RESEARCH

Assessment of Reliability of Secondary Traits in Selecting for Improved Grain Yield in Drought and Low-Nitrogen Environments

B. Badu-Apraku,* R.O. Akinwale, J. Franco, and M. Oyekunle

ABSTRACT

Grain yield of maize (*Zea mays* L.) has low heritability under low soil nitrogen (low N) and drought, necessitating the use of secondary traits with strong associations with yield for selection. A base index involving anthesis–silking interval, plant and ear aspects, ears per plant, and stay green characteristic is used for selection for yield under drought and low-N stresses. Reports are contradictory on the reliability of stay green characteristic for selecting for yield under drought stress and of ears per plant and anthesis–silking interval in selecting for low-N tolerance. Ninety extra-early inbreds were evaluated for 2 yr at three locations in Nigeria under low N and drought to confirm reliability of stay green characteristic for selecting for drought tolerance and of ears per plant and anthesis–silking interval for low N. Plant aspect and plant and ear heights were identified as the most reliable traits for simultaneous selection for yield under low N and drought in the extra-early inbreds. Stay green characteristic was unreliable for selecting drought tolerant genotypes while ears per plant and anthesis–silking interval were not among the reliable traits for selecting low-N tolerant genotypes. Ear height, plant and ear aspects, and stay green characteristic were identified by both path–coefficient and genotype main effect plus genotype × environment interaction (GGE) biplot analyses as reliable for selecting for low N and ear aspect, plant height, and anthesis–silking interval for drought tolerance.

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Abbreviations: GEI, genotype × environment interaction; GGE, genotype main effect plus genotype × environment interaction; GT, genotype × trait; PC, principal component; WAP, weeks after planting; WCA, West and Central Africa.

Maize is the most important cereal crop after rice (*Oryza sativa* L.) in West and Central Africa (WCA). *Striga hermonthica* (Del.) Benth, drought, and low-N stresses constitute the most important biotic and abiotic factors limiting its production. Therefore the development and use of maize germplasm with tolerance to multiple stresses are crucial for an increase in maize productivity. In maize, when drought occurs before and during flowering, a delay between pollen shedding and silk emergence is observed (Hall et al., 1982; Bolaños and Edmeades, 1996). Also, induced drought stress environments produced significantly lower grain yield, fewer ears per plant, and lower grain moisture percentage than the nonstressed site (Hall et al., 1982; Bolaños and Edmeades, 1996; DuPlessis and Dijhhuis, 1967; Chapman and Edmeades, 1999; Edmeades et al., 2000; Badu-Apraku et al., 2004b, 2005). In a study of the effect of drought screening methodology on genetic variances in Pool 16 Drought Tolerant Population, only grain moisture at harvest, ear height, and days to anthesis and silking had positive additive genetic variances but with lower narrow-sense heritability (Badu-Apraku et al., 2004a). However, there is limited information on the correlation between grain

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yield and other traits of extra-early maize under drought stress. This is mainly because the Maize Improvement Program of the International Institute of Tropical Agriculture (IITA) had until recently emphasized on the drought escape mechanism, which occurs when the plant completes critical physiological processes before drought sets in. This is quite desirable in varieties to be released to farmers in the areas of WCA where terminal drought is most prevalent. Since 2007, however, emphasis has shifted from the escape mechanism to drought tolerance at the flowering and grain-filling period, which is under genetic control and indicates the_presence of physiological mechanisms to minimize or withstand the adverse effects of drought if and when it occurs. Drought tolerant varieties are useful in the environments where drought occurs randomly and at any growth stage of the maize crop. This is quite relevant in WCA where drought occurrence is erratic with varying intensity and timing.

Bänziger et al. (1999) showed that improvement for drought tolerance also resulted in specific adaptation and improved performance under low-N conditions, suggesting that tolerance to either stress involves a common adaptive mechanism. Due to the low heritability of yield under stress conditions, secondary traits such as ears per plant, stay green characteristic, and anthesis–silking interval have strong associations with yield under low-N and drought conditions and have been used to select for higher levels of tolerance to the two stresses in maize (Lafitte and Edmeades, 1994; Bänziger and Lafitte, 1997a). At IITA, a base index that integrates increased grain yield under drought stress and well-watered environments with a short anthesis–silking interval, increased ears per plant, good stay green characteristic, and good scores for plant aspect and ear aspect under drought stress has been used since 2001 in selecting for drought tolerant early, intermediate, and late maturing maize genotypes (Menkir and Akintunde, 2001; Badu-Apraku et al., 2004a). Furthermore, the base index has since 2003 been used to characterize intermediate and/or late maturing maize (Menkir et al., 2003; Meseka et al., 2006) and early and extra-early maturing maize germplasm (Badu-Apraku, 2010) for tolerance to low N in WCA. Badu-Apraku et al. (2011a) reported that the most reliable traits for selection for improved grain yield under drought stress in the early maturing germplasm were ear aspect, ears per plant, anthesis–silking interval, and plant aspect. On the other hand, the best traits identified for selecting for improved yield under low N were plant height, days to silking, days to anthesis, ears per plant, anthesis–silking interval, stay green characteristic, ear aspect, and plant aspect. The authors concluded that the traits, anthesis–silking interval, ears per plant, ear aspect, and plant aspect, were the most reliable for the simultaneous selection for drought and low-N tolerant early maturing genotypes. Furthermore, stay green characteristic, earlier used in the base index for selecting for improved grain yield under drought and low-N stresses, was not identified as one of the reliable traits under drought conditions. Similarly, in another study by Badu-Apraku et al. (2011b) involving extra-early inbreds, a low correlation was obtained between grain yield and the stay green characteristic under drought stress and in low-N environments. The secondary traits that have been used to compute the base index for selecting for tolerance to the two abiotic stresses in extra-early genotypes were based on the results of the evaluation of early, intermediate, and late maturing germplasm (Bänziger et al., 1999; Menkir and Akintunde, 2001; Badu-Apraku et al., 2004b, 2011a). This is because there is limited information to ascertain drought adaptive traits of the extra-early germplasm. Similarly, there is limited information on the traits suitable for selection for tolerance to low N in the extra-early germplasm. During the last decade, extra-early inbreds and productive hybrids with tolerance to drought at the flowering and grain-filling periods and low N have been identified and are being vigorously promoted for adoption by farmers of WCA (Badu-Apraku et al., 2011b; Badu-Apraku and Oyekunle, 2012). Based on our experience, the efficiency of the base index for selecting drought and low-N tolerant genotypes could be greatly improved. A thorough assessment of the traits in the index with a view of identifying the most reliable for indirect selection for grain yields of extra-early maize germplasm under the two abiotic stresses is desirable. There is, therefore, a need to confirm the influence of drought stress and low-N effects on the effectiveness of the base index to select low-N and drought tolerant extra-early maize genotypes in WCA. The objectives of the present study were to (i) confirm whether the secondary traits, ears per plant, ear and plant aspects, and anthesis–silking interval identified by Badu-Apraku et al. (2011a) as the most reliable for simultaneous selection for improved grain yield under both drought stress and low-N conditions in early maize are also the most reliable for selecting drought and low-N tolerant extra-early maize, (ii) decompose the total correlation coefficients into the direct and indirect components using the sequential path coefficient model analysis to determine whether the inclusion of stay green characteristic in the selection indices for selection for improved grain yield under drought stress and low N is justified, (iii) to determine whether plant height and days to silking and anthesis, identified as reliable traits for inclusion in the base index for selecting low-N tolerant early genotypes, are appropriate, and (iv) compare the results of the sequential path analysis with those of the genotype main effect plus genotype × environment interaction (GGE) biplot. The results of this study should confirm the most reliable traits for computing the base indices for the selection for improved grain yield under drought stress and low N.

