

Yield Gains in Extra-Early Maize Cultivars of Three Breeding Eras under Multiple Environments

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ABSTRACT

Availability of extra-early maize cultivars has facilitated the expansion of maize production into savannas of West and Central Africa (WCA). Fifty-six extra-early maize cultivars of three breeding eras; 1995 to 2000, 2001 to 2006, and 2007 to 2012 were evaluated for 2 yr under 24 multiple-stress and 28 non-stress environments in WCA. Objectives of the study were to determine genetic improvement in grain yield of cultivars developed during the breeding eras, and identify high-yielding and stable cultivars across multiple-stress and non-stress environments. Average increase in yield of 44 kg ha⁻¹ yr⁻¹ (2.72%) and 67 kg ha⁻¹ yr⁻¹ (2.28%) were obtained under multiple-stress and non-stress environments. Yield gains from era 1 to era 3 under multiple stresses was associated with increased days to anthesis, reduced stalk lodging, and improved husk cover. Cultivars 2004 TZEE-Y Pop STR C₄, TZEE-W Pop STR QPM C₀, and TZEE-W Pop STR BC₂ C₀ of era 2; and TZEE-W Pop STR 107 BC₁, TZEE-W Pop STR C₅, and 2012 TZEE-Y DT STR C₅ of era 3 were high-yielding and stable across multiple-stress environments while 98 Syn EE-W from era 1, FERKE TZEE-W Pop STR, TZEE-W Pop STR C₃, and TZEE-Y Pop STR QPM C₀ from era 2, and TZEE-W Pop STR C₅, 2009 TZEE-OR₂ STR QPM, 2009 TZEE-W STR, TZEE-Y STR 106, and TZEE-W DT C₀ STR C₅ from era 3 were outstanding across non-stress environments and should be tested extensively and commercialized. Considerable improvement has been made in breeding for multiple-stress tolerant extra-early maize cultivars.

Core Ideas

- The study determined genetic improvement in grain yield of the cultivars during the breeding eras, investigated trait associations, and identified high-yielding and stable cultivars across multiple-stress and non-stress environments.
- The study revealed an annual genetic gain of 2.72 and 2.28% for the cultivars under multiple-stress and non-stress environments.
- Cultivars 2004 TZEE-Y Pop STR C₄, TZEE-W Pop STR QPM C₀, TZEE-W Pop STR BC₂ C₀ of era 2 and TZEE-W Pop STR 107 BC₁, TZEE-W Pop STR C₅, and 2012 TZEE-Y DT STR C₅ of era 3 were the highest yielding and stable across multiple-stress environments while 98 Syn EE-W from era 1, FERKE TZEE-W STR, TZEE-W Pop STR C₃, TZEE-Y Pop STR QPM C₀ from era 2, and TZEE-W Pop STR C₅, 2009 TZEE-OR₂ STR QPM, 2009 TZEE-W STR, TZEE-Y STR 106, TZEE-W DT C₀ STR C₅ from era 3 were the most outstanding across non-stress environments.
- We conclude that substantial progress has been made in breeding for multiple-stress tolerant extra-early maize cultivars in West and central Africa.

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MAIZE is an important staple food, animal feed, and industrial crop in sub-Saharan Africa (SSA). The savannas of the subregion offer ideal environments for maize production because they are characterized by high solar radiation, low night temperatures, low incidence of pests, and diseases. However, recurrent drought, low soil nitrogen (low-N), and *Striga hermonthica* (Del.) Benth. limit maize production and productivity in the savannas. Drought can reduce grain yield of maize by as much as 90% when it occurs at the most sensitive stage of the crop growth, that is, a few days before anthesis to the beginning of grain-filling period (NeSmith and Ritchie, 1992). Nitrogen is a major requirement for high levels of maize productivity but it is the most limiting nutrient in tropical soils. A fertilizer rate of 90 to 120 kg N ha⁻¹ is recommended for increased maize grain yield in WCA. However, fertilizer application rates are still far below the recommended doses in the subregion due to the unavailability or the exorbitant prices of inorganic fertilizer for resource-poor farmers. The estimated annual loss of maize yield due to low-N stress varies from 10 to 50% per year in the subregion (Wolfe et al., 1988). Breeding for tolerance to low-N offers the most economical and sustainable approach for increased maize yields in the subregion. *Striga* infestation can cause total crop failure (Badu-Apraku et al., 2010) and has often forced farmers in the subregion to abandon their farmlands.

Under field conditions, drought, *Striga* and soil nutrient deficiency occur simultaneously and the combined effects can be devastating (Cechin and Press, 1993; Kim and Adetimirin, 1997). For example, Badu-Apraku et al. (2004) reported a grain yield loss of 53% under drought and 42% under *Striga*

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Abbreviations: AMMI, additive main effects and multiplicative interaction; ASI, anthesis-silking interval; DAP, days after planting; EPP, ears per plant; G, cultivar; G × E, cultivar × environment interaction; GGE, genotype main effect plus genotype × environment interaction; E, environment; IITA, International Institute of Tropical Agriculture; IITA-MIP, International Institute of Tropical Agriculture Maize Improvement Program; Low-N, low soil nitrogen; IPCA1, interaction principal component axes 1; MI, multiple trait base index; SSA, sub-Saharan Africa; WAP, weeks after planting; WCA, West and central Africa; WECAMAN, West and Central Africa Collaborative Maize Research Network..

infestation. Consequently, breeding for extra-early (80–85 d to maturity) cultivars with enhanced tolerance to drought and resistance to *Striga* is crucial to improved productivity and stable maize production in WCA. Therefore, it is desirable to incorporate drought tolerance into cultivars that have resistance to *Striga* in the Sudan and northern Guinea savannas where intermittent drought is prevalent, as the two stresses occur together. Presently, farmers in *Striga* endemic agro-ecologies of WCA are demanding extra-early and early (90–95 d to maturity) cultivars with combined resistance or tolerance to *Striga* and drought and are unwilling to adopt maize cultivars that do not possess both adaptation to drought-prone environments and *Striga* resistance (Badu-Apraku et al., 2013a, 2013b, 2015b). Improvement for drought tolerance has most often resulted in specific adaptation and improved performance under low-N conditions, indicating that tolerance to either stress involves common adaptive mechanism (Bänziger et al., 1999; Badu-Apraku et al., 2011, 2015a). It is therefore becoming increasingly important to adopt a holistic approach to identify genotypes with tolerance to a range of stresses expected in the target environment in WCA instead of compartmentalizing different stresses (Badu-Apraku et al., 2010). During the past decade, the International Institute of Tropical Agriculture Maize Improvement Program (IITA-MIP) has therefore paid increasing attention and devoted scarce resources to develop new products endowed with high yield potential and stability across a broad range of moisture availability and growing conditions. Backcrossing, inbreeding, hybridization, the S_1 recurrent selection method and screening under drought, low soil N and artificial infestation with *S. hermonthica* have been used as strategies to develop several extra-early maturing source populations, cultivars and inbred lines, with tolerance to low-N, drought escape and/or tolerance to drought at the flowering and grain-filling periods as well as moderate levels of resistance to *S. hermonthica* and the maize streak virus. The availability of these extra-early maize cultivars has resulted in the expansion of maize production into new frontiers replacing the traditional cereal crops such as sorghum [*Sorghum bicolor* (L.) Moench] and pearl millet [*Pennisetum glaucum* (L.) R.Br.] in the savannas of WCA (IITA, 1992). Extra-early maize cultivars are more responsive to fertilizer application, faster in maturity and can be harvested much earlier in the season than the adapted sorghum and millet crops. The maize cultivars are thus used for filling the hunger gap in July in the WCA savannas when all food reserves are depleted after the long dry period and the new crop of the normal growing season is not ready for harvest. There is also a high demand for the extra-early maize in the West African forest zone for peri-urban maize consumers because they allow farmers to market the early crop at a premium price in addition to being compatible with cassava (*Manihot esculenta* Crantz), cowpea [*Vigna unguiculata* (L.) Walp.] and soybean [*Glycine max* (L.) Merr.] for intercropping (IITA, 1992). Another important advantage of the extra-early maize is that they provide farmers in the various agro-ecological zones with flexibility in the dates of planting. Extra-early maize can be planted when the rains are delayed or could be used for early plantings when the rainfall distribution is normal (Badu-Apraku et al., 2012).

