Agronomic traits associated with genetic gains in maize yield during three breeding eras in West Africa

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Abstract

Studies on genetic gains in grain yield in maize (*Zea mays* L) is crucial to identify traits of potential value and the necessary modifications in breeding methodologies and strategies for increased progress in future breeding efforts. Fifty early-maturing maize cultivars developed during three breeding eras were evaluated for 2 yr in two field experiments involving 16 multiple stress (drought, Striga-infested, and low soil nitrogen) environments and 35 optimum environments to determine the changes in agronomic traits associated with the genetic gains in grain yield over three breeding eras. The average rate of increase in grain yield was 30 kg ha^{-1} yr^{-1} corresponding to 1.59% annual genetic gain across multiple stresses. Among the agronomic traits under stress, only ears per plant (0.32% $year^{-1}$), ear aspect (-0.51% $year^{-1}$), plant aspect (-0.24% $year^{-1}$) and days to anthesis (0.11% $year^{-1}$) changed significantly ($P<0.05$ or <0.01) during the three eras. The increase in grain yield from the first to the third generation cultivars across stress environments was associated with significant improvements in plant and ear aspects, increased ears per plant and stay green characteristic. Under optimal growing environments, the increase in grain yield from the first to the third generation cultivars was 1.24% per annum and the gain was associated with significant improvements in plant and ear heights, plant and ear aspects, husk cover, and increased ears per plant. The results indicated that substantial progress has been made in breeding for cultivars with combined tolerance/resistance to the three stresses during the past 22 years.

Keywords: drought stress, maize cultivars,soil nitrogen, Striga resistance

Introduction

Maize (*Zea mays* L) production in the savannas of West Africa (WA) is constrained by the use of inappropriate varieties, *Striga hermonthica* (Del) Benth parasitism, low-N and drought, along with diseases and pests, although not as severe as in the forest and forest-savanna transition agro-ecologies. All of the constraints may occur simultaneously in the farmer's field, but in particular, drought stress aggravates Striga infestation and poor N uptake, resulting in zero or grossly reduced grain yield at the end of the season. The estimated annual loss of maize yield resulting from individual or combined effect of these constraints could be up to 100%, depending on severity and stage of manifestation in the field (Wolfe et al, 1988; Lagoke et al, 1991; Cechin and Press, 1993; Kim and Adetimirin, 1997; Badu-Apraku et al, 2004; Badu-Apraku et al, 2010). It is desirable to incorporate low-N tolerance into maize cultivars for increased productivity, especially cultivars that possess resistance to Striga and drought as the three stresses occur at the same time. Indeed, farmers in the Striga endemic agro-ecologies of sub-Saharan Africa (SSA) are presently demanding for cultivars that possess resistance to multiple stress factors and are unwilling to adopt maize cultivars that do not meet this requirement (Badu-Apraku et al, 2010).

The International Institute of Tropical Agriculture (IITA) has developed early maturing germplasm with tolerance or resistance to Striga, drought, and, to a lesser extent, low soil N in WA. Tolerance/resistance to the stresses has been increased in the germplasm through inbreeding, hybridization, backcrossing and recurrent selection, along with effective drought, Striga and, more recently, low-N screening methods. The breeding program has developed stress tolerant inbred lines, hybrids, open-pollinated varieties (OPVs) and quality protein maize (QPM) cultivars with resistance to multiple stresses. Many of the stress tolerant/resistant OPVs and hybrids derived from this program have been released and adopted by farmers in WA.

It is important for plant breeders to measure breeding progress by evaluating under the same environmental conditions the performance of cultivars developed and released over a period of time (Kamara et al, 2004; Tefera et al, 2009). Information on the genetic gains in improvement of grain yield and other traits in crops may help identify traits of potential value as well as the necessary modifications in breeding methodologies and strategies for increased progress in future breeding efforts. Many such studies have been conducted in developed countries in maize (Russell, 1984; Duvick, 1997; Tollenaar, 1989)

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and several other crops (Specht et al, 1999; Tefera et al, 2009). Only a few such studies have been conducted in SSA (Kamara et al, 2004; Badu-Apraku et al, 2013a,b). Most of the researchers also conducted additional studies to identify changes in other agronomic traits associated with the genetic gain in grain yield during the different breeding eras. In WA for example, Kamara et al (2004) reported a genetic gain of 0.41% per year for intermediate/late maturing maize cultivars released from 1970 to 1999 evaluated in the Nigerian savannas. The increase was associated with increased total biomass and kernel weight, and reduced plant height and number of days to flowering. Badu-Apraku et al (2013a) obtained 1.1% annual genetic gain under drought stress. Similarly, the average rate of increase in grain yield under optimum growing conditions was 40 kg ha^{-1} yr^{-1} with a genetic gain of 1.33% yr^{-1}. In another study involving cultivars developed during the breeding eras, Badu-Apraku et al (2013b) obtained yield increase of 41 kg ha^{-1} per year when Striga-infested and 34 kg ha^{-1} per year when Striga-free. For about 22 years, IITA's Maize Improvement Program has been involved in the development of early and extra-early germplasm, specially targeted to the savanna as well as the second growing season in the forest agro-ecologies. The 22 years have been classified into three breeding eras based on the specific strategies used for maize improvement: 1988-2000 (Era 1), 2001-2006 (Era 2) and 2007-2010 (Era 3). The strategies used for the development of the cultivars in each Era have been described in detail by Badu-Apraku et al (1999, 2001) and a total of 50 cultivars (15, 16, 19 cultivars for the eras) were developed during the three eras. In each era the optimum evaluation environment was much superior to the stress environments, although the genetic gain per era was highest for the multiple stress environments. Averaged across all environments in the study, productivity of the early maturing maize cultivars in WA has increased from 2512 kg ha^{-1} during Era 1 to 3207 kg ha^{-1} during Era 3, at the rate of 8.88% Era^{-1}, a total genetic gain of about 27% in the 22-year period covered by the three eras. There is a need to identify the plant traits associated with the genetic gains in grain yield under the different production conditions. The objective of the present study, therefore, was to evaluate the changes in agronomic traits associated with the genetic gains in grain yield over the three breeding eras.

