SELECTION FOR DROUGHT TOLERANCE IN TWO TROPICAL MAIZE POPULATIONS

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ABSTRACT

Drought is a major factor limiting maize (*Zea mays* L.) yield in much of the world. The need to breed maize cultivars with improved drought tolerance is apparent. This study compared two maize populations, ZM601 and ZM607 for drought tolerance during flowering, the most drought-vulnerable period for the maize plant. Cultivar ZM601 had been improved through recurrent selection for two cycles for drought tolerance at flowering plus one cycle under rainfed ("random") drought stress, while ZM607 had been improved for high yield for three cycles under favorable growing conditions. A set of 143 random S_1 lines from ZM601 was compared with 94 from ZM607 at two drought stressed and one well-watered environment for yield and secondary traits. The results did not show much difference in drought tolerance between ZM601 and ZM607. Differences between population means for grain yield, anthesis-silking interval (ASI), and number of ears per plant (EPP) were small. Frequency distributions for ASI and leaf rolling were different for the two populations. However, ZM601 had more lines with shorter ASI and less leaf rolling as compared to ZM607. Broad sense heritability of ASI was larger,while that of grain yield smaller, and the correlation between ASI and grain yield was larger at drought-stressed compared to unstressed sites. Absence of large differences in grain yield between ZM601 and ZM607 lines was attributed to little effect of the selection completed prior to this evaluation, to genetic similarities of the two populations prior to selection, and to large genotype-by-environment interaction between Mexico, where drought screening was conducted, and Zimbabwe, where this evaluation was conducted. Results confirmed the value of ASI (measured at drought-stressed sites) as an indirect selection criterion for improving grain yield under drought stress conditions.

Key Words: Anthesis, heritability, recurrent selection, secondary traits, *Zea mays,* Zimbabwe

RÉSUMÉ

La secheresse est un facteur majeur limitant la production du maïs (*Zea mays)* dans le monde. La nécessité de croiser les variétés de maïs avec des variétés résistantes à la sécheresse est apparente. Cette étude a comparé deux populations, ZM 601 et ZM 607 pour la tolérance à la sécheresse pendant la période de floraison, la periode la plus vulnérable pour le maïs. La variété ZM 601 a été amélioré à travers la sélection recurrente pour deux cycles pour la tolérance à la sécheresse à la floraison en plus d'un cycle pendant la période pluvieuse (au hazard) stress de sécheresse, alors que ZM 607 a été amélioré pour rendement élévé pour trois cycles dans des conditions favorables. Un ensemble de 143 races S pris au hazard de ZM 601 était comparé avec 94 races de ZM 607 à stress deux sécheresses et un environnement bien arosé pour le rendement et les traits sécondaire. Les résultats n'a pas montré de différence significative dans la tolérance à la sécheresse entre ZM 601 et 607. Les différences entre moyennes des populations concernant le rendement en grains, l'interval d'anthesis-silking, et le nombre d'oeillet par plante était petit. La distribution de frequence pour ASI et roulage des feuilles était differente pour les deux populations. Cependant, ZM 601 avait plus des lignes avec des coûts ASI et moins de roulage des feuilles comparé au ZM 607. L'héritabilité de ASI était très large, celle de rendement en grains faible, et la corrélation entre ASI et le rendement en grains était élévée pour les sites stressés par la sécheresse comparés aux sites non stressés. L'absence des différences larges dans le rendement en grains entre les races ZM 601 et 607 était attribué au faible effet de la sélection faite avant l'évaluation, aux similarités génétiques de deux populations avant la sélection, et à la grande intéraction génotype-environnement entre le Mexique ou dépistage a été conduit et le Zimbabwe ou l'évaluation a été conduite. Les résultats ont confirmé la valeur de ASI mesurée comme un critère de sélection indirect pour l'amélioration dans les conditions de stress de la sécheresse.