Several studies have been performed routinely to compare cultivars of different eras in the temperate zones in an effort to understand how genetic improvement has influenced important traits such as grain yield in maize by Castleberry et al. (1984), Duvick (2005), Campos et al. (2006), and Wang et al. (2011). Similarly, several comparisons of hybrids developed in different eras under contrasting N levels have been reported (Castleberry et al., 1984; Tollenaar et al., 1997; Sangoi et al., 2002; O'Neill et al., 2004). However, only limited studies have been performed to assess progress made in the extra-early maturing cultivars developed over years in WCA. Information on the genetic gains in extra-early cultivars is crucial for determining whether or not the investments in research in the subregion are justified and to gain a better understanding of how selection has influenced important traits such as grain yield in maize (Kamara et al., 2012; Badu-Apraku et al., 2013b, 2015a, 2015b). The limited information on genetic gains from selection make it difficult to ascertain completely the genetic gain that has been made for grain yield in relationship to N fertility, drought tolerance and *Striga* resistance in the numerous cultivars that have been released in WCA during the past two decades.

The extra-early varieties developed by International Institute of Tropical Agriculture (IITA) during the past three decades may be categorized into three breeding eras (1995–2000, 2001–2006, and 2007–2012). However, despite the tremendous advances in the improvement of the extra-early maize, information is completely lacking on the genetic gains in grain yield and other agronomic traits of the extra-early cultivars developed during the three breeding eras. The identification of traits of potential value and modifications in breeding methodologies and strategies are crucial for increased progress in future breeding of the extra-early maize cultivars (Badu-Apraku et al., 2015b).

The objectives of this study were to: (i) determine the gains in grain yield under multiple-stress and non-stress environments; (ii) identify traits associated with yield improvement during the three breeding eras under multiple-stress and non-stress environments, and (iii) identify high-yielding and stable cultivars under multiple-stress and non-stress environments for commercialization in the subregion.

MATERIALS AND METHODS

Development of Drought-Tolerant, *Striga* Resistant and Low-N Tolerant Extra-early Populations and Cultivars

Research on the extra-early maize has involved the development of base populations from which inbred lines have been extracted for the development of cultivars, inbreds, and hybrids. The initial strategy was to develop extra-early maturing drought escaping cultivars from local maize accessions for evaluation and release to farmers. A breeding program for *Striga* resistance in the extra-early maize was initiated in Côte d'Ivoire in 1994 by the West and Central Africa Collaborative Maize Research Network (WECAMAN) with backstopping by IITA. WECAMAN's efforts were to complement those of IITA to combat the threat posed by *S. hermonthica* to maize production in the WCA savannas. The initial emphasis of this collaborative program was to develop

maize populations, cultivars and inbreds that combined extra-earliness with resistance/tolerance to *S. bermonthica*, and drought. The emphasis of the breeding program has been the formation of high-yielding extra-early drought and *Striga* resistant/tolerant populations using drought tolerant and *Striga*-resistant germplasm from diverse sources identified through several years of extensive testing in WCA. Efforts were concentrated on the introgression of *Striga* resistance/tolerance into the extra-early maize populations and cultivars, using inbred lines from IITA (1368 STR, and 9450 STR) as the sources of resistance. Backcrossing, inbreeding, and hybridization were adopted in the breeding program. Among the products of the IITA-WECAMAN breeding program are two extra-early *Striga* resistant populations, one having white endosperm designated as TZEE-W Pop STR, and the other named TZEE-Y Pop STR with yellow endosperm (Fajemisin et al., 1999, Badu-Apraku and Fakorede, 2001). The details on the methodology adopted for the development of the two extra-early breeding populations have been described in detail by Badu-Apraku and Fakorede (2013). The populations were each subjected to recurrent selection for stress tolerance and enhancement of grain yield under stress and no-stress conditions. Following the development of the two extra-early populations, the main strategies adopted in the extra-early maturing maize component of the IITA-MIP are improvement of source populations using recurrent selection with reliable artificial *Striga* field infestation and screening methods to increase resistance to relevant stresses in the breeding materials, development of open-pollinated cultivars, inbred lines, and hybrids from source populations and germplasm enhancement (Badu-Apraku et al., 2016).

Several alleles control the expression of adaptation to drought-prone environments in maize. Therefore, a major strategy of the IITA-MIP has been to screen maize inbred lines with adaptation to drought-prone environments from diverse sources. The promising inbred lines with enhanced adaptation to drought-prone environments were also screened for *Striga* resistance under artificial infestation. The promising inbreds with better adaptation to both drought-prone environments and *Striga* resistance were evaluated for adaptive traits in the selected screening sites. The selected lines with genes for *Striga* resistance derived from *Zea diploperennis* H.H. Iltis Doebley and/or genes for drought tolerance at the flowering and grain-filling periods were also used for further introgression into the two extra-early maturing breeding populations undergoing S₁ family recurrent selection in our program. Further improvement of the extra-early populations under controlled drought and artificial *Striga bermonthica* infestation using the S₁ recurrent selection method has resulted in the development of new productive cultivars that combine enhanced levels of adaptation to drought-prone and low-N environments and improved levels of resistance to *Striga*. A total of 56 extra-early maturing cultivars and/or populations were developed during the breeding period (1995–2012) as shown in Supplementary Table S1.

Evaluation of Extra-Early Cultivars under Drought, Low-N, *Striga*-Infested, and Optimal Environments

Fifty-six extra-early maturing maize cultivars (Supplementary Table S1) comprising 14 from era 1, 17 from era 2, and 25 from era 3 were evaluated in three separate experiments under 24 multiple-stress (drought, *Striga*-infested and low-N) and 28 non-stress (high-N, *Striga*-free, and rainfed) environments in Nigeria, Benin, and Ghana in West Africa between 2013 and 2016 (Supplementary Table S2). The experimental design was 8 by 7 lattice with three replications. An experimental plot consisted of two rows, 4 m long, spaced 0.75 m apart with 0.40 m spacing between plants within the row in all experiments. Three seeds were planted per hill and seedlings were thinned to two per stand about 2 wk after planting (WAP), resulting in a final plant population density of 66,666 plants ha⁻¹.

In the first experiment, the cultivars were evaluated at Ikenne (6°53' N, 3°42' E, 60 m altitude, 1200 mm annual rainfall), Nigeria under managed drought during the dry seasons of 2013/2014, 2014/2015, and 2015/2016 and under terminal drought at Bagauda (12°00' N, 8°22' E, 580 m altitude, 800 mm annual rainfall), Dusu, Ejura, Fumesua, and Manga during the growing seasons of 2013 as well as Kpeve and Pokuase in 2014. The soil type at Ikenne is Eutric nitrisol while that of Bagauda is clay loam (Soil Survey Staff, 1999). The managed drought at Ikenne was achieved through an irrigation system that provided 17 mm of water per week up to 21 d after planting (DAP). Thereafter, the irrigation water was withdrawn until maturity, so that the maize plants relied on stored water in the soil for growth and development.

In the second experiment, the cultivars were evaluated at Ile-Ife (7°18' N, 4°33' E, altitude 244 m, 1100 mm annual rainfall) and Mokwa (9°18' N, 5°18' 4' E, altitude 457 m, 1100 mm annual rainfall), Nigeria under low-N (30 kg N ha⁻¹) in 2013 and 2014. The soil at Mokwa is a luvisol (Soil Survey Staff, 1999) with 0.27, 0.035 and 0.48% organic C, organic N and P content. On the other hand, the soil at Ile-Ife is characterized as Alfisol (Soil Survey Staff, 1999) with 0.084% organic N. The experimental fields were depleted of N by continuously planting maize for several years and removing the plant biomass after each harvest. Soil samples were taken each year before planting for all the test environments and N content was determined at the IITA soil laboratory at Ibadan. The total N in the soils was determined by Kjeldahl digestion and colorimetric determination on Technicon AAI Autoanalyser (Bremner and Mulvaney, 1982). Fertilizer was applied to bring the total available N to 30 kg ha⁻¹ for the low-N fields when the soil N was below 30 kg ha⁻¹. The N fertilizer was applied 2 WAP. Also, single superphosphate (P₂O₅) and muriate of potash (K₂O) were applied to the low-N blocks at the rate of 60 kg ha⁻¹. Each trial was kept weed-free with the application of herbicides and by hand weeding.

