

Breeding for improved drought tolerance in maize adapted to southern Africa

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Abstract

The difficulty of choosing appropriate selection environments has restricted breeding progress for drought tolerance in highly-variable target environments. Genotype-by-environment interactions in southern African maize-growing environments result from factors related to maximum temperature, seasonal rainfall, season length, within season drought, subsoil pH and socio-economic factors that result in sub-optimal input application. In 1997 CIMMYT initiated a product-oriented breeding program targeted at improving maize for the drought-prone mid-altitudes of southern Africa. Maize varieties were selected in Zimbabwe using simultaneous selection in three types of environments, (i) recommended agronomic management/high rainfall conditions, (ii) low N stress, and (iii) managed drought. Between 2000 and 2002, 41 hybrids from this approach were compared with 42 released and prereleased hybrids produced by private seed companies in 36-65 trials across eastern and southern Africa. Average trial yields ranged from less than 1 t/ha to above 10 t/ha. Hybrids from CIMMYT's stress breeding program showed a consistent advantage over private company check hybrids at all yield levels. Selection differentials were largest between 2 to 5 t/ha and they became less significant at higher yield levels. An Eberhart-Russell stability analysis estimated a 40% yield advantage at the 1-ton yield level which decreased to 2.5% at the 10-ton yield level. We conclude that including selection under carefully managed high priority abiotic stresses, including drought, in a breeding program and with adequate weighing can significantly increase maize yields in a highly variable drought-prone environment and particularly at lower yield levels.

Media summary

A new maize breeding approach shows significant yield increases in drought-prone environments in southern Africa.

Keywords

GxE, breeding progress, genotype, *Zea mays*

Introduction

Even though the challenge of developing drought tolerant crop varieties has generated an immense amount of literature, most practical breeding efforts remain focused on increasing productivity under favorable conditions where genetic variance, heritability and therefore breeding progress for grain yield are greatest. Apart from adapting crop phenology to rainfall patterns, multi-environment trials (METs) including trials grown under random drought conditions are often the only systematic approach exploited to increase yield stability of new crop varieties in drought-prone environments (e.g. Fukai et al. 1999; Shakhathreh et al. 2001).

Genotype-by environment (GxE) interactions are common under drought and make breeding progress difficult. GxE interactions may originate from environmental variation in the timing and severity of water deficits, genetic variation in flowering time, and nutrient deficiencies and toxicities whose occurrence and severity interact with water deficits (Bänziger and Cooper 2001; Cooper et al. 1999). Also, high error variances such as induced by variable plant stand or variable soil water holding capacity are intrinsic to many field trials grown under drought and impede selection decisions, particularly as such trials are often conducted far from breeding stations which tend to be placed at more favorable locations.

Even though there is extensive evidence that selection under target stresses may accelerate breeding gains for stress environments (Atlin and Frey 1990; Bänziger et al. 1997; Ceccarelli et al. 1992; Pederson and Rathjen 1981; Ud-Din et al. 1992), the difficulty of choosing appropriate selection environments, given a highly variable target environment, may limit the identification of superior genotypes (Blum 1979). While breeding programs in high-income countries may resort to real-time GIS information for adequately weighting information from METs (Podlich et al. 1999), those opportunities rarely exist in low-income

countries as there is a lack of both real-time GIS information and resources for conducting a large number of METs.

CIMMYT started in the 1970s to improve tropical maize for drought tolerance given that drought is an important factor limiting maize production in low-income countries (Edmeades et al. 1989). Progenies of experimental maize populations were evaluated under three carefully managed water supply levels: (i) flowering drought stress, (ii) grain-filling drought stress, and (iii) well-watered conditions. Selection was for an index that sought to maintain anthesis date and grain yield constant under well watered-conditions, increase grain yield and stem and leaf extension under drought and decrease anthesis-silking interval (ASI), leaf senescence and canopy temperature under drought (Bolanos and Edmeades 1993a). Compared to populations selected using METs, drought selections significantly increased grain yield across all water levels and decreased ASI and ear abortion under drought. Selection gains under drought were due to increased partitioning of dry matter to the growing ear, whereas biomass production, and likely water uptake, did not change (Bolanos and Edmeades 1993a and 1993b; Edmeades et al. 1993 and 1999).

