Heritability of Drought Adaptive Traits and Relationships with Grain Yield in Maize Grown under High Plant Population

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Abstract

In low-moisture stress areas with unpredictable rain-free season, high-plant population is suggested for screening maize genotypes with tolerance to drought at flowering as alternative to stressed normal plant density. To confirm efficiency of this option, randomly derived 196 S_1 lines from A-511 Maize Population were tested at two plant densities in combination with well watered and drought stressed at flowering. In each of the four environments, the S_1 lines were grown in 14 x 14 alpha lattice experimental design to estimate: (i) broad-sense heritability of each tested trait; and (ii) relationships between grain yield and drought adaptive traits. The broad sense heritabilities of flowering traits were relatively high across all growing conditions. In contrast, the heritability for number of ears per plant (EPP) increased with increasing plant density and/or drought stress as for yield and most other traits decreased. Besides, significant association of grain yield with its components and flowering traits observed across all growing conditions in the same direction and opposite direction, respectively. Although relationships of yield with the drought adaptive traits increased consistently with increasing stress, it was highly dependent on its components in all environments but only under stress condition on anthesis-silking interval (ASI). In addition to significant expression of desirable parameters for a population improvement in the stress tolerance, ASI and EPP are relatively easily measured on field as compared to other drought adaptive traits. Thus, the strong dependence of yield on both traits and their high heritability in each or combination of the two stresses have confirmed possibility of using them for screening drought tolerant maize under high plant density, specially in areas that lack rain-free season.

Keywords: Drought adaptive trait, high plant density, heritability

Introduction

In Ethiopia, about 40 % of the total maize growing area is located in drought stressed areas where it contributes less than 20 % to total production (Mandefro et al., 2001). This low productivity is mainly associated with moisture deficit since about 90% of the crop production is handled by small-scale farmers under rain-fed growing condition. Besides, studies have reported that drought stress is progressing aggressively and increased incidence is expected as climate change intensifies (Hillel and Rosenzweig, 2002). Under these circumstances, availability of drought tolerant

maize varieties is vital particularly for resource-poor farmers to reduce food insecurity and poverty.

   Although incidence of drought is unpredictable, maize is most sensitive to this stress during two weeks bracketing flowering that often results in barrenness and serious yield instability at farm level (Bolaños and Edmeades, 1996). For this reason, improvement of maize tolerance to drought at flowering and grain filling is suggested as the best option especially to smallholders who cannot afford additional inputs (Vasal *et al.*, 1999; Bänziger *et al.*, 1999). Furthermore, almost all investigators have emphasized that the unpredictable nature of drought dictates that varieties targeted for these areas should perform well both under stressed and favorable rainfall conditions. Based on this reality, simultaneous selection for grain yield potential in well-irrigated environments and at least for reduced barrenness and anthesis-silking interval under managed drought stress at flowering are recommended as a dependable procedure for improving tolerance to mid-season drought (Bolaños and Edmeades, 1996; Vasal et al., 1997). This indicates that grain yield alone cannot help to identify the adapted genotypes because of its reduced genetic variability and heritability under stress. Instead, secondary traits with high adaptive value under low-moisture stress at flowering like number of ears plant^{-1}, number of kernels ear^{-1}, number kernels plant^{-1}, and ASI have been considered as the most important tools for selection of drought tolerant genotypes. In addition to increased genetic variance and association with yield, these drought adaptive secondary traits have relatively high heritability under drought stress (Bolaños and Edmeades, 1996).

   The goal for implementation of managed drought stress at flowering is to expose genetic variability for traits indicative of the stress tolerance. In addition to availability of reliable rain free season at screening site, the appropriate timing and intensity of water deficit are critical factors in obtaining consistent improvement in drought tolerance (Bolaños and Edmeades, 1996). However, in some countries like Ethiopia, it is difficult to implement managed drought stress at flowering due to lack of appropriate screening site with reliable rain-free season. Under such condition, experiences have shown high possibility of interference of rain when inducing drought stress at flowering. Consequently, for areas with erratic rainfall, many investigators suggested screening under high plant density as alternative to direct selection under drought stressed normal-plant density (Dow *et al.*, 1984; Vasal et al., 1997). Regarding the stress adaptive traits, Edmeades et al. (2003) reported that the considerable gains in performance under high density and drought stress at flowering point to the reduction in ASI or increased EPP as the mechanism impairing tolerance to both. However, it should be kept in mind that estimate of the stress adaptive traits' genetic variability and heritability as well as their genetic correlation with grain yield applies only to environments sampled (Hallauer and Miranda, 1988; Falconer, 1989). Hence, when planning to improve specific trait or adaptation of elite population, priority should be given to estimation of the essential parameters for desirable traits under targeted or managed stress environment. Nevertheless, limited information is available about the drought adaptive traits reaction to high plant population size. Thus, the objectives of this study were to determine the drought adaptive traits'

heritability and their relationships with grain yield when randomly selected S_1 lines from A-511 Maize Population grown under high plant density.