In the third experiment, the cultivars were evaluated for yield potential and tolerance/resistance to *Striga* in 2013 and 2014 under artificial infestation with *S. bermonthica* in Benin, Nigeria, and Ghana. In Nigeria, the cultivars were evaluated at two *Striga* endemic locations in Mokwa and Abuja (9°16' N, 7°20' 20' E, altitude 300 m, 1500 mm annual

rainfall) from June to October, 2013 and 2014. In Benin, the cultivars were evaluated at two locations; Ina (9°30' N and 2°62'119 E, 1500 mm annual rainfall) in the northern Guinea savanna and Angaradebougou (11°33' N and 2°13' W, 1000 mm annual rainfall) in the Sudan savanna in 2013 and 2014. In Ghana, the cultivars were evaluated at Nyankpala (9°25' N, 0°58' W, 183 m altitude, and 1000 mm annual rainfall) in 2013 and 2014. The fields were fumigated with ethylene gas at about 7 d before planting to induce suicidal germination of *Striga* seeds in the soil. The *Striga* infestation method of IITA Maize Program was used (Kim, 1991). Three maize seeds and about 5000 germinable *Striga* seeds were placed per hill in each hole. The *Striga* seeds used for the trials were collected in the previous planting season from neighboring farmers' sorghum fields around Abuja and Mokwa in Nigeria, Ina and Angaradebougou in Benin, and Nyankpala in Ghana. The *S. bermonthica* seeds used for infestation were mixed with finely sieved sand in the ratio of 1:99 by weight and about 5000 germinable seeds were placed in each planting hole on the ridges, as described by Kim (1991). Fertilizer application was delayed until about 21 to 25 d after planting when 30 kg N ha⁻¹, 30 kg P ha⁻¹ and 30 kg K ha⁻¹ were applied as NPK 15–15–15. The reduced rate and delay in application of fertilizer were necessary to subject the maize plants to stress, a condition that favors the production of strigalactones, which enhances good germination of *Striga* seeds and attachment of *Striga* plants to the roots of host plants in *Striga* infested plots (Kim, 1991). Weeds other than *Striga* were controlled manually.

In the fourth experiment, the 56 extra-early cultivars were evaluated under non-stress growing conditions (rainfed, *Striga*-free, and high N) in 28 environments during the 2013 and 2014 growing seasons in Benin, Nigeria, and Ghana (Supplementary Table S2). All trials received 60 kg ha⁻¹ N, 60 kg ha⁻¹ P, and 60 kg ha⁻¹ K at planting with an additional 60 kg N ha⁻¹ top-dressed at 4 WAP except under *Striga*-free plots that received 30 kg N ha⁻¹, 30 kg P ha⁻¹, and 30 kg K ha⁻¹ as NPK 15–15–15 at about 21 to 25 DAP. Weeds were controlled with herbicides and/or manually.

Measured Traits

Data were recorded on drought-stressed, *Striga*-infested, low-N, and optimal plots. Days to 50% anthesis and silking were recorded as the number of days from planting to when 50% of the plants had shed pollen and emerged silks. The anthesis-silking interval (ASI) was calculated as the difference between days to 50% 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. Root lodging (percentage of plants leaning more than 30° from the vertical), and stalk lodging (percentage broken at or below the highest ear node) were recorded. Ears per plant (EPP) was obtained by dividing the total number of ears per plot by the number of plants harvested. Plant aspect was recorded on a scale of 1 to 9 based on plant type, where 1 = excellent and 9 = poor. Husk cover was rated on a scale of 1 to 5, where 1 = husks tightly arranged and extended beyond the ear tip and 5 = ear tips exposed. Ear aspect was recorded on a scale of 1 to 9, where 1 = clean, uniform, large, and well-filled ears and 9 = ears with undesirable features. In addition, stay-green characteristic was

recorded for the drought-stressed and low-N plots at 70 d after planting on a scale of 1 to 9, where 1 = almost all leaves green and 9 = virtually all leaves dead. Host plant damage syndrome rating (Kim, 1991) and emerged *Striga* plants were recorded at 8 and 10 WAP in the *Striga*-infested plots. *Striga* damage syndrome was scored per plot on a scale of 1 to 9 where 1 = no damage, indicating normal plant growth and high resistance, and 9 = complete collapse or death of the maize plant.

In the managed drought and low-N experiments, harvested ears from each plot were shelled to determine the percentage grain moisture. Grain yield in kg ha⁻¹ was adjusted to 15% moisture content and computed from the shelled grain weight. On the other hand, in the *Striga*-infested, *Striga*-free, well-watered and high N environments, grain yield (kg ha⁻¹) was computed based on 80% shelling percentage and adjusted to 15% moisture content.

Data Analysis

Broad-sense heritability (H) of grain yield were estimated for each environment as

$$H = \sigma_g^2 / (\sigma_g^2 + \sigma_{g \times e}^2 / e + \sigma_e^2 / re)$$

where σ_g^2 is the genotypic variance, $\sigma_{g \times e}^2$ is the genotype \times environment and σ_e^2 is the residual variance; e is the number of environments, and r is the number of replicates per environment. Ten (five each from multiple-stress and non-stress environments) out of the 52 environments with heritability of grain yield less than 0.30 were removed from all analyses (Supplementary Table S2).

Analyses of variance was performed across the remaining 19 multiple-stress and 23 non-stress environments on plot means of each trait with PROC GLM in SAS 9.3 using a RANDOM statement with the TEST option (SAS Institute, 2011). In addition, ANOVA was performed separately for the multiple-stress and non-stress environments. In the ANOVA, the location–year combinations (test environments), eras, replicates, blocks and interactions of each experiment were considered as random factors while cultivars were considered as fixed effects. Means were separated using the standard error.

The relationship between measured traits of maize cultivars and year of development across multiple stress and non-stress environments (i.e., stressed vs. optimal growing environments) was determined using regression analysis. The mean grain yield of the maize cultivars was used as the dependent variable and regressed on the year of breeding as independent variables to obtain regression coefficient (b value) across stress and optimal growing environments, using SAS. The b value was then divided by the intercept and multiplied by 100 to obtain the relative genetic gain per year (Badu-Apraku et al., 2009). Furthermore, the relationship between grain yield under multiple stress and non-stress environments as well as across the research environments was visualized for each breeding era using scatter diagrams. The regression analysis, including the parameters and the graphical display of the regression line and the distinction between the different eras were done using the Excel software in the Microsoft Office suite 2007. A multiple trait base index (MI) that integrated superior grain yield, EPP, anthesis-silking interval, plant and ear aspects, stay-green

characteristic, *Striga* damage rating and number of emerged *Striga* plants under multiple stress and outstanding grain yield under non-stress environments was used to select the top 15 and worst 10 hybrids (Badu-Apraku et al., 2015b). Each trait was standardized to minimize the effect of the different scales. A positive MI value was therefore considered an indication of tolerance/resistance to the multiple stresses while negative values indicated susceptibility. The MI was computed using the following equation:

$$MI = (2 \times YLD_{STR}) + YLD_{NSTR} + EPP - ASI - EASP - PASP - SGR - SD8 - SD10 - (0.5 \times ESP8) - (0.5 \times ESP10)$$

where

YLD_{STR} = Grain yield under multiple stress environments

YLD_{NSTR} = Grain yield under non-stress environments

EPP = Number of ears per plant under multiple stress environments

ASI = Anthesis-silking interval under multiple stress environments

EASP = Ear aspect under multiple stress environments

PASP = Plant aspect under multiple stress environments

SGR = Stay-green characteristic across drought and low-N environments

SD8 and SD10 = *Striga* damage rating at 8 and 10 WAP across *Striga*-infested environments.

ESP8 and ESP10 = Number of emerged *Striga* plants at 8 and 10 WAP across *Striga*-infested environments.

Repeatability of the traits (Falconer and Mackay, 1996) under multi-stress and non-stress conditions were computed on cultivar-mean basis using the following formula:

$$R = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{e} + \frac{\sigma_e}{re}}$$

where σ_g^2 is the genotypic variance, σ_{ge}^2 is the genotype \times environment and σ_e^2 is the residual variance; e is the number of environments, and r is the number of replicates per environment. Variances were estimated using REML method in SAS MIXED procedure.

The yield data of the 56 extra-early cultivars were subjected to the additive main effects and multiplicative interaction (AMMI) analysis to examine the relationships among cultivars (G), environments (E) and G \times E interaction. The AMMI model was described by Zobel et al. (1988), Gauch and Zobel (1988), and Crossa (1990). This analysis uses principal component analysis

to decompose the multiplicative effects (G \times E) into a number of interaction principal component axes (IPCAs). The genotype main effect plus G \times E interaction (GGE) biplot software Windows application that fully automates biplot analysis (Yan, 2001a, 2001b) was used for the AMMI analysis. The AMMI model equation of Sadeghi et al. (2011) was used. The AMMI biplot was used to obtain information on the cultivars that were the most suitable across multiple-stress as well as non-stress environments and to investigate the stability of cultivars in the contrasting environments. Three AMMI family models, AMMI0, AMMI1, and AMMI2 may be used for studying GEI in multi-environment trials. The most predictively accurate member of the AMMI model family is the AMMI0 because the GEI are small and buried in the noise. However, AMMI1 could be more accurate than AMMI0 when the GEI is only marginally significant. But where the AMMI2 captures more GEI than AMMI1, the AMMI2 model only decreases accuracy (Gauch et al., 2008) and therefore the AMMI1 was more appropriate and was adopted in the present study.