MATERIALS AND METHODS

Germplasm

Ninety extra-early inbred lines developed from four broad-based *S. hermonthica* and maize streak virus resistant populations were used in the two studies reported in this paper (Table 1). The inbred lines were derived from the two populations, TZEE-W Pop STR C_0 and TZEE-Y Pop STR C_0, and the crosses, TZEE-W SR BC_5 × 1368 STR, TZEE-W Pop STR × LD, and TZEF-Y SR BC_1 × 9450 STR. The method adopted for the development of the inbred lines has been described in detail by Badu-Apraku and Menkir (2006). The lines were developed by the pedigree breeding method with evaluation of topcross performance at the S_3 stage under *S. hermonthica* infestation at Ferkessedougou (9°3′ N, 5°10′ W, and mean annual rainfall of 1400 mm) and *S. hermonthica*-free conditions at Sinematialli (9°37′ N, 3°4′ W, and mean annual rainfall of 1200 mm), both in Côte d'Ivoire, during the rainy season of 1997. At the S_4 stage, 250 to 300 lines derived from each population were crossed to the corresponding base population as the tester. There was no conscious selection for drought tolerance. The yield performance of the lines per se, their combining abilities for grain yield, *S. hermonthica* damage rating, *S. hermonthica* emergence count, ears per plant, and other desirable agronomic characters across the two locations were used as criteria for selecting 90 to 100 S_4 lines, which were advanced to S_8.

Field Evaluations

Ninety extra-early maturing maize inbred lines developed by IITA were evaluated in Nigeria under managed drought stress during the 2007/2008 and 2008/2009 dry seasons in well-watered environments at Ikenne (6°53′ N, 3°7′ E, 60 m altitude, and 1500 mm annual rainfall) and low N (30 kg ha^{-1}) and high N (90 kg ha^{-1}) at Mokwa (9°18′ N, 5°4′ E, 457 m altitude, and 1100 mm annual rainfall) during the planting seasons of 2008 and 2009. A randomized incomplete block design (10 × 9 α lattice) with two replications was used for the drought stress and well-watered experiments as well as the N-response trials. Each experimental unit was a one-row plot with a row spacing of 0.75 m and length of 5 m. Distance between two adjacent plants within the row was 0.40 m in all trials. Three seeds were planted per hill. The maize plants were thinned to two per hill about 2 wk after emergence to give a final plant population density of 66,000 plants ha^{-1}.

In the first study conducted at Ikenne, the lines were evaluated under induced drought stress, which was achieved with a sprinkler irrigation system that supplied adequate water from planting through 21 d after planting. Thereafter, irrigation water was withdrawn (24 to 26 d before 50% anthesis) until maturity so that the maize plants relied on stored soil water for growth and development. During the first 3 wk, the plants were provided 12 mm of water per week by the sprinkler irrigation system (Menkir and Akintunde, 2001; Meseka et al., 2006; Badu-Apraku and Akinwale, 2011; Badu-Apraku et al., 2011b). The soil in the station at Ikenne is alfisol (U.S. soil taxonomy) and the experimental fields are flat and fairly uniform, with high water-holding capacity. The well-watered (rainfed) experiment at Ikenne was conducted during the growing season. Except for the well-watered treatments, all management practices were the same for both well-watered and drought stress experiments. Fertilizer was applied to

Table 1. Mean squares derived from ANOVA of measured traits[†] of 90 extra-early maize inbreds evaluated under drought stress and low-N environments in Nigeria between 2008 and 2009.

Source	df	YD	DS	DA	ASI	PH	EH	SL	PA	EA	EPP	HC	RL	LS1	LS2
Drought stress															
Environment (E)	3	204,552,812**	5,197**	4,264**	331**	171,596**	60,121**	233**	31**	9.34**	8.4**	4.9**	38.8**	65**	
Replication(E)	4	685,832 NS[‡]	29**	25**	3.6 NS	2,602**	717**	3.96 NS	12**	0.60 NS	0.5 NS	0.1 NS	9.43**	1.9 NS	
Block (E × replication)	64	519,226 NS	15**	9**	2.7 NS	482**	184**	4.99**	4**	0.51**	0.2 NS	0.2 NS	0.85 NS	2.5**	
Entry (G)	89	597,447**	33**	22**	5.7**	975**	329**	4.37**	3 NS	0.37*	1.3**	0.2 NS	1.11 NS	2.2**	
G × E	267	564,472**	15**	9**	3.6**	556**	222**	4.24**	4**	0.27 NS	0.7**	0.2 NS	1.18 NS	1.6**	
Error	292	390,421	7.0	4.0	1.0	198	101	817.0	2.6	0.26	0.3	0.2	1.05	1.0	
Mean ± SE		1,220 ± 312	56 ± 1.36	54 ± 1.04	2.50 ± 0.72	130 ± 7.04	56 ± 5.03	2.0 ± 0.84	3.2 ± 0.81	2.8 ± 0.26	0.8 ± 0.25	1.9 ± 0.2	0.6 ± 0.50	4.2 ± 0.50	
Low N environments															
Environment (E)	1	41,901,080**	1.8 NS	14.0 NS	22.9**	89,102**	55,878**	0.15 NS	1,460**	1,309.22**	14.65**	185**		370**	302**
Replication(E)	2	553,672 NS	4.98 NS	1.5 NS	10.4**	58 NS	4.3 NS	0.25 NS	0.31 NS	0.80 NS	0.82 NS	0.47 NS		0.35 NS	1.10 NS
Block (E × replication)	32	375,259**	13.6**	12.6**	1.1 NS	441**	188**	1.06 NS	1.11 NS	0.50 NS	0.31 NS	1.16 NS		0.94**	1.62**
Entry (G)	89	634,266**	17.1**	17.2**	1.0 NS	538**	196**	1.19 NS	1.96**	1.17*	0.39 NS	1.49**		0.94**	1.53**
G × E	84	293,513*	5.1 NS	5.9 NS	1.2 NS	141 NS	83**	1.26 NS	1.22**	0.82 NS	0.42 NS	1.23**		0.66**	0.94*
Error	141	198,214	4.2	4.7	1.4	131	54	1.15	0.73	0.83	0.36	0.81		0.4	0.67
Mean ± SE		837 ± 223	55 ± 1.03	52 ± 1.09	2 ± 0.59	118 ± 5.73	58 ± 3.69	0.6 ± 0.54	4.3 ± 0.43	4.5 ± 0.46	0.7 ± 0.30	5.0 ± 0.50		3.7 ± 0.32	4.9 ± 0.41

*Significant *F*-test at the 0.05 probability level.

**Significant *F*-test at the 0.01 probability level.

[†]ASI, anthesis–silking interval; DA, days to anthesis; DS, days to silk; EA, ear aspect; EH, ear height; EPP, ears per plant; HC, husk cover; LS1, stay green characteristic 1; LS2, stay green characteristic 2; PA, plant aspect; PH, plant height; RL, percent root lodging; SL, percent stalk lodging; YD, grain yield.

[‡]NS, not significant.

the well-watered and drought stress plots at the rate of 60 kg ha^{-1} each of N, P, and K at planting. An additional 60 kg ha^{-1} N was top-dressed at 2 wk after planting (WAP). The trials were kept weed free with the application of Atrazine and Gramoxone (Syngenta Crop Protection AG) as pre- and post-emergence herbicides at 5 L ha^{-1} each of Primextra (Syngenta Crop Protection PTY Limited) and Paraquat and subsequently, hand weeding.

In the second study conducted at Mokwa, the 90 extra-early maturing maize inbred lines used for the first experiment were evaluated in experimental fields, which were depleted of N by the continuous planting of maize and removal of the biomass after each harvest. Soil samples were taken from a depth of 0 to 15 cm of the top soil before planting. The N content was determined at the IITA soil laboratory at Ibadan, Nigeria. Fertilizers were applied to bring the total available N to 90 kg ha^{-1} for the moderately high-N field and 30 kg ha^{-1} for the low-N field as indicated by soil tests. The N fertilizer was applied at 2 WAP. Also, single superphosphate (P_2O_5) and muriate of potash (K_2O) were applied to both low-N and high-N blocks at the rate of 60 kg ha^{-1}. The evaluations under low and high N were done in adjacent blocks, separated about 10 to 15 m to minimize the flow of N across blocks. Other crop management practices were as described earlier for the first study.