Most assessments of progress of CIMMYT's drought tolerant maize populations were conducted in the environment where the populations were selected and it may be hypothesized that selection gains may be limited to the particular drought conditions in the selection environment. Byrne et al (1995) demonstrated a greater yield stability of one drought tolerant population as compared to its conventionally-selected counterpart across international testing locations, and improvements under drought were also associated with selection gains across a wide range of nitrogen supply levels (Bänziger et al. 1999 and 2002), indicating that a screening approach using managed drought screening environments may have wider merit.

In the 1997 season, CIMMYT initiated a program targeted at improving maize for the drought-prone mid-altitudes of southern Africa. The breeding program was product-oriented and therefore simultaneously addressed several high-priority constraints including drought, low N and major leaf and ear diseases. This paper describes the target environment, selection methodology used, selection differential to commercial check hybrids, and makes conclusions on breeding strategies that increase productivity in highly variable drought-prone environments.

Target environment

Maize is the main staple in southern Africa where it is grown on over 12 million hectares (FAOSTAT 2003). Information about maize growing environments and the relative importance of abiotic and biotic stress factors is sketchy (Bänziger and de Meyer 2002). Setimela et al. (2003) analyzed trial data from 290 well-adapted maize genotypes, over three years and 94 sites in southern Africa using sequential retrospective pattern analysis (DeLacy et al. 1996). Cluster analysis applied to the most prominent GxE interactions grouped trial sites into eight mega-environments mainly distinguished by season rainfall, maximum temperature, subsoil pH and N application. GIS information was available for season rainfall, maximum temperature and subsoil pH (Hodson et al. 2002) and used to map maize mega-environments (Table 1, Figure 1).

Table 1. Characteristics of maize mega-environments in southern Africa as identified through sequential retrospective pattern analysis of METs.

Maize mega environment	Maximum temperature (°C)	Season precipitation (mm)	Subsoil pH (water)	Area in southern Africa (10 ³ ha)	Area in southern Africa (%)
A	24-27	> 700	< 5.7	46,282	18.2
B	24-27	> 700	> 5.7	28,826	11.4
C	24-30	< 700		48,291	19.0
D	27-30	> 700	< 5.7	17,166	6.8
E	27-30	> 700	> 5.7	49,589	19.6
F	>30	> 700		17,146	6.8
G	>30	< 700		38,403	15.1
H	<24			7,897	3.1

Classification by maximum temperature distinguished different elevations – mega-environments A to E corresponding to the mid-altitudes, mega-environments F and G to the lowlands and mega-environment H to the highlands – but seem also related to disease incidence, with leaf diseases such as *Cercospora zea-*

maydis, *Puccinia sorghi*, and *Exserohilum turcicum* the most prevalent in mega-environments A and B, downy mildews occurring in mega-environments F and G, and *Puccinia polysora* and *Helminthosporium maydis* likely occurring mostly in mega-environment F. Information on subsoil pH originated from the FAO Digital Soil Map of the World that derived soil properties from soil types (FAO 1995). Soil analyses suggest that more areas are affected by low subsoil pH (e.g. Nyamangara et al. 2000) and therefore distinction between mega-environments A and B, and D and E rather imprecise.

