Genetic analysis of drought tolerance in adapted × exotic crosses of maize inbred lines under managed stress conditions

M. A. Adebayo · A. Menkir · E. Blay · V. Gracen · E. Danquah · S. Hearne

Abstract Introduced maize (*Zea mays* L.) germplasm can serve as sources of favorable alleles to enhance performance in new maize varieties and hybrids under drought stress conditions. In the present study, the combining abilities of 12 exotic maize inbred lines from CIMMYT and 12 adapted maize inbred lines from IITA were studied for grain yield and other traits under controlled drought stress. The inbred lines from each institution were separated into groups using SSR-based genetic diversity and were intercrossed using a factorial mating scheme to generate 96 hybrids. These hybrids were evaluated under both controlled drought stress and well-watered conditions at Ikenne in Nigeria in 2010 and 2011. Average mean yields of hybrids under drought stress represented 23 % of the average yield of hybrids under full irrigation. General combining ability (GCA) effects accounted for 49–85 % of the observed variation for several traits recorded under both well-watered and drought stress conditions. Specific combining ability effects for grain yield, though positive in most hybrids, were not significant under drought stress conditions. All the twelve exotic and nine adapted lines had positive GCA effects (female, male, or both) for grain yield under either drought stress or full irrigation, or both environments. EXL03 and EXL15 that had positive and significant female and male GCA effects for grain yield under both environments can be used to improve their adapted counterparts for grain yield and drought tolerance. Normalized difference vegetation index had weak but significant correlation with grain yield.

Keywords Drought tolerance · GCA · Maize germplasm · NDVI · SCA

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Introduction

Drought occurs when rainfall ceases and its distribution is erratic during the growing cycles of crops (Mir et al. 2012). Drought is most devastating to crop productivity (Toker et al. 2007; Hao et al. 2011; Mir et al. 2012) and most recalcitrant to breeding (Tuberosa and Salvi 2006). Drought stress could reduce grain yield by 17 % with the loss reaching as high as 80 % when severe stress coincides with flowering and

grain filling stages in maize (Edmeades 1992). Imminent climate change occasioned by increasingly erratic rainfall and global warming may aggravate drought stress in the near future and subject maize to more drought-affected environments (Bolanos and Edmeades 1996; Betran et al. 2003; Campos et al. 2004; Messmer et al. 2009; Hao et al. 2011; Mir et al. 2012). Developing maize varieties that are tolerant to drought is, therefore considered critical for increasing the world's maize production (Campos et al. 2004; Xiong et al. 2006) and ensuring global food security (Mir et al. 2012).

Breeding maize for drought tolerance has been a major activity at IITA and CIMMYT to help attain food security in sub-Saharan Africa (Monneveux et al. 2006). Inbred lines with superior breeding values for yield and tolerance to abiotic stresses have been used as base materials to develop high-yielding and drought-tolerant hybrids (Hallauer et al. 1988; Dhliwayo et al. 2009). The introduction and use of exotic germplasm with superior sources of drought tolerance permit the expansion of the genetic base of drought-tolerant adapted source germplasm for developing new maize hybrid with greater levels of tolerance to drought stress. Such exotic germplasm can be invaluable sources of novel/favorable genes for adaptation to environmental stresses for introgression into adapted germplasms (Kim et al. 1987; Eberhart et al. 1995; Dhliwayo et al. 2009). A wide array of inbred lines with tolerance to drought and other environmental stresses that are adapted to the lowlands and mid-altitudes have been released in sub-Saharan Africa by CIMMYT and IITA (Everett et al. 1994a, b; Menkir et al. 2003). These inbred lines possessing favorable alleles for tolerance to drought stress have been exchanged among scientists in both institutions (Dhliwayo et al. 2009; Wen et al. 2011).

