders have also developed a wide array of tropical, lowland, white and yellow endosperm maize inbred lines of both tropical and temperate genetic backgrounds (Kim et al. 1987; Menkir et al. 2004) that are well adapted to different agro-ecologies of SSA (Kim and Ajala 1996; Kim 1997; Kim et al. 1999). Elite inbred lines that were developed with genes for common traits are being exchanged between the two centers for maize improvement in SSA. However, incorporation of exotic materials into existing breeding program must be based on sound knowledge of the breeding values of the selected germplasm (Menkir et al. 2004; Nelson and Goodman 2008). This knowledge can be obtained after conducting a series of genetic and multi-location studies on the yield and agronomic performance of hybrids developed from such inbred lines. The concepts of general combining ability (GCA) and specific combining ability (SCA) effects defined by Sprague and Tatum (1942) have been widely adopted in maize breeding for selection of inbred lines as parents of hybrids. Additive gene action has been reported to be relatively more important than non-additive gene action for inbred lines that have not been tested, whereas non-additive gene action was more important than additive gene action for previously selected lines (Nass et al. 2000). Also, several authors have reported that GCA is more preponderant than SCA for grain yield in tropical maize germplasm (Derera et al. 2008; Dhliwayo et al. 2009; Adebayo et al. 2014).

The choice of suitable parental inbred lines for a single-cross maize hybrid development is contingent on the degree of genetic divergence existing between the parents; this variation determines the extent to which heterosis may be exploited (Moll et al. 1962; Adebayo et al. 2015; Abera et al. 2015). Earlier and recent works in maize breeding indicated that greater heterosis would be exploited in crosses of genetically distantly related parents than in those of closely related parents (East and Hayes 1912; East 1936; Johnson and Hayes 1940; Moll et al. 1962; Tracy and Chandler 2004). Heterosis has also played significant roles in the adaptation of maize to drought and other stress conditions (Tollenaar et al. 2004; Tollenaar and Lee 2006; Araus et al. 2010).

In this study, a subset of the new wide array of elite drought-tolerant inbred lines developed at CIMMYT and IITA were used for hybrid combinations to ascertain their performance for grain yield and other agronomic attributes under contrasting production environments. Therefore, the objectives of this study were: (i) to determine the combining ability and heterosis of 24 elite drought-tolerant maize inbred lines across diverse lowland environments, and (ii) to assess the interaction of the genetic effects for grain yield and other agronomic traits with environment.

Materials and methods

Genetic materials

Twenty-four lowland drought-tolerant maize inbred lines, 12 each from CIMMYT and IITA were used as source materials in this study (Table 1). The pedigrees of the inbred lines can be found in Adebayo et al.

(2014). The lines from each centre were previously separated into groups using microsatellite-based genetic diversity (Adebayo et al. 2015) and were intercrossed using a NCD II mating scheme to generate 96 hybrids that have been evaluated earlier under managed drought stress conditions as described in detail in Adebayo et al. (2014).

Field experiments

A trial composed of 100 maize hybrids—96 F_1 single-cross hybrids plus four hybrid checks—was evaluated in separate experiments at three different locations (Ikenne, Saminaka, and Bagauda) during the growing seasons of 2011 and 2012 under rainfed conditions.

Table 1 Line code, group, breeding centre, cross designation, and trait means of the 24 CIMMYT and IITA DT maize inbred lines selected for the 96 NCD II hybrids development

