Genetic Variances and Relationship among Traits of an Early Maturing Maize Population under Drought-stress and Low Nitrogen Environments

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ABSTRACT

Drought and low soil nitrogen (low N) are major causes of low grain yield of maize (*Zea mays* L.) in sub-Saharan Africa (SSA). An early maturing maize population, TZE-Y Pop DT STR, had undergone four cycles of selection for drought tolerance, followed by four selection cycles for resistance to *Striga hermonthica* (Del.) Benth., which is normally conducted under low N (about 30 kg N ha^{-1}). The objectives of this study were to estimate residual genetic variances, predict future gains from selection, and investigate inter-trait relationships in the population under drought-stress, low N and across research environments. North Carolina Design I was used to develop 250 full-sib progenies from the improved population, which were evaluated in three drought-stress and two low N environments in Nigeria, 2011 to 2013. Additive genetic variances were not significant for most traits under the research conditions. The predicted gains from selection for grain yield were 5.3, 8.5 and 7.5% cycle^{-1} under drought, low N, and across environments. These results suggested the absence of substantial genetic variability in the population to ensure progress from selection. Ears per plant (EPP), ear aspect (EASP), plant aspect (PASP), and stay green characteristic (STGR) were consistently identified as important secondary traits under both research conditions. We concluded that there is need to introgress new sources of favorable alleles for drought-stress and low N tolerance into the population for guaranteed progress from selection, using EPP, EASP, PASP, and STGR in combination with yield in a selection index under drought-stress and low N.

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Abbreviations: ASI, anthesis-silking interval; DA, days to 50% anthesis; DS, days to 50% silking; EASP, ear aspect; EHT, ear height; EPP, number of ears per plant; GT, genotype × trait; h^2, narrow sense heritability; i, standardized selection differential; IITA, International Institute of Tropical Agriculture; Low N, low soil nitrogen; NCD I, North Carolina Design I; PASP, plant aspect; PHT, plant height; RL, root lodging; SAS, statistical analysis system; SGR, stay green characteristic; SL, stalk lodging; SSA, sub-Saharan Africa; WAP, weeks after planting; WCA, West and central Africa.

THE DEMAND FOR MAIZE in SSA has continued to increase because it is an important staple food crop. Maize accounts for more than 15% of the total calorie intake by the population in SSA, along with its use in animal feed production and as raw material in some agro-allied industries (Badu-Apraku et al., 2012b). In West and central Africa (WCA), the maize crop has increasingly gained wider acceptability over other traditional cereal crops, such as sorghum [*Sorghum bicolor* (L.) Moench] and millet (*Penisetum typhoides* L.), because of its better adaptation to various agro-ecologies, responsiveness to fertilizer application, and relative ease of cultivation, processing and storage (Badu-Apraku, 2010; Badu-Apraku et al., 2010). Availability of early maturing maize cultivars (90–95 d maturity) has further enhanced the expansion of maize production into new frontiers in WCA, including marginal areas (where the annual rainfall is below 500 mm, or where the soils are sandy or shallow) in the subregion (Badu-Apraku et al., 2013a). The savannas of WCA, however, offer the ideal environment for

maize production because they are characterized by high solar radiation, low night temperature, and low incidence of diseases and pests. Unfortunately, maize production and productivity are severely constrained by recurrent drought and low soil nitrogen (low N), acting and interacting in these savannas. Edmeades et al. (1995) reported a 15% annual yield loss in maize production because of drought stress in SSA. Losses may, however, be much higher in the marginal areas. Furthermore, most farmers in WCA cultivate maize under low N conditions (McCown et al., 1992; Oikeh and Horst, 2001) because of inherently low levels of soil N, and high cost or nonavailability of inorganic fertilizers to the resource-poor farmers. Wolfe et al. (1988) indicated that N stress alone could account for maize yield losses as high as 50% in SSA. The impacts of drought on maize production and productivity are greatest on nutrient-depleted soils, particularly those with low N, with the poorest subsistence farmers being the most severely affected. The development, promotion, and adoption of improved maize cultivars with combined tolerance to drought and low N is crucial for improved productivity and sustained maize production in the subregion (DeVries, 2000; Badu-Apraku et al., 2010; Badu-Apraku et al., 2015a). Therefore, maize cultivars targeted to the drought-prone areas of WCA should also be tolerant to low N (Kim and Adetimirin, 1997; Badu-Apraku et al., 2015b).

Conventionally, breeders develop stress-tolerant maize populations, improve such populations through recurrent selection, and extract from the improved populations experimental cultivars and/or inbred lines for hybrid production (Badu-Apraku, 2006, 2007; Hallauer et al., 2010). A successful recurrent selection program is expected to increase the mean performance of individuals and also maintain the genetic variability within the population to facilitate continuous improvement in advanced cycles of selection. Therefore, breeders require information on genetic variability for quantitative traits to ascertain achievable progress from further selection in a population (Badu-Apraku, 2006, 2007; Hallauer et al., 2010). The magnitude and type of genetic variability in a breeding population suggest appropriate breeding method to be used for genetic improvement and reveal the limits of the selection scheme.

An early maturing yellow-endosperm maize population, TZE-Y Pop DT STR, possessing tolerance to both drought-stress and *S. hermonthica*, was developed at the International Institute of Tropical Agriculture (IITA) in 2007, using diallel crosses involving elite maize germplasm selected on the basis of extensive testing in WCA (Badu-Apraku and Yallou, 2009). The population has been improved for grain yield and other agronomic traits through four cycles of selection under induced drought stress, followed by four cycles of selection under artificial infestation of *S. hermonthica* with application of only 30 kg

N ha^{-1} during the selection process. The improved population is now designated as TZE-Y Pop DTC$_4$ STR C$_4$. Although the population was not intentionally improved for low N tolerance, it was hypothesized that selection for *Striga* resistance under low N (30 kg N ha^{-1}) conditions (Badu-Apraku, 2006, 2007) and selection for drought tolerance (Edmeades et al., 1995, 1997) in the population had resulted in improved adaptation of the population to low N conditions. Badu-Apraku et al. (2015b) confirmed that selection for *Striga* resistance and drought tolerance in early maturing maize populations enhanced tolerance to low N in the maize cultivars derived from the populations. However, information is completely lacking on the magnitude and type of genetic variability for grain yield and other traits in this population under drought-stress and low N environments.

