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Genetic Variances and Heritabilities of Early Yellow Maize Population Following Cycles of Improvement for Striga Resistance and Drought Tolerance.

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ABSTRACT

Drought and Striga are principal constraints to maize production in sub-Saharan Africa. An early yellow maize population, TZE-Y Pop DT STR that had undergone five cycles of selection for resistance to Striga, followed by three cycles of improvement for drought tolerance was investigated for yield gains, changes in genetic variances and inter-relationships among traits under drought-stress and optimum environments. Two hundred and forty S₁ lines comprising 60 each from the base population and subsequent populations from three selection-cycles improved for grain yield and drought tolerance, were assessed under drought and optimal environments in Nigeria, 2010 – 2012. Genetic improvements in grain yield of 423 and 518 kg ha⁻¹ cycle⁻¹ were achieved under drought-stress and optimum environments. Predicted improvements in selection for yield were 348 and 377 kg ha⁻¹ cycle⁻¹ under drought-stress and optimum environments, respectively. The highest yield observed in C₃ was accompanied by reduced days to silking, anthesis-silking interval, improved plant aspect, ear aspect, and increased plant height and ears per plant across research environments as well as improved stay green characteristic under drought. The level of genetic variability for yield and some few other traits were maintained under drought and optimal environments in the population. Presence of residual genetic variability for yield and other assayed traits in C₃ indicated that progress could be made from future selection in the population depending on the ability of breeders to identify outstanding genotypes and precision level of
experimentation. Substantial improvement has been made in yield and drought tolerance in $C_3$ of population.

**Abbreviations:** ASI, anthesis-silking interval; DAP, days after planting; DS, days to 50% silking; DA, days to anthesis; EPP, ear number per plant; GEI, genotype-by-environment interaction; HUSK, husk cover; IITA, International Institute of Tropical Agriculture; PHT, plant height; STGR, stay green characteristic; WAP, weeks after planting; WCA, West and Central Africa.

**RECURRENT DROUGHT,** *Striga hermonthica* infestation and soil nitrogen deficiency (Low N) are the most prominent limitations to sustainable maize production and productivity in West and Central Africa (WCA). Losses in grain yield resulting from *Striga hermonthica* damage on maize could be as high as 100% and force farmers to abandon their farms. About 40 million hectares of cereal fields in WCA alone are seriously infested by *Striga* spp., while at least 70 million hectares have moderate levels of infestation by the parasite (Lagoke et al., 1991). Edmeades et al. (1995) observed that 15% annual maize yield loss is caused by drought stress in the West African savannas. The authors concluded that yield losses could be higher in the marginal rainfall areas characterized by annual rainfall of less than 500 mm and sandy or shallow soils. Higher yield losses could be recorded if drought occurred at the most drought-sensitive stages of crop growth and development, particularly during flowering and grain filling periods (Denmead and Shaw, 1960; NeSmith and Ritchie, 1992). About 10 to 50% yield reduction in maize is attributed to stress due to low-N annually (Wolfe et al., 1988). Therefore, the development and genetic enhancement of maize for tolerance to low soil N is also very important for increased maize production and productivity (Betrán et al., 2003a). Most often, drought, damage due to *Striga*, and soil nutrient deficiencies occur simultaneously in the field, and the combined effects could be disastrous (Cechin and Press,
1993; Kim and Adetimirin, 1997). In a study conducted by Badu-Apraku et al. (2004), to examine the performance of cultivars with early maturity under induced moisture stress, *Striga* infestation and optimal (well-watered and *Striga*-free) conditions, drought reduced grain yield by 53% while 42% yield reduction resulted from *Striga* infestation. In a similar study, Badu-Apraku et al. (2010a) demonstrated yield reductions of 44, 65 and 40% under drought, *Striga* infestation and low N, respectively. In the northern Guinea and Sudan savannas where random drought stress is prevalent, it is important to introgress genes for drought tolerance into cultivars that possess resistance to *Striga*, since the two stresses occur simultaneously in the field. Badu-Apraku et al. (2013) observed that maize farmers in the *Striga* prone agro-ecologies of SSA urgently need cultivars that are tolerant to drought and resistant to *Striga* and will not adopt maize cultivars that do not possess these characteristics. It is therefore, important that maize breeding programs targeting the savannas of WCA pay special attention to at least drought stress and *Striga* infestation.

Maize breeding populations have been successfully improved for drought tolerance, yield and other desirable agronomic traits through recurrent selection (Badu-Apraku et al., 1997; Chapman and Edmeades, 1999; Monneveux et al., 2006). For example, Edmeades et al. (1995) obtained yield gains per cycle of 175 kg ha\(^{-1}\) (14%) under drought, 162 kg ha\(^{-1}\) (3%) under optimal growing conditions and 168 kg ha\(^{-1}\) (4.8%) across research environments in two early-maturing CIMMYT maize populations. Recurrent selection under induced drought stress at flowering and grain filling periods resulted in annual yield gain of 5% under moisture stress (Edmeades et al., 1999).

Several researchers have shown that dominance and additive genetic effects were equally important in the inheritance of yield in temperate maize populations while additive genetic effects were more important for other measured traits (Hallauer and Miranda, 1988; Han and Hallauer, 1989; Wolf et al., 2000). Similarly, Silva et al. (2004) investigated genetic
variances in tropical maize populations and indicated that even though the magnitude of dominance and additive effects are specific for populations, these may differ depending on the dominance and additive gene action of the segregating loci. Nevertheless, the few reports on the gene action modulating the inheritance of yield of tropical maize populations under drought stress are not many and also contradictory. For example, studies by Guei and Wassom (1992) revealed that the dominance genetic variance was greater than the additive for grain yield and ears per plant in two tropical maize populations. In contrast, the authors showed that the additive genetic variance was more important than dominance variance in the expression of flowering traits under drought. Furthermore, Badu-Apraku et al. (2004) reported that additive genetic variance and narrow sense heritabilities were moderate-to-large for yield and other measured traits in Pool 16 DT, after subjecting the population to eight selection cycles for increased yield under managed drought. They concluded that dominance genetic variance was equally important and needed to be considered in future selection programs.