Line	Group	Origin	Female (set)	Male (set)	Trait means			
					Grain yield (kg ha^{-1})	Silking dates (days)	Plant height (cm)	Ear aspect[§] (1–5)
EXL01	1	CIMMYT	1	4	1698	65.3	127.7	3.7
EXL04	1	CIMMYT	1	4	2266	66.3	134.7	2.8
EXL05	1	CIMMYT	1	4	1481	66.0	125.5	2.8
EXL24	1	CIMMYT	1	4	701	60.3	94.5	3.8
EXL10	2	CIMMYT	4	2	2634	60.7	135.0	2.5
EXL15	2	CIMMYT	4	2	3013	61.0	167.0	3.1
EXL16	2	CIMMYT	4	2	2336	62.3	129.8	2.8
EXL17	2	CIMMYT	4	2	2136	62.8	141.8	3.2
EXL02	3	CIMMYT	6	3	1808	60.8	125.3	3.2
EXL03	3	CIMMYT	6	3	1883	62.0	125.5	3.4
EXL06	3	CIMMYT	6	3	2341	62.8	128.0	3.1
EXL07	3	CIMMYT	6	3	1245	63.2	106.2	3.6
ADL34	4	IITA	5	1	2029	68.2	139.7	2.9
ADL35	4	IITA	5	1	1995	65.7	145.3	2.8
ADL36	4	IITA	5	1	2129	65.8	147.7	3.1
ADL39	4	IITA	5	1	2693	61.2	154.3	2.2
ADL31	5	IITA	2	6	1871	62.8	113.7	3.1
ADL41	5	IITA	2	6	1024	64.5	124.5	3.4
ADL33	5	IITA	2	6	2896	66.3	150.2	2.7
ADL47	5	IITA	2	6	2341	63.0	135.5	2.8
ADL27	6	IITA	3	5	814	69.3	129.0	3.8
ADL32	6	IITA	3	5	904	71.7	151.5	3.3
ADL37	6	IITA	3	5	2613	62.0	116.8	3.1
ADL38	6	IITA	3	5	2257	62.7	132.5	3.0
Mean					1963	64.0	132.6	3.1
SE					116	0.4	2.1	0.1
P of F for lines					***	***	***	***
P of F for env.					******	**	**	***
P of line × env.					***	ns	ns	**

ns mean squares not significant

[§] Ear aspect was visually rated on a scale of 1–5, where *1* clean, uniform, large, and well-filled ears and *5* rotten, variable, small, and partially filled ears

, * Mean squares significant at $p < 0.01$, 0.0001, respectively

Another trial comprising the 24 parental lines that were used for NCD II hybrids development and two inbred checks was established in adjacent block in each of the locations in each year. Ikenne is situated in the lowlands of the rainforest agro-ecological zone of Nigeria at an altitude of 60 m above sea level (masl), latitude 6°54′N, longitude 3°42′E, and average annual rainfall of 1421 mm while Saminaka is located in the northern guinea savannah at altitude of 730 masl, latitude 10°40′N and longitude 8°77′E, and an average annual precipitation of 1200 mm. Bagauda is situated in the Sudan savannah at 580 masl, latitude 12°00′N, longitude 8°22′E, and average annual rainfall of 800 mm.

Hybrids and checks were evaluated using a 10 × 10 triple-lattice design in three replications whereas the parental lines were arranged in a randomized complete block design (RCBD) with two replications in each of the three test environments. Hybrids and lines were randomized within each replicate. An experimental plot was 5-m long single row, with plants within a row spaced 0.5 m apart and 0.75 m distance between rows. Three maize seeds were planted per hill and later thinned to two plants 2 weeks after planting (2WAP) to attain a population density of 53,333 plants ha^{-1} in each trial. At Ikenne, basal application of NPK was done at the rates of 60 kg N, 60 kg P, and 60 kg K per hectare. An additional 60 kg ha^{-1} N of urea was applied as top dressing 4 weeks after planting (WAP). Prior to planting, soils at both Saminaka and Bagauda were treated with organic manure (cow dung). Application of fertilizer at both Saminaka and Bagauda was carried out at 2WAP when 60 kg ha^{-1} each of N, P, and K was applied as 15–15–15 NPK. Urea was used as top-dress at the rate of 60 kg ha^{-1} N 4 weeks later. At each location, weeds were controlled by applying a mixture of gramoxone and primextra as pre-emergence herbicides at 5.0 l ha^{-1} each of paraquat (*N*,*N*′-dimethyl-4,4′-bipyridinuim dichloride) and atrazine (2-chloro-4-ethylamino-6-isopropylamino-1,3,5-triazine) immediately after planting. Manual weeding was subsequently done to keep the plots weed-free.