Selection for grain yield alone without other suitable secondary traits under drought stress or low N may be ineffective, because heritability of grain yield is usually low under stressed conditions. For example, Bolaños and Edmeades (1993) observed a decline in estimates of heritability of grain yield with reduced yield levels during selection for drought tolerance in lowland tropical maize. However, some secondary traits showed high heritability as well as high or increased estimates of genetic correlations with grain yield under drought stress (Bolaños and Edmeades, 1996; Bänziger and Lafitte, 1997; Badu-Apraku et al., 2004). Several workers have studied the relative importance of secondary traits in selecting for improved grain yield under drought-stress and low N conditions but obtained varying results, with overlapping of identified traits under the different stresses, probably because of the stress factors and type of genetic materials used (Alabi et al., 2001; Bolaños and Edmeades, 1996; Bänziger and Lafitte, 1997; Bänziger et al., 2000; Badu-Apraku 2006, 2007; Badu-Apraku et al., 2004, 2011, 2012a). For example, Bänziger et al. (2000) recommended ears per plant (EPP), anthesis-silking interval (ASI), and stay-green character (STGR) as the most useful secondary traits under drought-stress and low N conditions, whereas Badu-Apraku et al. (2011) through genotype × trait (GT) biplot identified ear aspect (EASP), plant aspect (PASP), ASI, and EPP as the most reliable secondary traits under drought stress; days to 50% anthesis (DA), days to 50% silking (DS), STGR, ASI, plant height (PHT), EPP, EASP, and PASP under low N and ASI, EPP, EASP, and PASP across (drought stress and low N) environments. Furthermore, Badu-Apraku et al. (2012a) used both path co-efficient and genotype main effect plus genotype × environment interaction (GGE) biplot analyses to identify EASP, PHT, and ASI as important secondary traits for drought tolerance, whereas EHT, PASP, EASP, and STGR were identified for selection under low N conditions. Alabi et al. (2001) recommended the use of EPP, STGR, and ASI for selection under low N environments. Despite the

few differences in the reports from these and several other researchers, the IITA Maize Program conducts selection for improved grain yield under drought-stress and low N conditions by using a base index that incorporates high grain yield, increased EPP, reduced ASI, and outstanding expression of EASP, PASP, and STGR (Oyekunle and Badu-Apraku, 2013). Thus, further studies are required to validate the reliability of the secondary traits included in the base index of the IITA Maize Program. The identification and validation of secondary traits for selection for improved grain yield under contrasting stresses remains a relevant research area in maize breeding (Bolaños and Edmeades, 1993, 1996; Bänziger and Lafitte, 1997; Badu-Apraku et al., 2004). Therefore, the objectives of this study were to (i) determine the magnitude of residual genetic variability for grain yield and other traits in TZE-Y Pop DTC$_4$ STR C$_4$ under drought-stress, low N, and across (drought-stress and low N) environments; (ii) predict the response of TZE-Y Pop DTC$_4$ STR C$_4$ to selection under the contrasting research conditions; and (iii) investigate the inter-trait relationships under drought stress, low N, and across environments, using simple correlations, step-wise multiple linear regression and path co-efficient analyses.

MATERIALS AND METHODS
Generation of Progenies through the North Carolina Design I Mating Scheme

Fifty S$_0$ plants were randomly chosen as male parents from the reference population, TZE-Y Pop DTC$_4$ STRC$_4$. These male parents were divided into 10 sets of five male plants. Each male plant was crossed to five randomly selected female plants from the same reference population to generate 25 full-sib progenies per set, for a total of 250 full-sibs using the NCD I mating scheme (Comstock and Robinson, 1948). These progenies were generated during the 2011 growing season at the IITA–Ibadan breeding nursery.

Field Evaluations and Management

The 250 full-sib progenies were evaluated under managed drought stress at Ikenne (3°7′ E, 6°87′ N, 30 m ASL, 1200 mm annual rainfall) during the dry season of 2011/2012, natural drought stress at Kadawa (11°45′ N, 8°45′ E, 468.5 m ASL, 884 mm annual rainfall) during the 2012 growing season and at Ile-Ife (7°18′ N, 4°33′ E, 244 m ASL, 1200 mm annual rainfall) during the 2012/2013 late growing season (the second season of the year, usually shorter than the first). In addition, the progenies were evaluated under low N (30 kg N ha^{-1}) at Ile-Ife and Mokwa (9°18′ N, 5°4′ E, 457 m ASL, 1100 mm annual rainfall) during the 2012 growing season (Supplemental Tables S1 and S2). The trials were laid out in a 25 by 10 randomized incomplete block design with two replicates. Each experimental unit was a single-row plot, 3 m long, with row spacing of 0.75 m and hill spacing of 0.4 m within the row. Three seeds were planted per hill and thinning to two seedlings per hill was done at about 2 wk after emergence, resulting in a final population density of about 66,667 plants ha^{-1}. Fertilizer was applied to terminal drought-stressed plots at the rate of 60 kg each of N, P$_2$O$_5$ and K$_2$O ha^{-1} at 2 wk after planting (WAP) and 60 kg of N ha^{-1} at 4 WAP, whereas under managed drought, 60 kg each of N, P$_2$O$_5$ and K$_2$O ha^{-1} was applied at planting and 60 kg of N ha^{-1} was top-dressed at 3 WAP. The managed-drought trial was irrigated using the sprinkler irrigation system during the dry season. Irrigation water was applied at the rate of 17 mm per week to the drought plots for the first 4 wk, after which the irrigation was withdrawn till harvest maturity so that the plants could rely on stored soil moisture for growth and development. In contrast, terminal drought was achieved by planting the trials at such a time that drought coincided with 1 to 2 wk before flowering through grain-filling periods, towards the end of the growing season (terminal drought). The low N experimental fields were depleted of N by continuous planting of maize for several years; the biomass was removed after each harvest. The total N in the soils was determined by Kjeldahl digestion and colorimetric determination using Technicon AAII Autoanalyser (Bremner and Mulvaney, 1982). Based on the soil analyses, the N fertilizers were applied in two splits at 2 and 4 WAP to bring the total available N in the low N plots to 30 kg ha^{-1}. In addition, 60 kg each of P$_2$O$_5$ and K$_2$O were applied to the low N plots at 2 WAP. The drought-stress and low N fields were kept weed-free manually and by use of pre-emergence herbicide, atrazine (1-chloro-3-ethylamino-5-isopropylamino-2, 4, 6-triazine) and post-emergence herbicide, gramoxone (1,1-dimethyl-4, 4-bipyridinium dichloride) at 5 L ha^{-1} of primextra {atrazine (1-chloro-3-ethylamino-5-isopropylamino-2, 4, 6-triazine) + metolachlor [2-chloro-N-(2-ethyl-6-methylphenyl)-N-(2-methoxy-methylethyl) acetamide (56)]} and paraquat (1,1-dimethyl-4, 4-bipyridinium dichloride), respectively.