RESULTS

Analysis of Variance across Multiple-Stress and Non-Stress Environments

The combined ANOVA of the 56 extra-early maturing maize cultivars evaluated across the two research conditions (multiple-stress and non-stress conditions) showed highly significant ($p < 0.001$) mean squares for grain yield and all other measured traits for E, era, cultivar, and E \times cultivar (Supplementary Table S3). The ANOVA revealed that E, cultivar, and E \times cultivar sum of squares for grain yield accounted for 62.9, 7.9, and 10.0% of the total sum of squares across the multiple-stress and non-stress conditions (Table not shown). It is striking to note that the mean squares for the research conditions were highly significant ($p < 0.01$) for grain yield and all other measured traits. The research conditions sum of squares for grain yield explained 75.2% of the model sum of squares (Table not shown), indicating that each research condition was unique and that there was a need for separate ANOVA for each of the two research conditions. Similarly, across the non-stress environments the ANOVA revealed highly significant mean squares for grain yield and all other measured traits for E, Era, Cultivar, E \times Cultivar and E \times Era sources of variation (Supplementary Table S3). Across the multiple stress environments significant mean squares were recorded for grain yield and most other measured traits for E, Era, Cultivar, E \times Cultivar and E \times Era sources of variation. The few exceptions included Era mean squares for number of emerged *Striga* plants at 8 and 10 WAP, E \times Era mean squares for days to anthesis, days to silking, plant height, ear height, root lodging, ear aspect, the number of emerged *Striga* plants at 8 and 10 WAP and E \times Cultivar mean square for root lodging, ear aspect, the number of emerged *Striga* plants at 8 and 10 WAP (Supplementary Table S4).

The repeatability estimates of the traits ranged from 0.51 for ASI and EPP to 0.98 for days to anthesis under multiple-stress environments and from 0.46 for ASI to 0.96 for days to silking under non-stress environments. High repeatability estimates (i.e., ≥ 0.60) were recorded for most of the traits under multiple-stress and non-stress environments (Supplementary Tables S3 and S4).

Genetic Gains in Grain Yield of Cultivars of Three Breeding Eras under Multiple Stress and Non-Stress Environments

Under multiple stresses, grain yield ranged from 1817 kg ha⁻¹ for cultivars bred during 1995 to 2000 to 2303 kg ha⁻¹ for those developed during 2007 to 2012 (Table 1) with a corresponding genetic gain of 2.72% yr⁻¹ (Table 2). Under non-stress environments, grain yield ranged from 3212 kg ha⁻¹ for cultivars bred during era 1 to 3960 kg ha⁻¹ for those developed during era 3 with annual genetic gain of 2.28% yr⁻¹. The average rate of increase in grain yield was 44 kg ha⁻¹ yr⁻¹ under multiple stress and 67 kg ha⁻¹ yr⁻¹ under non-stress environments (Tables 1 and 2). The significant gain in grain yield under multiple-stress was associated with increased days to anthesis, decreased stalk

lodging, and improved husk cover. In contrast, no significant gain was achieved for grain yield during the breeding eras under non-stress environments. However, increased days to anthesis, plant and ear heights, stalk lodging, and EPP as well as decreased ASI, improved ear aspect and reduced ear rot were obtained under the non-stress environments (Table 2).

The regression analysis of the mean grain yield of the extra-early maize cultivars under multiple stress and non-stress environments showed clear separation of the maize cultivars into three distinct breeding eras (Fig. 1), with the exception of some few cultivars from the first and second eras that produced yields comparable to those of the third era extra-early cultivars. The third era extra-early cultivars displayed outstanding performance under both multiple-stress and non-stress environments. Grain yield of the extra-early cultivars under

Table 1. Grain yield and other agronomic traits of extra-early maize cultivars of three breeding eras evaluated under multiple-stress and non-stress conditions in Nigeria, Benin, and Ghana between 2013 and 2016.

Trait	Era	Number of cultivars	Stress conditions	Non-stress conditions
Grain yield, kg ha ⁻¹	1995–2000	14	1817 ± 23	3212 ± 26
	2001–2006	17	2075 ± 20	3609 ± 24
	2007–2012	25	2303 ± 17	3960 ± 20
Days to anthesis	1995–2000	14	53 ± 0.08	51 ± 0.07
	2001–2006	17	54 ± 0.07	53 ± 0.06
	2007–2012	25	54 ± 0.06	53 ± 0.05
Days to silking	1995–2000	14	55 ± 0.09	53 ± 0.07
	2001–2006	17	56 ± 0.08	55 ± 0.07
	2007–2012	25	56 ± 0.07	55 ± 0.06
Anthesis silking interval	1995–2000	14	2.6 ± 0.04	1.9 ± 0.03
	2001–2006	17	2.3 ± 0.04	1.8 ± 0.03
	2007–2012	25	2.3 ± 0.03	1.8 ± 0.02
Plant height, cm	1995–2000	14	147 ± 0.54	164 ± 0.47
	2001–2006	17	152 ± 0.48	169 ± 0.42
	2007–2012	25	153 ± 0.40	171 ± 0.36
Ear height, cm	1995–2000	14	67 ± 0.41	76 ± 0.41
	2001–2006	17	71 ± 0.37	81 ± 0.37
	2007–2012	25	72 ± 0.31	82 ± 0.31
Root lodging, %	1995–2000	14	7.8 ± 0.24	5.7 ± 0.17
	2001–2006	17	6.9 ± 0.21	5.4 ± 0.15
	2007–2012	25	6.2 ± 0.18	4.6 ± 0.13
Stalk lodging, %	1995–2000	14	11.8 ± 0.27	11.2 ± 0.25
	2001–2006	17	11.3 ± 0.24	10.4 ± 0.22
	2007–2012	25	9.6 ± 0.20	9.4 ± 0.19
Husk cover	1995–2000	14	3.0 ± 0.02	2.2 ± 0.01
	2001–2006	17	2.8 ± 0.02	2.2 ± 0.01
	2007–2012	25	2.8 ± 0.01	2.1 ± 0.01
Plant aspect	1995–2000	14	3.9 ± 0.03	2.7 ± 0.02
	2001–2006	17	3.6 ± 0.02	2.5 ± 0.02
	2007–2012	25	3.5 ± 0.02	2.4 ± 0.01
Ear aspect	1995–2000	14	4.1 ± 0.04	3.1 ± 0.02
	2001–2006	17	3.8 ± 0.04	2.9 ± 0.02
	2007–2012	25	3.6 ± 0.03	2.6 ± 0.01
Ear rot	1995–2000	14	2.9 ± 0.08	2.1 ± 0.05
	2001–2006	17	2.5 ± 0.07	1.9 ± 0.04
	2007–2012	25	2.7 ± 0.06	1.9 ± 0.03
Ears per plant	1995–2000	14	0.8 ± 0.004	0.91 ± 0.003
	2001–2006	17	0.8 ± 0.004	0.93 ± 0.003
	2007–2012	25	0.9 ± 0.003	0.94 ± 0.002

multiple-stress could predict the grain yield under non-stress environments with a corresponding R^2 value of 85% (Fig. 1).

Relationship among Grain Yield and Other Agronomic Traits under Multiple Stress and Non-Stress Environments

In the present study, grain yield had significant positive correlations with days to anthesis and silking, plant and ear heights, and EPP but significant negative correlations with ASI, root and stalk lodging, husk cover, plant and ear aspects, ear rot, stay-green characteristic, *Striga* damage at 8 and 10 WAP as well as the number of emerged *Striga* plants at 10 WAP across multiple stress environments (Table 3). Similarly under non-stress environments, significant positive correlations were obtained between grain yield and days to anthesis and silking, plant and ear heights, and EPP. However,

significant negative correlations were observed between grain yield and husk cover, plant and ear aspects, and ear rot. Correlations between most of the paired traits were also significant under multiple stress and non-stress environments (Table 3).

Performance and Stability of Extra-Early Maize Cultivars of Three Breeding Eras across Environments

The means of grain yield and other agronomic traits of top 15 and worst 10 cultivars selected using the multiple trait base index under multiple-stress and non-stress environments are presented in Table 4. The index values varied from -20.8 for TZEE-Y SR BC1 × 9450 STR S6 F₂ to 13.5 for TZEE-W STR 105. Grain yield ranged from 1215 kg ha⁻¹ for TZEE-Y SR BC1 × 9450 STR S6 F₂ to 2600 kg ha⁻¹ for TZEE-W

Table 2. Relative genetic gain, coefficient of determination (R^2), (a) slope, and (b) regression coefficients of grain yield and other agronomic traits of extra-early maize cultivars of three breeding eras evaluated under multiple-stress and non-stress conditions in Nigeria, Benin, and Ghana between 2013 and 2016.