Materials and Methods

A detailed description of the breeding methodology along with the field evaluation trials employed for cultivar development in the different eras, have been described by Badu-Apraku et al (2013a,b); only a brief description is presented here. Emphasis of the breeding program was on the development of high-yielding, early maturing (90-95 days to maturity), stress resistant or tolerant cultivars, with concentration on one stress factor in each era; a type of tandem selection. In essence, the best genetic materials in one era formed the base populations for improvement in the next era. Backcrossing, inbreeding, hybridization and recurrent selection have all been adopted as needed in the breeding program. Evaluation trials were carried out at different stages within each era, with a primary focus on the stress factor being considered during the era, while maintaining the level attained in those of the previous eras. Development of drought tolerant and maize streak virus (MSV) resistant populations and varieties was the main focus in Era 1. Pool 16 DT SR, developed through eight cycles of recurrent selection (Badu-Apraku et al, 1997) and subsequently converted for resistance to MSV disease (Badu-Apraku et al, 2012) was the main source population for developing the first generation of drought tolerant early maturing maize cultivars with resistance to the MSV disease between 1988 and 1993. This population, and some other germplasm from diverse sources identified through several years of extensive testing in WA were composited to form two base populations designated TZE-W Pop DT STR (white) and TZE-Y Pop DT STR (yellow) for improvement in Era 2, with specific focus on Striga resistance, using inbred lines from IITA (1368 STR, and 9450 STR) as the sources of resistance during the development of the populations. Although some of the germplasm used for the development of the two populations had been selected for drought tolerance (Pool 16 DT, for example), greater focus on breeding DT materials was in Era 3. Between 1988 and 2010, a total of fifty experimental cultivars were developed in the program; that is, 16 in Era 1, 19 in Era 2 and 15 in Era 3.

Field Evaluation of the 50 Cultivars

The 50 early-maturing maize cultivars developed during the three eras were evaluated in 2010 and 2011 in two sets of field experiments including 16 stress environments and 35 relatively normal (non-stress) environments. In each trial, a 10 x 5 randomized incomplete block design with three replications was used. A plot consisted of two rows, 5 m long, spaced 0.75 m apart with 0.40 m spacing between plants within a row. Three seeds were planted per hill and the resulting maize plants were thinned to two per stand about 2 wk after emergence to give a final plant population density of 66,000 plants ha^{-1}.

The stress environments consisted of induced drought stress at Ikenne during the 2009/2010 and 2010/2011 dry seasons; terminal drought stress (natural drought stress during the growing season especially towards the end of the season) at a drought-prone site, Bagauda in 2010 and 2011; artificial infestation with *S. hermonthica* for two years (2010 and 2011) at Mokwa and Abuja both in southern Guinea savanna agro-ecological zone of Nigeria where Striga is endemic, as well as Ina (9°30'N and 2°62'E, 1,500 mm annual rainfall) in the southern Guinea savanna and Angaradebougou (11°33'N and 2°13'E, 1,100 mm annual rainfall) in the northern Guinea savanna of Benin Republic; and low-N stress at Mokwa and Ile-Ife (rainforest ecology) also for 2010 and 2011. The induced drought stress at Ikenne was achieved by withdrawing irrigation water from 28 d after planting until maturity so that the maize plants relied on stored water in the soil for growth and development. The Striga infestation method developed by IITA Maize Program (Kim, 1991; Kim and Winslow, 1991) was used to artificially impose Striga stress on the varieties. Fertilizer application on the Striga-stress plots was delayed until about 30 d after planting when 30 kg ha^{-1} N, 26 kg ha^{-1} P, and 50 kg ha^{-1} K were applied as 15-15-15 NPK. The low-N stress plots also received only 30 kg N ha^{-1} rather than the recommended rate of 90 kg N ha^{-1}. Weeds other than Striga were controlled manually.

The 35 optimum environments included the non-stress counterparts of the stress environments described above; that is, full irrigation throughout the growing season at Ikenne, Striga-noninfested plots at Mokwa, Abuja, Ina and Angaradebougou, and recommended fertilizer rates of 120 kg N ha^{-1} at Mokwa and Ile-Ife. In addition, the varieties were evaluated under normal growing season environmental conditions at Saminaka, Samaru, Zaria in Nigeria and Nyankpala, Ejura, Fumesua and Yendi in Ghana. Table 1 provides information on the locations used in the study. All trials were conducted in 2010 and 2011. Apart from those that received specific treatments, 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 ha^{-1} N top-dressed at 4 wk after planting (WAP) and weeds were controlled manually.

