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Genetic variability for drought tolerance in early-maturing maize inbreds under contrasting environments

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Abstract

Drought severely constrains maize (*Zea mays* L) production in the savannas of West and Central Africa (WCA). Understanding the levels of drought tolerance in early-maturing maize inbreds is crucial for the development of drought-tolerant maize hybrids for the sub-region. A total of 156 inbred lines were evaluated under drought and well-watered conditions at Ikenne and Bagauda in Nigeria for 2 yr. The objectives were to (i) determine the levels of drought tolerance in early-maturing inbreds, (ii) assess the performance of the inbreds and relationship among traits under the contrasting environments, and (iii) identify the most stable inbreds across environments. Inbreds differed significantly ($p < 0.01$) in grain yield and other measured traits under drought and well-watered conditions. Grain yield of inbreds was significantly ($p < 0.01$) correlated with ears per plant ($r = 0.50$), anthesis-silking interval ($r = -0.55$), plant aspect ($r = -0.57$), ear aspect ($r = -0.35$) and stay-green characteristic ($r = -0.28$) under drought. Forty-eight percent of the lines were identified as drought tolerant with tolerance indices ranging from 0.17 to 15.31. Broad-sense heritability estimate was 43% for grain yield under drought and 47% under well-watered conditions. Drought reduced grain yield of the inbreds by 3-88%, averaging 52%. Biplot analysis identified inbreds TZEI 18, TZEI 56, TZEI 1, and TZEI 19 as the most stable across environments. The inbreds with high levels of drought tolerance could be utilised for the development of drought-tolerant hybrids and synthetic varieties as well as for introgression of tolerance genes into tropical maize breeding populations.

Keywords: drought, early-maturing inbred lines, heritability, maize, tolerance indices

Introduction

Food security is a major challenge confronting developing countries in West and Central Africa (WCA). The greatest contribution to food security is expected from maize (*Zea mays* L) because it is the most predominant staple crop grown by majority of rural populace in the savannas agro-ecologies of WCA. It serves as an important source of protein and calories for the poor rural dwellers in the sub-region and occupies an important position in the food, feed and agro-industrial economy of WCA. The savanna agro-ecology of WCA has the greatest potential for maize production and productivity due to its high incoming solar radiation, low night temperatures, adequate rainfall as well as low incidence of pests and diseases. However, despite the high potential of maize in the savannas, its productivity is threatened by several biotic and abiotic stresses. Prominent among the stresses are recurrent drought, parasitic weed, *Striga hermonthica* Del Benth and low soil nitrogen (low-N).

Due to climatic changes caused mainly by global warming, semi-arid and subhumid zones of WCA are characterized by high interannual rainfall variability, and drought or excess water occurrence at any time during the growing season (Haussmann et al, 2012). Recurrent drought is the major abiotic stress contributing to maize yield loss in the lowland savanna belt of WCA (Fajemisin et al, 1985). The risk of drought is particularly high in the Sudan savanna zone because rainfall is unreliable and its distribution is erratic in much of this area (Eckebil, 1991). Even in those lowlands with adequate precipitation for maize production, periodic drought can occur at the most drought-sensitive stages of the crop development, flowering and grain filling periods. Annual maize yield loss due to drought is estimated to be 15% in WCA (Edmeades et al, 1995). However, drought stress that coincides with silking and grain filling stages of maize growth and development could reduce yields by 50% and 20%, respectively (Denmead and Shaw, 1960). Other reports indicate that although drought may occur at any stage of maize growth and development, the greatest damage occurs when drought coincides with flowering and grain-filling periods and yield losses can be between 40 and 90% (NeSmith and Ritchie, 1992; Menkir and Akintude, 2001; Badu-Apraku et al, 2011a; Badu-Apraku and Oyekunle, 2012; Oyekunle and Badu-Apraku, 2013).

Presently, open-pollinated cultivars are the predominant maize types cultivated by farmers in the sub-region. The low rate of adoption of hybrids may be attributed to lack of availability of productive hybrids and well established private seed companies to

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provide adequate quantities of good quality hybrid seed in the sub-region. Breeding strategies adopted by the International Institute of Tropical Agriculture (IITA) and National Maize Improvement Programs in the sub region to overcome the problem include the development of several extra-early (80-85 days), early-maturing (90-95 days) and intermediate/late (100-120 days) inbred lines for production of superior hybrids. To accelerate the progress in developing outstanding hybrids by IITA for the sub region, knowledge and understanding of the breeding values of the available IITA early inbred lines in contrasting environments is highly desirable. This information would help in devising a viable breeding strategy to develop hybrids adapted to the target environments.

Information on the genotypic correlations between traits is of interest to breeders selecting for improved grain yield of early maize under contrasting environments. This information is required because it indicates the magnitude and direction of association among traits, correlated responses to selection, relative efficiency of indirect selection as well as permit the computation of appropriate multiple trait selection indices (Falconer and Mackay, 1996). Heritability of grain yield has been reported to be low under stress conditions (Badu-Apraku et al, 2004; 2005). Therefore, the use of secondary traits that have strong association with yield under stress conditions has been proposed for yield improvement. Under drought and low-N conditions, secondary traits such as number of ears per plant (EPP), rate of leaf senescence, and anthesis-silking interval (ASI) have been reported to have strong correlation with yield and have been exploited to select for higher levels of tolerance to the two stresses in maize (Lafitte and Edmeades, 1995; Bänziger and Lafitte, 1997; Badu-Apraku et al, 2011b). Lafitte and Edmeades (1995) reported strong correlations for maturity, plant height, and 100-kernel weight under low-N stress. Badu-Apraku et al (2011b) reported strong correlation between grain yield, days to silk, days to anthesis, stay green characteristics, ASI, plant height, ears per plant, ear aspect, and plant aspect under low-N conditions. Furthermore, Badu-Apraku et al (2011b) in a study of the relationships among traits of tropical early maize cultivars in contrasting environments reported that the most reliable traits for selection for improved grain yield under drought were plant and ear aspects, ASI, and EPP and indicated that stay green characteristics was not identified as a reliable trait for selection for drought-tolerant genotypes. In contrast, Badu-Apraku et al (2011c) in a study of the selection of extra-early maize inbreds under low N and drought at flowering and grain-filling for hybrid production reported weak association between grain yield and other traits under drought stress.