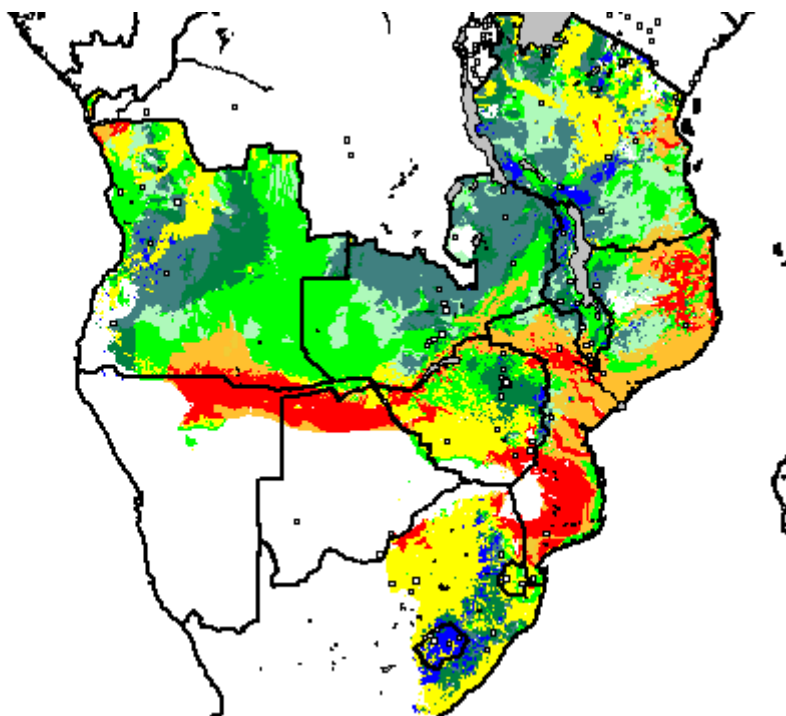


Figure 1. Maize mega-environments in southern Africa delineated by combinations of maximum temperature, season precipitation and subsoil pH. Table 1 lists colour codes. White areas with rainfall < 400 mm were excluded from the analysis. Squares indicate trial sites used for defining mega-environments. Climatic and edaphic data were from Hodson et al. (2002).

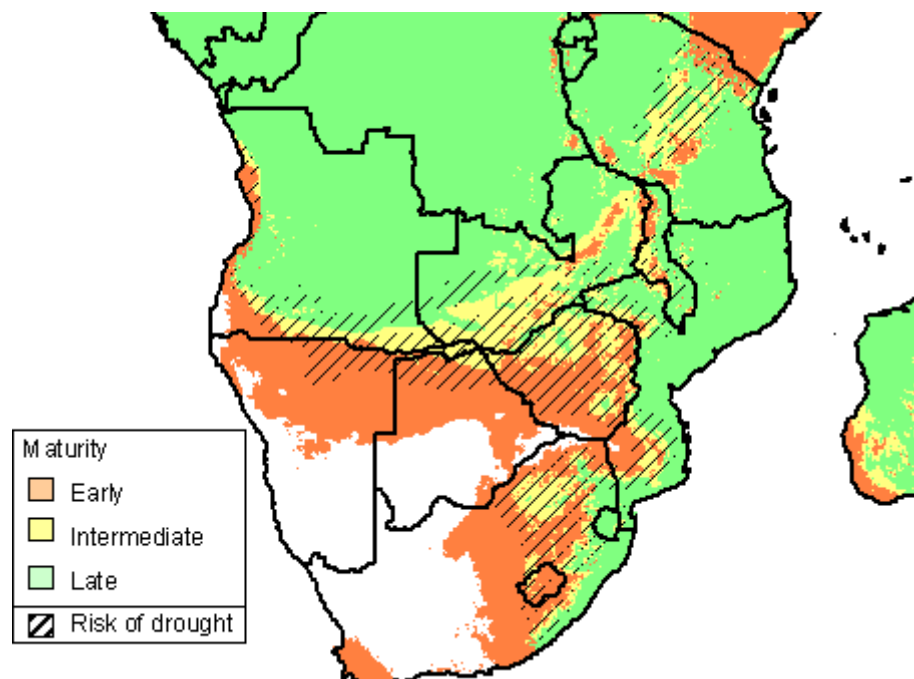


Figure 2. Growing season length and risk of drought in southern Africa. Early, intermediate and late maturity correspond to < 2000 °d, 2000-2250 °d and > 2250 °d (Kiniry et al., 1991). Risk of drought indicates areas where rainfall is less than 50% of potential evapotranspiration for a minimum of 20% of the season and in more than 50% of all years. Data are from Hodson et al. (2002).