There is a growing advocacy for the application of precision agriculture technologies as a vital component of crop breeding activities (Barker and Sawyer 2012). Applications of remote-sensing tools based on the use of irradiation to estimate green biomass status at field level are gaining prominence in maize breeding. One of such devices that has been proposed for high throughput phenotyping in tropical maize adaptation under water stress (Lu et al. 2012) is a spectroradiometer, otherwise known as Greenseeker handheld optical sensor unit (NTech Industries 2007,

Inc., USA). It is used to measure normalized difference vegetation index (NDVI). NDVI, which is a measure of crop biomass captured in a non-destructive manner through remote sensing, and has been reported to be correlated with grain yield in wheat (Raun et al. 2001; Freeman et al. 2007) and maize (Martin et al. 2006; Teal et al. 2006; Verhulst and Govaerts 2010). It has also been studied as a potential secondary trait for measuring tolerance to drought stress in maize (Lu et al. 2011).

Genetic analyses of selected drought-tolerant CIMMYT lines along with IITA drought tolerant lines will be useful to facilitate systematic exploitation of the introduced lines to develop productive new inbred lines with higher levels of tolerance to drought. Several researchers found that additive genetic effects play a major role in conditioning grain yield under drought stress in tropical (Chapman and Edmeades 1999; Edmeades et al. 1999; Derera et al. 2008; Dhliwayo et al. 2009) and temperate (Betran et al. 2003) maize germplasm. Derera et al. (2008) also found non-additive gene action playing important roles in controlling grain yield under both drought stress and favorable growing environments. However, limited studies have been conducted to determine the combining abilities of lowland exotic and adapted inbred lines under managed drought stress conditions to identify suitable exotic lines with good combining abilities for introgression. This study was thus conducted to (i) determine the gene action controlling grain yield under managed drought stress conditions, (ii) identify suitable adapted and exotic lines with good combining ability for introgression, and (iii) assess the relationship between NDVI and grain yield under both well-watered and drought stress conditions.

Materials and methods

Field trials

Forty-eight tropical lowland white drought-tolerant inbred lines were characterized for diversity using microsatellite markers (Adebayo 2012) which separated the lines into two major groups in line with their origin. Among these, 24 lines were selected for use in the current study. These inbred lines were a subset of the association panel from the two major groups of a

diverse collection of 359 advanced drought-tolerant maize inbred lines genotyped recently using 1,260 single nucleotide polymorphism markers (Wen 2011). The 24 maize inbred lines comprising 12 each from CIMMYT and IITA (Table 1) were assigned into six groups of four lines each to generate 96 single-cross hybrids. The four lines included in each group showed some level of relatedness based on pedigree and SSR-markers (Adebayo 2012).

The four lines in one group were used as females and crossed with the four lines in another group used as males in each set based on a modified North Carolina Design II mating scheme (Menkir and Ayodele 2005). Each line was used as female or male in different sets. The resulting 96 F$_1$ hybrids, (Group I × Group IV, Group V × Group II, Group VI × Group III, Group II × Group I, Group IV × Group VI, and Group III × Group V), along with four hybrid checks were evaluated in a trial under managed

drought stress and full irrigation at Ikenne (6°54′N, 3°42′E, altitude 60 m) during the dry seasons in 2010 and 2011. Two of the hybrid checks—Oba 98 and Oba Super 1—are commercial hybrid maize varieties in Nigeria, while the remaining two checks—M1026-7 and M1026-8—are drought-tolerant synthetic hybrids developed at IITA yet to be released for public use.

Ikenne receives little rainfall from November to March of each year. The rainfall amounts during the months when drought stress treatment was imposed are 0 mm for December 2010 and January 2011, 0 mm also for December 2011 and January 2012. Rainfall amounts recorded for February 2011 and 2012 were 49 and 55 mm, respectively. The soil at this site is eutricnitrosol (FAO classification). The experimental fields are flat and reasonably uniform, with high water-holding capacity (Menkir et al. 2009). Trials were planted in two adjacent blocks that received different irrigation treatments. The first block (Block 1)

Table 1 Line code, pedigree, group, adaptation, and maturity of the 24 exotic and adapted DT maize inbred lines selected for NCD II hybrids development

