Assessment of interrelationships among grain yield and secondary traits of early-maturing maize inbred lines under drought and well-watered conditions

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Abstract
Knowledge and understanding of interrelationships between grain yield and yield-related traits would ensure progress from selection in maize breeding programs through the use of appropriate selection indices. One hundred and fifty-six early-maturing maize inbreds were evaluated at five environments in Nigeria, for 2 years to assess the relationship between grain yield and yield-related traits of maize inbreds under drought and well-watered conditions. Genotypes, and genotype × environment interaction mean squares were significant (P<0.05) for grain yield and other measured traits under drought and well-watered conditions. Under drought, plant and ear aspects, ear height, ears per plant (EPP), leaf senescence, number of seeds per ear, and seeds per row had direct effects on grain yield, accounting for 76% of total variation. Under well-watered conditions, days to silking, ear aspect, ear height, EPP, ear length, 100-kernel weight, number of seeds per row, plant height, and stalk lodging had significant direct effects on yield. Genotype main effect plus genotype × environment interaction (GGE) biplot identified plant and ear aspects, days to anthesis and silking, ASI, EPP, stay green characteristic, plant and ear heights, ear diameter, number of seeds per ear, number of seeds per row, and ear length as the most reliable traits for indirect selection for grain yield improvement under both research conditions. Plant and ear aspects, ear height, stay green characteristic, number of seeds per ear, and number of seeds per row were identified by both path–coefficient and GGE biplot analyses as the most reliable traits for selecting for grain yield under drought. Ear aspect, EPP, days to silking, plant and ear heights, number of seeds per row, and ear length were the most reliable traits for selecting for improved grain yield under well-watered conditions.

KeyWords *Correlation, GGE biplot analyses, path–coefficient analysis, reliable traits, yield-related traits, Zea mays L.*

Introduction

Maize (*Zea mays* L.) is the most widely grown and consumed crop by urban and rural dwellers in West Africa. Its production has greatly increased in the savanna agro-ecological zones due to favorable environmental factors such as high solar radiation, adequate rainfall, low night temperature as well as low incidence of pest and diseases. However, its production is greatly constrained by *Striga hermonthica* parasitism, recurrent drought, and low soil nitrogen (N) (Badu-Apraku et al., 2003). It is therefore crucial to develop and make available maize varieties capable of mitigating the production challenges.

Drought is the single most important production constraint affecting maize production and productivity in the sub region. Edmeades et al. (1995) reported an estimated 15% annual maize yield loss from drought in the West African savannas and indicated that localized losses may be much higher in the marginal areas where the annual rainfall is below 500 mm and soils are sandy or shallow. Grain yield losses can even be greater if drought occurs at the most drought-sensitive stages of crop growth, such as the flowering and grain filling periods (Denmead and Shaw, 1960; Ne Smith and Ritchie, 1992). Changes in climatic conditions resulting from global warming have further increased the probability of drought, even in the forest agro-ecology of West and Central Africa (Fakorede et al., 2003). Therefore, maize breeding programs targeting the savanna agro-ecologies of the sub region should have drought tolerance as one of their major breeding priorities.

Information on the interrelationship among grain yield and yield related traits is desirable for designing appropriate breeding strategies most especially under stress conditions. Several statistical tools have been employed in the study of interrelationship among traits. The most commonly used methods by breeders include path coefficient analysis and genotype main effect plus genotype × environment interaction (GGE) biplot. Path coefficient analysis has been widely used in crop breeding to