Collection of Agronomic Data

Data were recorded on both stress and non-stressed environments in the study for number of days from planting to the day 50% of the plants had shed pollen (days to anthesis, DA) and emerged silks (DS), respectively. The anthesis-silking interval (ASI) was calculated as DS minus DA. Plant height was measured as the distance from the base of the plant to the height of the first tassel branch and ear height as the distance to the node bearing the upper ear. Root lodging (percentage of plants leaning more than 30 percent from the vertical), and stalk lodging (percentage broken at or below the highest ear node), disease reaction, and ear aspect, were also recorded. Ear number 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 5 based on plant type, where 1 = excellent and 5 = 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 based on a scale of 1 to 5, where 1 = clean, uniform, large, and well-filled ears and 5 = ears with undesirable features. In addition, leaf senescence scores were recorded for the drought-stressed plots at 70 d after planting on a scale of 1 to 10, where 1 = almost all leaves green and 10 = virtually all leaves dead. Host plant damage syndrome rating (Kim, 1991) and emerged Striga counts were made at 8 and 10 WAP (56 and 70 d after planting) in the Striga infested plots at Mokwa and Abuja. Maize 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, i.e., highly susceptible (Kim, 1991; Badu-Apraku and Lum, 2007). In the first and third studies, harvested ears from each plot were shelled to determine the percentage grain moisture. Grain yield was adjusted to 15% moisture and computed from the shelled grain weight. On the other hand, in the second study, grain yield was computed based on 80% (800 g grain kg^{-1} ear weight) shelling percent-

Table 1 - Description of the 14 locations used for evaluating early maturing maize cultivars developed during three breeding eras in West Africa, 2010-2011.

Country	Location	Code	Agro ecological zone§	Latitude	Longitude (m asl)	Altitude	Rainfall during growing season (mm)
Nigeria	Ikenne	IK	FT	6°53'N	3°42'E	60	1,200
Nigeria	Mokwa	MO	SGS	9°18'N	5°40'E	457	1,100
Nigeria	Zaria	ZA	NGS	12°00'N	8°22'E	640	1,120
Nigeria	Abuja	AB	SGS	9°15'N	7°20'E	300	1,500
Nigeria	Bagauda	BG	SS	12°01'N	8°19'E	520	900
Nigeria	Ile-Ife	IF	FT	7°28'N	4°32'E	280	1,200
Ghana	Nyanpala	NY	NGS	9°25'N	0°58'E	340	611
Nigeria	Saminaka	SK	NGS	9°50'N	6°45' E	264	1,000
Nigeria	Samaru	SM	NGS	12°00'N	8°22'E	640	1,120
Bénin	Angaredebou	AN	SS	11°32'N	3°05'W	297	1,000
Bénin	Ina	IA	SGS	9°58'N	2°44'W	358	900
Ghana	Yendi	YD	SGS	9°26'N	0°10'W	157	1,300
Ghana	Ejura	EJ	FT	7°38'N	1°37'E	90	1,108
Ghana	Fumesua	FM	FT	6°41'N	1°28'W	150	1,345

§ SGS = southern Guinea savanna; NGS = northern Guinea savanna; FT = forest-savanna transition zone; SS = Sudan savanna.

age and adjusted to 150 g kg^{-1} moisture content.

Statistical Analysis

Analysis of variance, combined across environments was performed on plot means for each trait with PROC GLM in SAS using a RANDOM statement with the TEST option (SAS Institute, 2001). In the combined ANOVA, the location-year combinations, replicates and blocks of each experiment were considered as random factors while entries were considered as fixed effects. Data relating to scores and counts were natural logarithm-transformed before the analyses of variance.

Correlation coefficients were computed between grain yield and other measured traits, as well as between each pair of the measured traits for the 50 maize cultivars under the different environmental conditions. Regression of each variable on year of cultivar development was done to estimate gain $year^{-1}$. Correlation analysis was done with the SAS package, version 9.2 (SAS Institute, 2001) while regression analysis, including the parameters and the graphical display of the regression line were done using the Excel software in the Microsoft Office suite 2007. In addition, R-factor analysis was used to study the association of agronomic traits with grain yield under each environment. R-factor analysis is based on correlation among traits with principal component analysis approach. Using this approach, each trait was expressed as a linear function of other traits and the best linear combination of variables was identified as the first principal factor or factor 1, which accounted for a larger proportion of the total variance for the set of data than any other factor. Other factors were determined similarly, with each subsequent factor explaining more of the residual variance than others after it. The principal component model used was:

$$X_i = a_{j1}F_1 + a_{j2}F_2 + \dots\dots\dots + a_{jn}F_n$$

where

X_i = vector of observed variable, i = 1,2, ………., n,

a_j = matrix of the factor loadings, j = 1, 2, ………, p, and F = vector of factors.