Collection of Agronomic Data

Data were recorded for DA and DS as days from planting to when 50% of the plants in a plot had shed pollen and extruded silks, respectively. The ASI was determined as the difference between DS and DA. Number of ears per plant (EPP) was obtained by dividing the total number of ears harvested per plot by the number of plants at harvest. Ear aspect was scored on a scale of 1 to 9, where 1 = clean, uniform, large, and well-filled ear and 9 = ears with undesirable features, whereas PASP was recorded on a scale of 1 to 9 based on plant type, where 1 = excellent and 9 = poor. Plant height (PHT) was measured as the distance from the base of the plant to the base of the first tassel branch and ear height (EHT) as the distance from the base of the plant to the node bearing the upper ear. Husk cover (HUSK) was scored on a scale of 1 to 5, where 1 = husk tightly arranged and extended beyond the ear tip and 5 = ear tips exposed. Root lodging (RL) was estimated as the percentage of plants leaning more than 30° angle from the vertical whereas stalk lodging (SL) was the percentage of plants broken at or below the top ear node. The STGR was scored for drought and low N plots at 70 d after planting on a scale of 1 to 9, where 1 = almost all leaves green and 9 = virtually all leaves dead. Grain weight of shelled ears harvested per plot was recorded and converted to kg ha^{-1} at 15% moisture content.

Statistical Analysis

Log transformation was performed on data related to counts, scales, and scores using the formula [log (counts + 1)], whereas the square root transformation was used for data in percentages before subjecting them to ANOVA using Statistical Analysis System (SAS) 9.3. (SAS Institute, 2011).

Analyses of variance were performed on plot means of grain yield and other measured traits separately under drought and low N, followed by combined analysis across environments with PROC GLM statement of SAS 9.3. (SAS Institute, 2011). Year–location combinations constituted environments in the present study. Results of the homogeneity tests for grain yield showed no significant differences among year–location combinations (data not shown), thus justifying the analysis across environments. The statistical model used for the combined ANOVA is as follows:

$$Y_{ijkln} = \mu + E_i + R_{j(i)} + S_{k(ij)} + M_{l(k)} + F_{n(kl)}$$
$$+ (EM)_{ikl} + (EF)_{ikln} + E_{ijkln}$$

where Y_{ijkln} is the observed measurement for the nth female within the lth male in the kth set of the jth replicate, within the ith environment; μ is the grand mean; E_i is the main effect of the environment, $i = 1,2$ or $1,2,3$ or $1,2,...5$; $R_{j(i)}$ is the effect of replicate nested within environment effect, $j = 1,2$; $S_{k(ij)}$ is the effect of set nested within replicate j by environment i, $k = 1,2,....10$; M_l is the effect of male nested within set, $l = 1,2,...5$; $F_{n(kl)}$ is the effect of the female within male by set k, $n = 1, 2,...5$; $(EM)_{ikl}$ is the interaction effect between environment and male nested within set, $(EF)_{ikln}$ is the interaction effect between environment and female nested within male within set, and E_{ijkln} is the error term.

Variance components were estimated by equating the observed mean squares to their expectations and solving for the desired component. The additive (σ^2_A) and dominance (σ^2_D) genetic variances were estimated from the components of variance derived from the mean squares of the ANOVA as follows: $\sigma^2_A = 4\sigma^2_m$ [inbreeding coefficient (F) = 0 for non-inbred plants], and $\sigma^2_D = 4\sigma^2_{f/m} - 4\sigma^2_m$. In this model, σ^2_m = component of variance due to genetic differences among males and $\sigma^2_{f/m}$ = component of variance due to females within males. The standard errors of the additive and dominance variances were estimated according to the method of Hallauer et al. (2010). Narrow-sense heritability (h^2) estimates among full-sib families were computed according to the method of Holland et al. (2003), and expected response to selection (R) was estimated using the following formula:

$$R = ih\sigma_A$$

where i is the standardized selection differential (selection intensity was 25% and i = 1.2711 for this study), h is the square root of the narrow-sense heritability, and σ_A is the standard deviation of breeding values (square root of the additive genetic variance). Gain per cycle for each trait was estimated as [(response to selection/mean) × 100]. Heritability estimates were rated as high (>60%), moderate (30–60%) or low (<30%), whereas predicted gain/cycle was rated as high (>20%), moderate (10–20%), and low (<10%) according to Johnson et al. (1955). The step-wise regression analyses were done using the Statistical Package for the Social Sciences, SPSS version 17.0 (SPSS Inc, 2007). Sequential path co-efficient analyses were performed to explain the causal relationships among traits under each and across research conditions using the procedure proposed by Mohammadi et al. (2003). The sequential stepwise multiple regression was used to organize the predictor traits into first, second, and third order based on their respective contributions to the total variation in grain yield with minimized multicolinearity (Badu-Apraku et al., 2012a, 2014). At first, all other traits were regressed on grain yield and those with significant contributions to grain yield at $P \leq 0.05$ were identified as first order traits. Subsequently, traits that were not identified as first-order traits were regressed on each of the first order traits to identify those with significant contributions to grain yield through the first-order traits and they were categorized as second-order traits. The procedure was repeated to identify traits in subsequent orders. The path co-efficients were the standardized b values from the output of the stepwise regression analysis (Mohammadi et al., 2003; Badu-Apraku et al., 2012a, 2014). The stepwise multiple regression analysis tested the significance of the path coefficients using t test at 0.05 level of probability and retained only traits with significant path coefficients and indicated the percentage of the variation they accounted for in the dependent variable.

RESULTS
Component of Variance, Heritability, and Predicted Gain per Cycle

Analyses of variance across drought environments revealed significant mean squares for environment, replications, sets-in-reps, males/sets-in-reps, and the interaction of environment with the males-within-sets for most measured traits (Table 1). However, the mean squares for most traits were not significant for the females in males/sets-in-reps and the interaction of environment with the females in males-within-sets. Under low N and across environments, all the sources of variation, except the interaction of environment with the females in males-within-sets, showed significant mean squares for most of the measured traits.

Estimates of additive genetic variance were significantly different from zero for PASP under drought, DA, DS, ASI, and STGR under low N and grain yield, DS and ASI across test environments (Table 2). However, dominance variances were not significantly different from zero for any of the measured traits under each and across research conditions. Because of negative estimates, additive variances of two traits each under drought and low N were equal to zero. Similarly dominance variances of nine traits under drought and seven traits each under low N and across environments were also equal to zero. As a result of the zero variances, the dominance to additive genetic variance ratio could be estimated for only EPP, ASI, and HUSK under drought, EPP, PHT, EHT, DA, EASP, and PASP under low N and PHT, EHT, EASP, PASP, SL, and STGR across environments. The dominance to additive genetic variance

Table 1. Analysis of variance for grain yield and other agronomic traits of full-sib families developed from TZE-Y Pop DTC$_4$ STR C$_4$ and evaluated under three drought, two low N, and across five environments, 2011 to 2013.