No	Line code	Pedigree	Group	Adaptation	Maturity
1	EXL01	[CML-384xCML-176]F3-107-3-1-1-B-B-B-B-B	1	Exotic	Intermediate/late
2	EXL04	CIMCALI8843/S9243-BB-#-B-5-1-BB-2-3-2-B-B	1	Exotic	Intermediate/late
3	EXL05	CIMCALI8843/S9243-BB-#-B-5-1-BB-4-3-4-B-B	1	Exotic	Intermediate
4	EXL24	ZEWAc1F2-254-2-1-B-1-BBB-B-B	1	Exotic	Intermediate
5	EXL10	La Posta Seq C7-F102-1-3-1-1-B-B-B-B-B	2	Exotic	Intermediate
6	EXL15	La Posta Seq C7-F180-1-1-2-1-B-B-B-B-B	2	Exotic	Intermediate
7	EXL16	La Posta Seq C7-F180-3-1-1-1-B-B-B-B-B	2	Exotic	Intermediate/late
8	EXL17	La Posta Seq C7-F18-3-2-1-1-B-B-B-B-B	2	Exotic	Intermediate
9	EXL02	[SYN-USAB2/SYN-ELIB2]-12-1-1-2-BBB-B-	3	Exotic	Intermediate/late
10	EXL03	95S43SR HG"A"-94-1-1-1-B-B-B-B-B-B-B	3	Exotic	Intermediate
11	EXL06	CL-04374=P43Cameroon-4-1-1-1-1-3-3-B*7-B-B-B	3	Exotic	Intermediate
12	EXL07	CL-04935=(PR8549xP23C2)-5-1-3-B*14-B-B-B-B-B-B	3	Exotic	Intermediate
13	ADL34	TZL-COMP3-C2-S2-34-4-1-2-B-B-B-B-B-B	4	Adapted	Late
14	ADL35	DTPL-W-C7-S2-7-1-1-1-1-B-5-B-B-B-B-B-B	4	Adapted	Late
15	ADL36	DTPL-W-C7-S2-1-2-1-1-5-B-1-B-B-B-B-B-B	4	Adapted	Intermediate/late
16	ADL39	T115x9071-2-1-7-B-B-B-B-B-B-B-B-B-B	4	Adapted	Intermediate
17	ADL31	(KU1403x1368)-7-2-1-B-B-B-B-B-B-B-B	5	Adapted	Intermediate
18	ADL41	1368xGT-MAS-Gk-37-1-1-1-B-B-B-B-B-B-B-B	5	Adapted	Intermediate
19	ADL33	ACR-86-8-1-2-1-1-1-B-1-B-B-B-B-B-B	5	Adapted	Late
20	ADL47	1368xMi82-33-1-1-B-B-B-B-B-B-B	5	Adapted	Intermediate
21	ADL27	1368xICAL224-1x1368-3-1-B-B-B-B-B-B-B-B-B-B	6	Adapted	Late
22	ADL32	161-B-B-B-B-B	6	Adapted	Late
23	ADL37	1368xB73LPAX 1368-17-2-2-1-B-B-B-B-B-B-B-B	6	Adapted	Intermediate/late
24	ADL38	BabangoyoxMO17LPAxBabangoyo-23-4-3-4-B-B-B-B-B-B-B-B	6	Adapted	Intermediate/late

received irrigation until the crop had attained physiological maturity whereas the second block (Block 2) received irrigation only for 28 days which was ~3 weeks before anthesis. The blocks were separated by four ranges, each 4.25 m wide, to restrict lateral movement of water from the fully irrigated block to the drought stress block. Overhead sprinkler irrigation system that dispensed 12 mm of water per week was used. All field management practices were uniform for both well-watered and drought stress trials. The hybrids were arranged in a 10×10 lattice design with three replications and were planted in single-row plots, 4 m long with spacing of 0.75 m between rows and 0.50 m spacing between plants within a row in each block. Three seeds were sown per hill and later thinned to two plants per hill 2 weeks after planting (2 WAP) to attain a population density of 53,333 plant/ ha^{-1}. Fertilizer was applied at the rate of 60 kg N, 60 kg P, and 60 kg K per hectare at planting. An additional 60 kg ha^{-1} N was applied in the form of urea as top dressing 4 weeks later. In each trial, gramoxone and primextra were applied 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). Subsequently, manual weeding was done to keep the trials weed-free.