Data collection

Data were recorded on plot basis on several agronomic traits in each experiment but those on silking dates (DTS), plant height (PLHT), ear aspect (EASP), and grain yield (GY) are presented in this report. DTS was recorded as the number of days from planting to when 50% of plants in a plot had emerged silks. PLHT and EHT were measured in centimetres (cm) as the distance from the base of the plant to the height of the first tassel branch and the node bearing the upper ear, respectively. EASP was visually rated on a scale of 1–5, where 1 = clean, uniform, large, and well-filled ears, and 5 = rotten, variable, small, and partially filled ears. The total number of plants and ears were counted in each plot at the time of harvest. EPP was computed as the proportion of total number of ears divided by the number of plants harvested. All ears harvested from each plot were weighed and shelled to determine grain weight and a representative grain sample was taken to determine percent moisture. Grain yield (GY), measured in kg ha^{-1} adjusted to 15% moisture content was calculated from grain weight and percent moisture.

Statistical analyses

Analysis of variance (ANOVA) was computed for the traits means of hybrids for each test environment to generate entry means adjusted for block effects according to the lattice design (Cochran and Cox 1960). Means of the measured traits of the parental lines across environments were also subjected to ANOVA in RCBD. To test the significance of hybrid × environment interaction, combined ANOVA was computed over the 2 years across the three locations. Replications, location-year combinations and incomplete blocks were considered as random effects while genotypes were considered as fixed effects. Each location-year combination was considered a test environment. All analyses were performed with PROC GLM in SAS (SAS Institute 2009) using a RANDOM statement with TEST option. The hybrids (sets) component of the variation was divided into variation due to male (sets), female (sets), and female × male (sets) interaction. The *F* tests for male (sets), female (sets), and female × male (sets) mean squares were computed using the mean squares for their respective interaction with environment. The mean square attributable to female (sets) × environment, and male (sets) × environment were tested using the mean square for female × male (sets) × environment whereas the mean square for female × male (sets) × environment was tested using the pooled error mean squares. The main effects of male (sets) and female (sets) represent the GCA effects while the female × male (sets) interaction represents SCA effects (Hallauer and Miranda 1988). For each location and across locations over the 2 years, estimates of male and female GCA for each line and SCA for each cross were calculated for grain yield using adjusted means after the check entries were omitted following the procedure of Singh and Chaudhary (1985). Spearman's rank correlation coefficients for grain yield were calculated between each pair of the environment means of the hybrids.

Mid-parent heterosis (MPH) and better-parent heterosis (BPH) of each cross for grain yield and other agronomic traits were calculated and expressed in percentages using trait means of parents and hybrids across the six environments, following the procedures of Falconer and Mackay (1996). For each trait, the mid-parent value of a cross was calculated as the mean of the two parental line means averaged across environments. Hence, MPH was computed as $[(F_1 - MP)/MP] \times 100$, where F_1 is the mean performance of the cross; MP is the mid-parent value given by $(P_1 + P_2)/2$; P_1 and P_2 are the mean values of parent 1 and parent 2 averaged across environments, respectively. BPH was calculated as $[(F_1 - BP)/BP] \times 100$, where BP = the better parent mean averaged across environments. Hybrid means were then regressed on mid-parent and better parent values separately for each cross.

Results

Per se performance of drought tolerant inbred lines

Parental lines and environments exhibited significant differences for all measured traits (Table 1). Highly significant line × environment interaction was also observed for grain yield and ear aspect. Per se grain yields of the lines averaged across the six environments varied from 704 to 3014 kg ha^{-1} with a mean of 1963 kg ha^{-1}. Lines matured at an average of 64 days after planting, attaining mean plant height of 132.6 cm and ear aspect rating of 3.1 (Table 1).

Combining ability of parental lines

In the combined ANOVA, environment, sets and sets × environment interaction were significant sources of variation for all measured traits except sets for ear aspect (Table 2). Hybrids (sets) and hybrids (sets) × environment interaction differed significantly for measured traits. Females (sets), males (sets) and their interactions with environment also differed significantly for all measured traits. Mean squares for females × males (sets) interaction was, however, not significant for grain yield, whereas females × males (sets) × environment interaction was significant for grain yield and ear aspect (Table 2). Individual set analyses for grain yield revealed that GCA effects (females, males, or both) were significant in all six sets and SCA effect was not significant in any set (Table 3). Similar results were observed for GCA effects for silking dates, plant height and ear aspect, but SCA effect was significant for silking dates in set 3 only, plant height in set 4 only, and ear aspect in set 2 only (Table 3). Partitioning the cross sums of squares for grain yield in each location and across locations over the 2 years revealed that GCA accounted for 83.3, 78.1, and 77.7% of the variation observed for grain yield at Bagauda, Saminaka, and Ikenen, respectively. Across locations, GCA contributed 91.1 and 80.0% to the variation in plant height and ear aspect, respectively. The ratio of the female GCA (55.0%) to male GCA (32.9%) sum of squares estimated for grain yield across the three locations over the 2 years was 1.7. Similarly, the ratios of the female GCA to male GCA sum of squares were greater than a unity for silking dates (1.1), plant height (1.3) and ear aspect (1.5).