determine the causal relationship between grain yield and its contributing components, and to identify those components with significant effects on yield for potential use as selection criteria (Board et al., 1997; Moghaddam et al., 1998; Samonte et al., 1998). Several breeders have utilized path-coefficient analysis for examining the direct and indirect effects of various yield-related characters on grain yield in an array of crop plants, including rice (*Oryza sativa* L.) Samonte et al. (1998), maize (Badu-Apraku, et al., 2012). Genotype main effect plus genotype × environment interaction (GGE) biplot analysis has also been used to assess the relationship among traits in tropical maize (Badu-Apraku and Akinwale, 2011; Badu-Apraku et al., 2011a, b, 2012).
The heritability of grain yield under stress conditions is usually low (Badu-Apraku et al., 2012). This necessitates the use of secondary traits with strong association with yield for indirect selection for yield improvement under stress conditions. Secondary traits such as ears per plant, stay green characteristic, and anthesis-silking interval have strong associations with yield under drought conditions and have been used to select for higher levels of tolerance to drought in maize (Lafitte and Edmeades, 1994; Banziger and Lafitte, 1997a). Maize breeders in IITA utilize a selection index that integrates increased grain yield under drought 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 for improvement of maize germplasm for tolerance to drought (Menkir et al., 2003; Meseka et al., 2006; Menkir and Akintunde, 2001; Badu-Apraku et al., 2004, Oyekunle et al., 2015). Badu-Apraku et al. (2011a) reported that the most reliable traits for selection for improved grain yield under drought in the early maturing germplasm were ear aspect, ears per plant, anthesis-silking interval, and plant aspect. Badu-Apraku et al. (2012) identified plant aspect and plant and ear heights as the most reliable traits for simultaneous selection for yield under low N and drought in the extra-early inbreds. In the same study, Badu-Apraku et al. (2012) indicated that ear aspect, plant height, and anthesis–silking interval were identified by both path–coefficient and genotype main effect plus genotype × environment interaction (GGE) biplot analyses as reliable for selecting for drought tolerance. 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 contrasting results call for a thorough assessment of the interrelationships among traits with a view to confirming the most reliable traits for indirect selection for grain yield of early maize germplasm under stress and non-stress environments. Furthermore, there is a need to re-examine the IITA base index used for selection of drought tolerant early maize genotypes in WA to confirm the most reliable traits for computing the base index for selection for improved grain yield under drought. The objectives of the present study were to (i) asses relationship between grain yield and yield-related traits under drought and well-watered conditions, (ii) confirm the reliability of the traits with direct and indirect contribution to yield improvement under drought identified in previous studies, and (iii) compare the results of the sequential path analysis with those of the genotype main effect plus genotype × environment interaction (GGE) biplot in identifying the most reliable traits for selection for improved grain yield under drought.

Materials and Methods

Genetic materials and agronomical trials

One hundred and fifty-six early-maturing maize inbred lines extracted from six diverse germplasm sources, TZE-W Pop DT STR C_0, WEC STR, TZE-Y Pop DT STR C_0, TZE Comp 5-Y C_6, TZE-W Pop x LD and TZE-W Pop x 1368 STR C_0, with tolerance or resistance to Striga and maize streak virus, and/or tolerance to drought were used for the present study. The procedures used in developing the inbred lines have been described in details by Badu-Apraku et al. (2007). The 156 inbred lines were evaluated using a 12 x 13 incomplete block design with two replications under drought and well-watered conditions. The lines were evaluated under managed drought at Ikenne (forest-savanna transitional zone, 6°87′ N, 3°70′ E, 60 m asl, 1500 mm annual rainfall) during the dry seasons of 2007/2008 and 2008/2009 and in well-watered environments during the growing seasons at Ikenne and Bagauda (Sudan savanna, terminal drought stress environment; 12°00′ N, 8°22′ E, 580 m asl, 800 mm annual rainfall) in 2008 and 2009.

The dry season experiments at Ikenne were irrigated using an overhead sprinkler irrigation system, which applied about 17 mm of water per week from planting until 28 days after planting thus allowing the crop to mature on stored soil moisture. Induced drought stress was imposed by withdrawing irrigation water 28 days after planting until physiological maturity. At Bagauda and Ikenne during the growing seasons, the plants relied on natural rainfall for growth and development. Except for the water treatments, all management practices for both well-watered and induced drought stressed experiments were the same. Each experimental unit was a one-row plot, 4 m long with a row spacing of 0.75 m and intra-row spacing of 0.4 m. Three seeds were planted per hill and the seedlings were thinned to two per hill about 2 weeks after emergence. A compound fertilizer (NPK 15:15:15) was applied at the rate of 60 kg N ha^{-1} 2 weeks after planting (WAP) for all experiments except those under induced drought that had the fertilizer applied at planting. An additional 60 kg N ha^{-1} urea was top-dressed 3 WAP. In all the trials, the field was kept weed-free through the application of a mixture of 5 l ha^{-1} each of gramoxone and primextra, as pre-emergence herbicides. Subsequently, manual weeding was done as necessary to keep the trials weed-free.

Data collection

Days to anthesis (DA) and silking (DS) were recorded as the number of days from planting to when 50% of the plants in a row had shed pollen and had emerged silks. Anthesis-silking interval (ASI) was computed as the interval in days between silking and anthesis. Plant (PH) and ear (EH) heights were measured as the distance from the base of the plant to the height of the first tassel branch and the node bearing the upper ear. Plant aspect (PASP) was based on overall plant type (plant and ear heights, uniformity of plants, cob size, disease and insect damage and lodging) on a scale of 1 to 5 where 1 = excellent plant type and 5 = poor plant type. Ear aspect (EASP) was based on freedom from disease and insect damage, ear size, uniformity of ears and was recorded on a scale of 1 to 5, where 1 = clean, uniform, large, and well-filled ears and 5 = rotten, variable, small, and partially or poorly filled ears. In addition, leaf senescence (LD) scores were recorded for the drought-stressed plots at 70 days after planting on a scale of 1 to 10, where 1 = 0–10% dead leaves and 10 = 90-100% dead leaves. The number of ears per plant (EPP) was computed as the proportion of the total number of ears at harvest divided by the number of plants at harvest. In addition to the above field data, ear length (EL), ear diameter (ED), number of rows per ear (KR), number of seeds per ear (SPE), and weight of 100-kernels (KW) were recorded. Under drought stress environments, ears harvested from each plot were shelled and used to determine percentage grain moisture and grain weight. Grain yield, adjusted to 15% moisture, was computed from the shelled grain weight. On the other hand, under well-watered environments, harvested ears from each plot were weighed and representative samples of ears were shelled to determine percent grain moisture. Grain yield adjusted to 150 g kg^{-1} moisture, was computed from ear weight and grain moisture assuming a shelling percentage of 80%.