PVC access tubes were installed in December 2010 and 2011 in both well-watered and drought stress blocks to monitor soil moisture content during the growing cycle of the crop. Soil profiles were dug in each block by inserting a 2 m long PVC access tube into each soil profile using specialized installation kits and procedures contained in access tube installation guide version 1.0 (Sentek Sensor Technologies 2003).

Soil moisture content measurements commenced at Ikenne 35 DAP in each year using a portable soil moisture monitoring system known as Diviner 2000 which had a display unit and a portable 1.6 m long probe with a Diviner Cable. With the 1.6 m probe soil moisture readings were taken at regular intervals of 10 cm down through the soil profile. Soil moisture content scores were taken through the wall of a PVC access tube by remote sensing following the procedures described in Diviner 2000 Portable Soil Moisture Monitoring Solution User Guide Version 1.5 (Sentek Pty Ltd). Data were recorded first on weekly basis and later on daily basis when the impact of water stress became very critical in each year. Data were

downloaded from the Diviner 2000 display unit on a desktop computer.

Normalized difference vegetation index (NDVI) measurement

The Greenseeker Handheld Optical Sensor Unit (Ntech Industries 2007, Inc.), installed with red sensor, red waveband centered at 650 ± 10 nm, and near infra-red (NIR) band centered at 770 ± 15 nm, was used to collect NDVI measurements in each block at Ikenne in 2010 and 2011. The device was held at a distance of about 60 cm above the canopy while each plot was traversed, starting from the beginning of the row to the end, and data were collected in log plots mode. A HP iPAQ installed with NTech capture programme for pocket PC was used to measure, compute and save NDVI scores directly from the Greenseeker. The device computes the NDVI according to the following formula:

$$\text{NDVI} = (R_{NIR} - R_{RED})/(R_{NIR} + R_{RED}),$$

where $R_{NIR} =$ the fraction of emitted NIR radiation returned from the sensed area (reflectance), and $R_{RED} =$ the fraction of the emitted red radiation returned from the sensed area (reflectance). Measurements were taken in each block at 3-leaf stage (2 WAP) as NDVI_1 and 8-leaf stage (4 WAP) as NDVI_2. The data were later transferred by syncing the iPAD to a synchronized desktop computer for further processing.

Agronomic data recording

Data were recorded from each plot in both drought-stress and fully irrigated blocks at Ikenne in 2010 and 2011. Days to 50 % anthesis (DTA) and days to 50 % silking (DTS) were recorded as the number of days from planting to when 50 % of plants in a plot sheded pollen, and had emerged silks, respectively. Anthesis-silking interval was computed as the difference between DTS and DTA. Ear aspect (EASP) was also 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. Leaf senescence (LFDTH) was rated in the drought stress block on a scale of 1–9 at 10 WAP, where 1 = almost all leaves were green and 9 = virtually all leaves were

dead. The total number of plants and ears were counted in each plot at the time of harvest. The number of ears per plant (EPP) was then computed as the proportion of the total number of ears at harvest divided by the total 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 analysis