Estimates of females and males GCA effects for grain yield in each of the test locations and across the three locations over the 2 years are presented in Table 4. Four CIMMYT lines (EXL02, EXL04, EXL05, and EXL06) and three IITA lines (ADL33, ADL41, and ADL47) had significant females and males GCA effects across locations, and mostly positive and significant GCA (females, males, or both) in all the three locations (Table 4). Further assessment of females × males (sets) × environment interaction using Spearman's correlation analysis revealed that the correlation between hybrid means for all pairs of the six environments was generally weak ($r = 0.07–0.62$), though mostly significant (Table 5) However, the correlation between hybrid means for the 2 years in each location was positive and highly significant (Bagauda/$r = 0.30$, $p < 0.01$; Ikenne/$r = 0.62$, $p < 0.0001$; Saminaka/$r = 0.48$, $p < 0.0001$).

Table 2 Sums of squares expressed as percentages of corrected sums of squares of measured traits of 96 single-cross maize hybrids evaluated in six diverse environments in Nigeria between 2011 and 2012

Source of variation	Df	Grain yield (kg ha^{-1})	Silking dates (days)	Plant height (cm)	Ear aspect (1–5)[a]
Env.	5	77.2***	78.4***	67.2***	12.6**
Sets	5	1.1**	1.8***	1.7***	2.2ns
Sets × env.	25	1.3***	0.3***	0.3**	5.6***
Hybrids (sets)	90	3.5***	6.0***	10.5***	12.9***
Hybrids (sets) × env.	450	5.6***	3.4***	4.4***	22.8***
Females (sets)	18	1.7***	2.9***	5.1***	5.7***
Males (sets)	18	1.4***	2.6***	4.3***	4.2**
Females × males (sets)	54	0.5ns	0.5**	1.0***	2.8*
Females (sets) × env.	90	1.9***	1.0***	1.4***	6.3***
Males (sets) × env.	90	1.7***	1.0***	1.2***	7.1***
Females × males (sets) × env.	270	1.9**	1.4ns	1.8ns	9.3*
Error	978	5.3	4.5	5.7	21.2

*, **, *** Data significant at $p < 0.05$, 0.01, and 0.0001, respectively

[a] Ear aspect was visually rated on a scale of 1–5, where *1* clean, uniform, large, and well-filled ears and *5* rotten, variable, small, and partially filled ears

Table 3 Abbreviated ANOVA table showing significance of females (GCA_f), males (GCA_m), and females × males (SCA) effects in individual sets for grain yield, silking dates, plant height, and ear aspect measured on the 96 maize hybrids across six diverse environments in Nigeria

Source of variation	Set 1	Set 2	Set 3	Set 4	Set 5	Set 6
Grain yield (kg ha^{-1})						
Females	***	**	***	ns	ns	**
Males	ns	*	**	***	**	**
Females × males	ns	ns	ns	ns	ns	ns
Silking dates (days)						
Females	***	**	***	*	***	**
Males	***	ns	ns	***	***	*
Females × males	ns	ns	*	ns	ns	ns
Plant height (cm)						
Females	***	***	***	***	ns	*
Males	**	**	**	***	***	***
Females × males	ns	ns	ns	*	ns	*
Ear aspect (1–5)						
Females	***	*	***	ns	**	*
Males	ns	ns	**	ns	**	*
Females × males	ns	*	ns	ns	ns	ns

*, **, *** Mean squares significant at $p < 0.05$, 0.01, and 0.0001, respectively; *ns* mean squares not significant ($p > 0.05$)

Heterosis

The regression of hybrid performance on the mid-parent values resulted in positive and significant ($p < 0.05$–0.0001) regression coefficients varying from 0.15 to 0.92 for grain yield and other traits (Table 6). R^2 values varied from 4% for ear aspect to 53% for silking dates with grain yield having 13% (Table 6). However, the regression of hybrid means on the better or high parent values resulted in a non-significant regression coefficients for grain yield ($p = 0.0894$, $R^2 = 2\%$) and other traits.