Most trials with sub-optimal N application clustered with trials in mega-environments D and E, which may be indicative of less fertile soil types in those areas or may simply be coincidental.

In this analysis of maize mega-environments, the effect of maturity on GxE was excluded by adjusting grain yield in each trial for anthesis date using a linear regression, and mega-environment classification was based on long-term averages of climatic data. Figure 2 shows growing season-length based on heat units (Kiniry et al. 1991) and areas where within-season drought – defined as precipitation being less than 50% of potential evapotranspiration for a minimum of 20% of the season – was estimated to occur in more than 50% of all years (Hodson et al. 2002). Unless adjusted for maturity, even small differences in maturity result in additional GxE (Bänziger and Cooper 2001) and seasonal variation in rainfall may contribute to additional GxE-by-year interactions (Podlich et al. 1999).

Socio-economic constraints further amplify bio-physical constraints in southern Africa. In spite of maize yield potentials of above 10 t/ha, fertilizer consumption on crop land averages less than 25 kg/ha and seems to have decreased over the past 10 years (FAOSTAT 2003) as farmers have faced increasing input costs and decreasing product prices. In southern Africa, nitrogen is likely the most limiting nutrient followed by phosphorus and other nutrients including zinc, sulfur, potassium, magnesium and calcium. Africa has only one sixth of the road network that India had in the 1950s before the onset of the ‘green revolution’ (Hazell and Johnson 2002), making access to markets and the delivery of bulky inputs such as fertilizer and lime difficult. Only about 5% of the cropped area is irrigated (FAOSTAT 2003).

Given an average maize yield of 1.3 t/ha, maize varieties with increased abiotic stress tolerance and significant genetic gains at the lower yield level could probably have a greater impact on maize production and food security in Africa than breeding focusing on a relative minority of farmers that crop under socio-economically and bio-physically favorable conditions. The challenge to breeding comes from the highly variable drought-prone environment, as evidenced by aggregated regional maize production which fluctuated from 7.6 to 22.7 million tons over the past 20 years (FAOSTAT 2003) and in close correlation with rainfall (Heisey and Edmeades 1999).

Selection approach

The selection approach initiated for southern Africa in 1997 initially used four types of selection environments: (i) recommended agronomic management/high rainfall conditions, (ii) low N stress, (iii) managed drought, and (iv) random drought (Table 2). In most years, however, the experiments under random drought had very low heritabilities due to uneven plant stand, and the information from those experiments typically contributed less than 10% to the overall selection decision. Selection was therefore mainly based on the other three selection environments i.e., recommended agronomic management/high rainfall conditions, low N stress and managed drought. All selection environments were in Zimbabwe and, apart from the random drought experiments, on reddish clay soils. The random drought experiments were on black clay soils and granitic sands.

Table 2. Environments and criteria used for selecting CIMMYT maize hybrids

Management	Season	# Sites	Selection criteria
Recommended/High rainfall	Main	2	Yield, disease resistance, lodging, husk cover
Low N	Main	1	Yield, ASI ¹ , leaf senescence, ears per plant, ear rot
Managed drought	Dry	1	Yield, ASI ¹ , leaf senescence, ears per plant
Random drought	Main	1-2	Yield