Materials and Methods

In 2003, the randomly derived 196 S_1 lines from Population A-511 were tested under the following four growing conditions: (i) Well-watered normal plant density (WWND), where about 44 400 plants ha^{-1} were established with a spacing of 30 cm between plants within rows, and irrigated at seven day intervals until maturity; (ii) well-watered high plant density (WWHD), where the plant density in environment 'i' was doubled with a spacing of 15 cm between plants; (iii) drought stressed normal plant density (DSND), where irrigation was suspended from 15 days prior to 50 % anthesis until 25 days after anthesis when one additional irrigation was applied, the plant population was the same as in 'i'; and (iv) drought stressed high plant density (DSHD), drought stressed as in 'iii' but with plant density increased as in 'ii'. Although combination of high plant density at environment 'iv' increased the stress intensity, the last two growing conditions (iii and iv) are considered as severe drought stress.

The study was conducted during off-season (November to March 2003) on station, where a furrow irrigation system was used to apply about 40 mm of water (estimated by partial flume) every seven days. Rain didn't interfere during conducting the trials on field, as there was drought in most part of the country. Soil texture of the trial site was clay loam. The 196 S_1 lines in each of the four environments were planted in 14 x 14 lattice design with two replications. In addition, one border row of A-511 was planted at both ends of each block. Each entry was planted in a 4.2 m long row using 0.75 m inter-row spacing, and intra-row spacing as determined above. The four trials were sown in adjacent blocks within the same field, while 5 m wide path was left between well watered and drought stressed conditions to avoid leaching to the stressed environments. Two seeds hill^{-1} were planted in all trials to ensure uniform stand and then thinned to the desired plant density (PD). As recommended by the center, 50 kg P_2O_5 and 25 kg N ha^{-1} was applied at planting, followed by a side dressing of 25 kg N ha^{-1} 35 days later. Data were collected for days to 50% anthesis (AD) and silking (SD), anthesis-silking interval (ASI) was computed by subtracting AD from SD, plant heights (PH), number of ears plant^{-1} (EPP), upper most ear length (EL in cm), number of kernels ear^{-1} (NKE), kernels plant^{-1} (NKP), number of primary tassel branches (TB), and hundred seeds weight (HSW). Besides, 1 to 10 scores of leaf senescence (SEN) were taken in each plot on two occasions near the end of grain filling stage and averaged, while grain yield (GY) plot^{-1} measured that reported in tons hectare^{-1} (t ha^{-1}) at 15% moisture content.

Detail descriptions of the methodologies used for estimating genetic covariance and genetic variance of the tested traits in each of the four environments are given elsewhere (Gezahegn et al., 2008). In brief, data were first tested for normality, and ASI was normalized using $\log_e \sqrt{(ASI+10)}$. Then they were analyzed using

environment (plant densities and moisture levels) as fixed factors, and genotype, incomplete blocks within replicates, and replicates within environment as random factors. Analysis of variance (Table 1) for each trait in each environment was carried out by Alpha software. However, a randomized complete block design (RCBD) was used for covariance estimation, using AGROBASE™ 20 software, since the relative efficiency of the alpha lattice over randomized complete block design (RCBD) was between 0 and 20 % for each tested trait. Besides, variance components for calculations of heritability and correlations were obtained from the RCBD analysis as indicated below. The genetic variances (σ^2_G) in each environment were estimated from the variance among S_1 lines, assuming no dominance effects (p = q = 0.5) (Hallauer and Miranda, 1988; Singh and Chaudhary, 1985). For each growing condition, the error variance (σ^2_E) is equal to mean square of error (MS_e), while σ^2_G was calculated on an environmental basis as: $\sigma^2_G = (MS_g - MS_e)/r$, where MS_g and MS_e were the mean squares of genotypes and error, respectively, and r number of replications. However, it has to be considered that the estimates of components of variance from one environment included a genotype x environment interaction (G x E) bias. Hallauer and Miranda (1988) reported that standard errors of estimates of σ^2_G were computed