Collection of Agronomic Data

Data were recorded on both drought stressed and well-watered plots in the first study, and low-N and high-N plots in the second study for days to silking, as the number of days from planting to when 50% of the plants had emerged silks, and days to anthesis, when 50% had shed pollen. The anthesis–silking interval was computed as the difference between days to silking and anthesis. Plant height was measured as the distance from the base of the plant to the height of the first tassel branch and ear height as the distance from the base to the node bearing the upper ear. Root lodging (percentage of plants leaning more than 30° from the vertical) and stalk lodging (percentage broken at or below the highest ear node) were also recorded. Number of ears per plant was obtained by dividing the total number of ears per plot by the number of plants harvested. Plant aspect was recorded on a scale of 1 to 5 based on plant type, in which 1 represented excellent and 5 represented poor. Husk cover was rated on a scale of 1 to 5, in which 1 represented husks tightly arranged and extended beyond the ear tip and 5 represented ear tips exposed. Ear aspect was scored on a scale of 1 to 5, in which 1 represented clean, uniform, large, and well-filled ears and 5 represented ears with undesirable features. In addition, stay green characteristic was recorded on a scale of 1 to 10, in which 1 represented 10% dead leaf area, 2 represented 20% dead leaf area, 3 represented 30% dead leaf area, 4 represented 40% dead leaf area, 5 represented 50% dead leaf area, 6 represented 60% dead leaf area, 7 represented 70% dead leaf area, 8 represented 80% dead leaf area, 9 represented 90% dead leaf area, and 10 represented 100% dead leaf area for the drought stressed plots at 70 d after planting and for the low-N plots at 8 and 10 WAP. In the drought stressed and low-N experiments, harvesting was done at physiological maturity (80–85 d after planting). Harvested ears from each plot were shelled to determine the percentage grain moisture. Grain yield was adjusted to 15% moisture and computed from the shelled grain weight. In the well-watered and high-N experiments, harvested ears of each plot were weighed and the grain yield was estimated based on 80% shelling percentage (800 g grain kg^{-1} ear weight) and adjusted to 150 g kg^{-1} moisture content. Even though the extra-early inbreds were evaluated under managed drought stress, well-watered, and low-N and high-N environments, only the results of the evaluations under drought stress and low N have been presented in this study.

Statistical Analysis

Analyses of variance, combined across environments were performed on plot basis for grain yield, days to silking and anthesis, anthesis–silking interval, ears per plant, plant height, percentage stalk lodging, stay green characteristic, ear aspect, plant aspect, and husk cover with PROC GLM in SAS using a RANDOM statement with the TEST option (SAS Institute, 2001). Analysis of variance for the selected traits of the inbreds was conducted separately for data collected from the drought stressed and well-watered and from the low-N and high-N environments. In the combined ANOVA, the location–year combinations, replicates, and blocks of each experiment were considered as random factors and entries were considered as fixed effects. Analysis of variance was also conducted for each environment (location–year combinations) and across all environments for each of the experiments to determine if genotype × environment interaction was significant. GGEbiplot software was used for trait-association and trait-profile analyses (Yan et al., 2000; Yan, 2001; Yan and Rajcan, 2002; Morris et al., 2004; Ober et al., 2005). Since the traits were measured in different units, the mean values for each entry were standardized using standard deviation method (scale = 1) (Yan and Tinker, 2005). The GGEbiplot program is available at www.ggebiplot.com. This is represented in the model equation below:

$$\mathbf{X}_{ij} = (\hat{Y}_{ij} - \mu - \beta_j)/d_j = \lambda_1 g_{i1} e_{1j} + \lambda_2 g_{i2} e_{2j} + \varepsilon_{ij}$$

in which Y_{ij} is the average genetic value for inbred i on trait j, μ is the grand mean, β_j is the mean of trait j across all inbreds, λ_1 and λ_2 are the first two singular values from the singular value decomposition of the corrected matrix $\mathbf{X}$, g_{i1} and g_{i2} are the associated eigenvectors for inbred (row) i, e_{1j} and e_{2j} are the associated eigenvectors for trait (column) j, d_j is the standardization value (standard deviation for trait j), and ε_{ij} is the residual or nonexplained part of the model.

Pearson coefficients of correlation were calculated using the inbreds means for all traits and the ordinal scaled traits, stalk lodging, plant and ear aspects, root lodging, stay green characteristic 1, and stay green characteristic 2, were transformed by natural logarithm function; Table 2 shows the coefficients and their significance. The PROC CORR procedure of SAS (SAS Institute, 2001) was also used to compute the correlation coefficients and the PROC REG for regression analysis. Sequential stepwise multiple regressions, a methodology proposed by Mohammadi et al. (2003), was used to organize the predictor variables into first, second, and third order paths on the basis of their respective contributions to the total variation in grain yield with minimal multicolinearity.

RESULTS

Analysis of Variance

Results of the ANOVA combined across years and locations under drought stress showed significant genotypic and genotype × environment interaction (GEI) mean squares ($p <$

Table 2. Pearson coefficients of correlation between pair of traits† across 90 extra-early maize inbreds evaluated under drought stress (lower diagonal) and low-N (upper diagonal) conditions in Nigeria between 2008 and 2009.

	YD	DA	DS	PH	EH	EPP	RL	SL	HC	PA	EA	ASI	LS1	LS2
YD		−0.20 NS‡	−0.23*	0.44**	0.44**	0.21 NS	–	−0.03 NS	−0.41**	−0.70**	−0.68**	−0.06 NS	−0.60**	−0.65**
DA	−0.23*		0.97**	0.14 NS	0.16 NS	−0.04 NS	–	−0.18 NS	0.09 NS	0.07 NS	0.14 NS	−0.14 NS	−0.03 NS	−0.08 NS
DS	−0.35**	0.91**		0.15 NS	0.18 NS	−0.05 NS	–	−0.15 NS	0.11 NS	0.09 NS	0.11 NS	0.09 NS	−0.03 NS	−0.08 NS
PH	0.47**	−0.23*	−0.19 NS		0.87**	0.08 NS	–	0.12 NS	−0.32**	−0.59**	−0.38**	0.07 NS	−0.43**	−0.50**
EH	0.44**	−0.08 NS	−0.08 NS	0.76**		0.17 NS	–	0.11 NS	−0.36**	−0.54**	−0.40**	0.12 NS	−0.41**	−0.48**
EPP	0.02 NS	0.23*	0.10 NS	−0.16 NS	−0.26*			−0.01 NS	−0.17 NS	−0.18 NS	−0.41**	−0.05 NS	−0.15 NS	−0.27*
RL	0.08 NS	−0.21*	−0.22*	0.20 NS	0.19 NS	−0.09 NS								
SL	0.16 NS	−0.19 NS	−0.17 NS	0.02 NS	0.13 NS	−0.21*	0.18 NS		0.21 NS	0.05 NS	0.07 NS	0.18 NS	0.09 NS	0.16 NS
HC	−0.06 NS	−0.01 NS	0.01 NS	−0.14 NS	−0.11 NS	0.17 NS	0.21*	−0.05 NS		0.60**	0.47**	0.08 NS	0.46**	0.43**
PA	−0.46**	0.25*	0.30**	−0.51**	−0.43**	0.01 NS	0.03 NS	−0.07 NS	0.20 NS		0.60**	0.08 NS	0.78**	0.80**
EA	−0.54**	0.27*	0.25*	−0.28**	−0.28**	−0.02 NS	−0.01 NS	−0.04 NS	0.18 NS	0.50**		−0.08 NS	0.56**	0.67**
ASI	−0.39**	0.29**	0.65**	−0.05 NS	−0.08 NS	−0.15 NS	−0.12 NS	−0.05 NS	0.05 NS	0.25*	0.12 NS		0.01 NS	0.02 NS
LS1	−0.06 NS	−0.04 NS	0.03 NS	−0.12 NS	0.01 NS	−0.05 NS	0.01 NS	0.22*	0.07 NS	0.25*	0.04 NS	0.16 NS		0.88**

*Significant at the 0.05 probability level in the test of hypothesis Ho: $\rho = 0$.

**Significant at the 0.01 probability level in the test of hypothesis Ho: $\rho = 0$.

†ASI, anthesis–silking interval; DA, days to anthesis; DS, days to silk; EA, ear aspect; EH, ear height; EPP, ears per plant; HC, husk cover; LS1, stay green characteristic 1; LS2, stay green characteristic 2; PA, plant aspect; PH, plant height; RL, percent root lodging; SL, percent stalk lodging; YD, grain yield.

‡NS, not significant.

0.01) for all measured traits except plant aspect, husk cover, and root lodging for the genotypes and ear aspect, husk cover, and root lodging for GEI (Table 1). Genotypic mean squares were significant ($p < 0.01$) for all traits under low-N conditions except anthesis–silking interval, percentage stalk lodging, and ears per plant under low N and mean squares for GEI were significant for grain yield, ear height, plant aspect, husk cover, stay green characteristic 1 (8 WAP), and stay green characteristic 2 (10 WAP) under low-N conditions.