¹ Anthesis-silking interval

The experiments under recommended agronomic management/high rainfall conditions were conducted at two locations, Harare (17.80 S, 31.05 E, 1468 masl) and Kadoma (18.32 S, 30.90 E, 1155 masl) both with 700-800 mm rainfall and 650-700 mm potential evapotranspiration during the season. The experiments under low N were also conducted at Harare using, except for N management, the same crop management practices as under recommended agronomic management. Low N experiments were grown in fields that were depleted of N by continuously cropping maize (main season) or irrigated wheat (winter dry season), removing all stover biomass after harvest and not applying any N fertilizer. The experiments under low N yielded on average 25-35% (1.5-3.5 t/ha) of the yields obtained under recommended agronomic management/high rainfall conditions (6-9 t/ha) which has shown to be optimal for expressing N stress

tolerance in tropical maize (Bänziger et al. 1997). The experiments under managed drought stress were conducted during the winter dry season in Chiredzi (21.03 S; 31.57 E, 392 masl). Three (early-maturing genotypes) to four (late-maturing genotypes) irrigations totaling 200 to 250 mm of water were applied at the beginning of the season and irrigation stopped at 43 to 57 days after planting (about 50 days before anthesis). The crop completed its lifecycle without any further irrigation or rain and typically yielded between 1-3 t/ha. More details about stress management are provided by Bänziger et al. (2000). All selection experiments were grown using 1-row plots, two replications and incomplete lattice designs.

In each selection environment, selection was for an index of grain yield and secondary traits, with secondary traits together being weighted about 50% (recommended agronomic management/high rainfall) or 75-100 % (low N, managed drought) of grain yield. Relatively greater weights were applied on secondary traits under conditions with low heritability of grain yield and high heritability and genetic variance of secondary traits. Under recommended agronomic management/high rainfall conditions, secondary traits included increased resistance to *Cercospora zae-maydis*, maize streak virus, *Exserohilum turcicum*, *Puccinia sorghi* and ear rots (*Fusarium* and *Diplodia* sp.), decreased stem and root lodging and increased husk cover. Under low N and managed drought, secondary traits included decreased ASI, decreased barrenness and decreased leaf senescence. These traits showed high heritability and high genetic correlation with grain yield under drought and N stress (Bänziger and Lafitte 1997; Edmeades et al. 1998). Ear rot resistance was also assessed under low N as N stress typically results in increased ear rot incidence. In each selection environment, a linear selection index was used. The information from each environment was then weighted equally to select the best genotypes across environments while adjusting for differences in anthesis date and plant height.

Realized selection differentials

Hybrids resulting from this selection approach were evaluated across eastern and southern Africa between 2000 and 2002 using replicated trials that included advanced maize breeding germplasm submitted by public and private breeding programs (Vivek et al. 2001, 2002 and 2003). Entries were grouped by maturity and evaluated in 2-row plots by collaborators from the public and private sector at 36-65 sites per year and trial. All hybrids in the following comparison had similar vigor (mostly three-way cross hybrids) and general adaptation to southern and eastern Africa, i.e. they did not include any exotic materials. Small differences in maturity among individual hybrids were excluded by adjusting grain yield in each trial for anthesis date using a linear regression.

Over the three years, a total of 42 hybrids from CIMMYT's stress breeding program were compared with 41 released and prereleased hybrids from five private seed companies (Monsanto, Pannar, Pioneer International, Seed-Co International and ZamSeed). Both groups included all hybrids submitted by CIMMYT's stress breeding program and private seed companies, i.e. they were not further selected for the purpose of this analysis. All trials included other hybrids (e.g. from IITA and public national breeding programs) that were not included in this study. Private seed companies had selected their hybrids using METs conducted under recommended agronomic management/high rainfall conditions and in some instances random drought, and using similar selection criteria to those used by CIMMYT under those conditions, high yield and improved disease and lodging resistance. Different to CIMMYT hybrids, private seed company hybrids had never been selected under low N or managed drought.