by taking the square root of $\dfrac{2}{r^2}\left[\dfrac{MS_g{}^2}{(n-1)+2} + \dfrac{MS_e{}^2}{(r-1)(n-1)+2}\right]$, where n was

number of S_1 lines. Accordingly, broad-sense heritability (h_b^2) for a specific trait in each environment was estimated on a progeny mean basis as $h_b^2 = \sigma^2_G /(\sigma^2_G + \sigma^2_E /r)$. Since it was not possible to distinguish between additive, dominant, and epistatic effects of the variance components, h_b^2 estimated the extent to which phenotypes were determined by the genotypes (Falconer, 1989).

Table 1. Analysis of variance and expected mean squares for S_1 lines in each environment.

Source	Degree of . freedom.	Mean square	Expected MS (MS)
Replication	r-1		
Genotypes	n-1	MSg	$\sigma^2_E + r\sigma^2_G$
Error	(r-1)(n-1)	Mse	σ^2_E
Total	rn-1		

Genetic and phenotypic correlations between grain yield and secondary traits in each environment were estimated using the formula given by Singh and Chaudhary (1985). Accordingly, genetic correlations (r_G) between pairs of traits were estimated as: r_G

$= \dfrac{\delta_{gxy}}{\sqrt{\delta^2_{gx} . \delta^2_{gy}}}$ where δ_{gxy} is the genotypic covariance of traits x and y; δ^2_{gx} and

δ^2_{gy} are genotypic variances of traits x and y. Similarly, phenotypic correlations (r_P)

were estimated as: $r_P = \dfrac{\delta_{Pxy}}{\sqrt{\delta^2_{Px} \cdot \delta^2_{Py}}}$ where δ_{Pxy} is phenotypic covariance of traits x

and y; and δ^2_{Px} and δ^2_{Py} are phenotypic variances of traits x and y, respectively. The significance of the correlation coefficients was determined using the Student t-test (Steel *et al.*, 1997).

Results and Discussion

Results of this study showed presence of significant genetic difference among the S_1 lines within population A-511 for each of the tested traits, which variance magnitude were influenced by variation in level of moisture and/or plant density (data not shown, see Gezahegn et al., 2008). Besides, genetic variability data for each of the traits was obtained as planned like in site with rain-free season since draught stress at flowering induced without interference of rainfall as mentioned above. Broad sense heritability (h_b^2) for GY, NKE, NKP, EL, HSW and PH, increased with decreasing stress or increasing GY level, while for EPP increased with increasing plant density and/or drought stress (Table 2). Unlike others, relatively high heritability recorded for flowering traits in all growing conditions, while NTB showed reduced expression when plant population size increased with no clear trend in different moisture regimes. Based on S_1 lines from six tropical populations evaluated across moisture regimes, Bolaños and Edmeades (1996) reported the highest h_b^2 for GY, NKP, NKE and kernel mass under well watered conditions while the same applied to EPP under severe drought stressed normal plant density. AD showed almost similar h_b^2 across plant densities as well as moisture regimes, which also agreed with the above investigators who noted decreased effects of environment on this trait. With Pool 26 Sequia, Guei and Wassom (1992) reported larger narrow sense heritability for GY, SD, and ASI under non-stress, and for AD and EPP under stress, but in the other maize population (La Posta Sequia) the highest heritability estimated for all the traits was under severe drought stressed normal-plant density. No clear trend was exhibited in SEN expression of h_b^2 across environments. This may be due to reduced effects of environmental stress as reported by Bolaños and Edmeades (1996). Although the order of h_b^2 reduction due to plant density change was relatively smaller as compared to moisture change, heritability for all traits except EPP were reduced with increasing stress or decreasing grain yield level. As Ceccarelli (1989) pointed out heritability are used to identify optimum environments for selection, and the relatively high heritability exhibited by EPP under stress (high plant density or drought) also reflected its decisive role in improvement the tolerance of a population to these adverse growing conditions. However, it should be noted that σ^2_G and h_b^2 were considered as over estimated since G x E variance cannot be assessed in each environment of this study.