Statistical analysis

Combined analysis of variance (ANOVA) across environments was conducted separately for data collected under drought stress and well-watered environments with PROC GLM in SAS using a random statement with the TEST option (SAS Institute, 2002). In the combined ANOVA, environment and inbreds were considered as random effects. Thus, a random model was used in the analysis. GGE biplot software was used for trait-association and trait profile analyses (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 GGE biplot program is available at www. ggebiplot.com. This is represented in the model equation below:

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

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 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 computed using the inbreds means for all traits. 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

Performance of early-maturing inbred lines under drought and well-watered conditions

Results of the combined analysis of variance of the inbred lines across environments revealed significant genotype, and genotype × environment interactions (GEI) mean squares ($P<0.05$) for grain yield and other measured traits except ear diameter under drought (Table 1). Similarly, environments mean squares were significant ($p < 0.05$) for all measured traits except the number of seed per ear and ear diameter. Under well-watered conditions, genotypes, environments, and GEI means squares were significant ($p < 0.05$) for grain yield and all other measured traits (Table 1).

Table 1. Mean squares from analysis of variance for grain yield and other agronomic traits of 156 early-maturing maize inbred lines evaluated under drought at Ikenne during 2007/2008 and 2008/2009 dry seasons and well-watered conditions at Ikenne in 2008 and 2009 and under natural drought stress at Bagauda in 2008.

Source of variation	df	Days to anthesis	Days to silk	Plant height	Ear height	Plant aspect	Ear aspect	ASI	Ears per plant	Grain yield	Ear length	100 kernel weight	No of row per ear	Leaf sene-scene	SPR	ED
Drought stress																
Environment (env)	1	2346.3**	4464.0**	252532.6**	82425.1**	33.0**	51.5**	317.3**	10.17**	52.7**	597.9**	3722.1**	4.7	6.4**	4.7	4.2
Block (rep x env)	24	2.4	8.1*	234.1*	125.5**	1.4**	0.4	2.9	0.12	0.2	3.1	9.9	9.7**	1.7**	10.0	0.8
Rep (env)	1	4.7	16.3	960.3**	527.8**	6.3**	0.3	3.8	0.01	2.3**	9.4	13.3	4.7	7.2**	8.7**	2.5
Inbreds	155	19.7**	34.5**	1148.3**	385.8**	2.3**	0.8**	5.0**	0.12**	0.7**	4.9**	15.8**	6.4**	2.1**	6.4**	2.3
Inbreds x Env	155	7.4**	15.3**	388.1**	140.2**	1.7**	0.5**	3.3**	0.11**	0.4**	5.0**	17.9**	6.3**	1.2**	6.0**	2.2
Error	286	2.4	5.3	142.3	53.6	0.7	0.3	2.3	0.03	0.1	2.5	10.5	4.5	0.7	4.2	2.1
Well-watered conditions																
Environment (env)	2	338.4**	31.3**	108465.9**	24468.8**	38.5**	11.6**	196.6**	5.42**	126.7**	618.4**	993.8**	81.9**		11.8**	740.4**
Block (rep x env)	24	3.6	3.1	1416.7	171.3**	1.2	0.6**	1.2	0.07**	0.7**	2.0	5.0	3.9		9.9**	1.66
Rep (env)	2	0.7	2.6	1195.9	47.6	1.0	0.2	0.6	0.01	0.2	0.1	8.8	0.5		5.6**	3.1**
Inbreds	155	22.4**	32.4**	2432.8**	388.1**	2.6**	0.9**	4.2**	0.13**	1.7**	7.1**	38.3**	10.6**		8.8**	1.8*
Inbreds x Env	310	4.4**	7.4**	1702.8*	140.4**	1.6**	0.6**	1.9**	0.09**	0.9**	3.6**	19.0**	5.7**		6.4**	2.2**
Error	441	2.6	3.4	1444.1	96.1	1.0	0.2	1.2	0.04	0.4	2.0	8.9	3.4		2.1	1.4