A wide variation was observed for the level of MPH existing among the measured traits of the hybrids. Mean percentage heterosis was positive for grain yield (199.7%) and plant height (47.9%) but negative for

Table 4 Estimates of females and males GCA effects for grain yield (kg ha^{-1}) of 24 CIMMYT and IITA DT inbred lines evaluated in factorial crosses in sets at Saminaka (SMK), Ikenne (IKN), and Bagauda (BGD) and across the three locations in Nigeria in the growing seasons of 2011 and 2012

LINE	SMK		IKN		BGD		ACROSS	
	GCA$_f$	GCA$_m$	GCA$_f$	GCA$_m$	GCA$_f$	GCA$_m$	GCA$_f$	GCA$_m$
EXL01	151.7	337.8*	−340.6	−65.6	−126.7	−139	−149.8	35.6
EXL04	104.0	554.4*	388.6*	192.4*	344.7*	−74.8	423.2*	206.7*
EXL05	157.5	832.9*	437.8*	−135.5	485.2*	155	434.0*	216.5*
EXL24	−1306.7	−499.4	−471.7	−77.2	−967	−1096.7	−1021.99	−561.8
EXL10	113.3	123.5	164	766.9*	−456.4	267.9	−81.4	442.3
EXL15	431.9*	−380.1	10.9	589.9*	−312	83.4	34.9	259.4
EXL16	36.4	239.6	197.5*	988.4*	−325.6	314.4*	−42.3	602.0*
EXL17	644.1*	88.5	−458.2	595.6*	−61.5	193.6	−14.1	274.7*
EXL02	705.6*	1052.4*	−257	−66.5	1077.0*	369.9*	483.2*	426.4*
EXL03	−128.0	−122.0	314.2*	121.1	95.1	276.6*	136	97.7
EXL06	917.3*	762.2*	1028.8*	71.1	104.1	24.9	698.4*	231.7*
EXL07	−48.7	−333.5	−617.8	−1209.2	−397	−438.9	−467.9	−702.1
ADL34	−872.0	−447.1	−423.8	39.5	−150.8	−31.9	−447.7	−112.4
ADL35	−833.8	−194.6	−618.6	−60.6	−336	−492.6	−601.2	−199.9
ADL36	−898.2	−187.9	−674.4	233.3*	−198.8	250.6	−637.8	113.7
ADL39	−605.1	−63.9	−537	−198.1	133.7	10.3	−377.6	−116
ADL31	−234.6	−318.9	662.3*	−168.1	−732.1	−433.6	−118.1	−320.5
ADL33	−114.5	305.2*	922.7*	859.9*	593.4*	509.6*	614.5*	602.9*
ADL41	322.8*	914.5*	173.5*	−379.2	719.7*	620.1*	426.3*	288.7*
ADL47	97.8	545.5*	1182.3*	155.6	278.3*	183.2	655.8*	278.6*
ADL27	341.2*	−1839.2	220.6*	−858.6	78.6	−603.1	220.7*	−1113.9
ADL32	353.1*	−943.1	473.9*	−207.2	434.2*	434.9*	542.5*	−93.8
ADL37	645.2*	−452.4	−446.6	−529.9	205.4	117.2	16.1	−384.1
ADL38	19.6	25.6	−1331.4	−658.1	−485.7	−500.9	−725.6	−472.3
SE	125.5	125.3	82.3	82.4	137.7	137.6	75.7	75.6

EXL CIMMYT inbred lines, *ADL* IITA inbred lines

* Estimate significantly different from zero at ≥2 SE

Table 5 Spearman's correlation analysis for grain yield (kg ha^{-1}) recorded in six environments in Nigeria between 2011 and 2012