Trait	Relative gain		R^2		a		b	
	Stress	Non-stress	Stress	Non-stress	Stress	Non-stress	Stress	Non-stress
	— % per year —							
Grain yield, kg ha ⁻¹	2.72	2.28	0.4299	0.3718	1633	2943.9	44.435**	66.983
Days to anthesis	0.20	0.24	0.1042	0.1579	52.542	51.197	0.1028**	0.1228**
Days to silking	0.15	0.21	0.0691	0.1173	55.131	53.11	0.0837	0.1113
Anthesis silking interval	-0.72	-0.61	0.1453	0.1143	2.5975	1.956	-0.0186	-0.012**
Plant height, cm	0.45	0.44	0.3029	0.311	144.42	160.98	0.6482	0.7104**
Ear height, cm	0.49	0.70	0.1548	0.2549	67.228	74.78	0.327	0.5202*
Root lodging, %	-1.56	-1.60	0.1293	0.1272	8.17	6.1976	-0.1278	-0.0991
Stalk lodging, %	-1.45	1.20	0.1628	0.0861	12.689	11.691	-0.1845**	0.1407**
Husk cover	-0.53	-0.68	0.221	0.2629	2.9902	2.3255	-0.0157**	-0.0159
Plant aspect	-0.85	-1.02	0.3496	0.3103	3.9979	2.8016	-0.0339	-0.0286
Ear aspect	-1.04	-1.28	0.3917	0.4187	4.2634	3.279	-0.0444	-0.0419**
Ears rot	-0.82	-1.26	0.0374	0.1556	2.9704	2.2475	-0.0243	-0.0283*
Ears/plant	0.53	0.23	0.292	0.3806	0.7859	0.9068	0.0042	0.0021*

* Significant at 0.05 probability level.

** Significant at 0.01 probability level.

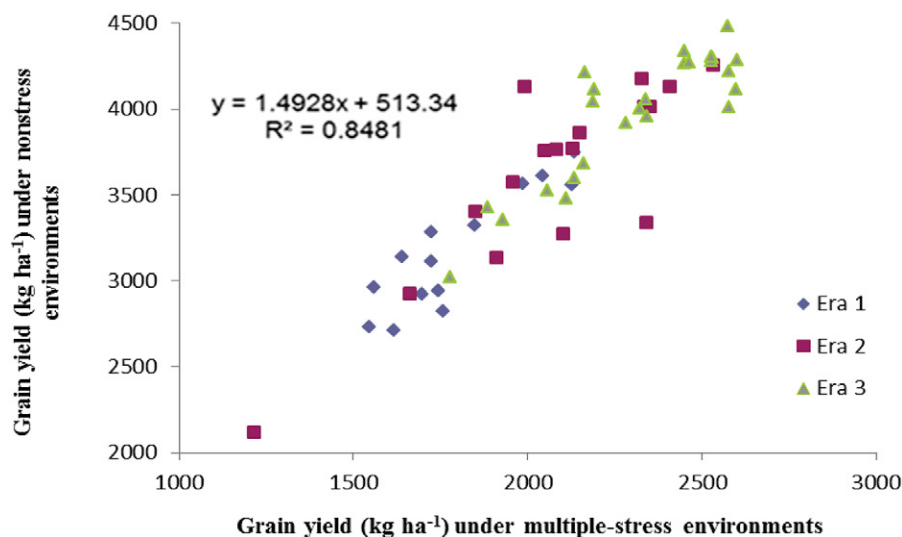


Fig. 1. Relationship between grain-yield of extra-early maturing maize cultivars developed during three breeding eras under multiple-stress and non-stress environments.

Table 3. Correlation coefficients of grain yield and other agronomic traits of extra-early maize cultivars of three breeding eras evaluated under multiple-stress (above diagonal) and non-stress conditions (below diagonal) in Nigeria, Benin and Ghana between 2013 and 2016.

Traits	Grain yield kg ha ⁻¹	Days to anthesis	Days to silking	ASI†	Plant height		Ear height		Root lodging		Stalk lodging		Husk cover		Plant aspect		Ear aspect		Ear rot		Ears per plant		SD10	SD8	STGR	ESP 8	ESP 10	
					cm	cm	cm	cm	%	%	%	%	%	%	%	%	%	%	%	%	%	%						%
Grain yield, kg ha ⁻¹		0.42**	0.36**	-0.40**	0.69**	0.64**	-0.63**	-0.57**	-0.78**	-0.82**	-0.89**	-0.29*	0.76**	-0.81**	-0.69**	-0.85**	-0.24	-0.27*										
Days to anthesis	0.64**		0.99**	-0.11	0.69**	0.72**	-0.59**	-0.55**	-0.64**	-0.59**	-0.43**	0.15	-0.59**	-0.39**	-0.53**	-0.15	-0.12											
Days to silking	0.59**	0.99**		0.05	0.66**	0.69**	-0.56**	-0.50**	-0.60**	-0.54**	-0.42**	0.06	-0.53**	-0.33*	-0.47**	-0.08	-0.05											
Anthesis-silking interval	-0.15	0.37**	0.47**		-0.24	-0.23	0.2	0.24	0.34**	0.27*	0.35**	0.09	-0.56**	0.42**	0.42**	0.46**	0.47**											
Plant height, cm	0.82**	0.80**	0.76**	0.05		0.84**	-0.48**	-0.36**	-0.62**	-0.80**	-0.70**	-0.23	0.41**	-0.50**	-0.59**	0.01	0.03											
Ear height, cm	0.80**	0.81**	0.78**	0.1	0.89**		-0.62**	-0.46**	-0.73**	-0.73**	-0.69**	-0.38**	0.37**	-0.55**	-0.63**	-0.08	-0.03											
Root lodging, %	-0.68	-0.45**	-0.43**	0.01	-0.48**	-0.59**		0.64**	0.68**	0.60**	0.58**	0.40**	-0.40**	0.53**	0.60**	0.24	0.25											
Stalk lodging, %	-0.66	-0.56**	-0.55**	-0.11	-0.39**	-0.56**	0.69**		0.64**	0.48**	0.57**	0.50**	-0.43**	0.59**	0.70**	0.36**	0.33*											
Husk cover	-0.80**	-0.71**	-0.70**	-0.2	-0.70**	-0.73**	0.66**	0.71**		0.75**	0.73**	0.51**	-0.62**	0.69**	0.81**	0.22	0.21											
Plant aspect	-0.94**	-0.77**	-0.75**	-0.08	-0.86**	-0.85**	0.68**	0.67**	0.85**		0.82**	0.29*	-0.58**	0.63**	0.73**	0.07	0.08											
Ear aspect	-0.95**	-0.69**	-0.64**	0.17	-0.84**	-0.80**	0.62**	0.59**	0.77**	0.92**		0.35**	-0.63**	0.74**	0.82**	0.21	0.24											
Ear rot	-0.52**	-0.56**	-0.56**	-0.27*	-0.46**	-0.52**	0.36**	0.60**	0.71**	0.58**	0.51**	-0.30*	-0.30*	0.35**	0.41**	0.31*	0.30*											
Ears per plant	0.63**	0.31*	0.26*	-0.29*	0.50**	0.47**	-0.46**	-0.33*	-0.46**	-0.57**	-0.56**	-0.38**	-0.66**	-0.69**	-0.70**	-0.38**	-0.40**											
Stay-green characteristic																												
Striga damage (8WAP)																												
Striga damage (10WAP)																												
Emerging Striga plants (8WAP)																												

* Significant at 0.05 probability level.

** Significant at 0.01 probability level.

† ASI Anthesis-silking interval; STGR = Stay green characteristic; SD8 = Striga damage at 8 WAP; SD10 = Striga damage at 10 WAP; ESP 8 = Emerged Striga plants at 8 WAP; ESP 10 = Emerged Striga plants at 10 WAP; WAP = weeks after planting.

Table 4. Grain yield and other agronomic traits of hybrids (the best 15 and the worst 10 based on the multiple base index) evaluated under multiple-stress (ST) and non-stress (NS) environments in West Africa between 2013 and 2016.