Average trial yields across the three years ranged from less than 1 t/ha to above 10 t/ha (Table 3). Reasons for low trial yields were wide-ranging, including drought, N stress, soil acidity and disease incidence, and not conclusively known in many cases. Hybrids from CIMMYT's stress breeding program showed a consistent advantage over private company hybrid checks at all yield levels. Selection differentials seemed largest between 2 to 5 t/ha and they became less significant at higher yield levels. Some of the trials were grown under managed N and drought stress. When they were excluded from the analysis, selection differentials remained of similar size. Selection differentials averaged 0.48 t/ha and 0.35 t/ha in trials grown under managed drought and managed N stress, respectively, indicating rather larger gains under drought than N stress. We also calculated linear regressions for each hybrid on average trial yield (Eberhart and Russell 1966). Based on those regressions, the advantage of CIMMYT hybrids over private company hybrids averaged 0.40 t/ha at the 1 ton yield level (1.24 t/ha versus 0.84 t/ha) and decreased to 0.25 t/ha at the 10 ton yield level (10.27 t/ha versus 10.23 t/ha).

Table 3. Selection differentials in trials grown across eastern and southern Africa of 42 CIMMYT hybrids selected for drought and N stress tolerance in Zimbabwe as compared to 41 private company check hybrids.

Average trial yield or stress type (t/ha)	# Trials	Grain yield		Yield advantage		Statistical significance of difference
		CIMMYT hybrids (t/ha)	Check hybrids (t/ha)	absolute (t/ha)	relative (%)	
All trials						
0-1	18	0.63	0.56	0.07	13	0.090
1-2	41	1.60	1.34	0.25	19	0.000
2-3	38	2.79	2.33	0.45	20	0.000
3-4	48	3.71	3.29	0.42	13	0.000
4-5	31	4.79	4.22	0.57	14	0.000
5-6	27	5.59	5.23	0.36	7	0.000
6-7	21	6.68	6.41	0.27	4	0.028
7-8	22	7.52	7.31	0.21	3	0.036
8-9	20	8.76	8.26	0.49	6	0.000
>9	7	9.66	9.37	0.30	3	0.084
Excluding trials under managed drought or low N (trials above 5 t/ha did not include any managed drought or low N trials)						
0-1	14	0.69	0.62	0.07	11	0.063
1-2	28	1.61	1.35	0.26	19	0.000
2-3	26	2.77	2.36	0.42	18	0.000
3-4	34	3.72	3.32	0.39	12	0.000
4-5	29	4.81	4.25	0.56	13	0.000
Only trials under managed stress						
Drought	17	3.01	2.53	0.48	19	0.000
Low N	28	2.33	1.97	0.35	18	0.003

There are several factors that could have influenced the expression of selection differentials in this study. CIMMYT and private seed company hybrids had a different germplasm base and they were not selected alongside each other. Some private seed company hybrids had been on the market for several years (but were still considered competitive) whereas all CIMMYT hybrids were recently selected. Most private seed company hybrids were tested at more locations and years before entering the trials, whereas selection of CIMMYT hybrids was mostly based on one to two year data in Zimbabwe. Several private seed companies had a longer term breeding program in the region than CIMMYT. These factors may have given an advantage or disadvantage to some individual hybrids. They are, however, unlikely to have influenced the relatively larger selection differential between the two groups under low yielding conditions, which is different to yield differences reported between old and recent hybrids selected using classical breeding approaches (Castleberry et al. 1984; Duvick and Cassman 1999; Tollenaar et al. 1997).

Breeding for drought tolerance – old and new insights

Early work in maize suggested that selection under dryland conditions may significantly reduce selection gains (Arboleda-Rivera and Compton 1974; Hallauer and Sears 1969) whereas selection under irrigated conditions may have some spill-over to dryland conditions (Johnson and Geadelmann 1989). As a consequence, many breeders adopted selection under high potential conditions followed by extensive multi-environment testing as the most effective approach to maize improvement. More recently, Duvick and Cassman (1999) and Tollenaar et al. (1994) concluded that modern maize hybrids have increased stress tolerance rather than a higher yield potential. While their results may be less an indication for the most effective breeding approach, they clearly show the importance of increased stress tolerance in successful hybrid varieties.