	Bagauda 2012	Ikenne 2011	Ikenne 2012	Saminaka 2011	Saminaka 2012
Bagauda 2011	0.30**	0.24*	0.21*	0.27**	0.19^{ns}
Bagauda 2012		0.26**	0.25*	0.45***	0.33**
Ikenne 2011			0.62***	0.33**	0.14^{ns}
Ikenne 2012				0.31**	0.07^{ns}
Saminaka 2011					0.47***

*, **, *** Correlation coefficients significantly different from zero at $p < 0.05$, 0.01, 0.0001, respectively; *ns* correlation coefficients not significantly different from zero

silking dates and ear aspect (Table 7). Top 10 highest-yielding hybrids displayed positive MPH that varied from 148 to 322% for grain yield (Table 7). Only three of them, namely; ADL32 × EXL06, ADL41 × EXL16, and EXL06 × ADL41, had MPH of >250% for grain yield, positive MPH for plant height and negative MPH for silking dates. Similarly, the bottom 10 hybrids recorded positive MPH values varying from 122 to 249% for grain yield, positive values for plant height and negative for silking dates. MPH values for ear aspect for the top 10 hybrids were mostly positive but the values for the bottom 10 hybrids did not follow any consistent trend (Table 7). All the top 10 hybrids are crosses involving CIMMYT and IITA lines out of which ADL47 featured in 50% and EXL06 in 30% of the crosses as either male or female parent. Thirty-six hybrids displayed positive MPH of 200% and above for grain yield (Fig. 1). Among these, 75% (27) are crosses involving CIMMYT and IITA lines, 16.6% involved only CIMMYT-derived lines, and 8.3% are crosses involving only IITA-derived inbred lines (Fig. 1).

Discussion

The significance of genotype × environment interaction (GEI) as a source of variation in SSA (Abdulai et al. 2007; Badu-Apraku et al. 2011) and the fact that both CIMMYT and IITA breeders work with highly diverse maize germplasm (Dhliwayo et al. 2009) has necessitated the conduct of multi-location trials and combining ability analysis for identifying useful inbred lines for population improvement for specific locations and those with wider adaptation across diverse production environments. The highly heterogeneous nature of the six test environments used in this study as reflected by the significant females × males (sets) × environment interaction accounted for the observed inconsistent performance of hybrids across locations. Also, the mostly significant but low rank correlations for all pairs of test environments suggests that crossover GEI effect may be responsible for the inconsistent lines and hybrids performance, and this may pose a great challenge to selection of superior lines and hybrids across the production environments. Crossover GEI effect involves inconsistent performance with changes in rank order with the consequence that some genotypes are superior in one environment while other genotypes are superior in another environment (Baker 1988). Derera et al. (2008) reported significant GEI with crossover effect in a set of drought-tolerant maize hybrids tested under stress and non-stressed environments in southern Africa. It was, therefore, suggested that where there is crossover GEI effects, different sets of lines and hybrids should be selected for a specific environment (Nass et al. 2000; Derera et al. 2008; Dhliwayo et al. 2009). The non-significant SCA effects for grain yield and other traits mostly observed in the individual sets analysis may be attributed to the few number of inbred lines that were used as female and male parents in each set. This might also account for non-significant SCA effect estimates for most crosses in this study. The significant sets × environment interaction may suggest variation in adaptation of parental lines to the

Table 6 Regression of hybrid performance on mid-parent values and percentage minimum, maximum, and mean values for mid-parent heterosis of 96 hybrids tested in six environments in Nigeria between 2010 and 2012

Trait	Regression analysis		Mid-parent heterosis (%)		
	Regression coefficient	R^2	Min.	Max.	Mean ± SE
Grain yield (kg ha^{-1})	0.21**	0.13	79.6	410.5	199.7 ± 0.17
Silking dates (days)	0.92***	0.53	−14.7	−6.4	−9.8 ± 0.08
Plant height (cm)	0.55***	0.43	29.9	65.3	47.9 ± 0.14
Ear aspect (1–5)[a]	0.15*	0.04	−29.0	25.5	−4.8 ± 0.002

ns data not significant

*, **, *** Data significant at 5, 1, and 0.01% probability levels, respectively

[a] Ear aspect scores, a scale of 1–5, where *1* clean, uniform, large and well-filled ears and *5* rotten, variable, small and partially filled ears