In this model, each of the n observed traits was described linearly in terms of n new, uncorrelated components F_1, F_2, ….., F_n and the components were grouped by varimax rotation method applied to the characteristic roots and vectors from the correlation matrix so that the resulting rotated factors were orthogonal. Traits loaded on each factor were sorted in descending order based on the value of the component attributable to the factor. To facilitate interpretation of the results, loaded component values of 0.4 or less were suppressed in the computer output and only the factors with eigenvalue ≥ 1 were retained. Factor analysis was done using the Statistical Packages for the Social Sciences (SPSS), version 17. Subsequent to factor analysis, SPSS was also used for stepwise multiple regression analysis of grain yield on all other traits to identify the best subset of traits for predicting grain yield as well as their order of importance under stress and non-stress conditions. This technique included in the regression model only the traits that contributed significantly to grain yield by systematically adding the traits, one at a time, to the model and terminating the analysis at the point where no other trait significantly contributed to grain yield at 0.05 level of probability specified by the researcher. The traits identified in the stepwise regression under stress conditions were individually adopted to predict grain yield under non-stress conditions, using the Excel software in Microsoft Office suite.

Results

Analysis of Variance under Multiple Stress and Non-stress Environments

The combined analysis of variance of the 50 early maturing maize cultivars evaluated under multiple stress (Table 2) and non-stress (Table 2) environments showed highly significant ($P < 0.01$) mean

Table 2 - Mean squares from the analysis of variance for grain yield and other agronomic traits of maize cultivars from three breeding eras evaluated under 16 multiple stress and 35 non-stress environments in Nigeria, Ghana and Benin Republic, 2010 and 2011.

Source of variation	DF	Grain yield kg ha^{-1}	Days to anthesis	Days to silking	ASI	Plant height, cm	Ear height, cm	Plant aspect	Ear aspect	Husk cover	% Root lodging	% Stalk lodging	EPP	Stay green character
						Multiple stress								
Environment, E	15	117935952**	1538.5**	1113.5**	140.4**	64454.0**	74777.6**	11.8**	143.7**	56.8**	246.8**	234.6**	1.57**	39.5**
Block (E × Rep)	176	1319862**	8.4**	8.9**	2.2**	434.9**	242.7**	0.8**	0.6**	0.7**	1.8**	0.8**	0.03**	0.9**
Rep (E)	28	2786291**	16.3**	19.6**	3.1**	633.0**	289.6**	0.6**	2.5**	0.5	4.9**	1.8**	0.06**	3.9**
Era	2	34459299**	0.2	1.4	0.5	2535.9**	346.6**	1.8**	13.1**	1.2	0.2	0.0	0.39**	2.1**
Cultivar (Era)	147	3266814**	33.1**	35.6**	3.2**	896.4**	227.5**	0.5**	1.3**	0.6	0.7	0.7*	0.05**	0.5
E × Cultivar (Era)	704	584284**	3.3**	4.8**	1.7**	172.3**	84.6	0.2**	0.4**	0.4	0.8	0.6*	0.02**	0.5
E × Era	30	795538**	3.4	4.3	1.2	177.5	91.8	0.1	0.7**	0.3	1.4	0.8	0.04**	0.4
Error	1190	402937	2.8	3.3	1.2	129.3	77.0	0.2	0.3	0.5	0.9	0.5	0.02	0.4
						Non-stress environments								
Environment, E	34	228785264**	2338.9**	1856.3**	82.2**	49178.2**	26209.6**	43.7**	61.9**	79.4**	133.6**	124.9**	1.53**	
Block (E × Rep)	412	1134849**	3.8**	4.8**	0.7**	346.3**	223.8**	1.1**	0.4**	0.3**	0.9**	0.7**	0.01**	
Rep (E)	6	6227585**	6.2**	8.6**	1.4**	1172.1**	839.1**	1.8**	1.0**	0.5**	2.5**	2.0**	0.05**	
Era	2	133599837**	0.3	0.5	1.5	17125.4**	8038.0**	16.0**	38.5**	3.7**	0.9	1.9*	0.22**	
Cultivar (Era)	147	9897354**	52.3**	63.3**	2.2**	2480.9**	907.2**	2.4**	2.1**	0.7**	1.7**	2.6**	0.04**	
E × Cultivar (Era)	1597	636002**	2.4**	2.9**	0.6**	168.4**	106.1	0.8	0.3**	0.2**	0.6**	0.6**	0.01**	
E × Era	68	903145**	2.6**	3.1**	0.7	215.3**	132.9*	1.2**	0.5**	0.3*	0.7**	0.7**	0.01*	
Error	2914	432607	1.5	1.8	0.6	145.9	99.6	0.7	0.2	0.2	0.5	0.5	0.01	

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

Table 3 - Grain yield and other agronomic traits of maize cultivars from three breeding eras evaluated under 16 multiple stress and 35 non-stress environments in Nigeria, Ghana, and Benin Republic, 2010 and 2011.