Although early-maturing inbred lines have the potential to perform well under limited water conditions through escape mechanism and/or presence of drought tolerance genes (Badu-Apraku et al, 2012), few studies have been conducted to determine the level of drought tolerance in early-maturing maize inbred lines developed by IITA. The magnitude and direction of association among traits of early maize inbreds under contrasting environment required further investigation. The objectives of the present study were to (i) determine the levels of drought tolerance in a set of IITA early-maturing inbred lines, (ii) assess the performance of early-maturing drought tolerant inbreds lines and the relationship between grain yield and other agronomic traits, and (iii) identify the most stable inbred lines across drought and well-watered conditions.

Materials and Methods

Experimental procedures

One hundred and fifty-six early-maturing maize inbred lines extracted from six diverse germplasm sources, TZE-W Pop DT STR C0, WEC STR, TZE-Y Pop DT STR C0, TZE Comp 5-Y C6, TZE-W Pop x LD, and TZE-W Pop x 1368 STR C0, with tolerance or resistance to Striga and maize streak virus, and/or tolerance to drought were used for the present study. The inbred lines were developed by West and Central Africa Collaborative Maize Research Network / International Institute of Tropical Agriculture (WECAMAN/IITA). The 156 inbred lines were evaluated using a 12 x 13 incomplete block design with two replications under both drought and well-watered conditions. The lines were evaluated under managed drought at Ikenne (forest-savanna transitional zone, 6°87'N, 3°70'E, 60 m asl, 1500 mm annual rainfall) during the dry seasons (November and March) of 2007/2008 and 2008/2009 and in well-watered environments during the growing seasons between May and August at Ikenne and June to September at Bagauda (Sudan savanna, terminal drought stress environment; 12°00' N,8°22'E, 580 m asl, 800 mm annual rainfall) in 2008 and 2009.

The dry season experiments at Ikenne were irrigated using an overhead sprinkler irrigation system, which applied about 17 mm of water per week from planting until 28 days after planting thus allowing the crop to mature on stored soil moisture. Induced drought stress was imposed by withdrawing irrigation water 28 days after planting until physiological maturity. The weekly rainfall pattern at drought screening site (Ikenne) is presented in Supplementary Figure 1. At Bagauda and Ikenne during the growing seasons, the plants relied on natural rainfall for growth and development. Except for the water treatments, all management practices for both well-watered and induced drought stressed experiments were the same. Each experimental unit was a one-row plot, 4 m long with a row spacing of 0.75 m and intra-row spacing of 0.4 m. Three seeds were planted per hill and the seedlings were thinned to two per hill about 2 weeks after emergence, resulting in a final plant population density of about 66,000 plants ha^{-1}. A compound fertilizer (NPK 15:15:15) was applied at the rate of 60 kg N ha^{-1}, 60 kg P ha^{-1}, and 60 kg K ha^{-1} 2 weeks after planting (WAP) for all experiments except those under induced drought that had the fertilizer applied at planting. An additional 60 kg N ha^{-1} urea was top-dressed 3 WAP. In all the trials, the field was kept weed-free through the application of a mixture of gramoxone (Shandong Dongtai Agricultural Chemistry Co Ltd), a foliar contact herbicide, and primextra (Syngenta Crop Protection Canada, Inc), a pre-emergence herbicide, at 5 l ha^{-1} each of gramoxone and primextra. Subsequently, manual weeding was done as necessary to keep the trials weed-free.

Data Collection

Days to anthesis and silking were recorded as the number of days from planting to when 50% of the plants in a row had shed pollen and had emerged silks. Anthesis-silking interval was computed as the interval in days between silking and anthesis. Plant and ear heights were measured as the distance from the base of the plant to the height of the first tassel branch and the node bearing the upper ear. Plant aspect was based on overall plant type (plant and ear heights, uniformity of plants, cob size, disease and insect damage and lodging) and was recorded on a scale of 1 to 5 where 1 = excellent plant type and 5 = poor plant type. Ear aspect was based on freedom from disease and insect damage, ear size, uniformity of of ears and was recorded on a scale of 1 to 5, where 1 = clean, uniform, large, and well-filled ears and 5 = rotten, variable, small, and partially or poorly filled ears. In addition, leaf senescence scores were recorded for the drought-stressed plots at 70 days after planting on a scale of 1 to 10, where 1 = 0–10% dead leaves; 2 = 10–20% dead leaves; 3 = 20–30% dead leaves; 4 = 30–40% dead leaves; 5 = 40–50% dead leaves; 6 = 50–60% dead leaves; 7 = 60–70% dead leaves; 8 = 70–80% dead leaves; 9 = 80–90% dead leaves, and 10 = 90-100% dead leaves. The total number of plants and ears were counted in each plot a few days before harvesting. The EPP was computed as the proportion of the total number of ears at harvest divided by the number of plants at harvest. In addition to the above field data, cob length, cob diameter, number of rows per cob and weight of 100 kernels were recorded. Ear length was measured with a ruler, ear diameter was measured with vernier calipers, and 100-kernel weight was determined using a metler balance. Under drought stress environments, ears harvested from each plot were shelled and used to determine percentage grain moisture and grain weight. Grain yield, adjusted to 15% moisture, was computed from the shelled grain weight. On the other hand, under well-watered environments, harvested ears from each plot were weighed and representative samples of ears were shelled to determine percent grain moisture. Grain yield adjusted to 150 g kg^{-1} moisture, was computed from ear weight and grain moisture assuming a shelling percentage of 80%.

Statistical Analysis

Analysis of variance (ANOVA) was first carried out for each environment. Thereafter, combined ANOVA across environments (locations × year) was conducted separately for data collected under drought stress and well-watered environments with PROC GLM in SAS using a random statement with the TEST option (SAS Institute, 2002). Environment and inbreds were considered as random effects. Thus, a random model was used in the analysis. Significant differences among inbred lines were tested with inbred x environment interaction mean squares while inbred x environment interaction was tested with error mean squares.