Mots Clés: Anthesis, heritabilité, sélection recurrente, traits secondaires, *Zea mays*, Zimbabwe

INTRODUCTION

Maize is the principal staple food crop produced and consumed by most households in eastern, central and southern Africa. Drought is a major cause of food insecurity for many households as it has been estimated to cause annual maize yield loss of 24 million tons in the developing world (Edmeades *et al*., 1995). During the 1991/92 summer season, southern Africa experienced its worst drought of the century, with maize production declining by 60% for the region as a whole (Rosen and Scott, 1992). In Zimbabwe, drought stress commonly limits maize production on about 77% of the arable land (Mashingaidze, 1984). Even in the high-potential regions, crops may be affected by mid- and late-season droughts.

Drought affects maize yields by restricting season length and through unpredictable stress that can occur at any time during the cropping cycle (Edmeades *et al*., 1994). Drought occurring at flowering leads to greater yield losses than when it occurs at other developmental stages (Grant *et al.,* 1989). In addition, by flowering time farmers can no longer adjust management practices, such as fertiliser application, weed control and replanting (Myers, 1985). Water deficit lasting only one or two days during tasselling or pollination may cause as much as 22% reduction in yield (Hall *et al.,* 1981). The genetic improvement of maize to better tolerate drought stress is thus, highly desirable.

Breeding for drought tolerance in maize is a complex task, not least because drought can affect the crop at any stage of development. Many breeders have focused on alleviating the effects of drought at flowering and during grain filling because maize is most vulnerable to drought at these times. A characteristic of maize under drought stress is a delay in silking resulting in an increase in the anthesis-to-silking interval (ASI), incomplete or nil fertilization, and decreased or nil kernel development (Hall *et al.,* 1984). By evaluating maize that is moisture-stressed during flowering, it is possible to identify maize genotypes capable of maintaining a short ASI, and achieving above-average grain yield. This approach is routinely used by CIMMYT to improve and develop drought tolerant maize populations, inbred lines and hybrids (Banziger *et al*., 2000). Other selection criteria, in addition to grain yield and ASI, may include number of ears per plant (EPP), ear aspect (visual assessment of quality), anthesis date, leaf rolling, rate of leaf senescence, and tassel size (Vasal *et al.,* 1997).

The choice of a selection strategy is critical to breeding for stress tolerance. Selection for drought avoidance or "escape" through earlier maturity can play a deciding role in whether a crop will yield anything, particularly in areas that have a very short growing season. However, given adequate rainfall, yield is usually positively correlated with late maturity in determinate annual crops such as maize, sorghum and sunflower (Edmeades *et al*., 1989), therefore, selection for earliness to avoid soil water deficits often means lower yields in years of adequate water supply (May and Milthorpe, 1962). Probably the most widely used strategy is to select for yield under non-stressed conditions, and then evaluate those selections at many sites with variable moisture availability or "random stress" (Myers, 1985). Underlying assumptions of this approach are that genes for drought tolerance are present in elite high-yielding material, even after the number of genotypes has been narrowed to the few evaluated under random stress, and that selection under optimum growing conditions can also increase performance in sub-optimum conditions (Russell, 1974). A third approach is to screen germplasm for yield and/or related traits under drought stress conditions (Blum, 1988). One problem with this approach is that as yields are very low under stress, microenvironment can greatly affect the performance of individual test plots, leading to large environmental error and poor separation of genotypic means. However, success can be achieved through use of very uniform sites and careful crop management, plus use of appropriate experimental designs and analyses, e.g., spartial or nearest-neighbor analyses. There is no consensus about the best strategy to use in breeding maize for drought tolerance, and some researchers recommend a combination of two or more of the above mentioned approaches. For the case of CIMMYT, two water regimes are used when selecting maize for drought stress tolerance: a) well-watered (WW); and b) water stress (WS), where irrigation is suspended about 25 days prior to anthesis until mid-grain filling, when one additional application is made. Later, selection for adaptation to specific ecologies, for yield potential, and yield stability is conducted through multi-location testing (e.g., Byrne *et al.,* 1995). The effectiveness of these different methods is however, largely unknown.