*, ** Significant at 0.05, and 0.01 probability levels, respectively.
SPR, number of seed per row; ED, ear diameter

Correlation among grain yield and other traits under drought and well-watered conditions

Significant positive phenotypic correlations were observed between grain yield and plant height (r_p = 0.65), ear height (r_p = 0.62), EPP (r_p = 0.50), ear length (r_p = 0.19), number of rows per ear (r_p = 0.25), number of seeds per ear (r_p = 0.61), and number of seeds per row (r_p = 0.70) while significant negative phenotypic correlations were observed between grain yield and days to anthesis (r_p = -0.66), days to silking (r_p = -0.71), ASI (r_p = -0.55), ear aspect (r_p = - 0.35), plant aspect (r_p = -0.57), 100-kernel weight (-0.18), and leaf senescence (r_p = -0.28) under drought (Table 2). Apart from ear length and ear diameter, EPP was significantly correlated with all other measured traits under drought. Under well-watered conditions, positive and significant correlations were detected between grain yield and plant height (r_p = 0.32), ear height (r_p = 0.49), ear length (r_p = 0.51), number of rows per ear (r_p = 0.41), ear diameter (r_p = 0.17) and EPP (r_p = 0.66), while significant negative correlations were observed between grain yield and days to anthesis (r_p = -0.25), days to silk (r_p = -0.41), ASI (r_p = -0.38), ear aspect (r_p = -0.69), plant aspect (r_p = -0.10) and stalk lodging (r_p = -0.17) (Table 2).

Sequential path analysis of relationships among grain yield and related traits under drought

Path coefficient analyses were performed in accordance with the causal relationships among traits under each research condition as shown in path diagrams depicted in Figs 1 and 2. Under drought, the stepwise regression analyses identified ear aspect, ear height, EPP, leaf senescence, number of seeds per ear, plant aspect, and number of seeds per row as traits with high direct effects on grain yield (data not shown). The seven traits accounted for 76% of the total variation in grain yield. Among the seven traits with direct effects on grain yield, ear aspect had the highest total effect (-0.15) on yield followed by EPP (0.14), plant aspect (-0.11), leaf senescence (-0.04), number of seeds per row (0.04) and the least was ear height and number of seeds per ear (0.01) (data not shown). Plant height contributed to yield indirectly through ear height, ear aspect, plant aspect, number of seeds per ear, and number of seeds per row. Days to silking had the highest indirect contribution to yield through plant aspect (-0.29) and ear height. Number of kernels per row had the highest indirect effect on yield through plant aspect (-0.04) and EPP (0.01). Ear length had highest indirect effect on yield through number of seeds per row (0.62), ear aspect, leaf senescence, number of seeds per ear, and the least was ear aspect (0.04).

Table 2. Correlation between grain yield and other agronomic traits of early-maturing inbred lines evaluated under drought (above diagonal) at Ikenne during 2007/2008 and 2008/2009 dry seasons and well-watered conditions (below diagonal) at Ikenne in 2008 and 2009 and at Bagauda during the 2008 growing season.

	Grain yield	Days to anthesis	Days to silk	ASI	Plant height	Ear height	Plant aspect	Ear aspect	Ears per plant	Ear length	Ear diameter	100-kernel weight	Row per ear	Leaf senescence	SPR	SPE
Grain yield	-	-0.66**	-0.71**	-0.55**	0.65**	0.62**	-0.57**	-0.35**	0.50**	0.19**	0.07	-0.18**	0.25**	-0.28**	0.70**	0.61**
Days to anthesis	-0.25**	-	0.93**	0.48**	-0.68**	-0.62**	0.32**	0.11**	-0.45**	0.04	0.00	0.35**	-0.17**	0.05	-0.37**	-0.44**
Days to silk	-0.41**	0.86**	-	0.76**	-0.69**	-0.63**	0.38**	0.14**	-0.51**	0.01	-0.01	0.31**	-0.20**	0.12**	-0.46**	-0.38**
ASI	-0.38**	-0.02	0.48**	-	-0.47**	-0.44**	0.34**	0.13**	-0.43**	-0.06**	-0.02	0.13**	-0.19**	0.20**	-0.26**	-0.31**
Plant height	0.32**	0.01	-0.11**	-0.24**	-	0.90**	-0.25**	0.02	0.42**	-0.08	0.02	-0.29**	0.18**	-0.10**	0.26**	0.35**
Ear height	0.49**	0.02	-0.17**	-0.37**	0.41**	-	-0.20**	0.02	0.41**	-0.12**	0.00	-0.29**	0.13**	-0.03	0.26**	0.31**
Plant aspect	-0.10**	0.19**	0.18**	0.05	-0.02	-0.04	-	0.51**	-0.19**	-0.49**	-0.15**	-0.17**	-0.33**	0.34**	-0.46**	-0.56**
Ear aspect	-0.69**	0.29**	0.39**	0.27**	-0.19**	-0.28**	0.19**	-	-0.24**	-0.34**	-0.03	-0.15**	-0.07	0.18**	-0.41**	-0.47**
Ears per plant	0.66**	-0.18**	-0.33**	-0.33**	0.17**	0.33**	-0.08**	-0.55**	-	-0.05	0.00	-0.22**	0.09*	-0.15**	-0.12**	-0.08*
Ear Length	0.51**	-0.18**	-0.20**	-0.12**	0.24	0.42	-0.06	-0.44**	0.39**	-	0.16**	0.40**	0.17**	-0.13**	0.27**	0.31**
Ear diameter	0.17**	-0.11**	-0.11**	-0.06	0.02	0.03	-0.07	-0.19**	0.11**	0.10**	-	0.10**	0.21**	-0.15**	0.09*	0.10**
100- kernel weight	0.01	-0.02	-0.08*	-0.15**	0.05	0.04	-0.08*	0.01	-0.03	0.08*	0.07	-	-0.03	-0.03	0.02	0.01
Row per ear	0.41**	-0.19**	-0.23**	-0.20**	0.04	0.18**	-0.10	-0.43**	0.37**	0.17**	0.19**	-0.06	-	-0.09*	0.07	0.17**
SPR														-0.26**	-	0.96**