In order to characterize the inbred lines for tolerance to drought, a base index was used (Badu-Apraku et al, 2011d; Oyekunle and Badu-Apraku, 2013). The index combined superior grain yield under drought with low values (i.e. desirable trait expressions) for plant aspect, ear aspect, and leaf senescence, short ASI, increased number of ears per plant, and grain yield under well-watered conditions. Since each parameter was standardized with a mean of zero and standard deviation of 1 to minimize the effects of different scales, a positive value indicated tolerance of lines to drought while a negative value indicated susceptibility of lines to drought. The base indices were estimated as follows:

Base index = [(2 x $Yield_{ds}$) + $Yield_{ww}$ + Cob per plant - ASI - Plant aspect - Ear aspect - Leaf senescence score], where ds = drought conditions, ww = well-watered conditions

Correlation analysis was computed among traits of inbred lines under drought and well-watered environments. The correlation analysis was carried out using the SAS package, version 9.2 (SAS Institute, 2002). Mean grain yield of inbreds under drought was regressed on mean grain yield of inbreds under well-watered environments.

Broad-sense heritability (Hn) and standard errors (SE) for heritability estimates were estimated according to Hallauer and Miranda (1988) from pooled male and female sums of squares. The equations used to estimate heritability and the standard errors of heritabilities were as follows:

$$Hb = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2 / e + \sigma_E^2 / re}$$

$$S.E.(Hb) = \frac{S.E.\sigma_G^2}{\sigma_G^2 + \sigma_{GE}^2 / e + \sigma_E^2 / re}$$

where σ^2_G = Genotypic variance, σ^2_{GE} = genotype x environment interaction variance, σ^2_E = environmental variance, e = number of environments, and r = replications.

Twenty-nine inbreds comprising the best 24 and the worst five entries in terms of grain yield were selected based on the results of the combined ANOVA across test environments. The inbred yield data were subjected to genotype main effect plus genotype × environment interaction (GGE) biplot analysis to decompose G + (G × E) interactions (Yan, 2001; Yan et al, 2000; 2007). The GGE biplot was used to identify the best inbreds in terms of yield and stability and the ideal genotypes across environments. The analyses were done using GGE biplot, a Windows application that fully automates biplot analysis, version 5.4 (Yan, 2001). The programme is available at www.ggebiplot.com (verified 23 September 2014). The GGE biplot model equation is:

$$Y_{ij} - Y_j = \lambda_1 \xi_{i1} \eta_{j1} + \lambda_2 \xi_{j2} \eta_{j2} + \Sigma_{ij}$$

where: Y_{ij} is the average yield of genotype i in environment j, Y_j is the average yield across all genotypes in environment j, λ_1 and λ_2 are the singular values for PC1 and PC2, ξ_{i1} and ξ_{j2} are the PC1 and PC2 scores, for genotype i, η_{j1} and η_{j2} are the PC1 and PC2 scores, for environment j, Σ_{ij} is the residual of the model associated with the genotype i in environment j. The data were neither transformed («Transform=0»), nor standardized («Scale=0»), and were environment centered («Centering=2»).

Results

Performance of early-maturing inbred lines under drought and well-watered conditions

Results of the combined analysis of variance of the inbred lines across environments revealed significant differences among genotypes and environments, as well as genotype × environment interactions for grain yield and all other measured traits under drought and well-watered conditions (Table 1). Means and ranges of the traits of the inbred lines under drought and well-watered conditions are presented in Table 2. Grain yield ranged from 0.03 t ha^{-1} for TZEI 151 to 1.92 t ha^{-1} for TZEI 17 under drought and from 0.50 t ha^{-1} for TZEI 74 to 3.13 t ha^{-1} for TZEI 18 under well-watered conditions. The grain yield reduction ranged from 1.6 % for TZEI 166 to 97.3% for TZEI 151 (data not shown). The mean grain yield ranged from 12 to 97% with an average of 48% of the average grain yield under optimal growing environments in the same environments (Table 2).

Under induced moisture stress, days to anthesis of the inbreds varied from 49 for TZEI 87 to 60 for TZEI 152; days to silking from 50 for TZEI 150 to 66 for TZEI 152; ASI from 0 for TZEI 17 to 6 for TZEI 152. Plant height of the inbreds ranged from from 64.7 cm for TZEI 116 to 172.5 cm for TZEI 72 (Table 2). Under well-watered conditions, days to anthesis increased compared to the value obtained under drought and ranged from 54 for TZEI 168 to 64 for TZEI 152. Similarly, days to silking ranged from 54 for TZEI 87 to 66 for TZEI 152; plant height ranged from 72.5 cm for TZEI 115 to 291.6 cm for TZEI 162. However, under well-watered environments, ASI decreased and ranged from 0.2 for TZEI 87 to 5.1 for TZEI 13; ear height from 36.8 cm for TZEI 156 to 81.4 cm for TZEI 148. On the average, drought reduced days to anthesis by 6.9%, days to silking (5.1%), EPP (16%), 100-kernel weight (17%), but increased ASI by 28%, and worsened plant aspect by 15%, ear aspect (17%), and stalk lodging (74%). The wide variation observed in in the performance of maize inbred lines for grain yield and other measured traits under drought and well-watered conditions reflected the extent of genetic variability as well as the severity of drought imposed during the flowering and grain filling periods.

Twenty inbred lines consisting of the best 10 and the worst 10, selected using the base index are presented in Table 3. TZEI 17 had the highest drought tolerance index (15.31) while TZEI 123 had the lowest (-14.60). The inbreds with the positive base index values had higher grain yield, increased EPP, shorter ASI, improved ear and plant aspects and delayed leaf senescence under drought. Thus, the best 10 inbred lines with positive base indices were classified as drought tolerant while the 10 inbreds with nega-

Table 1 - Mean squares from analysis of variance for grain yield and other agronomic traits of 156 early-maturing maize inbred lines evaluated under drought at Ikenne during 2007/2008 and 2008/2009 dry seasons and well-watered conditions at Ikenne in 2008 and 2009 and under natural drought stress at Bagauda in 2008.