Sources of variation	df	Grain yield	Days to anthesis	Days to silking	Anthesis-silking interval	Ears per plant	Plant height	Ear height	Ear aspect	Plant aspect	Husk cover	Root lodging	Stalk lodging	Stay green characteristic
Drought														
Environment (Env)	2	756485564**	3539.5**	4055.7**	67.95**	4.303**	790061**	375454**	76.16**	64.52**	109.15**	48.447**	34.130**	101.22**
Rep(Env)	3	846264	127.6**	54.1*	21.14**	0.051*	2820**	1637**	14.92**	7.00**	5.78**	0.028	0.223**	16.19**
Set(Env × Rep)	54	2246625**	14.1**	15.6**	3.95**	0.068**	1326**	798**	2.84**	3.60**	0.48**	0.095**	0.057**	2.43**
Male(Set)	40	1335782**	7.9**	8.3**	3.01**	0.031**	606**	211**	1.59**	2.08**	0.29**	0.050**	0.025	1.16**
Female(Set × Male)	200	722520	4.3	5.0*	1.75	0.022	237**	115ns	0.69	1.08*	0.18	0.033*	0.024	0.69
Env × Male(Set)	80	815041	9.6**	8.7**	2.26*	0.025*	392**	155**	0.87*	0.77	0.19	0.035*	0.025	0.98*
Env × Female(Set × Male)	400	668695	4.5	4.5	1.57	0.019	203	111	0.68	0.96	0.17	0.027	0.024	0.71
Error	720	654203	4.1	4.0	1.63	0.019	183	106	0.66	0.86	0.17	0.026	0.024	0.71
Low N														
Env	1	196989583**	5.0*	954.5**	820.84**	0.026	278229**	136595**	335.24**	286.23**	173.64**	1.704**	12.168**	161.60**
Rep(Env)	2	37100143**	154.8**	147.7**	6.66**	0.047*	6816**	5193**	0.51	9.50**	5.38**	0.012	0.325**	11.04**
Set(Env × Rep)	36	17609896**	10.4**	29.5**	6.98**	0.013	2146**	922**	5.56**	10.99**	2.50**	0.028	0.084**	9.48**
Male(Set)	40	2847367**	8.5**	15.7**	4.84**	0.020**	428**	209**	1.28**	1.32**	0.38	0.036**	0.122**	1.26**
Female(Set × Male)	200	1416620**	2.4**	3.7**	1.47**	0.014**	218**	141**	0.66**	0.95**	0.32	0.023	0.048**	0.53**
Env × Male(Set)	40	1333840	2.0*	1.8	1.07	0.011	276**	130*	0.58	0.97	0.42**	0.044**	0.048**	0.57*
Env × Female(Set × Male)	200	1215034	1.1	1.8	0.97	0.011	169	98	0.54	0.74	0.34**	0.025**	0.039**	0.49**
Error	480	1099398	1.2	1.7	0.90	0.011	144	90	0.48	0.72	0.28	0.019	0.028	0.38
Across														
Env	4	718719462**	1801.4**	2401.8**	276.59**	3.067**	513605**	242057**	123.72**	123.44**	100.42**	28.064**	20.972**	111.84**
Rep(Env)	5	15347816**	138.5**	91.5**	15.35**	0.050**	4418**	3059**	9.15**	8.00**	5.62**	0.021	0.264**	14.13**
Set(Env × Rep)	90	8391933**	12.6**	21.2**	5.16**	0.046**	1654**	848**	3.93**	6.56**	1.29**	0.068**	0.068**	5.25**
Male(Set)	40	2605684**	13.1**	18.5**	5.09**	0.032**	749**	288**	1.69**	1.90**	0.43**	0.050**	0.076**	1.29**
Female(Set × Male)	200	1066921**	4.2**	5.2**	1.82**	0.018	289**	160**	0.79**	1.09**	0.24	0.028*	0.037**	0.72*
Env × Male(Set)	160	1135347**	6.1**	6.1**	2.09**	0.020*	336**	143**	0.87**	1.00*	0.26*	0.037**	0.042**	0.91**
Env × Female(Set × Male)	800	906160	3.2	3.6**	1.38	0.017	185	105	0.61	0.90*	0.24*	0.027**	0.031**	0.60
Error	1200	832281	2.9	3.1	1.34	0.016	167	100	0.59	0.80	0.21	0.023	0.025	0.58

* Significant at 0.05 level of probability.

** Significant at 0.01 level of probability.

Table 2. Additive (σ^2_A) and dominance (σ^2_D) variances, narrow-sense heritability estimates (h^2), expected response cycle^{-1} (R) and % gain cycle^{-1} for grain yield and other agronomic traits of full-sib families developed from TZE-Y Pop DTC$_4$ STR C$_4$ and evaluated under three drought, two low N, and across five environments, 2011 to 2013.