Weyhrich et al. (1998) reported that the $S_1$ progeny selection scheme has been designed to improve population performance and facilitate rapid fixation of alleles, with deleterious alleles exposed to the environment for elimination during the initial stages of the selection program. In the absence of over dominance, the $S_1$ or $S_2$ family selection method is superior to other population improvement methods (Lamkey, 1992). Weyhrich et al. (1998) investigated the responses to selection of a maize population to seven methods of recurrent selection and showed that all the methods were effective for improvement in the population performance per se for yield. However, the greatest effect of selection for improved yield was observed using the $S_2$ progeny selection method. They concluded that the selection methods involving inbred progenies was responsible for the superior gains from selection in BS11 compared to other selection methods. Contrary to theoretical arguments that recurrent
selection involving inbred progenies is superior to mass selection and the half-sib recurrent selection methods, it has been demonstrated empirically that the S₁ or S₂ family selection is not always superior (Coors, 1999; Wardyn et al. 2009; Edward 2010). For example, Wardyn et al. (2009) demonstrated that predicted responses to S₁ or S₂ family selection did not show any advantages over half-sib methods in three maize populations. However, S₁ or S₂ family selection methods were unique and outstanding for improvement of inbred line performance while selection method involving half-sib progenies were superior for genetic enhancement of non-inbred progenies. Wardyn et al. (2009), explained that linkage disequilibrium, over dominance, and/or epistasis could profoundly influence predictions from selection programs. Similarly, Edward (2010) indicated that pseudo-over dominance because of linkage disequilibrium may limit responses to S₁ or S₂ family selection in maize breeding populations. Despite the limitations, the S₁ recurrent selection method capitalizes on additive gene action and has been extensively used to screen segregating families of maize at IITA. Using this recurrent selection method, several early Striga resistant/tolerant cultivars with outstanding performance in drought-prone environments have been developed and released in SSA. The early-maturing yellow maize population, TZE-Y Pop DT STR with combined drought tolerance and Striga resistance was derived from diallel crosses involving elite maize germplasm identified and selected based on years of extensive multi-location testing in WCA. Following the development of the population, the S₁ family recurrent selection method has been utilized to improve it for Striga resistance and tolerance to drought and low-N. The resulting improved population has been serving as a source population for extraction of outstanding maize products. Selection for early maturity has been conducted in the savanna and forest agro-ecologies of WCA, and several multiple stress tolerant cultivars have been developed. Several of these cultivars have been commercialized following wide testing in the sub-region. Outstanding inbred lines selected for tolerance to drought and Striga resistance
have been used for the development of early maturing varieties well adapted to drought-stress and *Striga* endemic zones. The selected lines are also utilized as sources of beneficial alleles for improvement of early tropical breeding populations. Recurrent selection methods have been employed to increase the frequency of beneficial genes to enhance tolerance to drought stress, while repeated self-pollination has also been employed to fix desirable genes. A major goal of the breeding program has been the genetic enhancement of the breeding populations for *Striga* resistance and tolerance to water deficit. Using this strategy, TZE-Y Pop DT STR has been remarkably improved through the *S*₁ recurrent selection program, aimed at concentrating beneficial genes in the breeding population. Through the recurrent selection and inbred-hybrid development programs, several inbred lines, open-pollinated cultivars and hybrids with tolerance to multiple-stress have been generated from the reference population (Badu-Apraku et al., 2006b; Badu-Apraku et al., 2008).

TZE-Y Pop STR had been subjected to five *S*₁ family recurrent selection cycles for improvement of *Striga* resistance level and upgrade of the grain yield performance under *Striga*-infested and non-infested environments (Badu-Apraku et al., 2007, 2008, and 2009). Sequel to this was three selection cycles of improvement for tolerance to drought. Thus, the population possess genes for combined resistance/tolerance to infestation by *Striga hermonthica* and drought stress. Selection and genetic drift in a target population may result in changes in gene frequencies and genetic variability. Consequently, following five selection cycles for improved yield and resistance to *Striga* and three cycles of selection for an upgraded level of drought tolerance in TZE-Y Pop DT STR, there is a need for information on changes in genetic parameters such as the genetic variability, heritability estimates, and genetic correlations due to recurrent selection in the population. Such information is highly desirable in determining the changes necessary in the population improvement methods and strategies that should be utilized to ensure continued gains from advanced selection cycles in
the population enhancement program. Information on the genetic variances and heritability estimates in the target population for yield and other traits is crucial for ascertaining the effectiveness and progress anticipated from future selection cycles. It is therefore important to verify whether there existed sufficient genetic variability for yield and other desirable agronomic traits in the target population to facilitate future genetic gains from S$_1$ progeny selection under drought stress as well as to confirm the appropriateness of the breeding methodology adopted in the maize improvement program of IITA.

The present study was designed to (i) examine the genetic gains in yield and other desirable traits assayed during the three cycles of improvement in TZE-Y Pop DT STR under drought stress and optimal environments; (ii) estimate genetic variability and predict future gains from selection in the two research environments, and (iii) determine changes in relationships among the measured traits due to selection in the population under drought stress environments.