*, ** Significant at 0.05, and 0.01 probability levels, respectively.
SPR, number of seed per row; SPE, number of seed per ear

Sequential path analyses of relationships among grain yield and related traits under well-watered conditions

Under well-watered conditions, days to silking, ear aspect, ear height, EPP, ear length, 100 kernel weight, number of kernels per row, plant height, and stalk lodging had significant direct effects on yield (data not shown). The nine traits contributed 69.9% of the total variation in grain yield. Ear aspect had the highest direct effect of (-0.71) followed by EPP (0.25), days to silking (-0.13), stalk lodging (0.11) while ear height and 100-kernel weight had the least direct effect (0.01). Plant aspect had indirect contribution to grain yield through days to silking, ear aspect, ear length, 100-kernel weight, number of kernels per row and plant height. ASI had the highest indirect effects on grain yield through days to silking, ear aspect, ear height, EPP, ear length, 100 kernel weight, number of kernels per row and plant height. Days to anthesis had the highest indirect effects through days to silking (0.91) (data not shown). Stalk lodging had a significant indirect effect on yield through ear height (0.45), followed by 100-kernel weight (-0.68), and the least was root lodging (0.13). Husk cover had a significant effect on yield through 100-kernel weight (0.69), ear length (0.53), number of kernels per row (0.64) and ear aspect (0.33).

Biplot analyses of trait relationships under drought environments

The vector view of the genotype by trait (GT) biplot showing the interrelationship among traits measured under drought is presented in Fig. 1. In the biplot dis-

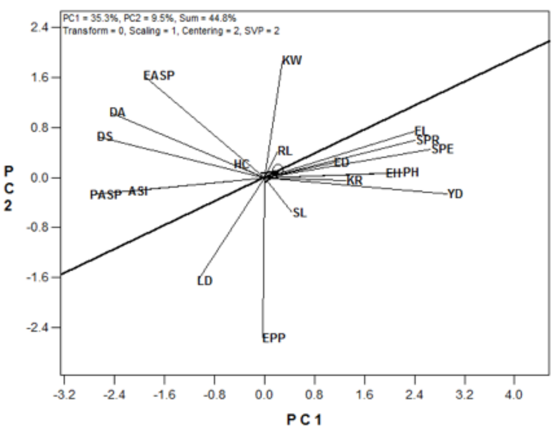

Figure 1 – A vector view of genotype × trait biplot showing interrelationships among traits of 156 early maturing maize inbreds evaluated under drought at Ikenne in 2007 and 2008 dry seasons. The data were not transformed (Transform = 0), standardized (Scale = 1), and were environment centered (Centering = 2). The biplot was based on genotype-focused singular value partitioning (SVP = 2) and is therefore appropriate for visualizing the relationships among traits.

ASI, anthesis–silking interval; DA, days to 50% anthesis; DS, days to 50% silking; EASP, ear aspect; EH, ear height; EPP, ears per plant; HC, husk cover; LD, Leaf senescence PASP, plant aspect; PH, plant height; ED, ear diameter; EL, Ear length; KW, 100-kernel weight; SPR, seed per row; SPE, seed per ear; RL, root lodging; SL, stalk lodging; KR, kernel row;YD, grain yield.