Sequential Path Analysis of Relationships Among Grain Yield and Related Traits Under Drought Stress Environments

Path coefficient analyses were performed in accordance with the causal relationships among traits under each research condition as shown in path diagrams depicted in Fig. 1 and 2. Under drought stress, the stepwise regression analyses identified husk cover, ear aspect, plant height, stalk lodging, and anthesis–silking interval as traits with high direct effects on grain yield. The five traits accounted for 52% of the total variation in grain yield. Among the five traits, ear aspect had the highest total effect (0.42) on yield followed by plant height (0.34), anthesis–silking interval (0.32) and percentage stalk lodging (0.13) and the least was husk cover (0.09) (Fig. 1). Plant aspect contributed to yield indirectly through plant height, ear aspect, and husk cover. Ear height had an indirect contribution to yield through stalk lodging and plant height. Ear aspect had the largest direct effect on yield followed by plant height, anthesis–silking interval, and percentage stalk lodging while husk cover had the least direct effect. Plant aspect had the highest indirect effect on yield through plant height (0.51) followed by ear aspect (0.49) and then husk cover (0.20). Ear height contributed to yield through plant height (0.76) and percentage stalk lodging (0.21); ears per plant contributed to yield indirectly through percentage stalk lodging. Days to silking contributed to yield through anthesis–silking interval. With the third order traits, stay green characteristic 1 contributed to yield through plant aspect (0.25) while days to anthesis contributed indirectly to yield through days to silking.

Sequential Path Analyses of Relationships Among Grain Yield and Related Traits Under Low-N Environments

In low-N environments, ear height, ear aspect, plant aspect, stay green characteristic 1, and days to silking had significant direct effects on yield, contributing 58% of the total variation in grain yield. Days to silking (–0.48) and ear aspect (–0.47) had the highest direct effects; stay green characteristic1 had the least direct effect (–0.15). Only ear height had a significant positive direct effect (0.17) on yield. Husk cover contributed to grain yield through plant aspect. Ear aspect and ear height had their highest indirect effects through plant aspect (0.46) (Fig. 2). Plant height had a significant indirect effect on yield through days to silking, plant aspect, ear aspect, and ear height with the highest effect through ear height (0.83). Stay green characteristic 1 had a significant effect on yield through all the five first-order traits; the highest contribution was through stay green characteristic 1 (0.47). Days to anthesis and anthesis–silking interval contributed to yield through days to silking while ears per plant had an indirect contribution to grain yield through ear aspect (–0.22).

Biplot Analyses of Trait Relationships in Drought Environments

Presented in Fig. 3 is the vector view of the genotype × trait (GT) biplot showing the interrelationship among traits measured under drought stress. In the biplot display, the rays

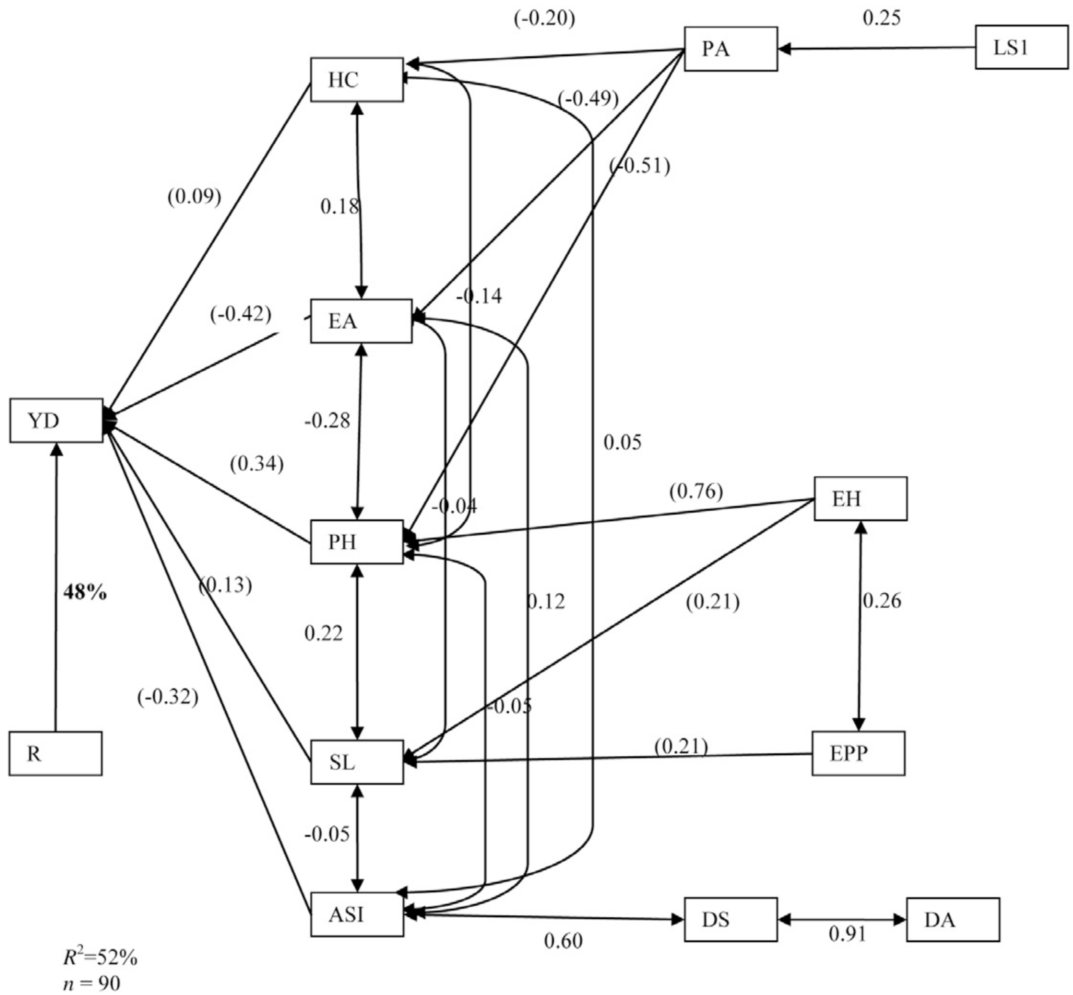

Figure 1. Sequential path analysis model diagram showing causal relationships of measured traits of extra-early maturing maize inbred lines evaluated under drought stress. Bold value is residual effect; values in parenthesis are direct path coefficients and other values are correlation. ASI, anthesis–silking interval; DA, days to 50% anthesis; DS, days to 50% silking; EA, ear aspect; EH, ear height; EPP, ears per plant; HC, husk cover; LS1, stay green characteristic 1; PA, plant aspect; PH, plant height; R, residual effect; SL, stalk lodging; YD, grain yield.

connecting the traits to the biplot origin are described as trait vectors. The cosine of the angle between vectors of any two traits measures the similarity or correlation between them relative to their effects on yield. Number of ears per plant, plant height, and ear height had angles less than 90° with yield and were therefore positively correlated with it; plant aspect and ear aspect had angles close to 180° with yield, indicating they were negatively correlated with yield, and days to anthesis and silking and anthesis–silking interval had very small acute angles among them, indicating very strong positive correlations with grain yield. Similarly, plant and ear aspects on the one hand and plant and ear heights on the other had positive correlations between them. Traits with short vectors such as stay green characteristic, percentage stalk lodging, and root lodging had weak and nonsignificant correlations with one another and with traits having long vectors. The biplot view in Fig. 4 was generated using the Auto Find QTL function of the GGE biplot (Yan, 2001) and it provides information on the reliability of the traits for indirect selection for improved grain yield under drought stress at $p < 0.01$ and R^2 value of ≥14.22%. The primary (principal component [PC] 1) and secondary (PC2) principal axes of the biplot accounted for about 67% of the total variation in grain yield. Based on this biplot, plant and ear aspects, days to silking, anthesis–silking interval, ears per plant, and plant and ear heights were identified as the most reliable traits for the indirect selection of grain yield under drought stress at $p < 0.01$ and R^2 value of 14.22%.