The objectives of this study were to: i) Compare the performance under drought and well-watered conditions of two maize populations developed by contrasting methods: ZM601 was improved for tolerance to flowering and grain-filling drought stress; ZM607 was improved for high yield under adequate moisture alone, and ii) calculate broad-sense heritabilities for traits associated with drought tolerance at flowering for these two maize populations.

MATERIALS AND METHODS

Germplasm. Cultivar ZM601 is a late maturing maize population with white, mixed dent and flint kernels, adapted to mid-altitude (800 - 1600 meters above sea level) environments. It was developed from a cross of EV7992 and a maize streak virus (MSV)-resistant conversion of CIMMYT's Population 43 (Magorokosho and Pixley, 1995). While EV7992 is a mid-altitude adapted, white, semi-dent late maturing population formed in the Tanzanian

National Maize Breeding Program. Population 43 (also known as 'La Posta') is a late-maturing, white dent 'Tuxpe_o' population with high yield potential and has been improved for MSV resistance in Nigeria. Cultivar ZM601 was improved through recurrent selection for drought tolerance through shuttle-breeding between Zimbabwe and Mexico for two cycles. For each cycle of improvement, randomly formed S_1 lines were simultaneously screened under managed drought stress in Mexico (Bola_os and Edmeades, 1993) and rainfed "random" stress in Zimbabwe, and lines combining good performance in both environments were selected. For each recurrent selection cycle, the chosen lines were randomly mated at least two times before developing new lines for further selection. A third cycle of improvement was conducted for ZM601 in Zimbabwe only, using "random" stress.

Cultivar ZM607 is also a late maturing maize population with white, mixed dent and flint kernels adapted to mid-altitude environments. It was developed from a cross of EV7992 and an MSV resistant conversion of CIMMYT's Population 44 (Magorokosho and Pixley, 1997). Population 44 (also known as 'AED-Tuxpeño' (AED = American Early Dent)) is a late-maturing, white dent population containing short-plant 'Tuxpeño' material, and is capable of high yields under favorable conditions. Cultivar ZM607 has been improved through S_1 recurrent selection for three cycles for high yield and resistance to foliar diseases under favorable growing conditions at CIMMYT, Zimbabwe and has not been selected specifically for drought tolerance. For each recurrent selection cycle, the chosen lines were randomly mated at least two times before developing new lines for further selection. Thus, ZM601C$_3$ and ZM607C$_3$ (C$_3$ identifies the third cycle of selection) have somewhat similar genetic backgrounds, but different selection histories.

Line formation. The S_1 lines were formed from the two populations at Harare during the 1993/94 growing season. The populations were planted on the same day and managed identically. A bulk of 600 F_2 seeds of each population (ZM601 C$_3$ and ZM607 C$_3$) was planted and individual plants were self-pollinated to obtain S_1 cobs. At harvest, rotten and small or partially filled ears were discarded. During the 1994 winter season, each S_1 was planted in a 4 m row for sib-mating to increase the quantity of seed for subsequent S_1 *per se* evaluation. At harvest, unsuitable ears were discarded as described above, and the remaining S_1 lines were kept as a random sample. For ZM601, 143 S_1 lines were retained while 94 S_1 lines were kept for ZM607.

Line evaluation. The 143 S_1 lines from ZM601, 94 S_1's from ZM607, plus three commercially important inbred lines (M162W, NAW5867 and K64R) were evaluated in a 15x16 alpha-lattice design at four locations (Table 1). The two random drought stress sites (Makoholi Experiment Station and Drewton Farm) and the high-rainfall location (CIMMYT Harare Research Station) were grown in summer under rainfed conditions, whereas the controlled drought stress site (Mzarabani Estate) was grown in winter with water applied entirely by irrigation. There were two replications per location, except for Mzarabani where three replications were used. For all trials, plots were single rows, 4 m long, over-planted and finally thinned to 53,333 plants per hectare. Standard maize production recommendations were followed for each respective area. The principal traits measured for the experimental lines are listed and defined in Table 2.