Theoretical considerations suggest that testing sites should be representative of production conditions and selection decisions weighted according to the relative economic value of the crop produced under stress and non-stress conditions (Rosielle and Hamblin 1981). However, the multitude of possible GxE

interactions that could occur due to different stress combinations and at different developmental stages of a crop (Blum 1979) seems to have discouraged greater investments in breeding approaches that target stress environments (see e.g. Villasenor Mir 2000). Where screening under carefully managed or selected drought conditions was used, genotypic variation in drought tolerance was often found (e.g. Dencic et al. 2000; Edmeades et al. 1999; Link et al. 1999; Molina et al. 2001; Sadeghian et al. 2000; Yadav et al. 2003). Accounts of selection progress after large-scale investments in stress screening approaches as suggested by Rosielle and Hamblin (1981), however, are rarely found.

Our results show that including selection under high priority abiotic stresses, such as drought and low N, in a routine breeding program and with adequate weighting can significantly increase maize yields in a highly variable drought-prone environment and particularly at lower yield levels. We think that several concepts during selection were particularly useful in guaranteeing breeding progress:

- All yield trials, corresponding to about 1000 hybrids annually, were conducted under the three types of selection conditions, (a) recommended agronomic management/high rainfall conditions, (b) low N stress, and (c) managed drought. As a result, selection for abiotic stress tolerance was already incorporated at early breeding stages when genetic variance and selection intensities were large. In classical breeding approaches, METs which expose new crop varieties to drought are typically conducted at later breeding stages when genotypes are fewer and genetic variance less.
- Drought and N stress were carefully managed to keep heritability high (see Bänziger et al. 2000). This differs from earlier selection attempts that used random drought conditions (see e.g. Johnson and Geadelmann 1989).
- Stress intensities were used that optimally express genotype-by-stress interactions in maize (Bänziger et al. 1997, Bolaños and Edmeades 1996), even if it meant that more severe stress intensities were applied than occur in the average target environment as mild stress intensities are less likely to result in significant genotype-by-stress interactions.
- Secondary traits whose variance increases under stress and whose heritability remains high (Bänziger and Lafitte 1997; Edmeades et al. 1998), and improved statistical design and analysis techniques (e.g. Gilmour 1998) were employed to keep heritability high.
- Selection decisions were made after adjusting for differences in flowering dates that otherwise would have contributed to GxE (Bänziger and Cooper 2001; Cooper et al. 1999)
- Selection was for good performance across selection environments as suggested by Rosielle and Hamblin (1981), not for the ratio of yield under stress and non-stress conditions which has sometimes being termed 'stress tolerance,' but is typically negatively correlated with yield (see e.g. Link et al. 1999).

Conclusions

It is only recently that carefully selected or managed abiotic stress screening approaches have been more widely used for assessing the stress tolerance of crop genotypes. Our results suggest that simultaneous selection for tolerance and resistance to abiotic and biotic stresses, while also monitoring performance under high potential conditions, can result in significant breeding progress in target environments where combinations of those stresses occur and particularly at lower yield levels. While assessing the effectiveness of various selection conditions for breeding progress in the target environment is inherently difficult, as large and long-term breeding investments are involved, breeders may have been too concerned with keeping heritability high while ignoring the need to adequately representing the target environment during selection. Managed stress screening approaches provide an opportunity to keep heritability high and adequately representing abiotic stress factors that are relevant in the target environment. It is desirable that more breeding programs use high-priority abiotic stresses in their mainstream breeding program, so that more experience on breeding approaches that effectively target stress environments can be gained. Such insights are particularly relevant for breeders in low-income countries that target production conditions that are stressed due to both biophysical and socio-economic reasons.

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