Biplot Analyses of Trait Relationships in Low-Nitrogen Environments

In low-N environments, the biplot display in Fig. 5 revealed a strong positive correlation among stay green characteristic 1, stay green characteristic 2, plant and ear aspects, and husk cover, between plant and ear heights, and between days to anthesis and silking. Yield had a positive correlation with plant and ear heights but a strong negative correlation with stay green characteristic 1 and

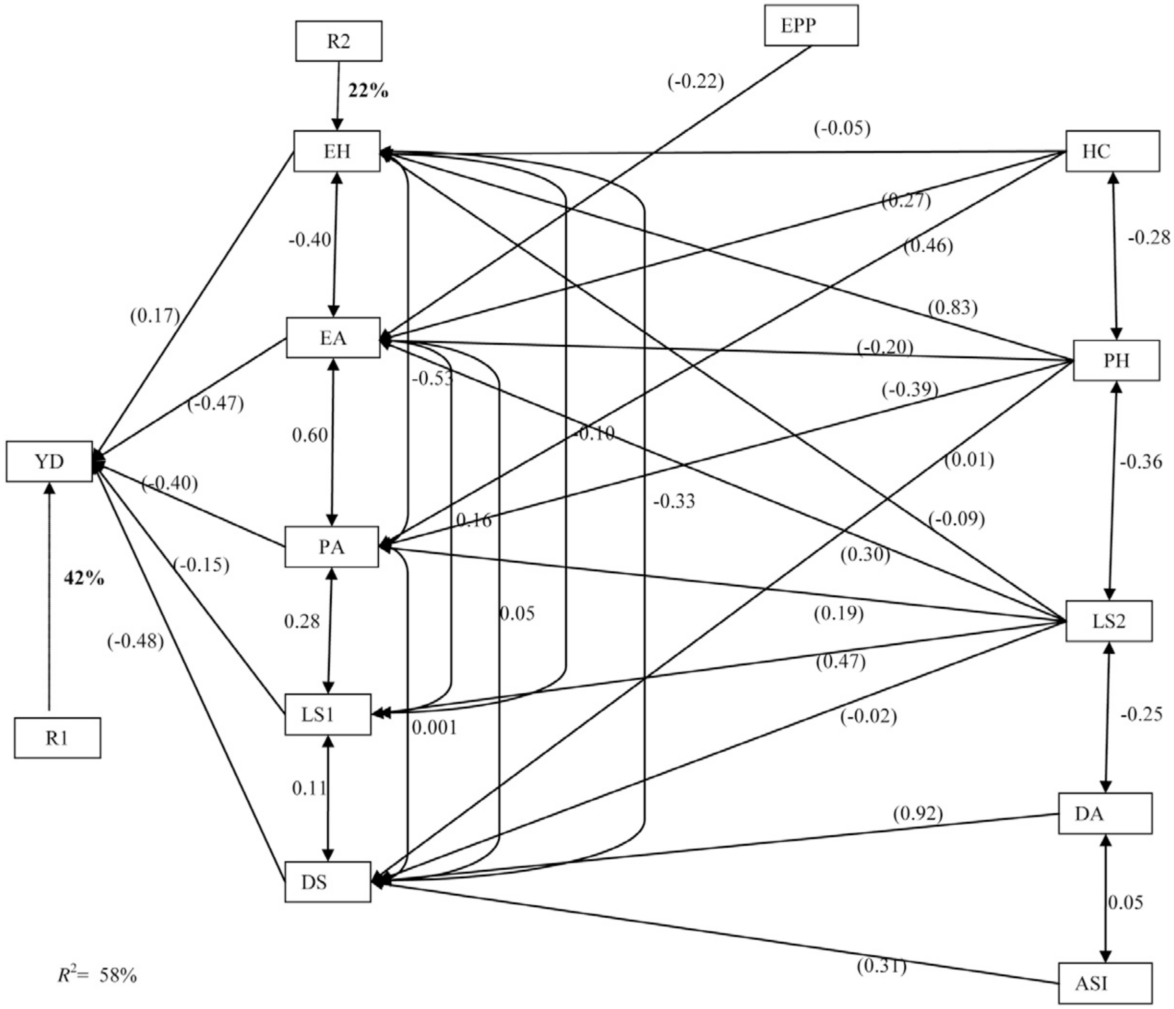

Figure 2. Sequential path analysis model diagram showing causal relationships of measured traits of extra-early maturing maize inbred lines evaluated under low-N conditions. Bold values are residual effects; values in parenthesis are direct path coefficient and other values are correlation coefficients. ASI, anthesis–silking interval; DA, days to 50% anthesis; DS, days to 50% silking; EA, ear aspect; EH, ear height; EPP, ears per plant; HC, husk cover; LS1, stay green characteristic 1; LS2, stay green characteristic 2; PA, plant aspect; PH, plant height; R1, residual effect 1; R2, residual effect 2; YD, grain yield.

2, plant and ear aspects, and husk cover. Ears per plant, anthesis–silking interval, and stalk lodging had short vectors, indicating that they were not strongly correlated with one another or with long vector traits. The first two principal components of the biplot in Fig. 6 accounted for about 81% of the total variation in yield. From the biplot display, stay green characteristics 1 and 2, plant and ear aspects, husk cover, and plant and ear heights were identified as the most reliable traits for yield improvement in low-N environments at $p < 0.01$ and R^2 value ≥21.48%.

DISCUSSION

The presence of genetic variability is of the utmost importance for progress from selection for improved grain yield under drought stress and low N. The observed significant genotypic mean squares for all measured traits except plant aspect, husk cover, and percentage root lodging indicate that good progress can be made in selecting for improved grain yield under the two stress environments. Furthermore, the significant means squares detected for GEI for most measured traits suggests that the extra-early inbreds should be tested in contrasting environments in multilocational trials to identify the most stable drought and/or low-N tolerant genotypes for hybrid development.

Correlation between genotypic and phenotypic values of cultivars evaluated under stress environments is often reduced due to significant GEI (Comstock and Moll, 1963). The lack of significant mean squares for GEI observed for ears per plant, anthesis–silking interval, days to anthesis and silking, ear aspect, plant height, percentage stalk lodging, percentage root lodging, and stay green characteristic under low N indicated that most of the traits used in the base index to select for tolerance to low N were stable and not affected by GEI. Hence the phenotypic and genotypic correlations between these traits and grain yield are not expected to be reduced under low-N stress. These results are in agreement with the findings of Badu-Apraku et al. (2011a). In contrast, the significant means squares detected for GEI for all