Statistical analyses. Analyses of variance (ANOVA) were initially conducted for each location using the statistical model for the alpha-lattice design (Patterson *et al.*, 1978). With only two exceptions, all individual site analyses for each trait showed no gain of efficiency from using the lattice design relative to the randomised complete block design (RCBD), and we therefore used unadjusted data for all combined, across-location ANOVAs (Gomez and Gomez, 1987).

Pearson's phenotypic correlation coefficients were calculated using SAS (SAS Institute, 1996). All percent data were transformed using the arcsine transformation before analysis. Genetic variances (σ^2_g), broad sense heritabilities (h^2_b) and their associated standard errors (SE) were estimated for each trait within each population at each location, according to Hallauer and Miranda (1981).

RESULTS AND DISCUSSION

Lower grain yield, larger ASI, fewer EPP and significant correlations of yield with ASI and EPP indicated that trials at Mzarabani and Drewton suffered more stress at flowering than trials at Harare and Makoholi (Tables 3 - 5) (Bolaños and Edmeades, 1993). Low grain yields at Makoholi were likely attributable to factors other than drought, probably a combination of low inherent soil fertility, leaching of nutrients due to heavy rainfall on sandy soil, and

possibly damage by nematodes (Dovi, 1995, personal communication). The average anthesis date did not differ for lines from the two populations (Table 3). This is a crucial fact to allow comparisons of drought tolerance among the lines, because it indicated that the lines were at similar phenological stage whenever moisture stress occurred.

Means and frequency distributions. There were no significant differences for mean grain yield of the lines from ZM601 and ZM607 under adequate moisture at Harare or when averaged across all four locations (Table 3). Small yield differences were recorded between lines of the two populations evaluated at the drought stressed sites. Absence of consistent yield differences between lines from ZM601 and ZM607 was surprising because their selection histories suggested that ZM607 might perform better than ZM601 at high yield sites, whereas ZM601 might have an advantage under drought stressed conditions. Our results indicated that concomitant selection for high yield under adequate and moisture-stressed conditions did not result in a significant yield advantage for ZM601 relative to ZM607 under drought stress. In other trials where ZM601 and ZM607 have been tested, no significant differences for grain yield, ASI or leaf senescence were observed between the two populations under optimal growing conditions, drought or low nitrogen stress (Banziger *et al.,* 1999).

Many secondary traits, including ASI, EPP, tassel size (TS), leaf rolling (LR) and leaf angle (LE) have been proposed as useful indirect selection criteria to improve maize yields under drought stress (Ludlow and Muchow, 1990; Edmeades *et al.*, 1997). Drought stress at flowering does not greatly affect days to pollen shed, but it often slows silk elongation and results in large ASI for drought-susceptible genotypes (Westgate, 1997). Decreased number of EPP may occur due to failure of fertilization (due to large ASI), or increased rate of kernel abortion due to water stress (Westgate and Bassetti, 1990). Large tassels are generally considered undesirable because they compete with the ear as a sink for photosynthates (Fischer *et al.,* 1987). Leaf rolling is a symptom of low leaf water status (Sobrado, 1987), and many breeders consider leaf rolling as counterproductive because it reduces radiation interception, photosynthesis and, therefore, yield. Erect leaves have been associated with higher yield under stress due to increased water-use efficiency and possible decreases in photo-oxidation as a result of less radiation flux per unit leaf surface area (Duncan, 1971).