Trait	Multiple stress environments			Non-stress environments		
	Era 1 (1988-2000) 15 cvs	Era 2 (2001-2006) 16 cvs	Era 3 (2007-2010) 19 cvs	Era 1 (1988-2000) 15 cvs	Era 2 (2001-2006) 16 cvs	Era 3 (2007-2010) 19 cvs
Grain yield, kg ha^{-1}	2176 ± 54.2	2286 ± 49.2	2606 ± 49.0	3398 ± 52.5	3615 ± 46.7	3957 ± 42.3
Days to anthesis	55 ± 0.50	55 ± 0.50	55 ± 0.40	53± 0.20	53± 0.10	53± 0.10
Days to silking	57 ± 0.40	57 ± 0.40	57 ± 0.40	54 ± 0.10	54 ± 0.10	54 ± 0.10
ASI, days	3 ± 0.12	3 ± 0.11	3 ± 0.10	2 ± 0.03	2 ± 0.03	2 ± 0.03
Plant height, cm	148 ± 2.30	151 ± 3.00	151 ± 2.80	164 ± 0.80	169 ± 0.70	170 ± 0.70
Ear height, cm	72 ± 2.40	73 ± 2.40	74 ± 2.20	77 ± 0.50	80 ± 0.50	82 ± 0.50
Root lodging, %	7.7 ± 0.10	7.9 ± 0.10	7.7 ± 0.20	4.0 ± 0.10	4.4 ± 0.20	4.3 ± 0.20
Stalk lodging, %	6.7 ± 0.20	6.8 ± 0.10	6.8 ± 0.20	5.4 ± 0.20	5.8 ± 0.20	5.5 ± 0.20
Husk cover	2.5 ± 0.05	2.5 ± 0.05	2.4 ± 0.04	2.3 ± 0.02	2.3 ± 0.02	2.3 ± 0.02
Plant aspect	3.2 ± 0.06	3.2 ± 0.06	3.1 ± 0.05	2.8 ± 0.02	2.6 ± 0.02	2.6 ± 0.03
Ear aspect	3.7 ± 0.05	3.6 ± 0.05	3.4 ± 0.05	2.9 ± 0.02	2.7 ± 0.02	2.6 ± 0.02
Ears per plant	0.8 ± 0.02	0.8 ± 0.02	0.9 ± 0.01	0.9 ± 0.005	0.9 ± 0.005	0.9 ± 0.004
Stay green characteristic	4.4 ± 0.09	4.4 ± 0.09	4.2 ± 0.07	-	-	-

squares for grain yield and nearly all other traits for most sources of variation. Under both conditions, era had no significant effect on flowering traits and under stress, Environment x Era interaction was not significant for 10 of the 12 agronomic traits assayed in this study (Table 2). Similarly in the stress environments, most of the mean squares associated with Era, Cultivar within Era and their interactions were not significant for husk cover (HC), root and stalk lodging, and the stay-green characteristic.

Relative to the non-stress environments, stress reduced grain yield by about 35%, delayed flowering by 2-3 days, increased ASI by 1 day, reduced plant and ear heights, increased lodging, and worsened husk cover, plant aspect and ear aspect (Table 3). On average, era had no effect on days to anthesis and silking, ASI, root and stalk lodging, plant aspect and ear aspect under both stress and non-stress environments (Table 3). Also under stress, era had no effect on plant and ear heights, although both increased significantly from Era 1 to Era 3 under non-stress environments. Era had no effect on EPP under non-stress environments but EASP, PASP, and EPP improved slightly, though significantly from Era 1 to Era 3 (Table 3).

Genetic Gains of Agronomic Traits under Stress- and Non-stress Environments

Under stress, grain yield per year increased at the rate of 1.59% (Table 4), a total gain of about 35% in the 22 years covered by the breeding program. Corresponding increase under non-stress conditions was 1.24%, about 27% total increase for the 22 years. Among the agronomic traits under stress, only EPP (0.32% year^{-1}), EASP (-0.51 year^{-1}) and ANTH (0.11% year^{-1}) changed significantly ($P < 0.05$ or < 0.01) during the three eras; changes associated with era in all other traits were not statistically significant ($P > 0.05$). Using the two probability levels as criteria, only PASP, ANTH, SILK, STLG, and RTLG did not change significantly under non-stress conditions during the breeding eras; all other traits changed in the

Table 4 - Percent genetic gain yr^{-1}, correlation coefficient between trait and the cultivar year of development (r-value), and probability that r = 0 for grain yield and other agronomic traits of maize cultivars from three breeding eras evaluated in 16 multiple stress and 35 non-stress environments in Nigeria, Ghana, and Benin, 2010 and 2012.

	Multiple stress environments			Non-stress environments		
Trait	% genetic gain yr^{-1}	r-value	P(r = 0)	% genetic gain yr^{-1}	r-value	P(r = 0)
Grain yield)kg ha^{-1})	1.59	0.69	<0.01	1.24	0.82	<0.01
EPP	0.32	0.52	<0.05	0.24	0.70	<0.01
Ear aspect	-0.51	-0.63	<0.05	-0.40	-0.41	<0.05
Plant aspect	-0.24	-0.39	<0.01	-0.81	-0.85	<0.01
Anthesis, days	0.11	0.50	<0.05	0.08	0.44	>0.05
Silking, days	0.08	0.37	>0.05	0.05	0.32	>0.05
Anthesis-silking interval (days)	-0.36	-0.25	>0.05	-0.80	-0.67	<0.01
Plant height (cm)	0.22	0.45	>0.05	0.28	0.64	<0.01
Ear height (cm)	0.18	0.27	>0.05	0.38	0.68	<0.01
Husk cover	-0.21	-0.25	>0.05	-0.38	-0.57	<0.05
Stalk lodging (%)	0.09	-0.03	>0.05	-0.63	-0.23	>0.05
Root lodging (%)	-0.01	-0.40	>0.05	0.25	0.01	>0.05
Stay green characteristic	-0.28	-0.28	<0.05	-	-	-