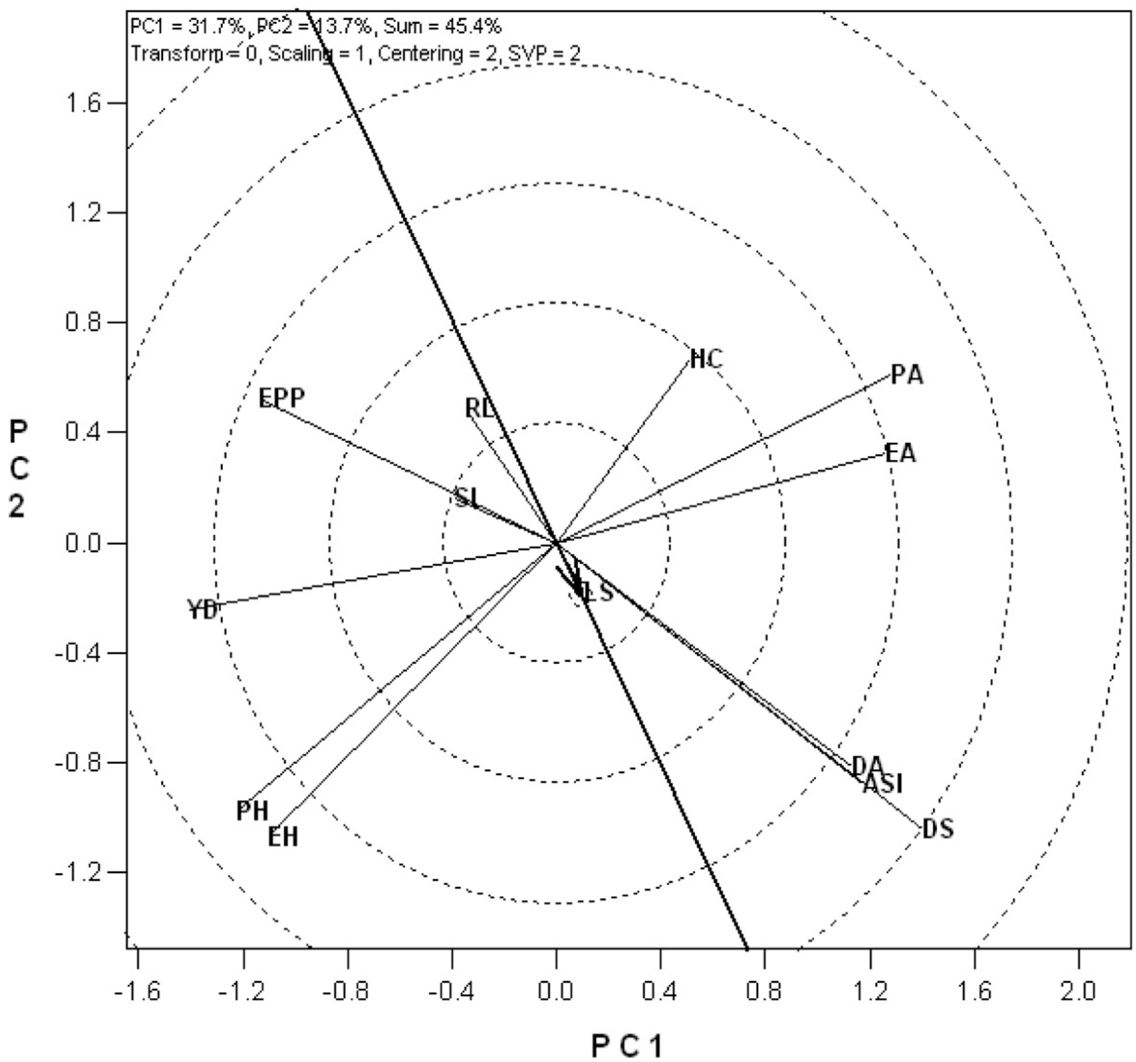

Figure 3. A vector view of genotype × trait biplot showing interrelationships among traits of 90 extra-early maturing maize inbreds evaluated under drought stress at Ikenne and Bagauda in 2007. The data were not transformed (Transform = 0), standardized (Scale = 1), and were environment centered (Centering = 2). The biplot was based on genotype-focused singular value partitioning (SVP = 2) and is therefore appropriate for visualizing the relationships among traits. Principal component (PC) 1 and PC 2 for model 2 explained 65.2% of the variation among traits. ASI, anthesis–silking interval; DA, days to 50% anthesis; DS, days to 50% silking; EA, ear aspect; EH, ear height; EPP, ears per plant; HC, husk cover; LS, leaf senescence; PH, plant height; RL, root lodging; SL, stalk lodging; PA, plant aspect; YD, grain yield.

traits except ear aspect, husk cover, and percentage root lodging suggested that the traits used in the base index to select for tolerance to drought stress were affected by GEI and therefore, the phenotypic and genotypic correlations between these traits and grain yield are expected to be reduced under drought stress. Therefore, the secondary traits, such as anthesis–silking interval, ears per plant, and ear aspect measured in this study are expected to improve the precision with which drought tolerant genotypes are identified, compared with measuring only grain yield under drought stress. Similar results were reported by Badu-Apraku et al. (2011a) for early maturing cultivars evaluated in similar research environments.

An important objective of the present study was to confirm the appropriateness of the traits in the base index for selecting extra-early genotypes for drought tolerance (Menkir and Akintunde, 2001; Badu-Apraku et al., 2004b, 2011a). The results of the GT biplot analysis revealed that stay green characteristic, percentage stalk lodging, and percentage root lodging had relatively short trait vectors, suggesting that they may be less important in evaluating extra-early genotypes for drought tolerance. Based on the genetic correlation with yield, ears per plant, plant and ear aspects, days to silking, anthesis–silking interval, and plant and ear heights were identified as the most reliable traits for indirect selection for improved grain yield under drought stress. In a similar study involving early maturing cultivars, Badu-Apraku et al. (2011a) identified number of ears per plant, anthesis–silking interval, and ear and plant aspects as the most reliable traits for selection for drought tolerant genotypes. The results of the present study suggest that days to silking and plant and ear heights are additional drought adaptive traits that should be

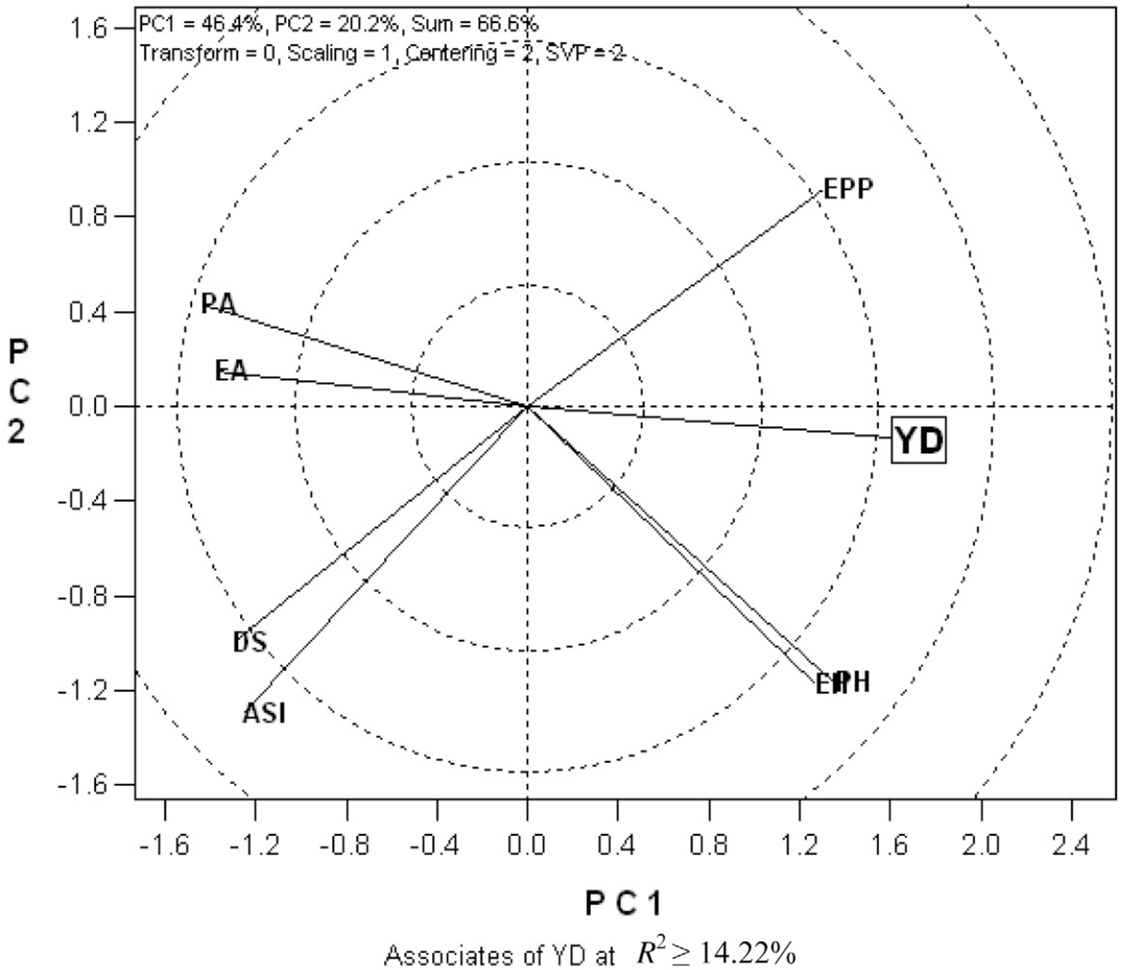

Figure 4. A vector view of the genotype × trait biplot displaying most reliable traits for indirect selection for yield (inside box) under drought stress at $p < 0.01$ and R^2 value of ≥14.22%. The data were not transformed (Transform = 0), standardized (Scale = 1), and were trait centered (Centering = 2). The biplot was based on genotype-focused singular value partitioning (SVP = 2) and is therefore appropriate for visualizing the relationships among traits. Principal component (PC) 1 and PC 2 for model 2 explained 66.6% of the variation among traits. ASI, anthesis–silking interval; DS, days to 50% silking; EA, ear aspect; EH, ear height; PA, plant aspect; PH, plant height; YD, grain yield.