The ZM601 lines had slightly shorter ASI and more EPP than lines from ZM607 (Table 3), suggesting better drought tolerance of ZM601 relative to ZM607. Comparisons of means for LR, TS and LE revealed no significant differences between the two populations. Frequency distributions for ASI and LR scores under drought stress, however, revealed important differences for lines from the two populations. Whereas positive (choice of the best fraction) or negative (discarding the worst fraction) selection based on grain yield under drought stress would have selected equal frequencies of lines from ZM601 and ZM607, use of the secondary traits ASI and LR would have chosen more lines from ZM601 and/or discarded more lines from ZM607 (Table 4). Thus, ZM601 lines showed a higher frequency or percent of drought adaptive traits relative to ZM607 lines.

Overall, the relatively small differences between ZM607 and ZM601 may have resulted from inherent parental differences between ZM601 and ZM607 before onset of selection for drought tolerance and high yield potential of the two populations, respectively. Alternatively, improvement of drought tolerance for ZM601 may have been slight because only three cycles of selection were conducted, two using managed drought stress in Mexico – where selection conditions may have been very different to the conditions in Zimbabwe where these trials were evaluated - and the third cycle relying on "random" stress (trials planted at drought-prone sites, during the normal crop season). In a related study, the means and frequency distributions for ASI were clearly different for sets of lines from ZM601 and Tuxpeño Sequía grown under drought stress; Tuxpeño Sequía, which had been selected for six cycles for drought tolerance under managed stress levels, had more lines than ZM601 with short ASI, and outyielded ZM601 under drought (Magorokosho and Pixley, 1997).

Phenotypic correlations among traits. The phenotypic correlation coefficients between grain yield and ASI were small (r = -0.08 to -0.21*) under adequate moisture conditions and became much larger (r = -0.40** to -0.43**) at moisture-stressed sites (Table 5). Similarly, the relationship between EPP and grain yield, also became stronger with increasing moisture stress (from 0.08 to 0.24** without stress, to 0.40** to 0.45** with moisture stress). The larger phenotypic correlation of EPP with grain yield under moisture stress may have been due to increased genetic variance for EPP under moisture stress relative to non stressed environments (Table 6). The magnitude of these correlation coefficients was generally very similar for the two populations in each environment. These results indicate that ASI and EPP are useful secondary traits to select for grain yield at moisture stressed sites, but less useful (if at all) under adequate moisture conditions. Similar results abound in literature (e.g., Bolaños and Edmeades, 1996; Edmeades *et al.,* 1994).

The number of days to 50% pollen shed (AD) was negatively correlated with grain yield for lines from both populations in all test environments (Table 5). This may have been due to early termination of the rains during the 1994/95 summer season, which subjected lines from both populations to drought stress during grain filling. Earlier

maturing lines produced higher yields as they completed their development before drought stress became severe. Selection for earliness has produced cultivars that perform well in environments with short rainy seasons, or where frequent mid-season droughts tend to coincide with flowering of late-maturing cultivars.

With adequate moisture, grain yield of maize and many other determinate crops is usually positively correlated with maturity and season length. Thus, earliness generally limits the yield potential of cultivars. A better alternative to early maturing, drought-escaping cultivars, therefore, may be to breed cultivars that are both tolerant to drought and responsive to good conditions. In a related study, Magorokosho and Pixley (1997) reported a significant positive correlation of grain yield with AD for the population Tuxpeño Sequía grown under drought conditions, indicating that drought tolerance enabled Tuxpeño Sequía to take advantage of a longer growing season even under drought stress. Such data challenge the widespread perception that escape through earliness is the best solution to maize cultivar requirements in drought-prone environments, particularly where a long rainy season is often interrupted by mid-season drought (e.g., much of Zimbabwe).

The correlation of leaf rolling with grain yield was negative and larger for lines of ZM607 (r = -0.20** to - 0.33**) than ZM601 (r = -0.13* to -0.14*). This probably reflects the fact that the variance for leaf rolling was less among lines from ZM601 than ZM607 under drought (Table 6). Correlations of grain yield with tassel size and leaf angle were small (Table 5).

In summary, grain yield under drought stress was correlated with plant processes related to biomass partition at flowering (ASI and EPP), and weakly associated with traits related to plant water status (leaf rolling, tassel size and leaf angle scores).