All the tested yield components and flowering traits showed significant genetic and phenotypic associations with grain yield in each environment (Table 3). Although these traits obtained their highest corresponding values under DSHD when drought and density stress combined, grain yield associated positively with its components and negatively with flowering traits in all growing conditions. Among the yield components, EPP, NKE and NKP were strongly associated with GY in each of the four environments while EL and HSW showed a tendency of increased relationship with increasing plant density and/or drought stress, but in a smaller magnitude. Results in this study were in agreement with S_1 to S_3 progenies tested across moisture regimes at Tlaltizapan, Mexico (Bolaños and Edmeades, 1996; Edmeades *et al.*, 1997). In the present study, genetic correlation of GY with EPP and EL showed significant trends as plant density changed as well as moisture availability, while significant trends reported only in EPP as water availability changed at Mexico.

The association of flowering traits with GY increased consistently with increasing drought and/or plant density stress. As a result, GY showed its highest dependency on these traits under DSHD where drought stress was combined with high plant density. The observed expression in AD for example indicated that it penalized late flowering more than early S_1 lines since low-moisture stress increased with time within DSND and DSHD. Bolaños and Edmeades (1996) also reported that AD and ASI correlated more strongly and more negatively with grain yield as drought intensified and yield levels declined. The consistent negative values estimated for these traits, especially under stress, indicated that earlier flowering S_1 progenies encountered less stress (escaped drought) during flowering or linked with increased GY potential than late flowering progenies. Moreover, studies demonstrated that progenies with reduced ASI and/or synchronized male and female flowering also gained high GY potential under stress (Guei and Wassom, 1992; Chapman and Edmeades, 1999). Thus as suggested by Bolaños and Edmeades (1996) selecting progenies that simply escape low-moisture stress by flowering early should be avoided in programs that focus on simultaneously increasing yield potential and tolerance.

AD showed non-significant trends as plant density changed under well watered conditions ($r_{gGY.AD}$ = -0.301 to –0.338) but significant trends within drought conditions ($r_{gGY.AD}$ = -0.531 to –0.723). In contrast, SD and ASI showed significant trends only as plant density changed under non moisture stress condition. The result demonstrated that both plant density and moisture availability, independently or in combination, induced significant effects on the association between flowering traits and GY. However, the magnitude varied across different studies, which need caution in interpretation. Besides, Hallauer and Miranda (1988) pointed out that genetic correlations inherently have large errors. In general, the potential use of the ASI to identify genotypes with tolerance to high density and drought stresses is well recognized (Dow et al., 1984; Edmeades et al., 2003). However, EPP as a measure of barrenness provides similar and perhaps more complete information at final harvest (Chapman and Edmeades, 1999). Thus ASI and EPP are the best drought and high plant density adaptive traits, which can substitute each other mainly in selection for drought tolerance.

Table2. Broad sense heritability (h_b^2) estimates of the tested traits of 196 randomly selected S1 lines derived from Population A-511 in each environment.

Environment	Estimation of h_b^2 in each of the four growing conditions			
Trait	WWND	WWHD	DSND	DSHD
GY	0.703	0.630	0.549	0.381
EPP	0.435	0.545	0.500	0.667
NKE	0.500	0.455	0.475	0.415
EL	0.462	0.346	0.349	0.211
NKP	0.541	0.529	0.481	0.440
HSW	0.602	0.539	0.349	0.347
AD	0.791	0.702	0.809	0.728
SD	0.713	0.702	0.791	0.682
ASI	0.775	0.680	0.692	0.704
PH	0.580	0.306	0.352	0.251
NTB	0.761	0.476	0.720	0.564
SEN	0.463	0.638	0.518	0.470

WWND=Well watered normal density; WWHD=Well watered high density; DSND =Drought stress normal density; DSHD= Drought stress high density; GY= grain yield in ton ha^{-1}; AD= days to 50% anthesis; SD= days to 50% silking; ASI= anthesis-silking interval; PH= plant height (cm); EPP= number of ears per plant; NKE= number of kernels ear[-1]; EL =ear length in cm; NKP= number of kernels plant[-1]; NTB= number of tassel branches; HSW= hundred seeds weight, SEN= leaf senescence.