considered for inclusion in the base index for characterizing extra-early germplasm for drought tolerance. This also suggests that the traits for selecting for drought tolerance in the extra-early germplasm could be different from those used for selecting drought tolerant early, intermediate, and late maturing maize germplasm. A plausible explanation for the differences in the traits identified for selecting for drought tolerance in the different maturity groups could be the differences in the mechanism of tolerance to drought stress. Most probably, the drought adaptive traits responsible for the drought tolerance in the extra-early germplasm used in the present study are different from those of the other three maturity groups. The finding that the stay green characteristic was not a reliable trait for selecting drought tolerant extra-early genotypes under drought stress is consistent with the results of Badu-Apraku et al. (2011b). Under low N, the pattern of the interrelationship among traits of the extra-early germplasm was different from that under drought stress (Fig. 4 and 6). Stay green characteristic, plant and ear aspects, husk cover, and plant and ear heights were identified as the most reliable traits for selecting for improved yield in low-N environments (Fig. 6). A strong positive correlation existed among the traits stay green characteristic, plant and ear aspects, and husk cover, indicating that measuring just one of these traits will suffice without sacrificing important information on the genotypes. In addition, ears per plant, percentage stalk lodging, and anthesis–silking interval were associated with short trait vectors, indicating that they were less important in evaluating extra-early genotypes for low-N tolerance. Therefore, these traits were not important under low N unlike the situation under drought stress whereas ears per plant and anthesis–silking interval were very important traits for selecting drought tolerant early genotypes. These results are contrary to the findings of Badu-Apraku et al. (2011a). In low-N environments, path analysis identified ear height, ear and plant aspects, stay green characteristic, and days to silking as traits with significant direct contributions to grain yield whereas the GT biplot identified stay green characteristic, plant and ear aspects, husk cover, and plant and ear heights as reliable traits for indirect selection for

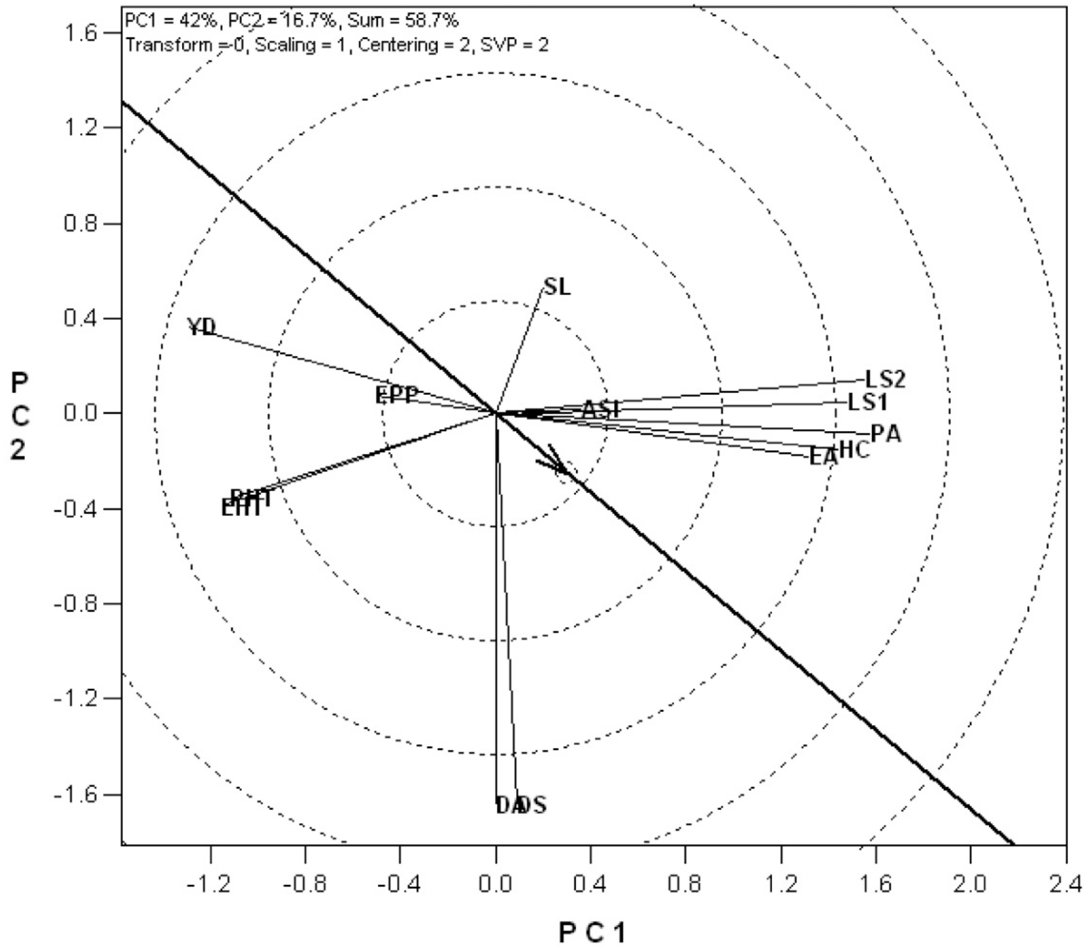

Figure 5. A vector view of genotype × trait biplot showing interrelationships among traits of 90 extra-early maturing maize inbreds evaluated under low N at Mokwa, Nigeria, in 2008 and 2009. The data were not transformed (Transform = 0), standardized (Scale = 1), and were trait centered (Centering = 2). The biplot was based on genotype-focused singular value partitioning (SVP = 2) and is therefore appropriate for visualizing the relationships among traits. Principal component (PC) 1 and PC 2 for model 2 explained 58.7% of the variation among traits. ASI, anthesis–silking interval; DA, days to 50% anthesis; DS, days to 50% silking; EA, ear aspect; EH, ear height; EPP, ears per plant; HC, husk cover; LS1, leaf senescence at 8 wk after planting (WAP); LS2, leaf senescence at 10 WAP; PA, plant aspect; PH, plant height; RL, root lodging; SL, stalk lodging; YD, grain yield.

grain yield. Ear height, plant and ear aspects, and stay green characteristic 1 were identified by both methods as reliable traits for selecting for low-N tolerant genotypes. Due to the high correlations between plant and ear heights on the one hand and stay green characteristic 1 and 2, plant and ear aspects, and husk cover on the other, the path analysis identified (as reliable traits) only ear height in the first trait pair and stay green characteristic 1 and plant and ear aspects in the second trait group.

In the present study, stay green characteristic, plant and ear aspects, husk cover, and plant and ear heights were identified as the most reliable traits in selecting for improved yield in low-N environments; number of ears per plant, plant and ear aspects, days to silking, anthesis–silking interval, and plant and ear heights were the most reliable in selecting for drought tolerant genotypes. Therefore, plant and ear aspects and plant and ear heights were identified as the most reliable traits for the simultaneous selection in the extra-early inbreds for improved yield under low-N and drought stress environments. These results are contrary to those of Badu-Apraku et al. (2011a) who reported that anthesis–silking interval, ears per plant, and ear and plant aspects were the most reliable for the simultaneous selection for drought and low-N tolerant early maturing genotypes. As indicated earlier, the differences in the results of the two studies could be due to the fact that the extra-early germplasm from which the extra-early inbreds were derived is different from those of the three other maturity groups and therefore different drought adaptive traits were present in the extra-early germplasm. It is striking that anthesis–silking interval and ears per plant, which have been used in the base index for selecting low-N tolerant early genotypes (Lafitte and Edmeades, 1994; Meseka et al., 2006; Badu-Apraku et al., 2011a), were not among the traits identified as reliable but the stay green characteristic used in the base index for selecting drought tolerant genotypes