Source of variation	df	Days to anthesis	Days to silk	Plant height	Ear height	Plant aspect	Ear aspect	ASI	Ear per plant	Grain yield	Ear length	100 kernel weight	No of row per ear
Drought stress													
Environment (env)	1	2346.3**	4464.0**	252532.6**	82425.1**	33.0**	51.5**	317.3**	10.17**	52.7**	597.9**	3722.1**	4.7
Block (rep x env)	24	2.4	8.1*	234.1*	125.5**	1.4**	0.4	2.9	0.12	0.2	3.1	9.9	9.7**
Rep (env)	1	4.7	16.3	960.3**	527.8**	6.3**	0.3	3.8	0.01	2.3**	9.4	13.3	4.7
Inbreds	155	19.7**	34.5**	1148.3**	385.8**	2.3**	0.8**	5.0**	0.12**	0.7**	4.9**	15.8**	6.4**
Inbreds x Env	155	7.4**	15.3**	388.1**	140.2**	1.7**	0.5**	3.3**	0.11**	0.4**	5.0**	17.9**	6.3**
Error	286	2.4	5.3	142.3	53.6	0.7	0.3	2.3	0.03	0.1	2.5	10.5	4.5
Well-watered conditions													
Environment (env)	2	338.4**	31.3**	108465.9**	24468.8**	38.5**	11.6**	196.6**	5.42**	126.7**	618.4**	993.8**	81.9**
Block (rep x env)	24	3.6	3.1	1416.7	171.3**	1.2	0.6**	1.2	0.07**	0.7**	2.0	5.0	3.9
Rep (env)	2	0.7	2.6	1195.9	47.6	1.0	0.2	0.6	0.01	0.2	0.1	8.8	0.5
Inbreds	155	22.4**	32.4**	2432.8**	388.1**	2.6**	0.9**	4.2**	0.13**	1.7**	7.1**	38.3**	10.6**
Inbreds x Env	310	4.4**	7.4**	1702.8*	140.4**	1.6**	0.6**	1.9**	0.09**	0.9**	3.6**	19.0**	5.7**
Error	441	2.6	3.4	1444.1	96.1	1.0	0.2	1.2	0.04	0.4	2.0	8.9	3.4

*, ** Significant at 0.05, and 0.01 probability levels, respectively.

Table 2 - Means, and ranges for grain yield and other traits of 156 early-maturing maize inbred lines evaluated under drought at Ikenne during 2007/2008 and 2008/2009 dry seasons and well-watered conditions at Ikenne in 2008 and 2009 and under natural drought stress at Bagauda in 2008.

	Drought				Well-watered conditions			
Traits	Mean	SE	CV	Range	Mean	SE	CV	Range
Flowering			- % -				- % -	
Days to 50% anthesis (no)	54	1.09	2.9	49-60	58	1.14	2.81	54-64
Days to 50% silk (no)	56	1.62	4.1	50-66	59	1.31	3.12	54-66
Anthesis-silking interval (days)	2.5	1.07	61.4	0-5.8	1.8	0.78	61.51	0.2-5.0
Yield components and yield								
Ear per plant (no)	0.64	0.20	44.4	0.2-0.96	0.80	0.14	25.43	0.4-1.2
Ear length (cm)	12.02	1.12	13.2	7.2-14.9	12.00	1.00	11.82	8.4-15.8
Ear diameter (cm)	3.52	1.01	40.7	2.2-5.8	3.61	0.99	38.88	2.4-4.8
Row per ear (no)	12.50	1.49	16.9	8.7-15.9	12.05	1.31	15.40	6-16
100 kernel weight (g)	18.22	2.29	17.8	12.0-22.9	21.92	2.11	13.59	12-33
Grain yield (t ha^{-1})	0.84	0.27	45.4	0.03-1.92	1.62	0.44	37.96	0.5-3.1
Agronomic								
Plant height (cm)	115.60	8.44	10.3	65-173	119.64	26.87	31.76	73-292
Ear height (cm)	61.03	5.18	12.0	25-91	52.27	6.93	18.76	37-81
Husk cover (1-5)	1.99	0.68	47.9	1.1-5.0	1.87	0.51	38.18	1.2-4.0
Plant aspect (1-5)	3.00	0.59	27.5	1.3-5.0	2.56	0.72	39.84	1.6-4.0
Ear aspect (1-5)	2.64	0.40	21.4	1.0-3.8	2.18	0.35	22.44	1.2-3.5
Stalk lodging (%)	17.97	10.61	83.5	0-100	4.76	3.41	10.13	0-25
Leaf death score (1-10)	3.71	0.59	22.6	1.3-6.4	-	-	-	-

tive base indices were drought susceptible. Under drought, the grain yield of TZEI 17 represented 83% of the yield under well-watered conditions in the same environment. On the whole, 75 inbred lines had positive base index values and were classified as drought tolerant while the 81 inbred lines with negative index values were drought susceptible (data not shown).

Correlation among grain yield and other traits under drought and well-watered conditions.

Significant positive phenotypic correlations were obtained between grain yield and plant height (rp = 0.65), ear height (rp = 0.62), EPP (rp = 0.50), ear length (rp = 0.19), and number of rows per ear (rp = 0.25) while significant negative phenotypic correlations existed between grain yield and days to anthesis (rp = -0.66), days to silking (rp = -0.71), ASI (rp = -0.55), ear aspect (rp = - 0.35), plant aspect (rp = -0.57), 100-kernel weight (-0.18), and leaf death (rp = -0.28) under drought (Table 4). Apart from ear length and ear diameter, EPP was significantly correlated with all other traits under drought. Highly significant phenotypic correlations existed between days to anthesis and days to silking (rp = 0.93); days to silking, and ASI (rp = 0.76); ear height and plant height (rp = 0.90); and plant aspect and ear aspect (rp = 0.51). However, there was low but significant correlations between ASI and leaf death (rp = 0.20); ear aspect and leaf death (rp = 0.18); ear aspect and ASI (rp = 0.13); days to anthesis and ear aspect (rp = 0.11) under drought (Table 4).