**MATERIALS AND METHODS**

**Development of the source population and the S$_1$ recurrent selection program**

An early-maturing *Striga* resistant and drought tolerant yellow source population, TZE-Y Pop DT C$_0$ STR C$_0$ was used for this study. The population was developed following recombination of the drought tolerant yellow germplasm sources, DR-Y Pool BC$_2$F$_2$, 9499 and KU 1414 using the half-sib method. The resulting early yellow population was named TZE-Y Pop. Subsequently, *Striga* resistant/tolerant genes from the IITA inbred line 9450 STR (Kim et al., 1987) was introgressed into TZE-Y Pop to improve the level of *Striga* resistance. This was followed by two cycles of backcrossing to the population. S$_1$ progenies were then generated and outstanding *Striga* resistant S$_1$ lines were selected and subjected to two cycles of random mating under artificial *Striga* infestation and induced moisture stress to
form TZE-Y Pop DTC₀ STR C₀. The methodologies and strategies employed for evaluation for resistance to *Striga* and the induced moisture stress management practices for selection for tolerance to drought at the different stages during the development of the population at various screening sites in WCA have been fully described by Badu-Apraku et al. (2007). In brief, the S₁ family selection scheme was initiated in the population in 1996 and has gone through five cycles of selection for improved yield and *Striga* resistance followed by three selection cycles for enhanced tolerance to drought. Progenies derived from cycles of genetic improvement were evaluated under artificial *S. hermonthica* infestation and non-infested conditions from 1996 to 2001 at Ferkéssedougou (Ferké) in Côte d’Ivoire and Abuja and Mokwa in Nigeria in 2003. From 196 to 256 progenies were screened per cycle, using a selection intensity of 25–30%. Based on the across locations data, 25–30% best S₁ progenies derived from the population were identified using the IITA base index that incorporated grain yield, *Striga* emergence counts, *Striga* damage rating at 8 and 10 WAP, and EPP assayed under *Striga*-infestation and/or non-*Striga* infestation (MIP 1996). The selected ears of the best S₁ families of each cycle of the population were intermated to form a new, enhanced population for the new cycle of selection. A minimum of three seasons were needed to complete a cycle of selection. By 2007, five cycles of selection for *Striga* resistance had been completed. The initial phase of the genetic enhancement for tolerance to drought tolerance was carried out under managed drought stress at Ferké and Sinématialli (Siné) in Côte d’Ivoire and Kamboinse in Burkina Faso (Badu-Apraku et al. (2008). Subsequently, drought screenings were conducted at Ikenne and Bagauda in Nigeria. The details on the improvement program have been described by Badu-Apraku et al. (2012a, 2015). In brief, at Siné, Ferké and Ikenne, the drought experiments were carried out using an overhead irrigation system which supplied seventeen millimetres of water per week during the dry season. The managed drought stress at Ferké and Siné was obtained by withdrawing
irrigation water from about two weeks before anthesis to the end of the growing season. In contrast, at Ikenne, planting was done during the dry season. Managed drought was obtained through suspension of the irrigation of the plants in the plots at 28 days after planting (DAP) until physiological maturity, thus compelling the plants to rely on stored water in the soil for growth and development. The soil at the testing site in Ikenne is characterized as Alfisol with experimental fields which are flat and uniform and have high water-holding capacity (Soil Survey Staff 1999). At Bagauda, plants were exposed to natural terminal drought which normally coincides with the flowering period and continues till harvest maturity. The optimal experiments were carried out at Ikenne during the major growing season (rain-fed). With the exception of the amount of water applied in the optimal environments, all management practices were similar for both optimal and drought experiments. The application of fertilizer and weed control in the optimal and drought-stressed plots were as described by Badu-Apraku et al. (2015). The best S₁ lines under drought stress were selected using the base index described by Meseka et al. (2006) and Oyekunle and Badu-Apraku (2012). A minimum of three seasons were necessary for completing a selection cycle for drought tolerance. The population had been subjected to five selection cycles for enhanced grain yield and Striga resistance as well as three cycles of genetic enhancement for grain yield and drought tolerance when the present experiment was commenced in 2011. However, at C₂ of the population, a study was conducted to determine the genetic variability of grain yield and other assayed traits under drought. Results of this study revealed low genetic variability for most measured traits and a recommendation was made for incorporation of new sources of drought tolerance genes into the population to accelerate progress from further selections in the population. Consequently, genes for drought tolerance were introgressed from the panel of drought tolerant inbreds from IITA and CIMMYT into the population. The introgression of
drought tolerance genes was followed by a cycle of selection and recombination to form the C₃ of the population.

**Field evaluations and crop management**

Sixty S₁ families each derived by self-pollination of non-inbred plants from the *Striga* resistant population, TZE-W Pop DT C₀ STR C₅ and the three cycles of selection for improved drought tolerance under drought stress, i.e. C₀ to C₃. The 240 S₁ families from C₀ to C₃ were tested under managed drought stress at Ikenne during the dry seasons of 2010/2011 and 2011/2012 and optimal environments at Ikenne in 2011 and 2012 and Kadawa all in Nigeria during the rainy season of 2011. Badu-Apraku et al. (2012a, 2015) have provided a complete description of the drought methodology adopted for evaluation of the cycles of selection in the present study. A 15 x 16 lattice with two replicates was used for the field evaluations. Single-row plots, each measuring 3 m with a row spacing of 0.75 m and distance between plants-within-row, 0.4 m were used. Three seeds were planted per hole, and the seedlings were thinned to two per hill about 2 wk after emergence to obtain a final plant population density of about 66,667 plants ha⁻¹. Application of fertilizer and weed management practices in the optimal and induced drought stress plots were carried out at Ikenne and Kadawa, following methods described by Badu-Apraku et al. (2015).

**Data collection**

Recorded data in both induced drought stress and optimal (rain-fed or well-watered) plots were as detailed by Badu-Apraku et al. (2015) for days to anthesis (DA), silking (DS), ASI, plant height (PHT) and ear height (EHT), root lodging (RL), stalk lodging (SL), stay-green characteristic (STGR, husk cover (HC), ear aspect (EASP), plant aspect (PASP), and the number of ears per plant (EPP). For trials under both drought and optimal environments, grain moisture was determined from shelled kernels from each plot. Grain yield for drought
trials was estimated from the shelled grain weight, adjusted to moisture content of 15 percent. However, for well-watered environments, grain weight was estimated from cob weight, assuming 80 % shelling percentage, adjusted to 15 percent moisture.

**Statistical analyses**

The plot means of the individual traits combined for the locations-within-year were subjected to analysis of variance (ANOVA) using PROC GLM command of SAS 9.3 (SAS Institute, 2011). In the combined ANOVA for each trait, the environments comprised the location–within-year combinations. In the model, the effects of environment, replication, incomplete blocks, the interactions of environment with cycle and genotype-within-cycle were assumed as random effects. In contrast, cycle and genotype-within-cycle effects were regarded as fixed effects in the computation of the means and standard errors per cycle while they were considered as random effects for the estimation of variance components. The analyses were performed separately for the managed drought and optimal growing conditions.