Table 5 - Components from varimax-rotated factor analysis for grain yield and other agronomic traits of 50 early maturing maize cultivars developed during three breeding eras and evaluated under 16 multiple stress and 35 non-stress environments in Nigeria, Ghana and Benin Republic, 2010 and 2011.

	Stress Environment				Non-stress Environment		
Trait	Factor 1	Factor 2	Factor 3	Factor 4	Factor 1	Factor 2	Factor 3
Grain yield	0.890				0.935		
Ear aspect	-0.845				-0.934		
Plant aspect	-0.835				-0.816		
Plant height	0.772				0.776		0.511
Ear height	0.747				0.809		
Ears per plant	0.718				0.711		
Days to anthesis		0.975				0.984	
Days to silk		0.955				0.974	
Husk cover			0.710				
Stay-green characteristic			0.634				
Root lodging			0.575				0.784
Anthesis-silking interval				0.877			0.531
Stalk lodging				0.406			0.834
Eigen value	4.46	2.29	1.67	1.17	4.93	2.57	1.83
% total variation explained	34.33	17.63	12.81	8.99	41.04	21.45	15.28
Cumulative variation	34.33	51.96	64.76	73.75	41.04	62.49	71.77

expected direction (Table 4). Regression of each trait on number of years from Era 1 to Era 3 showed similar responses under the two evaluation conditions, although the regression parameters differed under the two environmental conditions, especially with the R-value which, in most cases, was larger under non-stress than stress conditions (data not shown).

Traits Association under Multiple Stress and Non-stress Environments

Only three traits had significant r-values with grain yield under non-stress environments whereas for the stress environments, seven traits were significantly associated with grain yield (Supplementary Table 1). Under both environments, grain yield had positive r-values with EPP as well as with PHT under non-stress and EHT under stress conditions. All other significant correlations with grain yield were negative. Significant R-values were also observed between agronomic traits, with many more values reaching statistically significant levels under stress than non-stress conditions.

Grain yield and the other traits were grouped into four factors under stress and three under non-stress environments (Table 5). Together, the factors accounted for about 74% of the variance for all traits under stress, and 78% under non-stress. Pattern of component loadings on the factors were similar in the two group of environments; that is in both cases, factor 1 was grain yield and its determinants, factor 2 was flowering traits, and factor 3 along with factor 4 under stress conditions contained lodging and associated traits. It is particularly striking that traits associated with grain yield were almost exactly the same and nearly in the same order under both stress and non-stress conditions. In both cases, factor 1 carried about half of the total variation accounted for by all traits while the proportions accounted for by subsequent factors were much lower than that of factor 1. The influence of a factor on a particular trait is determined by the square of the factor loading for the trait (Lee and Kaltsikes, 1973; Fakorede, 1979). Therefore factor 1 accounted for 80% and 87% of the grain-yield variance under stress and non-stress environments, respectively. These values compare favorably with the R^2-values of about 88% from the stepwise multiple regression of grain yield on the variables loaded on factor 1 for each evaluation condition (Supplementary Table 2). In this regression, EASP alone accounted for 80 and 84% of yield variation under stress and non-stress environments while traits picked in subsequent steps of the regression model accounted for much lower proportions. Apart from EASP, the traits picked in the stepwise multiple regression model were all loaded and almost in the same order on factor 1 under stress but not so under non-stress conditions in which ANTH, that was not loaded on factor 1 was picked as the second most important grain-yield determinant. Regression of grain yield under non-stress conditions on each of the four traits identified in the stepwise multiple regression analysis for stress environments revealed that EASP and PASP predicted grain yield at similar rates per unit reduction in their ratings, with R^2 values of about 58 and 50%, respectively (Figure 1). The regression analysis also showed that cultivars that produced one ear per plant or were relatively tall under stress were high yielding under non-stress conditions, although the R^2 for PHT was much lower than those of the other traits.

Discussion

West Africa is endowed with diverse agro-climatological zones that potentially support high grain productivity of maize, provided the varieties that fit into each agro-ecological niche are available. Also, early in the maize improvement programs of WA