Under well-watered conditions, positive and significant correlations were detected between grain yield and plant height (rp = 0.32), ear height (rp = 0.49), ear length (rp = 0.51), number of rows per ear (rp = 0.41), ear diameter (rp = 0.17), and EPP (rp = 0.66), while significant negative correlations were observed between grain yield and days to anthesis (rp = -0.25), days to silk (rp = -0.41), ASI (rp = -0.38), ear aspect (rp = -0.69), plant aspect (rp = -0.10), and stalk lodging (rp = -0.17) (Table 4). Also, significant phenotypic correlations were observed between days to anthesis and days to silking (rp = 0.86); days to silking and ASI (rp = 0.48); and ear and plant heights (rp = 0.41). However, there was low but significant correlations between ear aspect and ASI (rp = 0.27); plant and ear aspects (rp = 0.19), days to anthesis and ear aspect (rp = 0.29) under well-watered conditions.

The *per se* performance of the inbreds under drought was regressed on the performance under well-watered conditions (Supplementary Figure 2). The grain yield of inbreds under well-watered conditions allowed modest prediction of grain yield of inbreds under drought. It was observed that for every one t ha^{-1} increase in grain yield of inbreds under well-watered conditions resulted in only 0.49 t ha^{-1} increases in grain yield under drought (Supplementary Figure 2). Regression analysis also revealed that the variation in grain yield of the inbreds under well-watered conditions explained 0.36 of the total variation in grain yield of inbreds under drought (Supplementary Figure 2).

Broad-sense heritability estimates of the inbreds for grain yield and other traits ranged from 2% for number of rows per ear to 66% for plant height under drought (Table 5). Under well-watered conditions, heritability estimates varied from 15% for plant aspect to 80% for days to anthesis. The broad-sense heritability estimate was 43% for grain yield under drought and 47% under well-watered conditions (Table 5). Relatively high heritability estimates were

Table 3 - Grain yield and other agronomic traits of the best 10 and worst 10 maize inbred lines across drought (DS) at Ikenne during 2007/2008 and 2008/2009 dry seasons and well-watered (WW) conditions at Ikenne in 2008 and 2009 and natural drought stress at Bagauda in 2008.

Name	Pedigree	Grain yield		Days to silking		ASI		Plant height		stalk lodging		Plant aspect		Ear aspect		Leaf death score	Ears per plant		Base index
		DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	WW	DS	DS	WW	
	Best inbred lines	--- t ha^{-1} ---				--- days ---		--- cm ---		--- % ---							--- no. ---		
TZEI 17	TZE COMP5-Y C6 S6 Inb 35	1.92	2.31	51	58	0.0	1.0	123.0	104.4	10	7.4	1.7	2.4	1.0	1.9	2.3	0.6	0.8	15.31
TZEI 129	TZE-Y Pop STR C0 S6 Inb 16-1-3	1.67	2.27	52	56	0.5	0.4	156.6	138.0	15	14.8	1.5	1.7	1.7	1.9	2.3	0.9	1.0	13.28
TZEI 31	TZE-W Pop x LD S6 Inb 4	1.75	2.58	51	55	0.6	1.4	132.5	134.2	22	2.9	1.9	1.8	2.4	2.2	2.0	0.9	1.0	12.70
TZEI 18	TZE-W Pop STR C0 S6 Inb 136-3-3	1.83	3.13	54	57	1.4	1.1	126.9	140.1	14	4.9	1.8	1.7	1.8	1.2	4.0	0.8	0.9	11.61
TZEI 16	TZE COMP5-Y C6 S6 Inb 31	1.42	2.15	54	59	1.2	1.3	120.8	120.7	13	7.4	2.0	2.0	1.8	1.6	1.3	0.8	0.9	11.57
TZEI 158	TZE-Y Pop STR C0 S6 Inb 102-2-2	1.67	2.28	51	56	0.8	1.1	132.7	131.2	12	4.5	1.7	2.3	1.9	1.9	3.2	0.7	0.8	10.73
TZEI 149	TZE-Y Pop STR C0 S6 Inb 66-2-2	1.54	1.86	51	55	1.5	1.3	144.4	113.7	24	12.3	1.6	2.6	1.6	1.8	3.2	0.7	0.7	9.36
TZEI 65	TZE-W Pop STR C0 S6 Inb 141-1-2	1.54	2.33	53	56	1.6	1.2	123.2	105.3	14	2.7	1.6	2.3	2.3	1.9	2.7	0.7	1.0	9.07
TZEI 1	TZE-W Pop STR C0 S6 Inb 1-2-4	1.39	3.02	55	59	1.7	2.2	131.9	127.7	18	6.9	1.9	1.6	2.2	1.6	3.6	0.9	1.0	9.05
TZEI 178	TZE COMP5-Y C6 S6 Inb 62-3-3	1.53	2.07	52	55	1.4	1.5	117.5	116.4	25	9.8	2.2	2.9	2.1	1.9	3.6	1.0	0.9	8.36
	Worst inbred lines																		
TZEI 184	TZE-Y Pop STR C0 S7 Inb 171-2-2	0.28	0.82	59	62	3.9	3.1	81.8	101.1	13	1.4	4.4	2.9	3.3	2.6	3.0	0.4	0.6	-8.58
TZEI 131	TZE-Y Pop STR C0 S6 Inb 16-3-3	0.27	0.83	59	63	3.9	3.0	107.0	120.6	19	0.6	4.2	2.9	2.9	2.8	4.0	0.4	0.5	-8.77
TZEI 53	TZE-W Pop STR C0 S6 Inb 60-1-4	0.07	0.93	56	59	2.6	2.0	116.0	135.6	15	0.8	3.7	2.5	3.4	2.3	3.6	0.2	0.7	-9.20
TZEI 118	TZE-Y Pop STR C0 S6 Inb 1-3-5	0.38	1.08	58	61	3.5	1.6	86.3	78.2	9	2.5	4.1	3.0	3.5	1.9	4.9	0.5	0.8	-9.46
TZEI 70	TZE-W Pop STR C0 S6 Inb 149-1-3B	0.24	1.72	64	61	5.7	1.4	102.7	132.4	6	0.9	4.9	3.0	3.1	2.2	3.5	0.3	0.6	-9.77
TZEI 143	TZE-Y Pop STR C0 S7 Inb 35-3-5	0.12	1.14	59	64	4.0	2.9	142.1	133.2	20	4.7	3.7	3.3	2.9	2.9	4.9	0.3	0.7	-10.32
TZEI 30	TZE-W Pop STR C0 S6 Inb 14-3-3	0.33	1.56	57	55	3.7	0.9	127.5	130.6	19	4.8	4.4	2.6	3.3	2.7	5.4	0.3	0.5	-10.45
TZEI 152	TZE-Y Pop STR C0 S6 Inb 68-3-3	0.13	0.58	66	66	5.8	2.1	114.7	142.0	30	4.0	4.5	3.2	3.1	2.9	3.9	0.8	0.5	-10.48
TZEI 127	TZE-Y Pop STR C0 S6 Inb 10-3-4	0.14	0.95	62	63	4.3	2.3	92.1	108.9	15	0.0	5.0	3.2	3.4	2.8	3.8	0.2	1.7	-11.88
TZEI 123	TZE-Y Pop STR C0 S6 Inb 3-1-2	0.06	0.58	60	60	4.7	1.3	117.7	121.2	18	11.3	4.6	3.6	3.4	3.5	6.0	0.5	0.4	-14.60
	Grand mean	0.84	1.62	56	59	2.5	1.8	115.6	119.0	18	4.8	3.0	2.6	2.6	2.2	3.7	0.7	0.8	
	SE	0.27	0.35	1.6	1	1.1	0.6	8.4	21.6	10.6	3.4	0.6	0.6	0.4	0.3	0.6	0.2	0.2	