Traits	$\sigma^2_A \pm$ SE	$\sigma^2_D \pm$ SE	σ^2_D/σ^2_A	h^2, %	R	% Gain/cycle
Drought environments						
Grain yield	62,255 ± 43,932	0 ± 72,221	0	21	144.5	5.3
Ears per plant	0.00045 ± 0.0011	0.0011 ± 0.0020	2.44	5.3	0.0062	0.76
Plant height	23.9 ± 19.8	0 ± 27.0	0	22	2.9	1.7
Ear height	6.9 ± 7.2	0 ± 11.7	0	14	1.3	1.5
Days to anthesis	0† ± 0.31	0 ± 0.47	‡	0	0	0.0
Days to silking	0 ± 0.31	0.31 ± 0.50	‡	0	0	0.0
Anthesis-silking interval	0.077 ± 0.10	0.040 ± 0.17	0.52	11	0.11	5.4
Ear aspect	0.10 ± 0.051	0 ± 0.075	0	32	0.22	4.1
Plant aspect	0.16 ± 0.065*	0 ± 0.11	0	34*	0.30	5.7
Husk cover	0.012 ± 0.01	0 ± 0.02	0	17	0.06	2.7
Root lodging	0.24 ± 0.45	0.01 ± 0.75	0.04	7.7	0.17	6.2
Stalk lodging	0.18 ± 0.18	0 ± 0.43	0	9.2	0.16	5.6
Stay green characteristic	0.03 ± 0.041	0 ± 0.070	0	9	0.061	1.5
Low N environments						
Grain yield	262,388 ± 142166	0 ± 233,875	0	29	351	8.5
Ears per plant	0.0013 ± 0.0011	0.0017 ± 0.0021	1.31	15	0.018	2.0
Plant height	20.5 ± 22.9	29.3 ± 35.7	1.43	15	2.2	1.2
Ear height	7.2 ± 11.3	35.7 ± 20.5	4.96	8.6	1.0	1.0
Days to anthesis	1.0 ± 0.38*	0.28 ± 0.47	0.28	53*	0.94	1.7
Days to silking	2.4 ± 0.69**	0 ± 0.80	0	77**	1.7	3.1
Anthesis-silking interval	0.66 ± 0.22*	0 ± 0.28	0	59*	0.79	48.6
Ear aspect	0.12 ± 0.064	0.0088 ± 0.11	0.07	28	0.23	4.3
Plant aspect	0.029 ± 0.075	0.18 ± 0.14	6.21	5.2	0.049	1.0
Husk cover	0 ± 0.09	0 ± 0.05	‡	0	0	0
Root lodging	0 ± 0.28	0 ± 0.88	‡	0	0	0
Stalk lodging	2.95 ± 1.48	0 ± 1.95	0	40	1.38	35
Stay green characteristic	0.13 ± 0.062*	0 ± 0.095	0	37*	0.28	7.6
Across environments						
Grain yield	104,766 ± 47500*	0 ± 66,236	0	36*	248	7.5
Ears per plant	0.00081 ± 0.00061	0 ± 0.0010	0	18	0.015	1.8
Plant height	24.7 ± 13.6	17.0 ± 18.2	0.69	31	3.5	2.0
Ear height	7.2 ± 5.4	14.9 ± 8.6	2.07	18	1.5	1.6
Days to anthesis	0.48 ± 0.24	0 ± 0.30	0	38	0.54	1.0
Days to silking	0.86 ± 0.33*	0 ± 0.40	0	53*	0.85	1.5
Anthesis-silking interval	0.21 ± 0.092*	0 ± 0.12	0	40*	0.36	18.8
Ear aspect	0.051 ± 0.031	0.020 ± 0.046	0.39	25	0.14	2.7
Plant aspect	0.057 ± 0.036	0.018 ± 0.059	0.32	21	0.14	2.8
Husk cover	0.014 ± 0.008	0 ± 0.01	0	24	0.07	3.4
Root lodging	0.088 ± 0.23	0 ± 0.36	0	5.6	0.09	4.0
Stalk lodging	0.49 ± 0.32	0.07 ± 0.46	0.14	24	0.44	13.2
Stay green characteristic	0.021 ± 0.025	0.026 ± 0.040	1.24	12	0.063	1.6

* Significantly different from zero at 0.05 level of probability.

** Significantly different from zero at 0.01 level of probability.

† Negative variances were treated as zero.

‡ Ratio could not be estimated.

ratio were >0.5 for two out of three traits under drought, four out of six traits under low N and two out of six traits across environments. Heritability estimates for grain yield were low under drought (21%) and low N (29%) but moderate (36%) across environments. The heritabilities ranged from zero for DA and DS to 34% for PASP under drought, zero for RL and SL to 77% for DS under low N and 5.6%

for RL to 53% for DS across environments. The predicted response to selection for grain yield was 144.5, 351, and 248 kg ha^{-1} cycle^{-1} corresponding to 5.3, 8.5, and 7.5% gain cycle^{-1} under drought, low N and across environments, respectively. The predicted gain per selection cycle was highest for RL (6.2%) under drought and ASI under both low N (48.6%) and across test environments (18.8%).

Step-wise Multiple Regression and Sequential Path Analyses

Under drought stress, the stepwise multiple regression analysis identified EASP, EPP, PASP, STGR, and ASI as traits with significant direct effects on grain yield accounting for about 72% of the total variation in grain yield (Table 3, Fig. 1). Among the five traits, ear aspect had the highest direct effect (−0.509) on yield, with the direct effect of the other four traits being relatively much lower (Fig. 1). Also among the five traits, only EPP had a positive direct effect on yield. Several other traits made indirect contribution to grain yield through one or more of these five first-order or primary traits. There were five traits in the second order or secondary group, including PHT, SL, DS, RL, and DA, with PHT being the only secondary trait that contributed indirectly to yield through all of the five primary traits, whereas SL contributed to yield through only one trait, STGR. Plant height had the highest indirect effect through PASP (−0.503) and the only positive indirect effect through EPP. The indirect contribution of the remainder four second-order traits to yield through the first-order traits are clearly depicted in Fig. 1. Only two traits, EHT and HUSK, were identified as the third-order traits with significant indirect effect on grain yield. While EHT had indirect effects through all the second-order traits, HUSK contributed indirectly through only three traits: DS (0.176), RL (0.157), and DA (0.145).

In the low N environments, seven traits (EASP, PASP, EPP, DS, EHT, SL, and STGR) were identified by step-wise multiple regression as the first-order contributors to grain yield. These traits explained about 75% of the total variation in grain yield (Table 3, Fig. 2). Ear aspect had the highest direct effect on grain yield (−0.419), whereas only EPP (0.199) and EHT (0.160) had positive direct contributions to yield. Only five traits (PHT, DA, HUSK, DS, and RL) were grouped into second order and there were no third-order traits under the low N conditions. The second-order traits made indirect contributions to yield through only three, four, or five first-order traits; none made contributions through all the seven first-order traits. Of the 18 indirect effects of the second-order traits through the first-order traits, 11 had positive values, four of which had indirect path coefficients of 0.532 to 0.81 (Fig. 2). All of the negative indirect effects had values <0.4.

Across environments, stepwise multiple regression also identified seven traits, which were the same as those identified under low N, together accounting for about 71% of the total variation in grain yield. Ear aspect alone accounted for nearly 60% of the total variation in grain yield (Table 3). Apart from EASP that had a direct path coefficient of −0.53, the first-order traits had direct values of <0.2 and only EPP (0.162) and EHT (0.089) had positive direct contributions to yield (Fig. 3). Here also, there

were only five second-order and no third-order traits. One of the second-order traits (DA) had indirect effect on yield through six of the seven first-order traits, whereas RL had indirect effect through only one of the first-order traits; that is PASP. Furthermore, 12 of the 19 indirect effects of the second-order traits through first-order traits on yield were positive, with DA (0.895) through DS and PHT (0.810) through EHT having the largest indirect effects. Apart from PHT (−0.54) through PASP, all negative indirect effects were <0.4 across environments (Fig. 3).

Based on the R^2 change values, EASP was the most important trait explaining more than 50% of the variation in grain yield under drought, low N, and across environments. The ASI under drought (0.6%), STGR under low N (0.8%) and EHT across environments (0.5%) were the least important traits under these respective research conditions (Table 3).

DISCUSSION

The generally low additive genetic variances for grain yield and most other traits in the present study suggested

Table 3. Unstandardized partial regression coefficients (b values), coefficients of determination (R^2), and R^2 change (DR2) from stepwise multiple regression of grain yield and other agronomic traits of full-sib families developed from TZE-W Pop DT C_4 STR C_4 and evaluated under drought, low N, and across environments, between 2011 and 2013.