Genetic variances and broad sense heritabilities. Genetic variance (σ^2_g) and to a lesser extent broad sense heritability (h^2_b) for grain yield was less at the more drought-affected sites for lines from both ZM601 and ZM607 (Table 6). Concomitantly and conversely, the σ^2_g and h^2_b for ASI increased for both populations. These trends, together with the increased correlation between grain yield and ASI (Table 5) suggest that ASI would be useful as a secondary trait to improve grain yield when selecting under drought stressed conditions. These findings corroborate literature reporting that genetic variance and broad sense heritability of grain yield often decline with increasing moisture stress (Blum, 1988; Rosielle and Hamblin, 1981; Bolaños and Edmeades, 1996). There are instances where selection for reduced ASI has been more effective than selection for grain yield under drought stress conditions (Bolaños and Edmeades, 1996).

Heritability for EPP was generally moderate (average of 42%) under drought stress conditions, despite small (albeit significant) estimates for σ^2_g (Table 6). Because of the small variance, selection for this trait may not be effective even though the correlation of EPP with yield under drought stress was high (Table 5). This contrasts with results from several drought tolerance studies in maize (e.g. Edmeades *et al.,* 1995; Bolaños and Edmeades, 1996), and suggests that stress levels in our trials were not severe enough to expose sufficient variability for EPP. It is also possible that previous studies evaluated germplasm with more genetic variance than ZM601 and ZM607 for this trait.

Heritability estimates for days to 50% anthesis (AD) were generally above 60% (Table 6). Although evaluated at few sites, h^2_b estimates for leaf angle score were moderate to high (50 and 71%), while those for tassel size and leaf rolling scores were low to moderate (21 to 63%).

CONCLUSIONS

Even though both populations are comprised of 50% EV7992 and 50% either EVPOP43 or EVPOP44 (both of Tuxpeño background), dissimilarity of ZM601 and ZM607 before the onset of selection may partly explain our failure to detect significant differences in grain yield after selecting the two populations differently. In addition, two selection cycles for drought tolerance under environmental conditions that were very different from those in Zimbabwe may not have been enough to create large differences in performance between the two populations. In other studies, Banziger *et al.* (1999) also did not find any significant differences in the performance of the same populations (ZM601 and ZM607) across a diverse range of environments in Southern Africa during regional trials conducted in 1998. In our study, a small advantage for ZM601 over ZM607 was observed for mean and frequency distribution for ASI, and number of EPP under drought stress.

The relative usefulness of secondary traits (e.g., ASI and EPP) as indirect selection criteria for a primary trait (e.g., grain yield) is determined by the magnitudes of their genetic variance, heritability and genetic correlation with the primary trait (Falconer, 1981). This study identified the utility of ASI as an indirect selection criterion for grain yield under drought stress conditions. A commonly used strategy at CIMMYT for drought stress breeding is to select lines combining short ASI under drought stress with good yield potential under non-stress conditions.

Usefulness of EPP as an indirect selection trait for grain yield under drought stress was suggested, but not conclusively established in this study. Our results, plus related literature, suggest that a selection index combining these secondary traits and grain yield should result in faster improvement of grain yield under drought stress than selection for grain yield alone.

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TABLE 1. Name, latitude, altitude, soil type, average annual rainfall and average monthly temperatures for the four sites where experiments were conducted*

Location	Latitude	Altitude masl**	Soil type	Average annual rainfall mm	Average hottest month	Temperature °C
Harare	18° S	1500	Deep fersiallitic red clay	800	29	14
Makoholi	20° S	1200	Granite derived sand	625	30	13
Drewton	20° S	1200	Granite derived sand	625	30	13

*Trials at Mzarabani were grown in winter, when all moisture was supplied by irrigation (no rainfall)
** masl = meters above sea level

TABLE 2. Traits measured for the S_1 *per se* evaluations carried out during the 1994/95 summer and 1995 winter seasons