obtained for days to anthesis and silking, plant and ear heights under drought. Similarly, high heritability estimates were observed for days to anthesis and silking, ASI and ear height under well-watered conditions (Table 5).

Biplot analysis of grain yield and stability of inbreds

The highly significant genotype effects and genotype × environment interaction of inbreds on grain yield and most measured traits under drought and well-watered conditions prompted the use of the GGE biplot to decompose the G + GE to determine the yield performance and stability of the inbreds across the environments. The GGE biplot for grain yield of the 29 early maturing maize inbreds comprising the best 24 and the worst five entries is shown in Supplementary Figure 2. The GGE biplot principal component (PC) axis 1 captured 61.7% while PC2 captured 17.8% of the total variation in inbreds. Thus, PC1 and PC2 together accounted for 79.5% of the total variation for grain yield of the inbreds (Figure 1). These results indicated that the biplot of PC1 and PC2 adequately reflected the environment-centered data.

In the GGE biplot display (Figure 1), the thick single-arrow black line that passes through the biplot origin (intercept of the vertical and horizontal axis) and the average tester (centre of the innermost concentric circle with an arrow) is referred to as the average-tester coordinate axis (ATC). The double-arrow line (ATC ordinate) separates entries with below-average means (to the left side of the line) from those with above-average means. A set of lines, parallel to the double-arrowed line, spans the whole range of the entries, grouping them based on their mean performance. The average performance of a genotype is approximated by the projection of its marker on the ATC. The stability of the genotypes is measured by their projection onto the average-tester coordinate y axis (ATC abscissa). The greater the absolute length of the projection the less stable is the genotype. Based on this information, inbred TZEI 35, TZEI 158, TZEI 177, TZEI 17, and TZEI 163 produced grain yields greater than the mean grain yield but had a long projection onto the average-tester coordinate y axis and were therefore the least stable. In contrast, inbreds TZEI 18, TZEI 56, TZEI 1, and TZEI 19 had outstanding yield performance and short projection onto the average-tester coordinate y axis and hence high yield stability across research environments (Figure 1).

Discussion

The significant variation observed among inbreds and environments for grain yield and other measured traits indicated that the test environments were unique and that adequate genetic variability existed among the early-maturing maize inbreds under drought and well-watered conditions. The wide ranged observed in grain yield, tolerance index and other measured traits supported the presence of adequate genetic variability in the early inbreds under drought. The presence of genetic variability among the early inbreds would allow significant progress from selection for improvements in most of the measured traits under drought. This result corroborates the findings of Badu-Apraku et al (2011d) and Badu-Apraku and Oyekunle (2012). The significant genotypic variation among the early inbreds in the measured traits is ex-

Table 4 - Correlation between grain yield and other agronomic traits of early-maturing inbred lines evaluated under drought (above diagonal) at Ikenne during 2007/2008 and 2008/2009 dry seasons and well-watered conditions (below diagonal) at Ikenne in 2008 and 2009 and and natural drought stress at Bagauda during the 2008 growing season.

	Grain yield	Days to anthesis	Days to silk	ASI	Plant height	Ear height	Plant aspect	Ear aspect	Ears per plant	Ear length	Ear diameter	100-kernel weight	Row per ear	Leaf death score
Grain yield	-	-0.66**	-0.71**	-0.55**	0.65**	0.62**	-0.57**	-0.35**	0.50**	0.19**	0.07	-0.18**	0.25**	-0.28**
Days to anthesis	-0.25**	-	0.93**	0.48**	-0.68**	-0.62**	0.32**	0.11**	-0.45**	0.04	0.00	0.35**	-0.17**	0.05
Days to silk	-0.41**	0.86**	-	0.76**	-0.69**	-0.63**	0.38**	0.14**	-0.51**	0.01	-0.01	0.31**	-0.20**	0.12**
ASI	-0.38**	-0.02	0.48**	-	-0.47**	-0.44**	0.34**	0.13**	-0.43**	-0.06**	-0.02	0.13**	-0.19**	0.20**
Plant height	0.32**	0.01	-0.11**	-0.24**	-0.90**	-0.25**	0.02	0.42**	-0.08	0.02	-0.29**	0.18**	-0.10**	
Ear height	0.49**	0.02	-0.17**	-0.37**	0.41**	-	-0.20**	0.02	0.41**	-0.12**	0.00	-0.29**	0.13**	-0.03
Plant aspect	-0.10**	0.19**	0.18**	0.05	-0.02	-0.04	-	0.51**	-0.19**	-0.49**	-0.15**	-0.17**	-0.33**	0.34**
Ear aspect	-0.69**	0.29**	0.39**	0.27**	-0.19**	-0.28**	0.19**	-	-0.24**	-0.34**	-0.03	-0.15**	-0.07	0.18**
Ears per plant	0.66**	-0.18**	-0.33**	-0.33**	0.17**	0.33**	-0.08**	-0.55**	-	-0.05	0.00	-0.22**	0.09*	-0.15**
Ear Length	0.51**	-0.18**	-0.20**	-0.12**	0.24	0.42	-0.06	-0.44**	0.39**	-	0.16**	0.40**	0.17**	-0.13**
Ear diameter	0.17**	-0.11**	-0.11**	-0.06	0.02	0.03	-0.07	-0.19**	0.11**	0.10**	-	0.10**	0.21**	-0.15**
100- kernel weight	0.01	-0.02	-0.08*	-0.15**	0.05	0.04	-0.08*	0.01	-0.03	0.08*	0.07	-	-0.03	-0.03
Row per ear	0.41**	-0.19**	-0.23**	-0.20**	0.04	0.18**	-0.10	-0.43**	0.37**	0.17**	0.19**	-0.06	-	-0.09*