Separate analyses of variance were performed on the data collected in 2010 and 2011 for each environment (drought stress and well-watered) to generate entry means adjusted for block effects according to an alpha lattice design (Patterson et al. 1978). Replications, years and incomplete blocks were considered as random effects while experimental hybrids were considered as fixed effects. Hybrids were then analyzed as a randomized complete block design (RCBD) because the lattice designs did not have significant advantage over RCBD. Analysis of variance was also conducted for the 96 single-cross hybrids according to a North Carolina Design II (Comstock and Robinson 1948) with hybrids nested within sets for each water treatment, and then combined across years. The variation among hybrids was partitioned into that due to male and female parents within sets and interaction between female and male parents pooled across sets. General combining ability (GCA) effects of both male and female parents were estimated for each line, and specific combining ability (SCA) effects were estimated as the interaction between parents. Significance of each effect was tested using the mean squares for their respective interaction with year. The mean squares due to GCA × year within sets and SCA × year within sets were tested for significance using the pooled error mean squares. All analyses were performed with PROC GLM in SAS (SAS Institute 2009) using a RANDOM statement with TEST option. Drought tolerance index (DTI) was computed as a percentage of GY loss due to drought stress on the yield realized under full irrigation (Menkir et al. 2003; Derera et al. 2008) as:

DTI (%) = [(yield under well-watered − yield under drought)/yield under well-watered] × 100.

Pearson's correlation coefficients were calculated using the mean values of all the measured traits. Also, linear regression models were used to determine the relationships between GY and NDVI using PROC REG in SAS (SAS Institute 2009).

Results

Results of the soil moisture content monitored with Diviner 2000 during the flowering periods of the maize crop under both well-watered and drought stress conditions in 2010/11 and 2011/12 dry seasons at Ikenne can be found in Adebayo (2012). As expected, the soil moisture content at every 10 cm depth down the soil profile in fully irrigated block was always higher than that of drought stress blocks. The volumetric water content assumes downward trend at every data point in the drought stress block while it fluctuates in the well-watered block because of weekly irrigation (Adebayo 2012).

In the analysis of variance combined over years, the sets had a significant effect on most traits except on NDVI_1 under both irrigation treatments, and EPP under full irrigation (Table 2). The year effect was significant for GY, NDVI_1, LFDTH, EASP, EPP, and NDVI_2 under drought stress. It was also significant for DTS, NDVI_1, NDVI_2, and ASI under full irrigation. Hybrids (sets) differed significantly for all measured traits under both irrigation treatments (Table 2). Hybrids × year interaction was significant for DTS, ASI, EASP, and NDVI_1 under full irrigation, and for LFDTH only under drought stress. Mean squares for both females (sets) and males (sets) were significant ($P < 0.05$) for most of the traits under both environments, except for males (sets) for GY and NDVI_2 and for females (sets) for NDVI_2 under drought stress, as well as for females (sets) for EPP, NDVI_1, and NDVI_2 and for males (sets) for NDVI_1 under full irrigation. The females × males interaction (SCA) was significant ($P < 0.05$) only for NDVI_2 under drought and for GY, EASP, EPP, and NDVI_2 under full irrigation. Also females × year (sets) interaction had significant effect on EASP and NDVI_1 but a weak effect on GY and EPP under full irrigation. Significant males × year (sets) interaction effects were detected for GY and NDVI_2 under drought stress, and for only ASI under full irrigation. The females × males × year (sets) interaction effects

were significant for NDVI_1 and LFDTH under drought stress, and also for ASI under full irrigation (Table 2).

Estimates of the females and males GCA effects and standard errors for GY of the 24 adapted and exotic DT maize inbred lines under both drought stress and well-watered conditions are presented in Table 3. Under drought stress, seven exotic and three adapted lines had significant and positive GCA effects for GY when they were used both as male and female parents. Four exotic and two adapted lines had significant GCA effects for GY when they were used both as male and female parents under full irrigation. Two exotic (EXLO3 and EXL15) and two adapted (ADL33 and ADL47) lines had significant and positive GCA effects for GY when they were used in crosses as both male and female parents under drought stress and full irrigation. Seventeen hybrids had significant SCA effects for GY under drought stress whereas 16 hybrids had significant SCA effects for GY under full irrigation (data not shown).