Trait (i)	Drought		
	b value	R^2	DR2
Ear aspect	−0.509	0.605**	0.605
Ears per plant	0.248	0.679**	0.075
Plant aspect	−0.246	0.707**	0.028
Stay green characteristic	−0.088	0.715**	0.008
Anthesis-silking interval	−0.080	0.721*	0.006

Trait (i)	Low N		
	b value	R^2	DR2
Ear aspect	−0.419	0.543**	0.543
Plant aspect	−0.208	0.644**	0.101
Ears per plant	0.199	0.688**	0.044
Days to silking	−0.176	0.711**	0.022
Ear height	0.160	0.727**	0.016
Stalk lodging	−0.100	0.740**	0.013
Stay green characteristic	−0.097	0.748**	0.008

Trait (i)	Across		
	b value	R^2	DR2
Ear aspect	−0.530	0.585**	0.585
Ears per plant	0.162	0.633**	0.048
Plant aspect	−0.187	0.660**	0.027
Stay green characteristic	−0.174	0.688**	0.027
Days to silking	−0.120	0.695*	0.008
Ear height	−0.089	0.701*	0.005
Stalk lodging	−0.079	0.706*	0.006

* Significant F test at 0.05 level of probability.

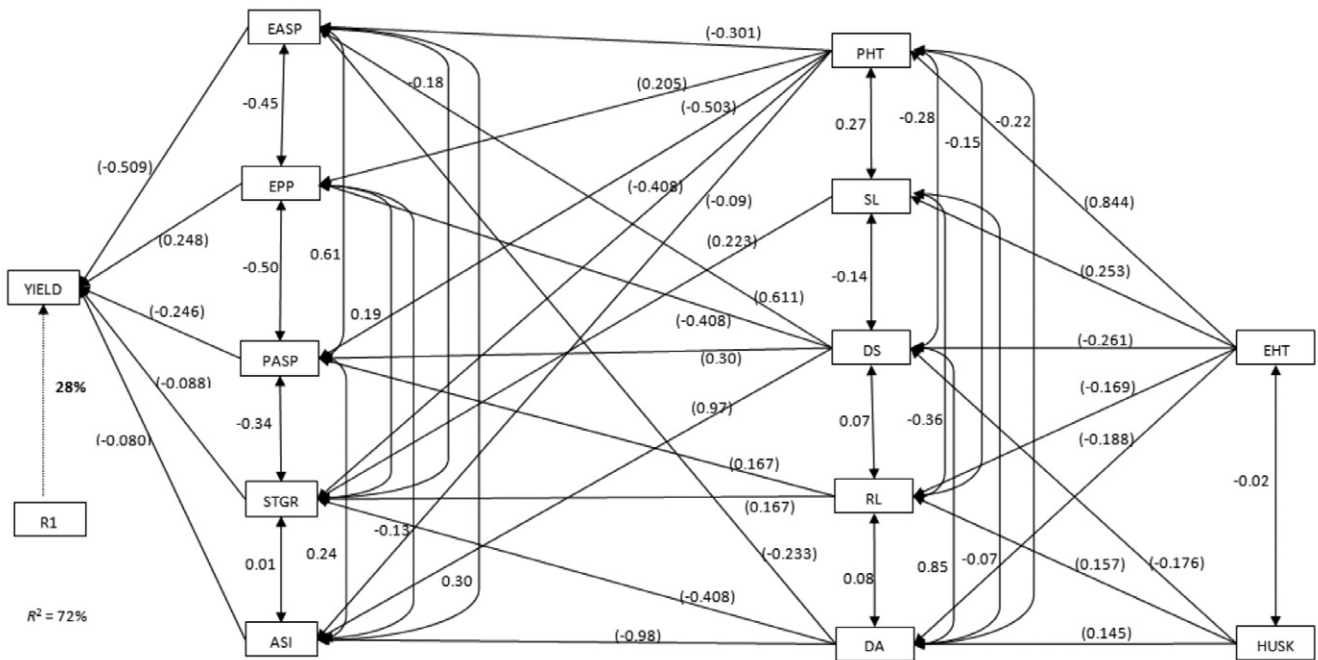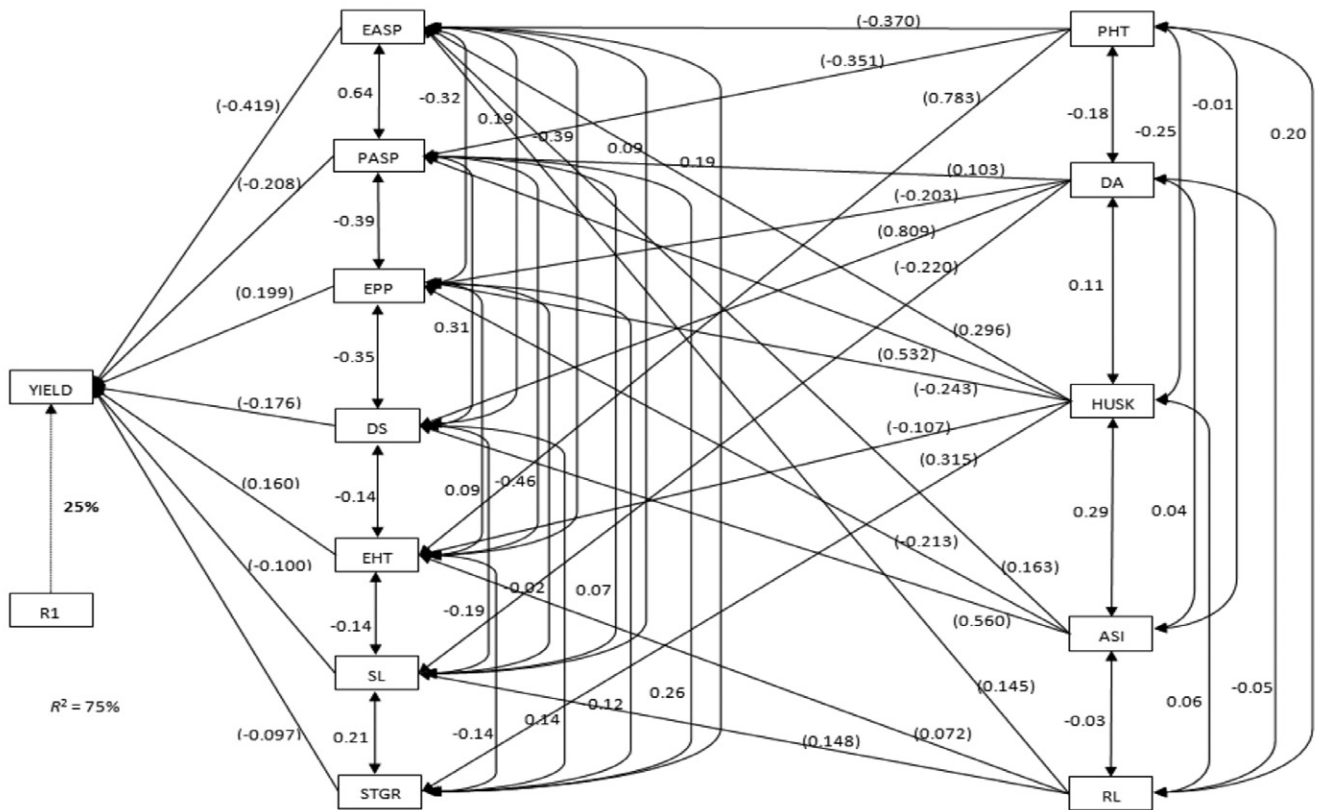** Significant F test at 0.01 level of probability.