*, **significant at 0.05, and 0.01 probability levels, respectively.

pected as the inbreds were extracted from six diverse germplasm sources. The significant interaction between inbreds and environments for grain yield and other measured traits suggested that the expression of these traits would be different in varying environments. This suggests the need to evaluate inbreds in contrasting environments to identify drought-tolerant genotypes with consistently favourable response in drought-prone environments. This result is in agreement with the findings of other workers (Badu-Apraku et al, 2003; 2011a; d).

Phenotypic variation observed for grain yield, ASI and EPP as well as for drought-adaptive traits e.g. leaf death score under drought suggested the importance of these traits in the identification and selection of drought-tolerant inbreds. Although days to 50% anthesis and silking were found to be earlier under drought than well-watered conditions, the mean value of ASI under drought was higher than that under well-watered conditions. This suggested that the ASI is an important indicator of drought-tolerance in maize. This result is in agreement with the findings of earlier workers (Edmeades et al, 1995; Menkir and Akintunde, 2001; Kamara et al, 2003) who reported that ASI is a useful drought-adaptive trait for selecting for drought-tolerance in maize.

The prolonged ASI together with reduction in grain yield, EPP, 100-kernel weight that occurred under drought contributed to the reduction in grain yield under drought. This result indicated that ASI, EPP, and 100-kernel weight should be used for improvement of grain yield under drought. The levels of reduction in grain yield and other related traits indicated the severity of drought imposed during the flowering and grain-filling periods in this study. The increased ASI might have induced barrenness (Bolaños and Edmeades, 1993a; Edmeades et al, 1993). Bolaños and Edmeades (1996) noted that correlation between grain yield and ASI is low under optimal management conditions but very strong under stress conditions. Herrero and Johnson (1981) and Edmeades et al (1993) also reported that delayed silking is associated with barrenness and appears to reflect reduced partitioning of assimilates to the developing ear at flowering. The grain yield reductions of 48% in the inbreds under induced drought in the present study fall within the limits reported by previous workers (NeSmith and Ritchie, 1992; Menkir and Akintunde, 2001; Badu-Apraku et al, 2005; Campos et al, 2006; Derera et al, 2008; Badu-Apraku et al, 2011d). The levels of yield reduction observed in the present study indicated that the screening methodology applied is appropriate to identified drought-tolerant inbreds for the production of suitable hybrids targeted for drought-prone environments.

Information on the inter-relationship among traits is important in designing effective selection programmes for crop improvement. Positive and significant correlations of grain yield with plant and ear heights indicated that tall plants are high yielding. However, this relationship is undesirable in maize breeding because they complicate simultaneous improvement for high yield and short statured lodging-resistant plants. The positive correlation of grain yield with its components such as ear diameter and length, 100-kernel weight and number of kernels per row has also been reported by other workers (Bolaños and Edmeades, 1996; Edmeades et al, 1997). The correlation coefficient values (r = -0.71 to 0.90) observed in the present study are similar to the values (r = -0.52 to 0.84) reported by Hallauer and Miranda (1988). Traits such as EPP which showed positive and significant correlation with grain yield can be improved simultaneously with grain yield during selection for higher grain yield. These traits could also be utilised as drought-adaptive traits during indirect selection for grain yield.

Heisey and Edmeades (1999) reported that maize is more susceptible to drought at flowering than most other crops because its florets develop virtually simultaneously and are usually borne on a single ear on a single stem. Unlike other cereals, the male and female florets in maize are spatially separated and pollen and fragile stigmatic tissue can be exposed to a desiccating environment during pollination and fertilization. The present study revealed that grain yield

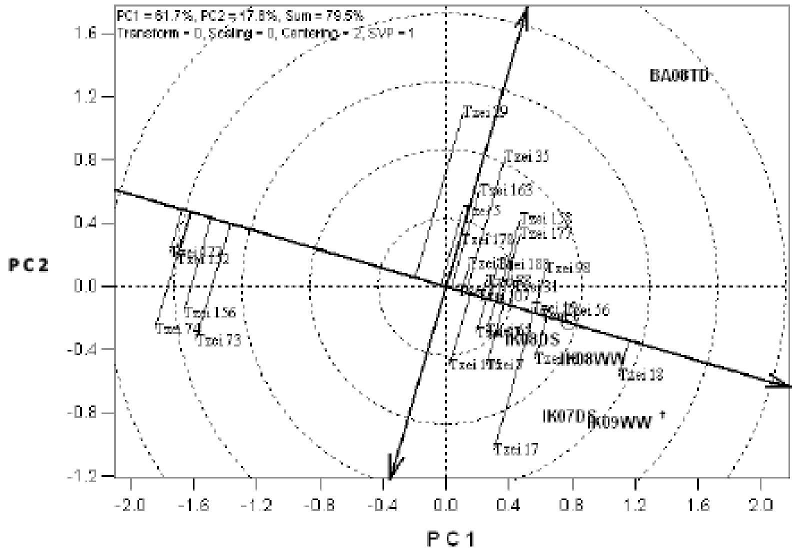

Figure 1 - Mean performance and stability of early-maturing maize inbreds in terms of grain yield as measured by principal components across contrasting environments. †IK07DS and IK08DS = Ikenne under drought during 2007/2008 and 2008/2009 dry seasons; IK08WW and IK09WW = Ikenne under well-watered in 2008 and 2009; BG09TD = Bagauda terminal drought in 2009.

under drought at flowering and grain filling periods is highly correlated with EPP and negatively correlated with days to 50% anthesis and silking, ASI, plant aspect, ear aspect, and leaf senescence. This implies that increase in grain yield is associated with a shorter ASI, reduced barrenness, lower leaf senescence, improved plant aspect and ear aspect. The results of this study are consistent with those of Bolaños et al (1993c) and Edmeades et al (1995) who identified the EPP and ASI to be important drought-adaptive traits for selecting for drought tolerance and yield potential in tropical maize.