Results from partitioning the cross sums of squares revealed that GCA accounted for over 70 % of the variation among hybrids for DTS and ASI under both irrigation treatments, for EASP under full irrigation and for LFDTH under drought stress (Table 4). GCA also accounted for 62 and 67 % of the variation for GY under drought stress and full irrigation, respectively

Table 2 Mean squares from the combined analyses of variance for the traits measured in hybrids evaluated under both well-watered and drought stress conditions at Ikenne in Nigeria in 2010 and 2011

Source of variation	Df	[1]GY (kg ha^{-1})	DTS (days)	ASI (days)	EASP (1–5)	EPP (no)	NDVI_1	NDVI_2	LFDTH (1–9)
Well-watered environment									
Year	1	11995239	333.8**	9.6*	1.9	0.01	0.5***	3.7**	–
Sets	5	44709757**	42.6**	16.1**	4.4*	0.1	0.003	0.1*	–
Hybrids (sets)	99	6479609***	10.3***	3.3***	0.8***	0.02***	0.001***	0.07***	
Hybrids × year (sets)	99	1484621.3	3.5**	1.0*	0.3*	0.01	0.001**	0.03	
GCA$_f$ (sets)	18	6704972*	15.0**	4.4***	1.0**	0.02	0.001	0.01	–
GCA$_m$ (sets)	18	6607642***	15.4***	4.0*	0.7**	0.02**	0.0004	0.02**	–
SCA (sets)	54	2195835**	2.8	1.0	0.2**	0.01**	0.0004	0.01*	–
GCA$_f$ × year (sets)	18	2183407*	2.9	0.4	0.3**	0.01*	0.001**	0.01	–
GCA$_m$ x year (sets)	18	947991	1.2	1.4*	0.2	0.01	0.0002	0.004	–
SCA × year (sets)	54	986147	1.9*	0.8	0.1	0.01	0.0003	0.004	–
Drought stress environment									
Year	1	82426623**	56.1	37.7	20.6*	1.1*	0.3**	0.6*	882.4**
Sets	5	15462783**	164.0**	69.6**	3.8**	0.4*	0.001	0.1**	21.2*
Hybrids (sets)	99	1812775***	38.3***	14.3***	0.7***	0.1***	0.001*	0.004***	6.2***
Hybrids × year (sets)	99	705644.0	10.2	5.1	0.2	0.04	0.001	0.002	1.7**
GCA$_f$ (sets)	18	1397510*	54.2**	18.4*	0.7**	0.1**	0.0003	0.02*	10.7**
GCA$_m$ (Sets)	18	1251998	53.4**	14.0**	0.9*	0.1*	0.001*	0.02	8.3***
SCA (sets)	54	546784	9.2	3.3	0.3	0.04	0.0005	0.01*	1.1
GCA$_f$ × year (sets)	18	584559	11.5	5.9	0.1	0.02	0.0003	0.01	1.7
GCA$_m$ × year (sets)	18	1061556*	8.9	2.8	0.4	0.02	0.0004	0.01**	0.9
SCA × year (sets)	54	562883	8.2	4.1	0.2	0.03	0.001*	0.004	1.2*

[1] *GY* grain yield; *DTS* days to 50 % silking; *ASI* anthesis-silking-interval; *EASP* ear aspect (1–5) where 1 = clean, uniform, large, and well-filled ears and 5 = rotten, variable, small and partially filled ears; *EPP* number of ears per plant calculated as ratio of plants harvested to ears harvested; *NDVI_1* and *NDVI_2* average NDVIs measured two and four WAP, respectively; *LFDTH* leaf death score (1–9) where 1 = almost all leaves are green and 9 = virtually all leaves are dead