Trait	Description
Grain Yield (GY)	Weight of shelled grain adjusted to t ha^{-1} at 12.5% moisture content.
Anthesis Date (AD)	Number of days from planting to 50% of plants shedding pollen.
Silking Date (SD)	Number of days from planting to 50% of plants with silks about 2 cm long.
Anthesis to Silking Interval (ASI)	SD minus AD.
Ears per Plant (EPP)	Number of cobs with at least one grain, divided by the total number of plants.
Leaf Rolling (LR)	Visual score: 1 (unrolled leaves) to 5 (rolled leaves). LR scores were recorded three times at weekly intervals commencing a week before flowering.
Leaf Erectness (LE)	Visual score: 1 (erect leaves) to 5 (lax leaves). LE scores were recorded three times at weekly intervals during the post-flowering period

TABLE 3. Grain yield (t ha^{-1} at 12.5% moisture content), anthesis to silking interval (ASI) (days), number of ears per plant (EPP), anthesis date (AD) (days) and leaf rolling score (LR) for S_1 lines from ZM601 and ZM607 evaluated at four locations of varying moisture levels during the 1994/95 summer or 1995 winter season

Trait	Population	Nonstress	Environment stress	Across

		HA [†]	MK	MZ	DF	AC
Grain yield	ZM601	3.45	1.71*	0.22**	0.76*	1.54
	ZM607	3.46	1.87	0.20	0.90	1.61
ASI	ZM601	0.14	0.97	4.23	4.20**	2.39*
	ZM607	0.02	1.04	4.25	4.78	2.53
EPP	ZM601	1.38	1.30*	0.90**	0.75*	1.06*
	ZM607	1.36	1.21	0.82	0.77	1.02
AD	ZM601	72.77	74.66	74.37	79.74	75.38

[†] HA=Harare, MK=Makoholi, MZ=Mzarabani, DF=Drewton and AC=Combined across locations
*, ** = significant at P<0.05 and at P<0.01, respectively, for pair-wise comparison of means of the two populations within a column

TABLE 4. Percent of the 143 ZM601 and 94 ZM607 lines among the best and worst of all 237 S_1 lines evaluated under drought stress at Mzarabani and Drewton during the 1994/95 summer or 1995 winter season

	Best Worst	ZM601	ZM607
			% of lines
Grain yield	$\geq$ 0.64 t ha^{-1}	10	11
	$\leq$ 0.25 t ha^{-1}	12	7
Anthesis-silking Interval	$\leq$ 3 days t ha^{-1}	51	39
	$\geq$ 5 days	31	42
Leaf rolling[†]	$\leq$ 2.5	46	34
	$\geq$ 3.0	34	46

[†] Visual score: 1 = best (unrolled leaves) to 5 = worst (rolled leaves)

TABLE 5. Linear phenotypic correlation coefficients for grain yield with various traits determined for 143 S_1 lines from ZM601 and 94 S_1 lines from ZM607, evaluated at four locations of varying moisture levels during the 1994/95 summer season and 1995 winter season

Traits	Population	Location				
		Non-stress		Moisture-stressed		Across
		HA[†]	MK	MZ	DF	AC
r yield.asi[‡]	ZM601	-0.08	-0.12*	-0.42**	-0.40**	-0.40**
	ZM607	-0.21*	-0.20**	-0.43**	-0.42**	-0.44**
r yield.epp	ZM601	0.24**	0.08	0.44**	0.40**	0.42**
	ZM607	0.13	0.21**	0.45**	0.44**	0.46**
r yield.ad	ZM601	-0.43**	-0.24**	-0.18**	-0.40**	-0.54**
	ZM607	-0.34**	-0.15*	-0.18**	-0.45**	-0.48**
r yield.lr	ZM601	-	-0.13*	-	-0.14*	-0.34**
	ZM607	-	-0.20**	-	-0.33**	-0.44**
r yield.ts	ZM601	-	0.05	-	0.13*	0.13**
	ZM607	-	0.01	-	0.04	0.16**
r yield.le	ZM601	-	-0.14**	-	-	-0.14**
	ZM607	-	-0.21**	-	-	-0.21**