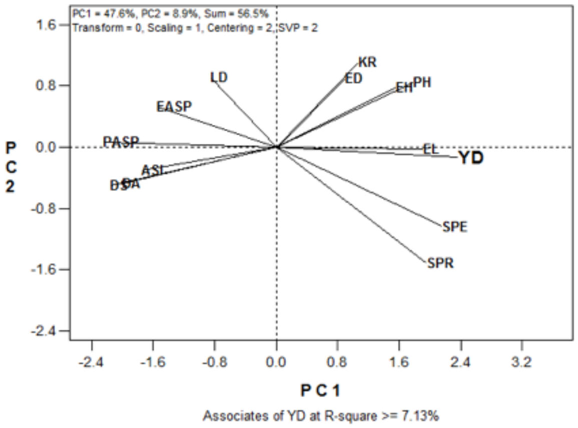

Figure 2 - A vector view of the genotype × trait biplot displaying most reliable traits for indirect selection for yield (inside box) under drought at p < 0.01 and R^2 value of ≥7.13%. The data were not transformed (Transform = 0), standardized (Scale = 1), and were trait centered (Centering = 2). The biplot was based on genotype-focused singular value partitioning (SVP = 2) and is therefore appropriate for visualizing the relationships among traits.

ASI, anthesis–silking interval; DA, days to 50% anthesis; DS, days to 50% silking; EASP, ear aspect; EH, ear height; LD, Leaf senescence PASP, plant aspect; PH, plant height; ED, ear diameter; EL, Ear length; SPR, seed per row; SPE, seed per ear; KR, kernel row; YD, grain yield.

play, the rays 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 the traits relative to their effects on grain yield. Number of kernels per row, ear and plant heights, ear diameter, number of seeds per ear, number of seeds per row, ear length, EPP, and 100-kernel weight had very small acute angles with yield, indicating very strong positive correlations with grain yield. On the other hand, leaf senescence, plant and ear aspects, days to anthesis and silking, and ASI had angles close to 180°; silking, plant and ear aspects were negatively correlated with yield. Plant and ear aspects, days to anthesis and silking, ASI had very small acute angles among them, indicating very strong positive correlations between them. Similarly, number of kernels per row, ear and plant heights, ear diameter, number of seeds per ear, number of seeds per row, ear length, EPP, 100-kernel weight had positive correlations between them. Traits with short vectors such as percentage stalk and root lodging, and husk cover had weak and nonsignificant correlations with one another and with traits having long vectors.

The biplot view in Fig. 2 was generated using the Auto Find QTL function of the GGE biplot (Yan, 2001) and provides information on the reliability of the traits for indirect selection for improved grain yield under drought at $p < 0.01$ and R^2 value of 7.13%. The primary (principal component [PC] 1) and secondary (PC2) principal axes of the biplot accounted for about 56.5% of the total variation in grain yield. Based on this biplot, plant and ear aspects, days to anthesis and silking, ASI, leaf senescence, number of kernels per row, ear and plant heights, ear diameter, number of seeds per ear, number of seeds per row, and ear length were identified as the most reliable traits for indirect selection of grain yield under drought.

Biplot analyses of trait relationships under well-watered conditions

Under well-watered conditions, the biplot display in Fig. 3 revealed a strong positive correlation between grain yield and plant and ear heights, EPP, husk cover, number of kernels per row, root and stalk lodging, 100-kernel weight and ear length. Grain yield had negative correlations with plant and ear aspects, ASI, days to anthesis and silking. Ear diameter had short vectors, indicating that it was not strongly correlated with long vector traits. The PC1 and PC2 together in biplot in Fig. 4 accounted for about 47.6% of the total variation in yield. The biplot revealed that plant and ear heights, ear length, EPP, ear diameter, number of rows per kernel, ASI, plant and ear aspects, days to anthesis and silking were identified as the most reliable traits for yield improvement under well-watered conditions at $p < 0.01$ and R^2 value of 5.67%.

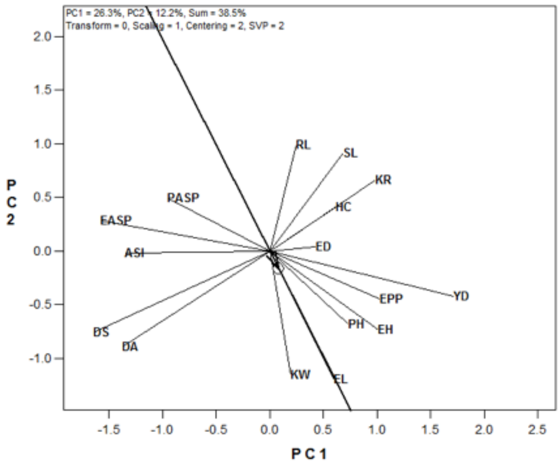

Figure 3 - A vector view of genotype × trait biplot showing interrelationships among traits of 156 early maturing maize inbreds evaluated under well-watered conditions at Ikenne and Bagauda in 2008 and 2009 rainy seasons. The data were not transformed (Transform = 0), standardized (Scale = 1), and were 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.