Table 7 Mean grain yield and mid-parent heterosis (%) of measured traits of top 10 and bottom 10 selected from 96 NCDII maize hybrids tested in six environments in Nigeria between 2010 and 2012

Hybrid	Grain yield (kg ha^{-1})	Mid-parent heterosis (%)			
		Grain yield	Silking dates	Plant height	Ear aspect
Top 10					
EXL06 × ADL47	7218	198	−8.8	54.3	−22.0
ADL32 × EXL06	7097	322	−12.7	56.2	−29.0
ADL33 × EXL15	6829	148	−8.7	42.0	−22.8
ADL47 × EXL16	6828	183	−9.3	48.5	−12.7
ADL41 × EXL16	6615	288	−10.2	60.8	−24.6
ADL47 × EXL17	6609	194	−11.1	50.1	−18.6
ADL33 × EXL16	6517	172	−10.3	43.1	−16.4
ADL47 × EXL10	6501	153	−9.3	48.1	3.7
EXL03 × ADL47	6464	190	−9.1	47.2	−11.9
EXL06 × ADL41	6454	276	−10.1	52.1	−13.8
Mean of Top 10	6713.2	212.4	−9.96	50.24	−16.81
SE	85.8	19.1	0.38	1.8	2.9
Bottom 10					
EXL24 × ADL35	4506	249	−10.7	44.5	−7.5
EXL24 × ADL39	4473	168	−10.7	42.6	−3.3
EXL01 × ADL35	4401	144	−7.3	45.0	3.1
EXL24 × ADL34	4391	222	−12.7	45.1	−14.7
ADL37 × EXL07	4382	122	−9.6	57.9	16.9
ADL39 × ADL27	4250	145	−10.0	41.7	8.5
ADL36 × ADL27	4127	189	−9.0	41.7	4.5
ADL38 × EXL07	4126	138	−9.3	54.2	10.8
ADL34 × ADL27	4028	183	−11.6	49.3	−1.5
ADL35 × ADL27	3788	180	−10.1	40.5	6.1
Mean of bottom 10	4247.2	174.0	10.1	46.3	2.3
SE	72.2	12.5	0.47	1.8	2.9

EXL CIMMYT inbred lines, *ADL* IITA inbred lines

conditions of the test environments. The significant GCA and GCA × environment interaction effects and non-significant SCA effects indicate the importance of additive genetic effects in controlling grain yield in this germplasm, suggesting that genetic gains can be achieved through selection. The magnitudes of the ratios of the sum of squares of female GCA to male GCA have been used to determine the traits that may be under the influence of maternal cytoplasmic effects (Kang 1994; Derera et al. 2008; Adebayo et al. 2014). In the present study, the greater contributions of the female GCA when compared with the male GCA to the cross sum of squares for grain yield and other measured traits in these set of inbred lines suggest that the traits might have been influenced by some cytoplasmic genes of the mother plants. The finding was contrary to earlier workers who reported equal contributions of the female and male parents to total variation for grain yield and some other agronomic traits under both full irrigation and drought stress conditions (Derera et al. 2008; Adebayo et al. 2014). It is, therefore, imperative that vigorous plants with satisfactory per se performance for grain yield and good eye appeal must be carefully selected from this set of inbred lines as mother plants for hybridization process.

High percentages of heterosis recorded for grain yield particularly for the high-yielding hybrids