Cultivar	YIELD†		DYSK		ASI		PLHT		PASP		EASP		EPP		STGR		SDRI		SDR2		ESPI		ESP2		YRD		BI	
	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS	ST	NS
	— kg ha ⁻¹ —		— cm —																									
TZEE-W STR 105	2525	4304	57	56	2.1	1.8	154	170	3.5	2.2	3.4	2.5	0.90	0.95	3.8	2.8	3.5	3.5	29.0	37.1	41.3	13.5						
2012 TZEE-W DT STR C ₅	2576	4220	55	53	2.1	1.7	155	168	3.4	2.4	3.5	2.6	0.89	0.97	3.8	2.7	3.4	3.4	32.4	42.7	38.9	12.5						
2009 TZEE-OR ₁ STR	2577	4010	56	56	2.3	1.8	163	175	3.0	2.2	3.3	2.4	0.87	0.93	3.4	2.7	3.6	43.3	51.3	35.7	12.0							
TZEE-W STR 105 BC ₁	2600	4285	57	56	2.4	1.9	154	174	3.4	2.2	3.3	2.5	0.85	0.93	3.8	2.7	3.3	31.7	40.9	39.3	12.0							
TZEE-W DT C ₀ STR C ₅	2597	4114	55	54	2.1	1.7	157	170	3.4	2.4	3.5	2.7	0.88	0.94	3.9	2.9	3.5	31.9	40.0	36.9	11.1							
TZEE-W STR 108	2573	4486	57	55	2.5	1.8	154	173	3.3	2.1	3.4	2.5	0.86	0.96	3.6	2.8	3.4	38.6	50.9	42.6	10.5							
TZEE-W STR 108 BC ₁	2186	4044	58	56	2.4	2.0	152	170	3.4	2.3	3.4	2.5	0.87	0.94	3.8	2.6	3.0	29.3	40.7	45.9	10.3							
TZEE-W Pop STR C ₅	2530	4298	57	55	2.3	2.0	155	173	3.3	2.2	3.4	2.6	0.86	0.94	4.0	2.9	3.5	39.0	47.8	41.1	9.5							
2004 TZEE-W Pop STR C ₄	2532	4254	56	55	2.4	1.7	155	173	3.3	2.3	3.5	2.5	0.87	0.93	3.9	2.7	3.5	42.0	54.3	40.5	9.2							
TZEE-W STR 104	2527	4279	57	55	2.4	1.8	149	173	3.4	2.2	3.4	2.5	0.84	0.94	3.9	2.8	3.4	39.2	50.0	40.9	8.6							
TZEE-W Pop STR QPM C ₀	2410	4129	58	56	2.5	1.7	155	174	3.4	2.4	3.4	2.5	0.86	0.93	3.6	2.8	3.5	40.1	47.7	41.6	8.4							
TZEE-W STR 104 BC ₁	2448	4264	57	55	2.4	1.7	153	170	3.6	2.3	3.4	2.5	0.84	0.94	3.8	2.8	3.5	31.4	44.1	42.6	8.3							
TZEE-W STR 107 BC ₁	2322	4006	57	56	2.2	1.8	155	172	3.4	2.2	3.6	2.6	0.87	0.94	3.4	3.0	3.6	36.7	54.2	42.0	8.2							
TZEE-W STR 107	2281	3921	58	56	2.1	1.9	155	173	3.4	2.2	3.4	2.6	0.84	0.92	3.6	2.9	3.4	40.0	50.2	41.8	8.1							
2009 TZEE-OR ₂ STR	2450	4341	57	55	2.4	1.8	164	180	3.3	2.3	3.6	2.4	0.87	0.95	3.7	3.0	3.7	41.0	54.8	43.6	7.7							
99TZEE-Y STR C ₀	1757	2825	55	53	2.5	1.8	151	165	3.8	2.8	4.0	3.3	0.81	0.92	4.4	3.6	4.3	44.6	54.0	37.8	-10.0							
99 TZEE-Y STR C ₀	1743	2944	53	50	2.4	1.6	142	155	4.2	2.9	4.1	3.2	0.78	0.91	4.8	3.3	4.3	31.1	44.1	40.8	-10.1							
EY 99 QPM	1848	3321	55	53	3.1	2.2	145	165	3.8	2.6	4.2	3.2	0.82	0.93	4.4	3.5	4.5	43.4	55.8	44.4	-11.8							
TZEE-W ST x GUA 314 BC ₁	1638	3139	56	53	2.8	2.0	143	163	3.7	2.7	4.1	3.2	0.79	0.93	4.1	3.5	4.4	56.4	66.3	47.8	-12.7							
95 TZEE-Y	1698	2924	56	54	2.7	2.0	145	164	4.1	2.7	4.1	3.3	0.79	0.92	5.2	3.3	4.3	39.6	51.8	41.9	-13.1							
CSP SR x TZEE-Y STR	1545	2734	55	54	2.6	2.3	144	158	4.1	2.8	4.4	3.3	0.82	0.89	4.2	3.5	4.6	39.9	53.8	43.5	-13.3							
97TZEE-Y 2-C ₁	1722	3113	53	52	2.5	1.8	144	159	4.2	2.8	4.7	3.2	0.80	0.92	4.8	3.4	4.2	44.7	55.3	44.7	-13.4							
TZEE-W-SR BC ₅ (RE)	1614	2711	53	51	2.3	1.8	144	157	4.1	3.0	4.4	3.5	0.81	0.89	5.0	3.5	4.5	58.3	71.2	40.5	-16.1							
TZEE-Y Pop STR C ₀	1557	2961	53	51	2.7	1.7	141	159	4.2	3.0	4.4	3.3	0.74	0.90	5.0	3.7	4.8	44.8	58.3	47.4	-19.6							
TZEE-Y SR BC ₁ x 9450 STR	1215	2115	54	53	2.6	1.9	135	152	4.3	3.3	4.6	3.6	0.73	0.89	5.0	3.4	4.7	31.9	40.2	42.5	-20.8							
S ₆ F ₂																												
Mean	2112	3666	56	54	2.4	1.8	151	169	3.6	2.5	3.8	2.8	0.83	0.93	4.1	3.1	3.9	39.1	50.5	42.4								
Sed	71	76	0	0	0.2	0.1	2	2	0.1	0.1	0.1	0.1	0.02	0.01	0.2	0.1	0.2	0.1	0.2	4.5	4.8							

† YIELD = grain yield; DYSK = days to anthesis; ASI = anthesis-silking interval; PLHT = plant height; EASP and PASP = ear and plant aspects; EPP = ears per plant; STGR = stay-green characteristic; SDRI and SDR2 = *Striga* damage rating at 8 and 10 WAP; ESPI and ESP2 = emerged *Striga* plants at 8 and 10 WAP; BI = multiple base index.

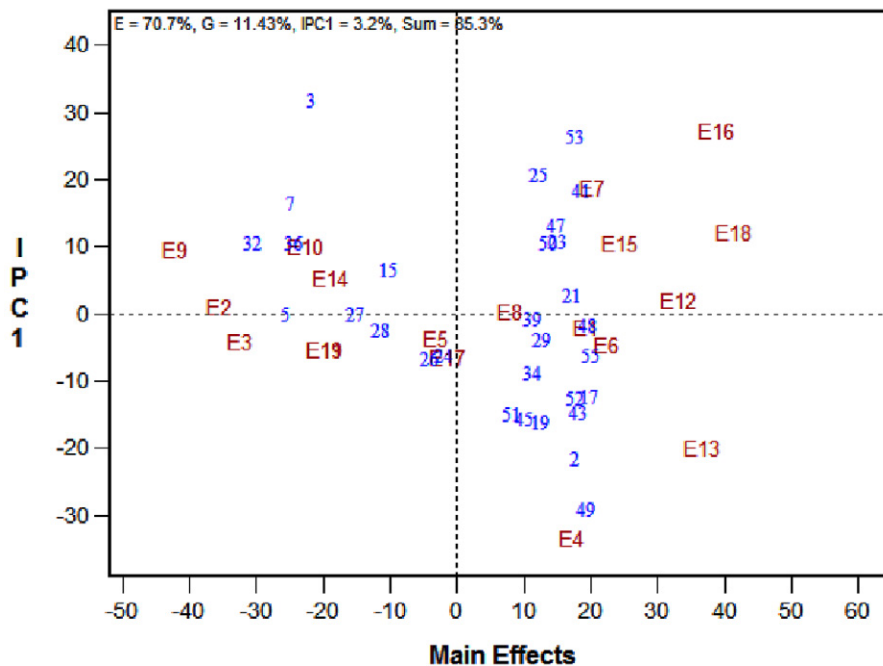


Fig. 2. Mean performance and stability of 56 extra-early maturing maize cultivars of three breeding eras in terms of grain yield as measured by principal components across 19 multiple-stress environments in West Africa between 2013 and 2016. E1 = Ikenne drought, 2013/2014; E2 = Ikenne drought, 2014/2015; E3 = Ikenne drought, 2015/2016; E4 = Abuja *Striga*-infested, 2013; E5 = Abuja *Striga*-infested, 2014; E6 = Angaradebou *Striga*-infested, 2013; E7 = Angaradebou *Striga*-infested, 2014; E8 = Bagauda drought, 2013; E9 = Dusu drought, 2013; E10 = Ina *Striga*-infested, 2013; E11 = Ina *Striga*-infested, 2014; E12 = Ile-lfe low-N, 2013; E13 = lfe low-N, 2014; E14 = Kpeve drought, 2014; E15 = Mokwa low-N, 2013; E16 = Mokwa low-N, 2014; E17 = Mokwa *Striga* infested, 2013; E18 = Mokwa *Striga*-infested, 2014; E19 = Nyankpala *Striga*-infested, 2013.