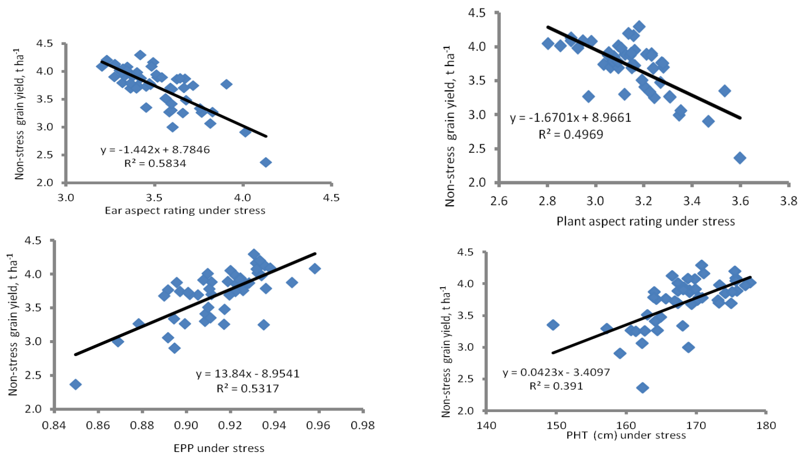

Figure 1 - Predicted grain yield under non-stressed environments as a function of performance of EASP, PASP, EPP, and PHT under stress environments for 50 early maturing maize cultivars developed during three breeding eras and evaluated in Nigeria, Ghana and Benin Republic in 2010 and 2011.

countries, researchers realized that maize production in the different ecologies was constrained by myriads of diseases. The experiences of early plant breeders therefore led to an important concept in maize breeding in WA that the first logical step in varietal improvement is resistance breeding (Fakorede et al, 1993). Indeed, breeding for disease resistance has continued to be a very important aspect of our effort at improving yield in WA. Establishment of IITA in Nigeria actually catalyzed maize improvement activities in the WA sub region. In collaboration with national programs, IITA developed and deployed varieties resistant to diseases such as the maize streak virus and downy mildew disease as well as identified and systematically tackled other biotic and abiotic constraints to maize production. Presently, Striga resistance, drought tolerance and low-N tolerance are receiving high-value attention in the maize breeding programs of the sub region. One remarkable observation about the successful outcome of the breeding efforts is the increased grain yield production of the varieties under the stress for which they are improved and the value-added production increase under non-stress conditions. Improving maize for each specific constraint has always led to improved yielding ability of the maize germplasm in the sub region. For example, breeding for streak resistance more than doubled grain yield under streak pressure while the streak resistance varieties performed equally with or better than the non- streak resistance counterparts under streak-free environments (Efron et al, 1989; Fakorede et al, 1993). Similarly, grain yield of Striga resistance varieties under Striga pressure is almost always more than double that of non-Striga resistance varieties, especially in farmers' field. Results obtained in the present study involving 50 open-pollinated varieties developed in three eras lead to the conclusion that Era 3 (or latest era) varieties are greatly improved in stress resistance over those of earlier eras. Improvement has been linear for resistance to multistress conditions, to barrenness brought about by Striga infestation, low-N or drought and to premature leaf senescence that results in reduced yield and excessive stalk breakage. Newer varieties have stronger roots. They require essentially the same amount of time to reach maturity as older varieties; flowering dates and grain moisture levels at harvest have not changed through the years. The result is that new varieties outyield those developed in earlier eras in all environments, with the yield advantage of the latest era varieties being greatest when environmental conditions are most favorable.

Theoretically, the ultimate goal of breeding for stress tolerance/resistance is for the resulting varieties to perform under stress equally with or better than their performance under non-stress conditions. Relative to Era 1, yield of the Era 3 varieties was 35% higher than that of era 1 under the multiple stress conditions in this study, and about 30% higher yielding than Era 1 varieties under non-stress conditions. In other words, to take full advantage of the genetic improvement of maize performance under stress conditions, the resulting varieties must be complemented by recommended agronomic practices especially under near normal natural conditions such as adequate rainfall. However, when environmental factors are overwhelmingly limiting, the era 3 varieties cushion the adverse effects and minimize the risk of partial or total crop failure that would have occurred if era 1 varieties were grown by the farmers, and this is the unquantifiable benefit of breeding for stress tolerance in maize.

Breeders are always desirous of identifying effective approaches to varietal improvement, one of which is indirect selection for a primary trait such as yield, through a secondary trait. This approach is particularly desirable in situations where the heritability of the primary trait is low because of harsh environmental conditions in which selection must be done, as has been the case with selection for resistance/tolerance to the three stresses, Striga parasitism, drought and low-N in WA. The large volume of data accumulated over the long period of the selection program reported here provided an opportunity to thoroughly investigate the secondary traits for effective indirect selection for maize grain yield under the stress conditions. Several statistical methods were used; ANOVA along with standard errors for comparison of means, correlation, linear as well as stepwise multiple regression, and factor analysis for data reduction into few groups (or factors), with each group containing related traits only. Our results showed consistently that traits with similar basic physiology were highly correlated; for example, anthesis with silking, plant height with ear height, ear aspect with plant aspect, and ear number with grain yield. Although the statistical methods used in the analyses have the same underlying principles, they elicited different aspects of the «raw material» which is basically variation; ANOVA determined the presence of variation while the other methods examined relationships, with the regression models highlighting causes and effects. The results of the present study also showed that factor analysis truly restructures inter-relationships to make data interpretation easier, and this is its advantage over correlation and regression analyses. The 12-13 quantitative traits were reduced to 3 or 4 groups of traits called factors. Theoretically, uses of factor analysis could be exploratory, confirmatory or as a measuring device (Kim, 1975; Fakorede, 1979). In the present study, we used the analysis to (i) explore and detect the patterning of variables with a view to discovering new concepts and possible reduction of data and (ii) confirm the expected number of orthogonal factors and their loadings. The output was used in stepwise multiple regression analysis to determine the order of importance of traits most relevant to grain yield improvement under stress and non-stress conditions. Overall, plant and ear aspects, along with ears per plant came out loud and clear as important secondary traits for grain-yield improvement under both stress and non-stress conditions. These three traits are relatively easy to determine, although ear and plant aspects are rather subjective and require experience to minimize the effects of the subjectivity. With more refinements in their method of determination, both traits, along with ear number may be effective as selection criteria and consequently reduce the cost of selection programs for varietal improvement.