Prediction of inbreds performance based on the per se performance of the lines under well-watered environments is crucial for genetic gain from selection under drought. The grain yield of inbreds under well-watered conditions allowed modest prediction of grain yield of inbreds under drought. The significant positive correlation (r = 0.6) observed between grain yield of inbreds under drought and well-watered environments indicated that assessment of inbred lines under optimal conditions would be useful for predicting the performance of the lines under drought. This information is invaluable for preliminary elimination of low-yielding inbred lines under well-watered environments. This is advantageous where large numbers of inbreds are expected to be screened under drought and there are limited drought screening facilities.

In the present study, the broad-sense heritability estimates for grain yield and other traits were higher than those reported by Mhike et al (2011) who recorded 21.2% for grain yield, 55.4% for days to anthesis, 16.9% for EPP, 31.6% for plant height and 71% for ASI. In contrast, the heritability estimates for grain yield in the present study are lower than that reported by other workers (Badu-Apraku et al, 2004b; Aminu and Izge, 2012; Oyekunle and Badu-Apraku, 2013). Aminu and Izge (2012) reported 60.73% heritability for grain yield of maize under drought conditions in the Northern Guinea and Sudan Savannas of Nigeria. However, the heritability estimates for grain yield, days to anthesis, stalk lodging, ear aspect, and leaf senescence were relatively lower under drought compared to well-watered conditions. The high heritability estimates for days to anthesis and silking, plant and ear heights and ASI under drought and well-watered conditions indicated that these traits may be effectively utilised for direct phenotypic selection. This suggested that selection of high yielding inbreds with improved ear aspect, stalk lodging resistance and delayed leaf senescence under drought could be used in developing superior hybrids for drought-prone areas. The relatively low heritability estimates for grain yield, ear and plant aspects, EPP and leaf senescence under drought and well-watered conditions implies that direct phenotypic selection for these traits may not be effective. This suggests the use of indirect selection and selection indices to determine the underlying genetic merits of the traits (Mhike et al, 2011).

The means for ear and plant heights of inbreds in the drought environments were similar to or larger than those obtained in the well-watered environments. The reduction in grain yield and other traits obtained under drought in the present study was 6.9-48%, indicating that reproductive and productive traits were more susceptible to drought than the

Table 5 - Broad-sense heritability estimates for grain yield and other agronomic traits of early-maturing maize inbred lines under drought and well-watered environments.

Traits	Drought	Well watered
Days to anthesis	62 ± 7.2	80 ± 10.5
Days to silk	56 ± 5.3	77 ± 11.3
Plant height	66 ± 6.4	30 ± 6.4
Ear height	64 ± 4.5	64 ± 12.2
Plant aspect	26 ± 8.1	15 ± 3.3
Ear aspect	38 ± 6.3	33 ± 2.6
ASI	34 ± 4.2	55 ± 10.2
Ear per plant	8 ± 2.0	31 ± 7.1
Grain yield	43 ± 9.2	47 ± 6.5
Ear length	3 ± 1.1	49 ± 5.7
100 kernel weight	13 ± 4.2	50 ± 8.5
No of rows/ear	2 ± 0.5	46 ± 6.2
Leaf death score	43 ± 6.3	-

vegetative traits. These results corroborate the earlier findings that the more severe the drought, the fewer the kernels and ears produced per plant and the lower the grain yield (Russell, 1984; Bolaños and Edmeades, 1993b; Kamara et al, 2003; Badu-Apraku et al, 2005). The coefficients of variation associated with drought were consistently larger than those associated with the well-watered environments. The ASI appeared to have much larger coefficients of variation than the primary traits from which it was derived i.e days to anthesis and silking. This result demonstrated the effectiveness of the screening methodology in the present study. This finding is similar to that reported by Badu-Apraku et al (2005).

In the present study, 75 out of 156 inbred lines were identified to be drought tolerant. The relatively large number of drought-tolerant inbred lines with varying levels of drought tolerance observed in the present study is expected because the inbred lines were developed from six diverse germplasm sources with resistance to Striga and tolerance to drought. The selected S_0 plants from each population had been advanced to S_6 or S_7 through inbreeding with selection under artificial Striga infestation and drought (Badu-Apraku et al, 2006). Several promising early-maturing maize inbred lines that combined above average grain yields under drought with low plant and ear aspects, short ASI, slow rate of leaf senescence and increased EPP have been identified in the this study. Some of the identified inbreds have been used in study reported by Oyekunle and Badu-Apraku (2013) where the authors observed high GCA male and female effects for inbreds TZEI 31, TZEI 17, TZEI 129, and TZEI 157 and identified them as testers both as male and female parents under either drought or well-watered conditions.

In conclusion, there was high genetic variability in the inbreds for grain yield, tolerance indices, and other measured traits under drought and well-watered conditions. Grain yield of inbreds was significantly correlated with EPP, ASI, plant aspect, ear aspect and stay-green characteristic under drought. Forty-eight percent of the lines were identified as drought-tolerant inbred lines. Broad-sense heritability estimate was relatively low for grain yield under drought and well-watered conditions. Biplot analysis identified inbreds TZEI 18, TZEI 56, TZEI 1, and TZEI 19 as the highest yielding and most stable across environments. The outstanding inbred lines with high levels of drought tolerance could therefore be utilised for the development of drought-tolerant hybrids and synthetic varieties or the genes for drought tolerance may be introgessed into tropical breeding populations. New inbred lines could also be generated through recycling of promising inbred lines.

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