The estimate of genetic variances for assayed traits were obtained by equating the observed to the expectation of mean squares and calculating the desired components as proposed by Hallauer et al. (2010). The incomplete block effect of the model was disregarded, and the error variance was estimated. Standard error for genetic variance and heritability estimates were computed based on the method proposed by Hallauer et al. (2010). The estimates of genetic variances and heritabilities among S1 families of the different cycles were compared for differences by pair-wise test of estimates using the standard errors. The predicted selection gain was based on C3 alone and was determined using the method of Hallauer et al. (2010), as follows:

\[ G = k \frac{\sigma^2_g}{\sigma_p} \]
Where $k$ is the standardized selection differential for $S_1$ families (based on 20% selection pressure, $k = 1.3998$) and $\sigma_g^2$ is the genetic variance, and $\sigma_p$ represents the square root of the phenotypic variance. The predicted selection gains may have been inflated based on the proportion contributed by the non-additive genetic variances to $\sigma_g^2$. Edwards (2008) proposed a more accurate method for predicting gains from selection, which involves the use of the additive variance instead of genetic variance as the numerator. This method provides more accurate predictions of gain from selection with inbred progeny than the method proposed by Hallauer et al. (2010). However, the method is more complex, and the computation is more challenging and was therefore not adopted in the present study. The differences among the cycle means were tested for significance using the least significant differences (LSD). Linear contrast was carried out using SAS 9.3 (SAS Institute, 2011) to partition the cycle mean squares of measured traits into single degrees of freedom for orthogonal comparisons which involved $C_0$ vs $C_1+C_2+C_3$, $C_1$ vs $C_2+C_3$ and $C_2$ vs $C_3$ for yield and most of the other assayed traits under drought stress and optimal growing environments. The $b$ values obtained from regression of the measured trait on the selection cycles provided an estimate value of realized gain per cycle while the percentage response per cycle was estimated as (realized gain cycle$^{-1}$ / intercept) x 100. The significance of the slope $b$ was tested using the $t$ test at 0.05 probability level.

The Statistical Package for Social Sciences, SPSS version 17.0 (SPSS Inc, 2007) was used to carry out the step-wise regression analyses on the assayed traits. Subsequently, sequential path diagrams were used to explain the cause and effect relationships among traits in the cycles $C_0$ and $C_3$ of selection for tolerance to drought as described by Mohammadi et al. (2003). Badu-Apraku et al. (2012a, 2014 and Talabi et al., 2017) have described in detail the procedures adopted for the sequential stepwise multiple regression analysis in the present study.
RESULTS

Analysis of variance and progress from selection under different environments

Combined analyses of variance revealed significant cycle effect for yield and other traits assayed under drought stress (DS) and optimal (WW) environments (Table 1). Significant environment effects were obtained for measured traits except for yield, ASI, plant aspect, and EPP under drought stress and DS under optimal environments. The G x E interaction mean squares were significant for yield, PHT, PASP and EASP under drought-stress and optimal environments. A significant G x E interaction was also observed for STGR under drought. Under drought, mean yield varied from 803 kg ha\(^{-1}\) for C\(_2\) to 2384 kg ha\(^{-1}\) for C\(_3\) and, under optimal environments, from 1831 kg ha\(^{-1}\) for C\(_2\) to 3737 kg ha\(^{-1}\) for C\(_3\) (Table 1). The most advanced cycle of selection, C\(_3\) significantly (\(P<0.05\)) yielded higher than the preceding cycles of selection under the two research conditions (drought-stress and optimal growing environments). In addition to the higher grain yield in C\(_3\), there were decreased DS and ASI, improved PASP and EASP, and increased PHT and EPP under drought stress and optimal growing environments. Stay green characteristic of C\(_3\) under drought was also better than those of the other selection cycles. The yield gain per cycle from C\(_0\) to C\(_3\) was 423 kg ha\(^{-1}\) (202 %) under drought and 518 kg ha\(^{-1}\) (48 %) under optimal environments. The predicted selection gain cycle\(^{-1}\) was 348 kg ha\(^{-1}\) for yield under drought and 377 kg ha\(^{-1}\) under optimal environments. The mean squares from linear contrast of cycles revealed significant effects for the comparisons of C\(_0\) vs C\(_1\)+C\(_2\)+C\(_3\), C\(_1\) vs C\(_2\)+C\(_3\) and C\(_2\) vs C\(_3\) for yield and most other traits assayed under drought and optimal environments (Table 2). The few exceptions included the contrasts C\(_0\) vs C\(_1\)+C\(_2\)+C\(_3\) for ASI under optimal environment, and C\(_1\) vs C\(_2\)+C\(_3\) for ASI and STGR under drought. The contrast C\(_2\) vs C\(_3\) accounted for 74 and 72 % of the total cycle mean squares for yield under drought and optimal environments, respectively. Similarly, the
contrast C2 vs C3 contributed over 70% to the total cycle effects of other traits assayed under drought and optimal environments except for DS and ASI under optimal environments.

**Genetic variance and broad sense heritability estimates**

Under drought, genetic variance estimates showed significant effects for yield, DA, EHT and EPP in C0; grain yield, DA, DS, PHT, EHT, HUSK, and EPP in C1; DA, ASI, EHT and EPP in C2 and grain yield, EASP and EPP in C3 (Table 3). The heritability estimates followed similar trends. Under optimal environments, significant genetic variance and heritability estimates were obtained for all traits assayed in cycles C0, C1, C2 and C3 except EPP in C0, PASP in C1, grain yield, ASI, PASP, EASP and EPP in C2, ASI, PHT, EHT, PASP and EPP in C3 (Table 4).

**Step-wise multiple regression and sequential path analyses**

The ears per plant, ASI and EASP were identified by the stepwise multiple regression analysis as traits with significant contributions to yield, accounting for about 66% of the total variation in yield among the S1 lines developed from the base population (cycle C0) of TZE-Y Pop DT STR and evaluated under drought (Fig. 1). Among these three traits, EPP had the highest and only positive direct effect (0.470) on yield while those of the other two traits had negative effects and were relatively much lower (Fig. 1). Indirect contributions were made by several other traits to yield through one or more of the first order traits. Among the five traits (PASP, DS, DA, EHT and STGR) in the second order, DS made indirect contribution to yield through all the three primary traits while the others indirectly contributed to yield through only one of the first order traits. The highest positive indirect effect (0.870) was made by DS through ASI while the highest negative indirect effect (-0.850) was contributed by DA through ASI. The remaining indirect contributions of the three second order traits to yield through the first order traits are illustrated in Fig. 1. Only two measured traits, PHT and...
HUSK were identified as the third order traits with significant indirect effect on yield. While PHT had indirect contributions through four of the second order traits, the HUSK made indirect contribution through only one trait, PASP (0.268).