ASI, anthesis–silking interval; DA, days to 50% anthesis; DS, days to 50% silking; EASP, ear aspect; EH, ear height; EPP, ears per plant; HC, husk cover; PASP, plant aspect; PH, plant height; ED, ear diameter; EL, Ear length; KW, 100-kernel weight; RL, root lodging; SL, stalk lodging; KR, kernel row; R1, residual effect 1; R2, residual effect 2; YD, grain yield

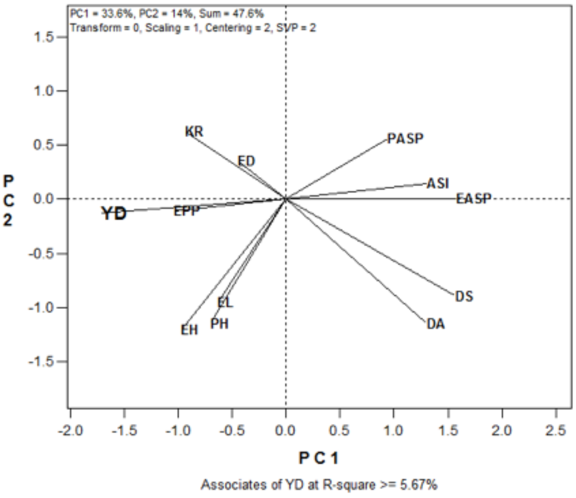

Figure 4 - A vector view of the genotype × trait biplot displaying most reliable traits for indirect selection for yield (inside box) under well-watered conditions at $p < 0.01$ and R^2 value of ≥5.67%. The data were not transformed (Transform = 0), standardized (Scale = 1), and were trait centered (Centering = 2). The biplot was based on genotype-focused singular value partitioning (SVP = 2) and is therefore appropriate for visualizing the relationships among traits.

ASI, anthesis–silking interval; DA, days to 50% anthesis; DS, days to 50% silking; EASP, ear aspect; EH, ear height; EPP, ears per plant; PASP, plant aspect; PH, plant height; ED, ear diameter; EL, Ear length; KR, kernel row; YD, grain yield.

Discussion

The presence of genetic variability among the lines for grain yield and other agronomic traits under drought and well-watered conditions indicated that significant progress could be made in selecting for improved grain yield and other traits under drought and well-watered conditions. The significant genotype GEI mean squares for the most measured traits under the two research conditions suggested that the inbreds should be evaluated in contrasting environments to allow identification of the most stable drought tolerant lines for the development of drought tolerant hybrids adaptable to drought prone environments. This result implied that most of the secondary traits used in selecting for tolerance to drought were affected by GEI and hence, the correlation between grain yield and secondary traits could be reduced due to drought. This result is in agreement with the finding of Badu-Apraku et al. (2011a, 2012).

The presence of significant positive phenotypic correlations between grain yield and plant height, ear height, EPP, ear length, and number of rows per ear indicated that improvement in these traits would contribute to significant progress in grain yield under drought and well-watered conditions. Similarly, the existence of negative correlations between grain yield and days to anthesis and silking, ASI, ear aspect, plant aspect, 100-kernel weight, and leaf senescence under drought and well-watered conditions indicated that these traits might have direct or indirect effects on grain yield under the two research conditions. These results justified the inclusion of most of these traits in the base index for selection of genotypes for tolerance to drought. This result is in agreement with the findings of earlier workers (Badu-Apraku et al., 2011b; Badu-Apraku and Oyekunle, 2012; Oyekunle et al., 2015).

An important objective of the present study was to assess the relationship among the traits and identify those with direct and indirect effects on grain yield. The knowledge of interrelationships between grain yield and its associated traits will improve the efficiency of breeding programs through the use of appropriate selection indices. The result of the path analysis revealed that ear aspect, ear height, EPP, leaf senescence, number of seeds per ear, plant aspect, and number of seeds per row had direct contribution to grain yield under drought. The direct contribution of ear aspect, EPP, plant aspect, and leaf senescence justified the inclusion of these traits in the base index for selection of genotypes for tolerance to drought. However, the number of seeds per row, ear height and the number of seeds per ear should also be considered in the base index for effective selection of drought tolerant genotypes. Similarly, the identification of days to silking, ear aspect, ear height, EPP, ear length, 100-kernel weight, kernel row, plant height, and stalk lodging with significant direct effects on yield suggested that these traits could be used in selecting for improved grain yield under optimal growing conditions. The high direct contribution of ear aspect, EPP, and ear height to yield under drought and well-watered conditions suggested that these traits could be used simultaneously for improving grain yield under the two research conditions.