*, **, *** Significant at $p < 0.05$, 0.01, and 0.0001, respectively

Table 3 Estimates of females and males GCA effects for GY of 24 adapted and exotic DT inbred lines evaluated in factorial crosses in sets under drought and well-watered conditions at Ikenne in Nigeria in 2010 and 2011

| Line | Grain yield (kg ha^{-1}) | | | |
| | Drought stress environment | | Well-watered environment | |
	GCA$_f$	GCA$_m$	GCA$_f$	GCA$_m$
EXL01	−685.1	449.9*	−1612.0	−432.4
EXL04	−336.4	233.6*	−63.6	575.9*
EXL05	−456.4	599.0*	39.6	278.2*
EXL24	−414.8	169.4*	−1030.0	−336.7
EXL10	541.3*	119.0	−191.7	768.3*
EXL15	491.4*	578.6*	345.5*	1400.0*
EXL16	89.9	333.6*	405.4*	1373.6*
EXL17	329.4*	461.8*	−474.1	779.3*
EXL02	401.9*	309.5*	−149.5	−213.6
EXL03	350.4*	209.2*	343.0*	270.1*
EXL06	−314.4	−105.1	1363.2*	1072.7*
EXL07	253.8*	306.2*	107.7	−563.4
ADL34	−678.4	−512.5	−1028.0	−710.1
ADL35	−684.2	−530.2	−847.6	−785.4
ADL36	−495.0	−541.3	−821.2	−220.5
ADL39	−606.0	308.7*	−1273.0	−950.3
ADL31	73.4	−72.4	493.8*	103.8
ADL33	226.3*	208.7*	1149.4*	289.7*
ADL41	698.5*	138.8*	1265.6*	57.8
ADL47	494.8*	416.7*	1412.6*	1213.1*
ADL27	−312.3	−1227.0	187.9*	−1920.0
ADL32	483.5*	−533.4	1053.6*	−1204.0
ADL37	405.6*	−544.9	−332.4	−656.8
ADL38	−143.0	−158.3	−343.4	−189.7
SE	61.19	61.16	81.20	81.23

* Significantly different from zero at ≥2SE

Table 4 Percentages of hybrid sums of squares contributed by female GCA and male GCA, and SCA for selected traits evaluated under drought and well-watered environments for 2 years at Ikenne in Nigeria

| Traits | Irrigation treatment | GCA$_f$ | GCA$_m$ | SCA |
		Percentages of hybrid sums of squares		
Grain yield (kg ha^{-1})	Drought	33	29	38
	Well-watered	34	33	33
Silking dates (d)	Drought	40	39	21
	Well-watered	39	40	21
Anthesis-silking-interval (d)	Drought	44	33	23
	Well-watered	38	35	27
Ear aspect (1–5)	Drought	29	38	32
	Well-watered	43	28	29
Number of ears per plant	Drought	31	26	43
	Well-watered	25	27	48
[a]NDVI_1	Drought	13	38	49
	Well-watered	30	19	51
NDVI_2	Drought	27	30	43
	Well-watered	18	35	47
Leaf death score (1–9)	Drought	48	37	15
	Well-watered	–	–	–

[a] NDVI_1 and NDVI_2 measured with a Greenseeker at two and four WAP, respectively

Discussion

The level of stress imposed on experimental hybrids in drought stress blocks was monitored during the two seasons to attain adequate stress intensity that elicited differential responses of hybrids in this study. The volumetric soil water content within the maize root zone of 30–60 cm in the well-watered environment was nearly doubled that in the drought stress block (Adebayo 2012). The average GY of hybrids recorded under drought was 23 % of that recorded under well-watered conditions which fell within the range of 20–30 % yield reduction that has been considered as severe drought stress in other studies (Bolanos and Edmeades 1996; Banziger et al. 2000). Significant variation for GY under drought observed in this study was an indicator of expression of differential levels of tolerance to drought in maize hybrids. Rosielle and Hamblin (1981) and Derera et al. (2008) have also reported differential responses of tropical maize hybrids to drought tolerance. The absence of significant hybrids × year interaction suggested that

(Table 4). Differences attributable to SCA were more than 30 % for GY, EPP, NDVI_1, and NDVI_2 under both irrigation treatments and for EASP scores under drought stress (Table 4).