For the S<sub>1</sub> lines developed from the cycle C3 of TZE-Y Pop DT STR population, and tested under drought stress, five traits including EASP, PASP, EPP, ASI and HUSK were identified as the first order contributors to yield. About 83 % of the total variation in grain yield were attributable to these traits (Fig. 2). The EASP made the highest direct contribution to yield (~0.513), while only EPP (0.311) and HUSK (0.124) had positive direct effects on yield. Only four traits, DS, DA, EHT, and SGC were categorized into second order group and these made contributions through five, four, three and two second order traits, respectively. Out of the 14 indirect contributions of the second order traits, seven effects were positive values, three of which had indirect path coefficients higher than 0.800 (Fig.2). Plant height was identified as the only third order trait which contributed through EHT (0.791) to grain yield.

**DISCUSSION**

The observed significant differences (P< 0.01) among the four cycles of S<sub>1</sub> families for yield and all other traits assayed under drought and optimal growing environments indicated that genetic variability existed in the early-maturing yellow breeding population TZE- Y Pop DT STR studied and that genetic gains could be achieved for the original cycle and the subsequent recurrent selection cycles (Badu-Apraku et al., 2011a; 2016; Berilli et al., 2013). The highly significant environment effects (P< 0.01) for all traits assayed except for yield, ASI, PASP and EPP under drought and DS, ASI and EPP under optimal conditions, was an indication that the research environments in Nigeria varied in terms of climatic and edaphic conditions. Furthermore, the presence of significant G x E interaction means squares for most
of the measured traits under drought stress and optimal growing environments suggested that there were differences in the responses of the S1 lines in the different cycles to environmental variations, and that the research environments were discriminating enough in the identification of outstanding cultivars in the recurrent selection procedure (Badu-Apraku et al., 2016). The observed significant G x E interaction for grain yield, PHT, PASP and EASP under both research conditions and the STGR under drought may be due largely to differences in the environmental factors, particularly soil type, temperature, amount of rainfall, and disease pressure at the testing sites in Nigeria. This is also an indication of the uniqueness of the environments in the identification of outstanding cultivars. Furthermore, the significant G x E interaction effects for yield and most other traits in the base index for identification for tolerance to drought indicated that the genotypic correlations of these traits with yield was expected to reduce under drought stress. In contrast, the non-significant G x E interaction for DS, ASI and EPP under both drought and optimal conditions suggested that there would be consistency in the rankings of traits of the genotypes in the contrasting environments (Badu-Apraku et al., 2016).

The mean of a trait is a parameter of paramount importance in population improvement because a high population mean indicates that a shorter time is required to achieve the targeted level of progress and vice versa (Hallauer et al., 2010). The relatively high cycle-mean grain yields recorded for C3 as well as the significant yield gains achieved from C0 to C3 under drought stress and optimal growing environments, confirmed the significant improvements in yield achieved in the advanced cycles of selection. This result, therefore suggested that a relatively shorter period would be required to achieve substantial progress in advanced cycles. It was also striking that the relatively high mean yield obtained for C3 was accompanied by decreased silking dates, reduced ASI, improved plant and ear aspects and increased plant height and number of ears per plant under drought and optimal
environments, as well as improved STGR under drought. The ASI, STGR, PASP, EASP and EPP are secondary traits included in the IITA selection index for identification of superior cultivars under drought conditions (Meseka et al. 2006; Badu-Apraku et al., 2013b). Edmeades et al. (1993) and Bänziger et al. (2000) demonstrated that selection efficiency for tolerance to drought could be improved through utilization of secondary traits that could be easily measured, have high heritability and strong correlations with yield under the stress factor. Therefore, to achieve significant genetic enhancement for improved yield under drought, Bänziger and Lafitte (1997) combined information from selected secondary traits in a Smith-Hazel index and obtained an average of 14% improved selection efficiency compared with selection for yield alone. A similar base index is also used by IITA scientists for selecting for drought tolerance under drought and optimal growing environments (Badu-Apraku et al., 2013b).

The yield gain cycle\(^{-1}\) from C\(_0\) to C\(_3\) was very high (202%) under drought and moderately high (48%) under optimal conditions. This suggested that there was high frequency of favourable drought tolerance alleles in the early yellow population for continued progress from future recurrent selection program, as additional cycles of recombination took place (Halward and Wynne, 1992). Furthermore, results of the present study revealed that predicted gain per cycle for grain yield (348 kg) under drought was relatively smaller compared with that under optimal conditions (377 kg). This result is contrary to the findings of Badu-Apraku et al., (2016) who studied the Striga-resistant and drought-tolerant early-maturing white population, TZE-W Pop DT C\(_3\) STR C\(_5\) under drought stress and well-watered environments. The authors reported that the genetic variances generally decreased for yield and other traits assayed in advanced cycles of the population under drought and well-watered conditions except for yield and ear height under well-watered conditions. Similarly, heritability estimates for yield and other measured traits decreased in the advanced
cycles of selection in the population under drought but increased in advanced cycles under well-watered conditions. Realized gain from selection for yield was 0.291 t/ha, corresponding to 30.5% per cycle under drought and 0.352 t/ha with a corresponding gain of 16.7% per cycle under well-watered conditions. Predicted selection gain based on C3 was 0.282 and 0.583 t/ha under drought and well-watered conditions. Low estimates of genetic variance, heritability and predicted gains from selection for yield and other traits suggested the need to introgress drought tolerance genes into the TZE-W Pop DT C3 STR C5 population (Badu-Apraku et al., 2016). A plausible reason for the contrasting results of the two studies is that the two populations were derived from different sources of germplasm and might have varied in the mechanisms by which they achieved drought tolerance.