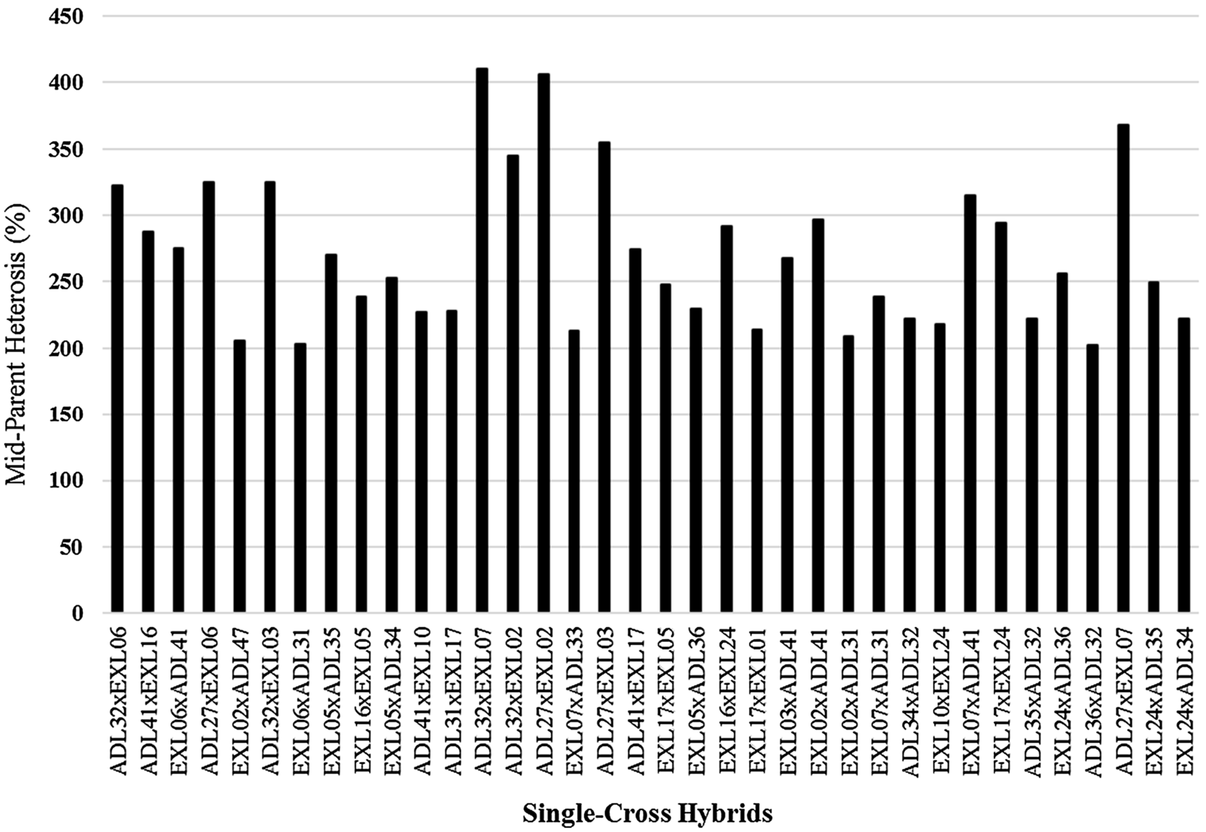

Fig. 1 Mid-parent heterosis (%) of grain yield displayed by 36 single-cross hybrids with highest values evaluated in six environments in Nigeria between 2011 and 2012

obtained from crosses of CIMMYT and IITA germplasm suggests that lines from both institutions possess genes that are complimentary. Abera et al. (2015) reported similar findings in crosses involving a different set of CIMMYT-derived lines and locally adapted Ethiopian inbred lines. The negative mean percentage heterosis recorded for silking dates and ear aspect, and the positive mean percentage heterosis for plant height corroborated the results of Menkir and Ayodele (2005) who used similar lowlands germplasm. The significant regression coefficients of the hybrid means on mid-parent values for grain yield and other measured traits indicate that high yielding hybrids generally resulted from crosses of inbred lines possessing genes for high productivity and other desirable agronomic characteristics.

While the lines that were identified as having good potentials in each location may be recombined to develop new populations for the extraction of new sets of productive inbred lines that are well suited for the particular location, the seven good general combiners; four from CIMMYT (EXL02, EXL04, EXL05, and EXL06) and three from IITA (ADL33, ADL41 and ADL47) identified in this study may be recombined into a more robust recurrent population for developing productive inbred lines with wider adaptation. Most of these seven lines were involved in the crosses of the ten highest yielding hybrids that exhibited appreciable heterosis, and can be adopted directly in single-cross hybrid development. Our results further supported the reports by earlier workers (Dhliwayo et al. 2009; Adebayo et al. 2014; Abera et al. 2015) that novel and useful alleles may be sourced from introduced or exotic germplasm for the improvement of locally adapted material for better hybrid maize productivity and agronomic performance.

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