The other secondary traits like NTB, SEN and PH were insignificant in their association with GY under DSND and WWHD (Table 3). Although PH importance in density response and lodging resistance is well documented (Edmeades et al., 2003), it was moderately and positively significant in its association with GY in extremely contrasting environments under WWND and DSHD. No clear explanation can be provided for this phenomenon, but tall plants are known for having a long duration in gaining maturity, which in turn is associated with increased yield when adequate water is available and minimized lodging occurs. In line with this assumption, Bolaños and Edmeades (1996) pointed out that the use of single row plots for evaluation, favored tall progenies to capture additional radiation when surrounded by shorter neighbors. Even so, they warned that such an advantage would not be expressed in large plots, and this positive r_G may reverse sign under drought conditions. Fortunately, in the present study, the exaggerated high positive correlation under WWND reduced due to increased plant density under WWHD without the use of increased plot size. Edmeades *et al.* (1997) noted that PH, NTB and SEN are highly heritable and easily measured, but are not strongly associated with grain yield under stress conditions. However, it should be considered that highly heritable traits can be easily altered by selection.

Phenotypic associations (r_P) of GY with its components and with flowering traits showed almost the same trend and sign but with smaller magnitude than their genetic correlations (Table 3). The results, except for HSW, were in agreement with the studies conducted at Tlaltizapan (Bolaños and Edmeades, 1996; Edmeades *et al.*, 1997). Nevertheless, the differences between phenotypic and genotypic associations in the present study were more pronounced as compared to their reports. This implies that

environmental correlations for the same traits were probably higher in the present study than in their study at Tlaltizapan. However, Chapman and Edmeades (1999) reported highly significant phenotypic associations of GY with AD and ASI under drought conditions (-0.80 and –0.89) but non-significant under well-watered conditions, which exceeded the magnitude estimated under drought conditions in this and other studies mentioned above.

Table 3. Genetic and phenotypic correlation of the tested traits with grain yield of S_1 lines derived from Population A-511 evaluated in four environments at Melkasa, 2003.

	Genetic correlation (r_G) with grain yield			
Traits	WWND	WWHD	DSND	DSHD
EPP	0.61**	0.77**	0.84**	0.85**
NKE	0.62**	0.63**	0.78**	0.80**
EL	0.23*	0.37**	0.54**	0.60**
NKP	0.70**	0.68**	0.73**	0.76**
HSW	0.31**	0.25**	0.30**	0.34**
AD	-0.30**	-0.33**	-0.53**	-0.72**
SD	-0.34**	-0.57**	-0.74**	-0.88**
ASI	-0.21*	-0.53**	-0.69**	-0.82**
PH	0.50**	0.13	0.13	0.50**
NTB	-0.03	-0.07	0.11	-0.16
SEN	-0.29**	-0.04	0.03	-0.06
	Phenotypic correlation (r_G) with grain yield			
	WWND	WWHD	DSND	DSHD
EPP	0.46**	0.64**	0.65**	0.70**
NKP	0.48**	0.49**	0.62**	0.64**
EL	0.22*	0.32**	0.37**	0.38**
NKP	0.47**	0.51**	0.60**	0.67**
HSW	0.25**	0.21*	0.40**	0.48**
AD	-0.29**	-0.32**	-0.37**	-0.43**
SD	-0.35**	-0.52**	-0.52**	-0.65**
ASI	-0.24**	-0.45**	-0.61**	-0.66**
PH	0.45**	0.19*	0.29**	0.38**
NTB	-0.01	-0.07	0.09	-0.05
SEN	-0.10	-0.07	-0.10	-0.22*

See Table 2 for abbreviations. *, ** indicates significance at P = 0.05 and P = 0.01, respectively.

In other study that based on testcrosses of inbred lines rather than randomly derived S_1 lines from elite populations, phenotypic correlations of GY with PH, EPP, EL, HSW, NKP, AD, SD and ASI under high plant density (60,000 plants ha^{-1}) were 0.56, 0.84, 0.72, 0.01, 0.69, 0.14, -0.33, and -0.66, respectively (El-Lakany and Russell, 1971). Similarly, using 25 hybrids at a stand of 98,800 plants ha^{-1}, the estimated simple correlation coefficients for GY with SD, ASI, and PH were –0.58, -0.86 and 0.20 respectively, (Buren *et al.*, 1974). Both studies observations for PH, EPP, NKE, SD, and ASI under high plant density agreed with the results obtained at Melkasa that also confirmed EPP and ASI as the most important adaptive traits of drought and/or high plant density stress. Generally, as low-moisture stress and/or plant density levels

increased, GY became increasingly dependent on EPP, NKP and ASI, and less on HSW. Thus, this study ascertained importance of ASI and EPP as selection tools for improvement of drought tolerance under low-moisture stressed normal-plant density in areas with rain free season as well as under drought stressed high-plant density in areas with unpredictable rain-free season.

Acknowledgments

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