It is not surprising that higher predicted gain per selection cycle was obtained under drought stress than optimal growing conditions because the recurrent selection scheme placed greater emphasis on grain yield performance under drought than under optimal conditions. This could also have been due to biased estimation of the predicted gain cycle⁻¹ at C3, under optimal conditions as the yield gain was about 36.2% higher than that of the drought condition.

In a recurrent selection program, estimating heritability for a trait from the genetic variance components is useful to determine the amount of progress that could be made in the improvement of that trait. Genetic variance which is directly related to heritability estimates initially increased for yield and other traits assayed from C0 to C1 but declined from C1 to C2 and subsequently showed a marked increase from C2 to C3. Although this result showed inconsistent patterns in the genetic variance as selection progressed under drought and optimal conditions, it is interesting that the highest progress made was from C2 to C3 which was the most advanced cycle of selection for drought tolerance in the present study. This progress is not surprising and could be attributed to the introgression of beneficial alleles for
drought tolerance from selected drought tolerant inbred lines from IITA and CIMMYT drought tolerant inbreds into the population at C₂, followed by a selection cycle and recombination to reconstitute the C₃ of the population. Significant linear contrast observed for the orthogonal comparisons indicated that there were wide differences among the contrasts. However, the over 70 % of the total cycle mean squares attributable to the comparison between C₂ and C₃ indicated that gains from selection resulted from the introgression of beneficial alleles for drought tolerance followed by one selection cycle and recombination. The high genetic variance observed for grain yield in the C₃ under both research conditions indicated that most probably there was genetic variability for most of the traits assayed to facilitate the response to continued selection for improvement of yield in the population. This might have resulted from the selection of desirable genes for both tolerance to drought and improved performance under optimal conditions at particular loci of the S₁ lines as influenced by factors such as the recombination rate, selection intensity, mutation rate, genetic drift, the mating systems, population structure, and genetic linkage (Hallauer and Miranda, 1988). In addition, the high genetic variation for grain yield in the C₃ correlated with a moderately high broad-sense heritability estimates compared to C₂. This observation was anticipated as it justified the fact that heritability is the fraction of the variance of a trait within a population that is due to genetic factors. The moderately high heritability estimates recorded for yield, DS, EPP and EASP under drought in C₃ indicated higher probability of improving the early yellow population for these traits in subsequent cycles of the recurrent selection program. The reduction in the genetic variance of S₁ lines in C₂ might have occurred probably due to a more intense selection pressure imposed on the measured traits at the C₁ to C₂ stage.

Path co-efficient analysis facilitates the examination of the magnitude of varying contribution of different agronomic traits to grain yield in the form of cause and effect
(Wright1921;1923; Dewey and Lu, 1959). It describes the effective measure of direct and indirect causes of association and illustrates the relative importance of each factor involved in contributing to the final product i.e. grain yield. Under drought, EPP, EASP and ASI were identified as the first order traits assayed with significant direct effects on grain yield of the S₁ progenies, thus suggesting that these traits played key roles in the improvement of yield under moisture stress conditions. In addition, this result did not only show that EPP, EASP and ASI were important secondary traits contributing to drought tolerance (Badu-Apraku et al., 2011a; 2013b; Talabi et al., 2017) but also, it revealed that the progress from selection under drought using grain yield along with the secondary traits in a selection index would be greater than selecting for grain yield alone (Badu-Apraku et al., 2013b; Bänziger et al., 2000). Therefore, it may be concluded that there was effective direct selection for these traits in C₀.

Furthermore, among the traits placed in the second order, DS made significant indirect contributions to yield through the three first-order traits and made the highest positive indirect contribution to grain yield through ASI. The DS also showed a high positive association with DA among the second order traits, with the two traits having direct effects on ASI in C₀ under drought accounting for the observed variation in grain yield. Several workers (Bänziger and Lafitte, 1997; Betrán, et al., 2003; Badu-Apraku et al., 2011a; 2013b; Talabi et al., 2017) have reported that reduced ASI contributed to increased yield under drought stress.

Under drought stress, the sequential path co-efficient analysis was very effective in providing an insight into the variations observed in grain yield of the S₁ families at C₃, as indicated by the co-efficient of determination (r²) of 83%. Among the five first order traits, EASP, PASP, EPP, ASI and husk cover identified as having direct effects on grain yield, three of them, ASI, EPP and EASP were also categorized as the first order traits with direct contribution to grain yield at C₀, indicating the consistency and the importance of these three
traits as selection progressed from C₀ to C₃. Similarly, the C₀ and C₃ S₁ lines evaluated under drought conditions identified common second order traits, except PASP at C₀, in their indirect contributions to grain yield. The obvious direct contributions of DS and DA to reduced ASI as well as the direct effects of STGR on both EASP and EPP indirectly accounted for the superior yield performance of the C₃ S₁ lines in water-deficit environments.

CONCLUSIONS

The high realized genetic gains from selection for improved yield under drought and optimal growing environments could be attributed to the introgression of sources of favourable genes for drought tolerance into the C₂ of the population, followed by one S₁ family cycle selection and recombination. Furthermore, high genetic variability, heritabilities and predicted gains for yield and other assayed traits in the most advanced cycle of improvement in the population indicated that further improvement of such traits is possible in future selection cycles in the population depending largely on the ability of the breeders to identify outstanding genotypes and the precision levels of the experiments. In addition, EPP, EASP, ASI, PASP and husk cover contributed directly to high grain yields under drought conditions both in C₀ and C₃ confirming the high reliability of the traits for effective selection for improved yield under drought stress. The ASI, EPP and EASP were consistent and reliable secondary traits under drought as selection progressed from C₀ to C₃ confirming their effectiveness for index selection for drought tolerance.

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sincere appreciation to the staff of the Maize Improvement Program of IITA for technical assistance.

REFERENCES


Figure caption

Fig. 1. Path analysis model diagram showing causal relationships of measured traits of early maturing $S_1$ lines developed from cycle $C_0$ of TZE-Y Pop DT STR evaluated under drought stress at Ikenne during the 2010/2011 and 2011/2012 dry seasons in Nigeria. Bold value is the residual effect; values in parenthesis are direct path coefficients while other values are correlation coefficients. $R_1$ is residual effects; ASI, anthesis–silking interval; DA, days to 50 % anthesis; DS, days to 50 % silking; EASP, ear aspect; EPP, ears per plant; HUSK, husk cover; PASP, plant aspect; PHT, plant height; STGR, stay green characteristics; and YIELD, grain yield.