[†] HA=Harare, MK=Makoholi, MZ=Mzarabani, DF=Drewton, AC=Across locations
[‡] ASI=anthesis to silking interval, EPP=ears per plant, AD=days to anthesis, LR=leaf rolling score, TS=tassel size, LE=leaf erectness
*, ** = significant at P<0.05 and at P<0.01, respectively

TABLE 6. Estimates and their standard errors (in parentheses) for genetic variance (σ^2_g) and broad sense heritability (h^2_b) for several traits for S_1 lines from ZM601 and ZM607 evaluated
at four locations of varying moisture levels during the 1994/95 summer and 1995 winter seasons

ZM601			Grain yield	ASI	EPP	AD	LR	TS	LE
Nonstress	HA†	σ^2_g	1.11 (± 0.16)	0.43 (± 0.09)	0.17 (± 0.02)	2.54 (± 0.46)			-
		h^2_b	0.70 (± 0.08)	0.19 (± 0.09)	0.51 (± 0.06)	0.73 (± 0.09)			-
MK		σ^2_g	0.16 (± 0.07)	1.12 (± 0.39)	0.05 (± 0.02)	4.43 (± 0.95)	0.06 (± 0.05)	0.11 (± 0.07)	(
		h^2_b	0.35 (± 0.15)	0.40 (± 0.14)	0.37 (± 0.13)	0.36 (± 0.14)	0.21 (± 0.14)	0.23 (± 0.15)	(
Stress	MZ	σ^2_g	0.02 (± 0.06)	0.73 (± 1.04)	0.01 (± 0.00)	3.81 (± 0.72)			-
		h^2_b	0.35 (± 0.19)	0.35 (± 0.16)	0.26 (± 0.13)	0.59 (± 0.12)			-
DF		σ^2_g	0.06 (± 0.02)	3.19 (± 0.69)	0.02 (± 0.00)	5.75 (± 1.15)		-	(
		h^2_b	0.52 (± 0.13)	0.59 (± 0.13)	0.53 (± 0.12)	0.66 (± 0.13)		-	(
ZM607									
Nonstress	HA	σ^2_g	0.71 (± 0.20)	0.08 (± 0.11)	0.04 (± 0.02)	2.27 (± 0.50)			-
		h^2_b	0.61 (± 0.12)	0.18 (± 0.18)	0.35 (± 0.13)	0.68 (± 0.10)			-
MK		σ^2_g	0.05 (± 0.08)	0.51 (± 0.37)	0.02 (± 0.01)	1.91 (± 0.92)	0.19 (± 0.07)	0.14 (± 0.07)	(
		h^2_b	0.12 (± 0.20)	0.25 (± 0.18)	0.04 (± 0.15)	0.63 (± 0.16)	0.44 (± 0.17)	0.35 (± 0.18)	(
Stress	MZ	σ^2_g	0.02 (± 0.08)	0.76 (± 1.50)	0.03 (± 0.01)	2.41 (± 0.64)			-
		h^2_b	0.38 (± 0.25)	0.32 (± 0.22)	0.47 (± 0.14)	0.67 (± 0.16)			-
DF		σ^2_g	0.03 (± 0.02)	6.50 (± 1.42)	0.01 (± 0.00)	5.60 (± 1.31)		-	(
		h^2_b	0.36 (± 0.18)	0.69 (± 0.15)	0.43 (± 0.18)	0.65 (± 0.15)		-	0.63 (± 0.15)

† ASI=anthesis to silking interval, EPP=ears per plant, AD=days to anthesis, LR=leaf rolling score, TS=tassel size, LE=leaf erectness
‡ HA=Harare, MK=Makoholi, MZ=Mzarabani, DF=Drewton