Fig. 1. Path analysis model diagram showing causal relationships of measured traits of early maturing full sib progenies evaluated under drought stress at Ikenne, Ile-Ife, and Kadawa, 2011 to 2013. Bold value is the residual effect; values in parenthesis are direct path coefficients while other values are correlation coefficients. R1 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; RL, root lodging; SL, stalk lodging, and YIELD, grain yield
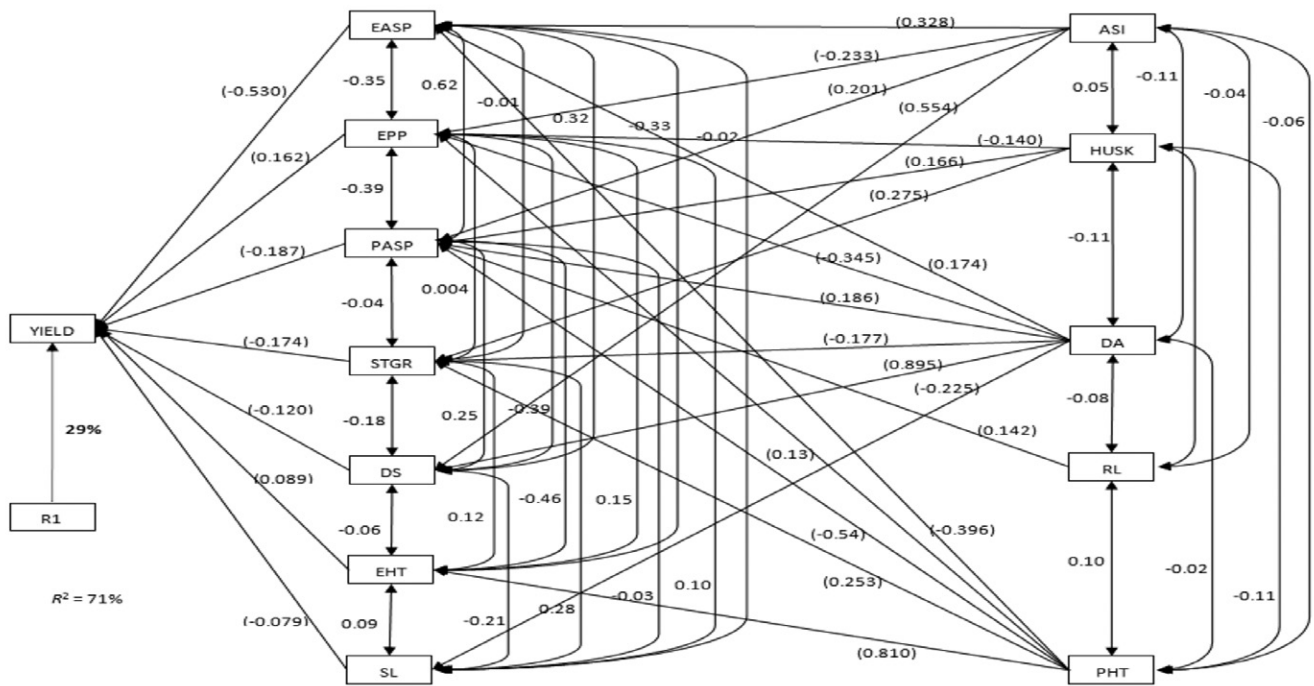

Fig. 2. Path analysis model diagram showing causal relationships of measured traits of early maturing full sib progenies evaluated under low N at Mokwa and Ile-Ife, 2012. Bold values are residual effect; values in parenthesis are direct path coefficient and other values are correlation coefficients. R1 is the 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; RL, root lodging; SL, stalk lodging, and YIELD, grain yield.

Fig. 3. Path analysis model diagram showing causal relationships of measured traits of early maturing full sib progenies evaluated evaluated across five environments, that is, three drought (Ikenne, Kadawa, and Ile-Ife) and two low N (Ile-Ife and Mokwa) environments, 2011 to 2013. Bold values are residual effect; values in parenthesis are direct path coefficient and other values are correlation coefficients. R1 is the 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; RL, root lodging; SL, stalk lodging, and YIELD, grain yield.

that little or no further progress would be possible from selection for improved yield in the population under drought, low N, and across environments. Similar results were reported by Badu-Apraku et al. (2013b), who obtained low genetic variability in an extra-early maize population after three cycles of selection for drought tolerance. The authors therefore recommended introgression of new sources of favorable alleles for drought tolerance into the population for guaranteed progress from further selection. In contrast, Badu-Apraku et al. (2004) observed moderate-to-large additive genetic variance and narrow-sense heritability estimates for grain yield and other traits in an early maturing maize population, Pool 16 DT, after eight cycles of recurrent selection for improved grain yield under water stress. Similarly, Miti et al. (2010) reported adequate genotypic variation for low-N tolerance among maize landraces in an experiment conducted using S_1 family recurrent selection to select for low-N tolerance among 96 landraces in Zimbabwe and concluded that these landraces could be improved by selection. The difference between our results and those of other workers are attributable to differences in the research conditions, the genetic base of the maize populations used for the studies, the parental control, and selection intensity.

Heritability estimates provide insight into how effectively a trait could be transmitted from parents to their offspring (Burton, 1952; Ariyo, 1995; Hallauer et al., 2010).