The relationship of GY with NDVI_2 was strong (r = 0.64***) under full irrigation. Also, GY was positively and significantly correlated with EPP (r = 0.8***) under drought stress. GY was, however, negatively and significantly correlated with DTS under drought (r = −0.7***) and with EASP under both environments (r = −0.8**).

hybrids had consistent performance across seasons, which was consistent with the result of Derera et al. (2008). It thus appears that superior hybrids with enhanced drought tolerance and high yield potential can be selected.

The preponderance of additive genetic effects for GY and other traits under both irrigation treatments indicate that genetic gains can be achieved to further improve these traits. Genetic gains from selection can be realized for traits that are controlled by additive genetic effects (Betran et al. 2003; Derera et al. 2008; Hallauer 2010). Non-additive genetic effects were also important in controlling GY, ear aspect, and number of EPP under well-watered conditions, consistent with results reported in other studies (Pswarayi and Vivek 2008; Derera et al. 2008; Dhliwayo et al. 2009). The observed similar proportions of GCA sums of squares for GY for female and male under well-watered conditions suggests that both parents made equal contributions to this trait. Although the males and females had similar GCA effects for GY under drought stress in this set of germplasm, the differences observed for anthesis-silking-interval, number of EPP and LFDTH underscore the importance of maternal effects for drought tolerance as earlier suggested by Derera et al. (2008). The contributions of SCA effects to the variation in GY, ear aspect, and number of EPP (>30 %) under drought suggests that non-additive gene action also played an important role in controlling these traits, which were similar to the results reported in other studies (Derera et al. 2008; Dhliwayo et al. 2009). The contribution of SCA effects was also sizeable for the control of NDVI which is measure of green biomass. The observed difference in percentages of variance due to male and female GCA for EASP scores under drought suggests that paternal effects play an important role in controlling the trait, which contrasts with the report of Derera et al. (2008). This was contrary to expectation because the seed parent would determine the appearance of the maize ears as a result of the effects of cytoplasmic factors.

Most of the exotic lines that had significant GCA effects for GY under both environments combine the genes for drought tolerance and high yield potential in their crosses. Two lines namely, EXL03 and EXL15, were outstanding because they combined well with other lines under both drought stress and full irrigation. These inbred lines can be used as superior sources of drought tolerance for improvement of adapted germplasm. Similarly, two adapted lines namely, ADL33 and ADL47 that combined well with other inbred lines under both drought stress and full irrigation can serve as base material for crossing with exotic lines to generate source populations for new generation of maize inbred lines with higher levels of drought tolerance and productivity. Efforts are under-way to recombine these good combiners into source population for developing new productive inbred lines.

The significant and positive correlation between GY and NDVI, particularly at 8-leaf stage, in our study was in agreement with the results of several other workers (Araus et al. 2010; Islam et al. 2011; Lu et al. 2011). A stronger relationship that existed between NDVI and GY under full irrigation indicates the potential predictive value of aboveground biomass for GY in maize under optimum growing conditions (Teal et al. 2006; Islam et al. 2011). This was also attributed to the maximum biomass which is accumulated later at seedling stage in cereals (Cabrera-Bosquet et al. 2011). Hybrid maize genotypes that accumulate higher aboveground biomass at the vegetative stage often produce high GY when growing conditions are optimal than when there is drought stress. In this study, NDVI at 8-leaf stage explained less variation in GY under full irrigation compared to what has earlier been reported in wheat and maize, when NDVI was normalized by the number of days of growth (Raun et al. 2001; Teal et al. 2006).

This study shows the rationale for sourcing favorable and unique alleles from exotic germplasm to improve adapted germplasm for drought tolerance in sub-Saharan Africa. Earlier efforts at utilizing exotic drought-tolerant germplasm from CIMMYT, Mexico, for drought tolerance breeding programs in sub-Saharan Africa were successful, leading to expression of appreciable levels of tolerance in the resultant germplasm (Sawkins et al. 2006).

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