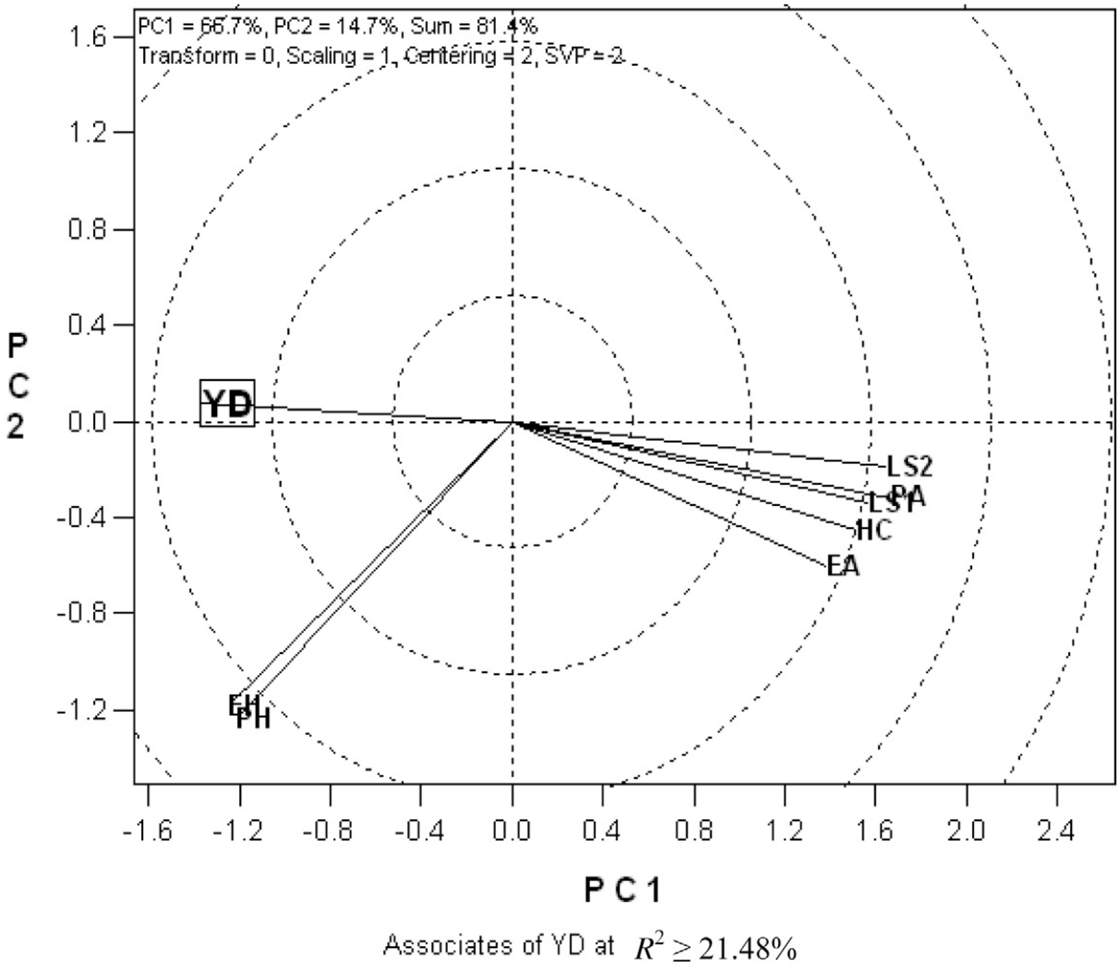

Figure 6. A vector view of the genotype × trait biplot displaying most reliable traits for indirect selection for yield (inside box) under low N at $p < 0.01$ and R^2 value of ≥21.48%. The data were not transformed (Transform = 0), standardized (Scale = 1), and were trait centered (Centering = 2). The biplot was based on genotype-focused singular value partitioning (SVP = 2) and is therefore appropriate for visualizing the relationships among traits. Principal component (PC) 1 and PC 2 for model 2 explained 81.4% of the variation among traits. EA, ear aspect; EH, ear height; EPP, ears per plant; HC, husk cover; LS1, leaf senescence at 8 wk after planting (WAP); LS2, leaf senescence at 10 WAP; PA, plant aspect; PH, plant height; YD, grain yield.

(Badu-Apraku et al., 2011a) had a significant direct effect on yield only in low-N environments. The results of the ANOVA showed that the extra-early genotypic mean squares were not significantly different for anthesis–silking interval and ears per plant, implying that these traits would not be useful in discriminating among the genotypes under low N. They were also among the three traits in the GT biplot with short trait vectors (Fig. 5), confirming their low discriminating abilities. Days to silking had a significant direct effect on yield under low N but was not identified as a reliable trait by the GT biplot due to its very low correlation with yield (Fig. 5) even though it had a long trait vector.

Another important objective of the present study was to gain an insight into the interrelationship among the traits used in the base index for selection for improved grain yield under both drought stress and low N. The results of the path analyses showed that the secondary traits with significant direct effects on grain yield under drought stress were husk cover, ear aspect, plant height, stalk lodging, and anthesis–silking interval; under low N, the most reliable traits were ear height, ear and plant aspects, stay green characteristic 1, and days to silking. Therefore, contrary to the results of the GT biplot, the path analyses identified only ear aspect as the trait common to the two stresses that could be used for the simultaneous selection for drought tolerance and low N.

Comparison of the results of the GGE biplot and path analyses revealed that both methods identified ear aspect, plant height, and anthesis–silking interval as important traits directly contributing to yield under drought stress. Several earlier studies had identified ear aspect and anthesis–silking interval as strong predictor traits for yield improvement under drought stress due to their strong genetic correlations with yield under stress conditions (Bänziger and Lafitte, 1997a, 1997b; Bolaños et al., 1993; Bolaños and Edmeades, 1996; Edmeades et al., 1997; Badu-Apraku et al., 2004a, 2004b, 2011a). The identification of plant and ear heights among the reliable traits for selecting drought tolerant genotypes indicated that they are important traits for selection for drought tolerance. On the other hand, the path analysis included percentage stalk lodging and husk cover among traits with significant direct effects on yield whereas the GT biplot did not. In contrast, ears per plant, which was among the reliable traits identified by the GT biplot for selection for improved yield under drought stress, was not among the traits with a high direct contribution to yield identified by the path analysis. Earlier studies by Bänziger and Lafitte (1997a, 1997b), Edmeades et al. (1997), and Badu-Apraku et al. (2004a, 2011a) reported that ears per plant is an important secondary trait for selecting for improved grain yield under drought stress. Failure of the path analysis to identify ears per plant as directly contributing to yield under drought stress could be due to the high correlation with percentage stalk lodging. This is explained by the fact that the angle between the vectors of number of ears per plant and percentage stalk lodging in the GT biplot was close to zero. It is evident from the results of the present study that path analysis showed higher sensitivity to multicolinearity and spurious correlations than the biplot analysis because the biplot displays the relationship among traits graphically, based on their correlations. If any two traits show high correlations, path analysis considers one of them as directly contributing to the target trait while the second trait contributes indirectly to the target trait through the first trait (Wright, 1921; Li, 1975). Therefore, the correlations among traits with significant direct contributions to target traits are relatively low. Based on this information, the path analysis demonstrated that ears per plant is contributing to yield through percentage stalk lodging. Similarly, ear height was considered to have contributed indirectly to yield through plant height and percentage stalk lodging. The results of the two statistical methods are not exactly the same because they identified reliable traits for selection based on different statistics. Path analysis uses partial regression coefficients while GT biplot uses genetic correlation among traits and the discriminating ability of the traits. In addition, while path analysis recognizes multicolinearity among traits, the GT biplot is less responsive to the statistical difficulty in identifying reliable traits for indirect selection for a target trait.

To improve maize yield under drought stress and low-N conditions, indirect selection under low N and drought is very important (Bänziger and Lafitte, 1997a, 1997b; Brancourt-Hulmel et al., 2005) as this strategy will increase gains from selection for yield through the exploitation of specific adaptation. The identification of plant and ear aspects and plant height as the most reliable traits for the simultaneous selection for improved yield under low-N and drought stresses indicated that tolerance of extra-early maturing maize cultivars to both stresses may involve similar adaptive mechanisms. This justifies the use of the same base index for selecting tolerant genotypes under both stresses. These findings are consistent with those of several earlier workers (Lafitte and Edmeades, 1994; Bänziger and Lafitte, 1997a, 1997b; Bänziger et al., 2006). Furthermore, the results of the GT biplot and path analysis indicated that selecting for increased plant height and good ear and plant aspects under either drought or low-N stress would result in simultaneous improvement in yield under both low-N and drought environments. In addition, both statistical tools revealed that the stay green characteristic, which is used in the base index for selecting drought and low-N tolerant genotypes, was not among the most reliable traits identified under drought stress even though it was among the most reliable under low-N environments. Therefore, its value as an adaptive trait in the selection index for selecting drought tolerant extra early is not justified.

An important practical implication of the results of this study is the possibility of selecting in one of the stress environments and being effective also in the other. In this case, selection under low N will be the obvious choice because it is easier and cheaper to accomplish. Results of the present study revealed that the reliable traits under low N, ear and plant aspects and plant height, cut across other stress environments (drought and low N), confirming the hypothesis of Badu-Apraku et al. (2011a) that improvement of grain yield under low N indirectly results in improved yield in the other research environments. It is also important to note that the traits plant and ear aspects and plant height were reliable for selecting stress tolerant early and extra-early genotypes, which implied that the same base index could be used for selecting for drought and low-N tolerance in the four maize maturity groups.

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