STR 105 BC₁ under multiple-stress and 2115 kg ha⁻¹ for TZEE-Y SR BC₁ × 9450 STR S6 F₂ to 4486 kg ha⁻¹ for TZEE-W STR 108 under non-stress environments. All the cultivars with positive index values yielded above 2000 and 3900 kg ha⁻¹ under multiple-stress and non-stress environments, respectively. Furthermore, most of the cultivars with the positive index values when compared with those with negative index values had higher grain yield, delayed flowering, higher plant height, reduced plant and ear aspects, increased ears per plant, delayed senescence, decreased *Striga* damage syndrome (8 and 10 WAP) and reduced number of emerged *Striga* plants (8 and 10 WAP). The yield reduction for both tolerant/resistance genotypes were similar to those of their susceptible counterparts. Mean grain yield under multiple stress was 42% lower than mean grain yield under non-stress environments.

The yield performance and stability of the 56 extra-early maturing maize cultivars of the three breeding eras evaluated under multiple stress and non-stress environments are presented in the AMMI biplot (Fig. 2 and 3). The vertical dotted line of the AMMI biplot represents the grand mean for grain yield, while the horizontal dotted line (y ordinate) represents the interaction principal component axes 1 (IPCA1) value of zero. Cultivars located close to the horizontal line have small interactions with the environment and are considered to be more stable than those farther from it. The farther a cultivar is to the right side of the grand mean line, the higher the grain yield. Across multiple stress environments, E (environment), G (cultivar), and the IPCA1 accounted for 70.95, 10.64, and 3.0% of the total variation in the sum of squares for grain yield, respectively giving a total sum of 84.6%. This indicated that the biplot was effective in explaining both the main

effects as well as in decomposing the G × E interaction across multiple stress environments (Fig. 2). The cultivars 22 (2004 TZEE-Y Pop STR C₄), 23 (TZEE-W Pop STR QPM C₀), 24 (TZEE-W Pop STR BC₂ C₀), 25 (TZEE-W STR 107 BC₁), 41 (TZEE-W Pop STR C₅), and 54 (2012 TZEE-Y DT STR C₅) produced yields greater than the grand mean and had near zero IPCA1 score, indicating that they were the most stable across multiple stress environments. The cultivars 2 (TZEE-W STR 104 BC₁), 49 (TZEE-W STR 105), and 55 (TZEE-W DT C₀ STR C₅) produced yields greater than the grand mean but had positive interactions with IPCA1 indicating that they were adapted to high yield environments while the cultivars 47 (2009 TZEE-W STR) and 53 (2012 TZEE-W DT STR C₅) yielded higher than the grand mean but showed strong negative interaction with IPCA1 indicating that they were adapted to low yield environments.

Across non-stress environments, the variation in grain yield attributable to E, G, and the IPCA1 were 54.3, 22.6, and 5.1%, respectively. The cultivars 8 (98 Syn EE-W), 15 (FERKE TZEE-W STR), 19 (TZEE-W Pop STR C₃), 31 (TZEE-Y Pop STR QPM C₀), 41 (TZEE-W Pop STR C₅), 46 (2009 TZEE-OR₂ STR QPM), 47 (2009 TZEE-W STR), 50 (TZEE-Y STR 106), and 55 (TZEE-W DT C₀ STR C₅) produced yields greater than the grand mean and had near zero IPCA1 score, an indication of their superior stability across non-stress environments (Fig. 3). Cultivars such as 49 (TZEE-W STR 105) and 52 (TZEE-W STR 108) yielded higher than the grand mean but showed strong positive interaction with IPCA1 indicating that they were adapted to high yield environments. Based on the AMMI analysis era 3 cultivar 41 (TZEE-W Pop STR C₅) was identified as high

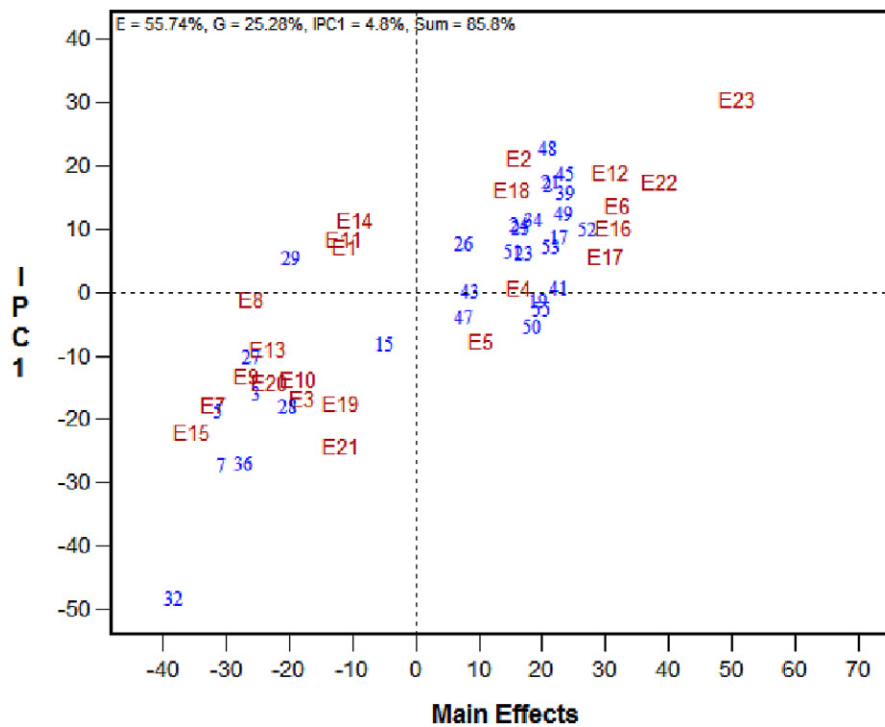


Fig. 3. Mean grain yield and stability of selected 56 extra-early maturing maize cultivars of three breeding eras as measured by principal components across 23 non-stress environments in West Africa between 2013 and 2016. E1 = Abuja *Striga*-free, 2013; E2 = Abuja *Striga*-free, 2014; E3 = Angaradebou rainfed, 2013; E4 = Angaradebou rainfed, 2014; E5 = Angaradebou *Striga*-free, 2013; E6 = Bagauda rainfed, 2014; E7 = Fumesua rainfed, 2014; E8 = Ina rainfed, 2013; E9 = Ina *Striga*-free, 2014; E10 = Ina rainfed, 2013; E11 = Ife high-N, 2013; E12 = Ife high-N, 2014; E13 = Ikenne rainfed, 2013; E14 = Ikenne rainfed, 2014; E15 = Mania Hari rainfed, 2013; E16 = Mokwa high-N, 2013; E17 = Mokwa high-N, 2014; E18 = Mokwa *Striga*-free, 2013; E19 = Manga rainfed, 2013; E20 = Nyankpala rainfed, 2013; E21 = Nyankpala rainfed, 2014; E22 = Zaria rainfed, 2013; E23 = Zaria rainfed, 2014.

yielding and stable both under multiple-stress and non-stress environments. Furthermore, both AMMI analysis and the multiple trait index consistently identified the cultivars 23 (TZEE-W Pop STR QPM C₀), 25 (TZEE-W STR 107 BC₁), and 41 (TZEE-W Pop STR C₂) as outstanding under multiple stress environments and 41 (TZEE-W Pop STR C₂) as well as 55 (TZEE-W DT C₀ STR C₂) under non-stress environments.

DISCUSSION

The presence of significant mean squares for grain yield and most other measured traits for Environment (E), Era, and Cultivar under multiple stress, non-stress, and across multiple stress and non-stress environments indicated that the test environments were unique and that there were significant differences among the cultivars of the different eras in grain yield and most other measured traits. These results are consistent with the findings of Badu-Apraku et al. (2011) and Badu-Apraku and Oyekunle (2012). The presence of significant E × Cultivar and E × Era mean squares for grain yield and most measured traits under multiple stress and non-stress environments indicated differential responses of the genotypes and the need to identify high-yielding and stable cultivars across environments, as reported by Sabaghnia et al. (2008); Moghaddam and Pourdard, (2009). This result confirmed the need for extensive testing of cultivars in multiple environments, including location and years before cultivar recommendations are made in the subregion (Badu-Apraku et al., 2011, 2015b).