Conclusions

The average rate of increase in grain yield was 30 kg ha^{-1} yr^{-1} corresponding to 1.59% annual genetic gain across the multiple stresses, Striga, drought and low N. The increase in grain yield from the first to the third generation cultivars across stress environments was associated with significant improvement in plant and ear aspects, increased EPP and stay green characteristic. Under optimal growing environments, the increase in grain yield from the first to the third generation cultivars was 1.24% per annum and the gain was associated with significant improvement in plant and ear heights, plant and ear aspects, husk cover, and increased EPP. The results of the present study indicated that substantial progress has been made in breeding for cultivars with combined tolerance/resistance to the three stresses during the past 22 years.

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Supplementary Table 1. Correlation coefficients among grain yield and other agronomic traits for 50 early maturing maize cultivars developed during three breeding eras and evaluated under 16 multiple stress (below diagonal) and 35 non-stress (above diagonal) environments in Nigeria, Ghana and Benin Republic, 2010 and 2011.

	Grain yield	Days to anthesis	Days to silking	ASI	Plant height	Ear height	Root lodging	Stalk lodging	Husk cover	Plant aspect	Ear aspect	EPP
Grain yield		0.24	0.20	-0.17	0.38**	0.24	0.05	0.01	-0.16	-0.19	-0.30*	0.51**
Days to anthesis	-0.31*		0.96**	-0.45**	0.07	-0.02	-0.06	-0.19	0.11	0.12	0.08	0.32*
Days to silking	-0.34*	0.80**		-0.20	-0.02	-0.10	-0.04	-0.23	0.11	0.12	0.08	0.30*
ASI	-0.27	0.15	0.35*		-0.24	-0.22	0.04	0.01	-0.10	-0.04	-0.03	-0.18
Plant height	0.21	-0.48**	-0.45**	-0.39**		0.78**	0.06	0.34*	0.11	-0.07	0.04	0.17
Ear height	0.44**	-0.68**	-0.51**	-0.49**	0.91**		-0.01	0.29*	0.21	0.01	0.13	0.07
Root lodging	-0.41**	0.10	0.18	0.52**	-0.48**	-0.51**		0.32*	0.15	0.07	-0.02	0.05
Stalk lodging	0.18	-0.50**	-0.34*	-0.20	0.46**	0.34*	-0.15		0.06	0.03	0.03	-0.02
Husk cover	0.21	0.01	-0.01	-0.26	0.21	0.24	-0.27	-0.04		0.41**	0.47**	-0.03
Plant aspect	-0.32*	0.39**	0.46**	0.07	-0.41**	-0.31*	0.01	-0.13	0.26		0.41**	-0.07
Ear aspect	-0.20	-0.14	0.04	0.06	-0.26	-0.04	0.02	0.06	-0.03	0.39**		-0.19
EPP	0.34*	0.01	-0.22	-0.19	0.16	0.03	-0.17	0.02	-0.03	-0.25	-0.37**	
Stay green characteristic	-0.50**	0.03	0.16	0.26	-0.24	-0.18	0.13	-0.11	-0.11	0.17	0.53**	-0.22

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

Supplementary Table 2. Partial regression coefficients (b-value) and coefficients of determination (R^2) from the stepwise regression analysis of grain yield (kg ha^{-1}) on several other agronomic traits of 50 early maturing maize cultivars developed during three breeding eras and evaluated under 16 multiple stress and 35 non-stress environments in Nigeria, Ghana and Benin Republic, 2010 and 2011.

Stress environments

No. of traits in model	μ	[1]EASP	PASP	EPP	PHT	R^2	ΔR^2	*P*(b-value=0)
1	7419.92	-1425.39				0.804	0.804	0.000
2	8070.54	-1180.69	-479.99			0.839	0.035	0.000
3	5078.94	-854.71	-474.48	2142.73		0.864	0.025	0.003
4	2108.55	-758.83	-283.72	2600.47	10.92	0.879	0.015	0.024

Non-stress environments

No. of traits in model	μ	EASP	SILK	PASP	R^2	ΔR^2	*P*(b-value=0)
1	8706.42	-1838.29			0.836	0.836	0.000
2	13246.43	-1823.95	-84.489		0.856	0.020	0.015
3	14106.91	-1531.63	-93.527	-442.892	0.871	0.015	0.006

[1]EASP = Ear aspect, PASP = Plant aspect, EPP = Number of ears per plant, PHT = Plant height (cm), SILK = Number of days from planting to 50% of the plants silking, ΔR^2 = increase in R^2 attributable to the addition of another variable to the model.