Low narrow-sense heritability estimate observed for most measured traits under drought, low N and across environments is an indication that the scope for improvement of most traits in the population is limited. However, introgression of genes for tolerance to drought stress and low N into the population could guarantee continued progress from selection for improved grain yield under these stress conditions. The predicted response to selection for grain yield of 144.5, 351, and 248 kg ha^{-1} cycle^{-1}, with a corresponding gain cycle^{-1} of 5.3, 8.5, and 7.5%, under drought, low N, and across environments, respectively, are low but compared favorably with the realized gains reported by Edmeades et al. (1995, 1997). Edmeades et al. (1995) obtained yield gains of 259 kg ha^{-1} cycle^{-1} (12.4%) and 115 kg ha^{-1} (1.5%) cycle^{-1} after three cycles of recurrent selection under drought stress in two maize populations, La Posta Sequia and Pool 26 Sequia, respectively, whereas Edmeades et al. (1997) compared grain yields of the base population with those of the advanced cycles of four drought-tolerant maize populations under four environments of differing N levels, and obtained gains of 210 kg^{-1} ha^{-1} cycle^{-1} for S_1 selection and 86 kg^{-1} ha^{-1} cycle^{-1} for full-sib selection. Predicted response to selection is, however, highly theoretical and some of the underlying assumptions may or may not remain valid under actual field conditions. This has often resulted in discrepancies between predicted gains and realized gains from selection

(Badu-Apraku et al., 2012b; Hallauer et al., 2010). While the predicted gain is based on parameter estimates obtained from a reference population for one cycle of selection, realized gains are estimated across several cycles of selection. The genetic, phenotypic, and environmental variances do not usually remain constant during selection cycles as assumed when predicting gains from selection.

Information on the type of gene action governing the inheritance of traits in a population guides the breeder on what objectives to design for the population. When additive gene action is more important than the non-additive gene action, development of both open-pollinated varieties (OPVs) and hybrids should be the goal. If non-additive gene action is more important than the additive gene action, hybrid production should be the goal. However, in the present study, more than half of the dominance variances were equal to zero because of negative estimates, whereas a few of the additive genetic variances were also equal to zero under each and across research conditions. Out of the 13 traits assayed, dominance to additive genetic variance ratio could be estimated for only three under drought and six each under low N and across environments. Therefore, no valid conclusions could be made about which of the gene actions governed the inheritance of most of the traits in this population.

An important objective of the present study was to investigate causal relationships among traits under drought, low N, and across test environments. Results of our study were compared with those of several studies conducted in SSA with the same objective. Under drought conditions, in our study, EASP, EPP, PASP, STGR, and ASI were identified as the most important traits contributing to the variation in grain yield, suggesting their reliability as secondary traits under drought stress. Using genotype × trait (GT) biplot analysis in an earlier study, Badu-Apraku et al. (2011) identified EASP, PASP, ASI, and EPP as the important secondary traits for selection under drought stress. Therefore, the inclusion of the traits in the IITA base selection index for improved grain yield under drought stress is well justified. Furthermore, in our study, plant height had indirect effects through all the five first-order traits (EASP, EPP, PASP, STGR, and ASI), whereas DS contributed through four of the five traits, suggesting that they should be considered as traits of potential value in drought experiments. Although EHT and HUSK were identified as third-order traits, EHT had significant effect on grain yield through all the second-order traits, suggesting that EHT is also of potential value in breeding for drought tolerance in maize. Similar results were obtained by Badu-Apraku et al. (2012a), who identified EPP, PASP, EASP, DS, ASI, PHT, and EHT as the most reliable traits in selecting for drought-tolerant genotypes in extra-early maize inbred lines. The authors suggested that DS, PHT, and EHT were additional drought-adaptive traits that should be considered for inclusion in the IITA base index for characterizing extra-early maturity maize for drought tolerance. Similarly, Bänziger and Lafitte (1997) also identified reduced barrenness (increased EPP) and shortened ASI, along with delayed leaf senescence, as reliable secondary traits for selection of superior genotypes under drought-stress and low N conditions. In their study, however, PASP, EASP, PHT, and EHT were not identified as important secondary traits for yield improvement.

In our study, traits identified as most reliable indirect selection criteria for maize grain yield improvement under low N environments included four of the five traits identified under drought (EASP, PASP, EPP, and STGR) plus three others (DS, EHT, and SL). These seven traits were similarly identified as the most reliable indirect selection criteria across environments. Obviously, secondary traits useful as indirect selection criteria for improved grain yield in maize under drought may vary with the type of genetic material and the geographical location of experiments, but some traits appear to be consistent under different research factors. Four traits, namely, PASP, EASP, EPP, and STGR, consistently identified in this study had also been identified by Badu-Apraku et al. (2011), through GT biplot analysis, as the most important secondary traits for selecting superior genotypes under drought-stress and low N environments in genetic materials different from the ones used in the present study. Bänziger and Lafitte (1997) similarly identified delayed leaf senescence (STGR), reduced barrenness (EPP), and shortened ASI as reliable secondary traits for selection of superior genotypes under drought-stress and low N conditions.

All of these seemingly important traits for indirect selection for yield improvement are easy to determine because they are based more or less on visual selection or counting. However, interpretation, application, and extrapolation of research findings on the traits must be done cautiously for several reasons. First, determination or quantification of some of the traits, such as PASP, EASP, and STGR, is subjective and only experienced scientists and research technicians can score them accurately. Although, for many years, these traits have been part of traits determined in maize trials conducted in WCA, maize breeders have paid little or no attention to them as selection criteria perhaps because of the subjectivity in their determination. Breeders are now giving greater attention to these traits, and the need to minimize the subjectivity in their determination is now obvious. In addition, there is need for more specific studies on these traits using diverse maize types, including OPVs, inbred lines and hybrids from different maturity groups and subjecting the data to several statistical and biometrical methods of analysis, such as those used in the present study. If the results from such studies are consistent with the findings reported here, maize breeders may need to select for the traits to minimize costs and efforts on selection for yield improvement. Second, results of this and similar studies suggest that selection for

EHT and/or PHT should improve yield. This may be done only under the stress conditions evaluated in the studies because the stresses normally reduce both PHT and EHT, which are known to be positively correlated with grain yield in tropical maize. Selection for increased plant height under optimum production conditions will increase lodging and this will be detrimental to grain production. Third, some ontogenic pairs of traits consistently demonstrated high positive relationships in our present study as well as in those conducted earlier. Some examples in the present study are PHT with EHT and DS with DA, both of which had high positive correlation coefficients ($r > 0.8$) and are either loaded on the same order of traits or one of the traits in a pair acts on yield through the other, with a high positive indirect path coefficient. Selection for improved grain yield using one of the traits in a pair as an indirect selection criterion or as a component in a selection index will suffice.

CONCLUSIONS

We concluded that the scope of improvement for most of the traits in TZE-Y Pop DT C$_4$ STR C$_4$ maize population was limited under drought stress, low N, and across environments because of the low additive variances, heritability estimates and predicted gains from further selection for the traits. Four traits, namely, EASP, EPP, PASP, and STGR, were identified as important secondary traits, which could be included in a base index together with grain yield when selecting for improved grain yield under drought-stress, low N and across both stress conditions. We recommended introgression of new sources of favorable alleles for tolerance to drought stress and low N into the population to facilitate rapid progress from further selection for improved yield in the population.

Supplemental Information Available

Supplemental information is available with the online version of this manuscript.

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