The results of the GT biplot analysis revealed that percentage stalk and root lodging, and husk cover had relatively short trait vectors, indicating that they may be less important in evaluating early genotypes for drought tolerance. This result corroborated the findings of Badu-Apraku et al. (2012). The small acute angle observed between grain yield and number of kernels per row, ear and plant heights, ear diameter, number of seeds per ear, number of seeds per row, ear length, EPP, and 100-kernel weight indicated the existence of very strong positive correlations between grain yield and the traits. Based on the genetic correlation with yield, GT biplot identified plant and ear aspects, days to anthesis and silking, ASI, leaf senescence, ear and plant heights, ear diameter, number of seed per ear, number of seeds per row, and ear length as the most reliable traits for indirect selection for grain yield under drought. This result is in agreement with the findings of Badu-Apraku et al. (2011b, 2012) who identified EPP, plant and ear aspects, days to silking, ASI, and plant and ear heights as the most reliable for improved grain yield under drought. The present study identified the stay green characteristic (leaf senescence) as a reliable trait for selecting genotypes for tolerance to drought in an early maturing germplasm. This result is in disagreement with the findings of Badu-Apraku et al. (2011b, 2012) who reported that stay green characteristic was not a reliable trait for selecting for drought tolerance. The plausible explanation for the difference in the studies might be due to the fact that drought adaptive traits responsible for the drought tolerance in the early germplasm used in the present study are different from those of the extra-early used in the earlier studies. The results of the present study suggested that days to anthesis and silking, number of seeds per row, ear and plant heights, ear diameter, number of seeds per ear, and ear length are additional drought adaptive traits that should be considered for inclusion in the base index for identification of early germplasm for drought tolerance.

The presence of strong positive correlations between grain yield and plant and ear heights, EPP, husk cover, number of kernel per row, root and stalk lodgings, 100-kernel weight and ear length under well-watered conditions indicated that selection for improvement in any of these traits would lead to improvement in grain yield under well-watered conditions. The identification of plant and ear heights, ear length, EPP, ear diameter, number of seed per row, ASI, plant and ear aspects, days to anthesis and silking by GT biplot as the most reliable traits under well-watered conditions indicated that these traits could be used for yield improvement under well-watered conditions.

The results of the present study revealed that both GT biplot and path analyses identified plant and ear aspects, ear height, leaf senescence, number of seeds per row as important traits directly contributing to yield under drought. Several studies have identified ear aspect as strong secondary trait for yield improvement under drought due to the strong genetic correlations with yield under stress conditions (Banziger and Lafitte, 1997a, b; Bolanos et al., 1993; Bolanos and Edmeades, 1996; Edmeades et al., 1997; Badu-Apraku et al., 2011a). The identification of plant aspects, ear height, stay green characteristic, number of seeds per row among the reliable traits for selecting drought tolerant genotypes by both methods indicated that they were important traits for selection for drought tolerance. On the other hand, the path analysis included EPP and number of seeds per ear among traits with significant direct effects on yield whereas the GT biplot did not. In contrast, days to anthesis and silking, ASI, plant height, ear diameter, number of seeds per ear, and ear length, were among the reliable traits identified by the GT biplot for selection for improved yield under drought; these traits were not identified to have a high direct contributions to yield by the path analysis. It was surprising to note that EPP which was among the secondary traits with high direct effect on grain yield by path analysis was not among the most reliable traits identified by GT biplot. However, earlier studies by Banziger and Lafitte (1997a, b), Edmeades et al. (1997), and Badu-Apraku et al. (2004, 2011a) reported that EPP is an important secondary trait for selecting for improved grain yield under drought. Therefore, EPP could still be retained in the base index for the selection of drought tolerant genotypes. The results of the GT biplot and path analyses indicated that plant and ear heights, plant and ear aspects, days to anthesis and silking, ASI, ear length, and number of seeds per row were the most reliable secondary traits for improving grain yield under well-watered conditions. The identification of plant and ear aspects, ear height, and number of seeds per row by both methods under drought and well-watered conditions indicated that selecting for increased ear height, good plant and ear aspects, and increased number of seeds per row under either drought or well-watered conditions would result in simultaneous improvement in yield under both drought and optimal growing environments. For progress to be made under drought and well-watered conditions, the base index used in selecting for drought genotypes (Meseka et al., 2006, Badu-Apraku et al., 2012, Oyekunle et al., 2015) should be modified to include plant and ear heights, days to anthesis and silking, ear length, and number of seeds per row. The implication of the results of the present study is that selecting genotypes in one of the research environments would also be effective in the other. However, it would be easier and cost effective to select under optimum conditions rather than under drought environments. Since the results of the present study revealed that plant and ear aspects, ear height, and number of seed per row were the most reliable traits under both drought and well-watered conditions, improvement of grain yield under well-watered conditions would indirectly result in improved grain yield in drought environments.

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