The high repeatability estimates ($\geq 60\%$) observed for most measured traits under multiple-stress and non-stress

environments indicated that the expression of the traits would be consistent under the two research conditions.

A major objective of the present study was to determine the gains in grain yield and other agronomic traits of 56 extra-early maturing cultivars under multiple stress and non-stress environments during three breeding eras. The genetic gain of 2.72% yr⁻¹ with the average rate of increase in grain yield of 44 kg ha⁻¹ yr⁻¹ obtained for the extra-early cultivars under multiple stresses, and the annual genetic gain of 2.28% under non-stress environments is higher than the gains reported for the early maturing cultivars by Badu-Apraku et al. (2015b) under similar multiple stress and non-stress environments. The authors reported the average rate of increase in grain yield under optimal growing conditions to be 40 kg ha⁻¹ yr⁻¹ with a genetic gain of 1.3% yr⁻¹, and a gain of 30 kg ha⁻¹ yr⁻¹, an annual genetic gain of 1.2% across 16 stress environments. In another study involving the same 56 extra-early cultivars, Badu-Apraku et al. (2016) reported genetic gains in grain yield of 2.56% under *Striga*-infestation and 1.3% annual genetic gain under *Striga*-free conditions. Results of the evaluation of the extra-early cultivars under low N and high N revealed annual genetic gains in grain yield of 2.14 and 2.56%, respectively while under drought stress and optimal conditions, the cultivars showed genetic gains of 1.99 and 1.94% per year, respectively (Badu-Apraku et al., unpublished data, 2016, Improvement in grain yield and low nitrogen tolerance in extra-early maturing maize cultivars of three breeding eras evaluated under low and high nitrogen environments). The genetic gains obtained in the present study under the individual stresses are also greater than those reported

in earlier studies for early maturing cultivars. For example, Badu-Apraku et al. (2013b) reported an average genetic gain in grain yield of 1.7% per era when 50 early maturing cultivars were evaluated under *Striga* infestation per se. Furthermore, Badu-Apraku et al. (2013a) reported 1.1% annual genetic gain for the early maturing cultivars under drought stress while the average rate of increase in grain yield under optimum growing conditions was 40 kg ha⁻¹ yr⁻¹ with a genetic gain of 1.3% yr⁻¹. In a study involving the evaluation of the 50 early maturing cultivars under low and high-N environments, Badu-Apraku et al. (2015a), reported genetic gains of 165 and 225 kg ha⁻¹ (0.55 and 0.94% per year) in grain yield, respectively. Relative gain per period (that is, gain in grain yield in a period per unit yield in the previous period) was 30 kg ha⁻¹. The genetic gains under low- and high-N environments were exactly the same. The differences in the genetic gains reported in the present study and those of the early maturing cultivars could be due to the differences in the environments under which the cultivars were evaluated, the stress level imposed during the evaluations, the type of material evaluated, that is, extra-early vs. early maturing cultivars, methods of development of the cultivars, breeding periods and number of cultivars involved in the evaluations (Badu-Apraku et al., 2015a). In the present study, extra-early maturing open-pollinated cultivars were evaluated under the three major stress factors limiting maize production and productivity in the savannas of WCA as well as natural, non-stress environments

The mean grain yield under multiple stresses in the present study was 42% lower than mean grain yield under non-stress environments. This is relatively greater than the mean grain yield reduction of 34 to 37% obtained across stress environments by Badu-Apraku et al. (2004, 2015b) for early maturing cultivars. The differences in the level of yield reduction in the different studies could be attributed to differences in the levels of resistance/tolerance to the three stresses of the extra-early maize cultivars used in the present study (Akaogu et al., 2012; Badu-Apraku et al., 2015a, 2015b).

The high genetic gains in grain yield under both multiple stress and non-stress environments in the present study is not surprising because during the development of the second and third era extra-early cultivars, a major strategy of the IITA maize program was to select maize inbred lines with enhanced adaptation to drought-prone environments from diverse sources. The promising inbred lines were also screened for *Striga* resistance under artificial infestation. The inbreds with better adaptation to both drought-prone environments and/or genes for drought tolerance at the flowering and grain-filling periods as well as *Striga* resistance genes from *Zea diploperennis* were used as sources of genes for further introgression into the two extra-early maturing breeding populations which were undergoing S₁ family recurrent selection in our program. Further improvement of the extra-early populations under controlled drought and *Striga hermonthica* parasitism using the S₁ recurrent selection method has resulted in the generation of new productive cultivars that combine enhanced levels of adaptation to drought-prone and low-N environments and improved levels of resistance to *Striga*.

In the present study, the significant gain in grain yield under multiple-stress environments was associated with increased days to anthesis, decreased stalk lodging and improved husk

cover. It is striking that none of the measured traits in the multiple base index was associated with the gains in grain yield under the multiple stress environments. The lack of significant gains in grain yield under non-stress environments could be due to the fact that emphasis in the breeding program was more on improvement of traits under multiple-stresses than under optimal growing conditions. However, the increased days to anthesis, plant and ear heights, stalk lodging, and EPP as well as the decreased ASI, improved ear aspect and reduced ear rot obtained under the non-stress environments suggested that the selection index improved yield under multiple-stresses but resulted in delayed flowering, increased plant and ear heights as well as increased stalk lodging of the cultivars under optimal growing conditions. Badu-Apraku et al. (2014) found that gains in grain yield of early maturing maize cultivars of three breeding eras under multiple stresses were associated with significant improvement in plant and ear aspects, increased EPP and stay green characteristic while under optimal growing environments, the gain was associated with significant improvement in plant and ear heights, plant and ear aspects, husk cover, and increased EPP. The findings of these authors are not consistent with our results under multiple-stress but are in partial agreement with our findings under non-stress environments in the present study. The differences in the maturity groups might have accounted for these results.

The regression analysis of the mean grain yield of the extra-early maize cultivars across stress and optimal growing environments showed clear separation of the maize cultivars into three distinct breeding eras, with the exception of some few cultivars from the second era producing yields which were comparable to those of the first and third eras. In general, the regression analysis separated the extra-early maize cultivars into three groups closely corresponding with the three breeding eras. This result indicated that substantial progress has been made in breeding cultivars with combined resistance and/or tolerance to drought, *Striga* and low-N during the past two decades. This result corroborates the findings of Badu-Apraku et al. (2013a, 2013b, 2015b). The strong positive association between the performance of the cultivars across both multiple-stress and non-stress environments indicated that cultivars selected across multiple-stress environments may also have superior performance under non-stress environments and, to a limited extent, vice versa.

In the present study, the multiple-stress environments consisted of drought, *Striga*, and low-N conditions and provided an opportunity to select the outstanding cultivars for further testing across the different environmental conditions. The AMMI biplot was an invaluable tool for the identification of superior cultivars across the multiple environmental conditions. The cultivar TZEE-W Pop STR C₅ was identified as high yielding and stable both under multiple-stress and non-stress environments suggesting that it has a broad adaptation to the growing environments in WCA. The results of this study are of special interest because drought, low-N, and *Striga* occur simultaneously under field conditions in WCA and when this happens, the combined effect can be devastating (Cechin and Press, 1993; Kim and Adetimirin, 1997; Badu-Apraku et al., 2015b). The superior performance of the cultivars under varying environmental conditions is of utmost importance as

maize varieties targeted to the drought-prone areas of WCA must also be tolerant to low-N, resistant/tolerant to *Striga* and have competitive yield under non-stress conditions. These results suggest that the outstanding cultivar should be extensively tested in on-farm trials in WCA and vigorously promoted for adoption and commercialization to contribute to food security in the subregion.

It is noteworthy that out of the 15 best cultivars identified by the multiple trait index, only TZEE-W Pop STR QPM C₀, TZEE-W STR 107 BC₁, and TZEE-W Pop STR C₅ under multiple-stress environments; TZEE-W Pop STR C₅ and TZEE-W DT C₀ STR C₅ under non-stress environments were identified by the AMMI biplot as high yielding and stable. This result is expected because entries selected by AMMI were based on only the yield data while those selected by the multiple trait index involved grain yield and other stress adaptive traits. Cultivars confirmed as outstanding by both AMMI and the multiple trait index will undoubtedly be outstanding and should contribute to food security and improved livelihoods of resource poor farmers in the subregion who produce maize under multiple-stress environments.

CONCLUSIONS

The annual genetic gain of 2.72 and 2.28% under multiple-stress and non-stress environments indicated that considerable progress has been made in breeding for multiple-stress tolerant extra-early maize cultivars in the subregion. The genetic gains in grain yield under multiple-stress environments was associated with increased days to anthesis, decreased stalk lodging, and improved husk cover. Commercialization of the outstanding extra-early maturing cultivars identified in the present study would contribute to food security and improve the livelihoods of farmers in SSA.

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