Fig. 2. Path analysis model diagram showing causal relationships of measured traits of early maturing $S_1$ lines developed from cycle $C_3$ of TZE-Y Pop DT STR and evaluated under drought stress at Ikenne during the 2010/2011 and 2011/2012 dry seasons in Nigeria. Bold value is the residual effect; values in parenthesis are direct path coefficients while other values are correlation coefficients. $R_1$ is residual effects; ASI, anthesis–silking interval; DA, days to 50 % anthesis; DS, days to 50 % silking; EASP, ear aspect; EPP, ears per plant; HUSK, husk cover; PASP, plant aspect; PHT, plant height; STGR, stay green characteristic; and YIELD, grain yield.
Table 1. Response/cycle, grain yield and other traits of S1 families derived from four cycles of selection in early yellow population evaluated under drought (DS) at Ikenne during the 2010/2011 and 2011/2012 dry seasons and under optimal conditions (WW) at Ikenne during the 2011 and 2012 growing seasons and at Kadawa during the 2011 growing season in Nigeria.

<table>
<thead>
<tr>
<th>Cycle</th>
<th>Grain yield, Kg/ha&lt;sup&gt;†&lt;/sup&gt;</th>
<th>Days to Silking</th>
<th>ASI</th>
<th>Plant height</th>
<th>Plant aspect</th>
<th>Ear aspect</th>
<th>Stay green characteristic</th>
<th>EPP</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>DS</td>
<td>WW</td>
<td>DS</td>
<td>WW</td>
<td>DS</td>
<td>WW</td>
<td>DS</td>
<td>WW</td>
</tr>
<tr>
<td>C&lt;sub&gt;0&lt;/sub&gt;</td>
<td>918</td>
<td>1993</td>
<td>60</td>
<td>57</td>
<td>5.0</td>
<td>1.2</td>
<td>158.1</td>
<td>167.8</td>
</tr>
<tr>
<td>C&lt;sub&gt;1&lt;/sub&gt;</td>
<td>968</td>
<td>1887</td>
<td>60</td>
<td>58</td>
<td>4.8</td>
<td>1.5</td>
<td>157.8</td>
<td>166.4</td>
</tr>
<tr>
<td>C&lt;sub&gt;2&lt;/sub&gt;</td>
<td>803</td>
<td>1831</td>
<td>61</td>
<td>57</td>
<td>5.6</td>
<td>1.4</td>
<td>148.3</td>
<td>161.8</td>
</tr>
<tr>
<td>C&lt;sub&gt;3&lt;/sub&gt;</td>
<td>2384</td>
<td>3737</td>
<td>56</td>
<td>55</td>
<td>3.5</td>
<td>0.8</td>
<td>181.5</td>
<td>185.0</td>
</tr>
<tr>
<td>Grand Mean</td>
<td>1173</td>
<td>2457</td>
<td>60</td>
<td>57</td>
<td>4.7</td>
<td>1.1</td>
<td>156.7</td>
<td>170.1</td>
</tr>
<tr>
<td>LSD</td>
<td>104.9</td>
<td>117.3</td>
<td>0.6</td>
<td>0.4</td>
<td>0.39</td>
<td>0.16</td>
<td>3.62</td>
<td>2.40</td>
</tr>
<tr>
<td>Environment (E)</td>
<td>ns</td>
<td>**</td>
<td>ns</td>
<td>ns</td>
<td>**</td>
<td>ns</td>
<td>*</td>
<td>**</td>
</tr>
<tr>
<td>Cycle (G)</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>G x E</td>
<td>**</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>ns</td>
<td>**</td>
<td>**</td>
</tr>
<tr>
<td>Realized gain</td>
<td>423</td>
<td>518</td>
<td>-1.21</td>
<td>-0.94</td>
<td>-0.39</td>
<td>-0.15</td>
<td>6.06</td>
<td>4.68</td>
</tr>
<tr>
<td>% response cycle&lt;sup&gt;†&lt;/sup&gt;</td>
<td>202</td>
<td>48</td>
<td>-1.93</td>
<td>-1.58</td>
<td>-6.67</td>
<td>-9.49</td>
<td>4.14</td>
<td>2.95</td>
</tr>
<tr>
<td>Predicted gain cycle&lt;sup&gt;†&lt;/sup&gt; (based on cycle 3 of the population)</td>
<td>348</td>
<td>377</td>
<td>1.0</td>
<td>0.76</td>
<td>0.39</td>
<td>0.08</td>
<td>0.80</td>
<td>1.42</td>
</tr>
</tbody>
</table>

<sup>†</sup>C<sub>0</sub>, C<sub>1</sub>, C<sub>2</sub> and C<sub>3</sub> refers to the base population, cycle 1, cycle 2 and cycle 3, respectively.
Table 2. Sum of squares from linear contrast of grain yield and other traits of S1 families derived from four cycles of selection in an early yellow population evaluated under drought (DS) at Ikenne during the 2010/2011 and 2011/2012 dry seasons and under optimal conditions (WW) at Ikenne during the 2011 and 2012 growing seasons and at Kadawa during the 2011 growing season in Nigeria.

<table>
<thead>
<tr>
<th>Cycle</th>
<th>Grain yield</th>
<th>Days to Silking</th>
<th>ASI</th>
<th>Plant height</th>
<th>Plant aspect</th>
<th>Ear aspect</th>
<th>Stay green characteristic</th>
<th>EPP</th>
</tr>
</thead>
<tbody>
<tr>
<td>C₀ vs C₁+C₂+C₃</td>
<td>1</td>
<td>36889190**</td>
<td>70337674**</td>
<td>305**</td>
<td>183**</td>
<td>21*</td>
<td>0.2ns</td>
<td>2239*</td>
</tr>
<tr>
<td>C₁ vs C₂+C₃</td>
<td>1</td>
<td>59502597**</td>
<td>175112390**</td>
<td>499**</td>
<td>1148**</td>
<td>11ns</td>
<td>43.1**</td>
<td>7265**</td>
</tr>
<tr>
<td>C₂ vs C₃</td>
<td>1</td>
<td>280545770**</td>
<td>626682342**</td>
<td>1988**</td>
<td>969**</td>
<td>478**</td>
<td>49.3**</td>
<td>107877**</td>
</tr>
</tbody>
</table>

Contributions (%) of linear contrasts to the total sums of squares

<table>
<thead>
<tr>
<th>Cycle</th>
<th>Grain yield</th>
<th>Days to Silking</th>
<th>ASI</th>
<th>Plant height</th>
<th>Plant aspect</th>
<th>Ear aspect</th>
<th>Stay green characteristic</th>
<th>EPP</th>
</tr>
</thead>
<tbody>
<tr>
<td>C₀ vs C₁+C₂+C₃</td>
<td>1</td>
<td>9.79</td>
<td>8.07</td>
<td>10.92</td>
<td>7.96</td>
<td>4.12</td>
<td>0.22</td>
<td>1.91</td>
</tr>
<tr>
<td>C₁ vs C₂+C₃</td>
<td>1</td>
<td>15.79</td>
<td>20.08</td>
<td>17.87</td>
<td>49.91</td>
<td>2.16</td>
<td>46.54</td>
<td>6.19</td>
</tr>
<tr>
<td>C₂ vs C₃</td>
<td>1</td>
<td>74.43</td>
<td>71.86</td>
<td>71.20</td>
<td>42.13</td>
<td>93.73</td>
<td>53.24</td>
<td>91.90</td>
</tr>
</tbody>
</table>

*, ** Significantly different at 0.05 and 0.01 levels of probability

C₀, C₁, C₂ and C₃ refers to the base population, cycle 1, cycle 2 and cycle 3, respectively.
Table 3. Genetic variances and heritability estimates of S<sub>1</sub> families derived from four cycles of selection in early yellow population evaluated under managed drought at Ikenne during the 2010/2011 and 2011/2012 dry seasons in Nigeria.

<table>
<thead>
<tr>
<th></th>
<th>Genetic variances</th>
<th>Heritability</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>C&lt;sub&gt;0&lt;/sub&gt;</td>
<td>C&lt;sub&gt;1&lt;/sub&gt;</td>
</tr>
<tr>
<td>Grain yield</td>
<td>50858±20488*</td>
<td>89438±26423**</td>
</tr>
<tr>
<td>Days to anthesis</td>
<td>1.38±0.57*</td>
<td>1.45±0.53*</td>
</tr>
<tr>
<td>Days to silking</td>
<td>1.26±1.05</td>
<td>2.88±1.18*</td>
</tr>
<tr>
<td>ASI</td>
<td>0.73±0.41</td>
<td>0.56±0.40</td>
</tr>
<tr>
<td>Plant height (cm)</td>
<td>72±40</td>
<td>73±29*</td>
</tr>
<tr>
<td>Ear height, cm</td>
<td>45±16*</td>
<td>38±18*</td>
</tr>
<tr>
<td>Husk cover</td>
<td>0.014±0.016</td>
<td>0.039±0.018*</td>
</tr>
<tr>
<td>Plant aspect</td>
<td>0.0049±0.018</td>
<td>0.0202±0.017</td>
</tr>
<tr>
<td>Ear aspect</td>
<td>0.011±0.011</td>
<td>0.029±0.011*</td>
</tr>
<tr>
<td>EPP</td>
<td>0.006±0.003*</td>
<td>0.014±0.004**</td>
</tr>
<tr>
<td>Stay green characteristic</td>
<td>0.029±0.023</td>
<td>0.000±0.032</td>
</tr>
</tbody>
</table>

*, ** Significantly different at 0.05 and 0.01 levels of probability

C<sub>0</sub>, C<sub>1</sub>, C<sub>2</sub> and C<sub>3</sub> refers to the base population, cycle 1, cycle 2 and cycle 3, respectively.
Table 4: Genetic variances and heritability estimates of $S_1$ families derived from four cycles of selection in early yellow population evaluated under optimal conditions at Ikenne during the 2011 and 2012 growing seasons and at Kadawa during the 2011 growing season in Nigeria.

<table>
<thead>
<tr>
<th></th>
<th>Genetic variances</th>
<th>Heritability</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$C_0^\dagger$</td>
<td>$C_1$</td>
</tr>
<tr>
<td>Grain yield</td>
<td>9058±35298$^\ast$</td>
<td>99918±43546$^\ast$</td>
</tr>
<tr>
<td>Days to anthesis</td>
<td>1.65±0.47$^{**}$</td>
<td>1.79±0.53$^{**}$</td>
</tr>
<tr>
<td>Days to silking</td>
<td>2.42±0.67$^{**}$</td>
<td>2.02±0.63$^{**}$</td>
</tr>
<tr>
<td>ASI</td>
<td>0.25±0.08$^{**}$</td>
<td>0.19±0.09$^{*}$</td>
</tr>
<tr>
<td>Plant height (cm)</td>
<td>83±23$^{**}$</td>
<td>60±20$^{**}$</td>
</tr>
<tr>
<td>Ear height, cm</td>
<td>30±10$^{**}$</td>
<td>20±9$^{*}$</td>
</tr>
<tr>
<td>Husk cover</td>
<td>0.058±0.020$^{*}$</td>
<td>0.051±0.019$^{*}$</td>
</tr>
<tr>
<td>Plant aspect</td>
<td>0.0325±0.0145$^{*}$</td>
<td>0.0093±0.0112</td>
</tr>
<tr>
<td>Ear aspect</td>
<td>0.018±0.007$^{*}$</td>
<td>0.030±0.010$^{**}$</td>
</tr>
<tr>
<td>EPP</td>
<td>0.003±0.002</td>
<td>0.007±0.003$^{*}$</td>
</tr>
</tbody>
</table>

$^\ast$, $^{**}$ Significantly different at 0.05 and 0.01 levels of probability

$^\dagger$ $C_0$, $C_1$, $C_2$ and $C_3$ refers to the base population, cycle 1, cycle 2 and cycle 3, respectively.
Fig. 1.
Fig. 2.

178x115mm (300 x 300 DPI)