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RESEARCH

Efficiency of Managed-Stress Screening of Elite Maize Hybrids under Drought and Low Nitrogen for Yield under Rainfed Conditions in Southern Africa

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ABSTRACT

Maize (*Zea mays* L.) yields in southern Africa are low, due largely to drought and low-N stress. Selection of stress-tolerant genotypes by CIMMYT is conducted indirectly under managed stress conditions, although the selection efficiency of this approach is not known. A retrospective analysis of 704 elite hybrid trials conducted from 2001 to 2009 was used to determine the relative ability of optimal, low-N, and managed drought trials to predict performance under the conditions of random abiotic stress and low-N fertility usually faced by African farmers. Well-fertilized trials in the rainy season were categorized as having experienced random abiotic stress if mean yield was <3 t ha^{-1} and the yield–anthesis date correlation was <0.1; otherwise they were classed as optimal. High genetic correlations were estimated between random abiotic stress and low-N or optimal conditions. Heritability was highest under optimal conditions and lowest under random abiotic stress. Indirect selection under low-N and optimal conditions was more efficient than direct selection under random abiotic stress or indirect selection under managed drought, especially for early maturing genotypes, but direct selection was most efficient for predicting performance under low N. Elite maize hybrids tolerant to random abiotic stress can be most efficiently selected under optimal and/or low-N conditions while low-N tolerant genotypes should be selected directly under low N.

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Abbreviations: *H*, broad-sense heritability; w^2, repeatability.

Maize (*Zea mays* L.) is the most important crop in eastern and southern Africa in area harvested and the contribution of calories and protein to diets (FAO, 2011). Yields in Africa are considerably lower than the world average because the cultivation of maize is often prone to drought and low soil fertility (primarily N but also P and other nutrient deficiencies) in addition to biotic stresses (FAO, 2010). There are also often complex interactions among these stresses, such as drought hindering nutrient uptake. Maize grain yield is reduced by up to 80% under drought and low-N conditions (Betrán et al., 1997; Bänziger et al., 1997, 2006). Drought events are expected to increase in the coming years in Africa due to climate change (Williams and Funk, 2010). Average fertilizer use in Africa in 2007 was 19 kg ha^{-1} of arable land and had decreased by 11% from 1997; by comparison farmers in Asia and western Europe applied 205 and 199 kg ha^{-1}, respectively (IFDC, 2010). High fertilizer and transport costs make it unlikely that fertilizer use in maize production in eastern and southern Africa will increase greatly in the near future. Further,

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expansion of maize cultivation into marginal and less fertile lands will increase the percentage of area affected by drought and low-N stress (FAO, 2010), accentuating the need to select genotypes tolerant to these conditions.

For breeding stress-tolerant maize, selection can be either conducted directly under stress, indirectly under optimal conditions, or under both optimal and stress conditions (Byrne et al., 1995). Assuming the same selection intensity under optimal and stress conditions, the relative efficiency of indirect selection for grain yield under stress is a function of the broad-sense heritability (*H*) under optimal and stress conditions and the genetic correlation between yield under stress versus nonstress conditions (Atlin and Frey, 1990; Falconer and Mackay, 1996). The efficiency of indirect selection will be higher than that of direct selection if *H* is higher in the indirect test environment and if the genetic correlation between the indirect and direct selection environments is high.

Inconsistent results have been reported with respect to the genetic correlation between performance under optimal and low-N conditions and *H* of grain yield in such test environments, with some authors suggesting an advantage for direct selection under low-N conditions (Lafitte and Edmeades, 1994; Bänziger et al., 1997; Mandal et al., 2010) and others for indirect selection under optimal conditions (Gallais et al., 2008; Anbessa et al., 2010). Bänziger et al. (1997) showed that the genetic correlation between optimal and low-N conditions declines with increasing difference in mean yield between the stress and nonstress environments. Therefore, the different results of the studies mentioned are likely related to the variation in yield reduction due to stress.

While genotypes can be easily selected under different levels of soil N, their selection under unpredictably variable abiotic stress conditions such as drought and heat is made difficult by random occurrence and intensity of such conditions. As a result there are few reports on the efficiency of indirect selection in managed drought and low-N conditions to improve grain yield under random abiotic stress conditions such as encountered in eastern and southern Africa. The maize breeding program of the International Maize and Wheat Improvement Center (CIMMYT) selects for grain yield under managed stress conditions, such as flowering- and grain-filling-stage drought stress imposed by withholding irrigation in the dry season and low-N stress imposed by planting trials without fertilization in fields that have been depleted of N by growing crops without fertilization and removing the resulting biomass; these managed-stress screens are used in all replicated yield testing stages. The objective of such trials is to simulate a clearly defined stress that is relevant in farmers' fields (Bänziger et al., 2000). These screens appear to have been effective in generating hybrids that perform well in low- and high-yielding environments in Africa (Bänziger et al., 2006). However, it is not known to what extent evaluation under managed drought, managed low-N, and optimal conditions contributes to selection gains. Managed drought stress trials are usually conducted in the dry season when temperature, daylength, humidity, and disease pressure may differ from the main growing season. Managed low-N stress trials are conducted at stress levels causing more than 70% grain yield reduction (Bänziger et al., 1997), which may not reflect all N-stress scenarios occurring in the target environment. Bänziger et al. (1999) also found correlated responses to selection under drought for response under low-N stress. While Venuprasad et al. (2007) indicated that rice (*Oryza sativa* L.) genotypes selected in managed drought trials were also adapted to randomly occurring drought, information on the relative efficiency of indirect selection under optimal, managed drought, and low-N conditions for genotypes adapted to random abiotic stress occurring in the main growing season in eastern and southern Africa is, to the best of our knowledge, lacking in maize.

The objectives of this study were to (i) estimate *H* of maize grain yield in and the genetic correlation among optimal, managed drought, random abiotic stress, and low-N conditions and (ii) use these estimates to evaluate to what extent indirect selection under managed drought or low-N conditions is predictive of grain yield under random abiotic stress conditions relative to selection under optimal conditions. With managed drought and low-N selection trials providing clearly defined abiotic stress conditions, the results may also indicate the extent to which drought and low-N stress were responsible for the stress conditions occurring in a large set of trials (704 trials conducted over 9 yr in up to 93 locations in 17 countries) conducted in the target environment in eastern and southern Africa.

MATERIAL AND METHODS

Experimental Design

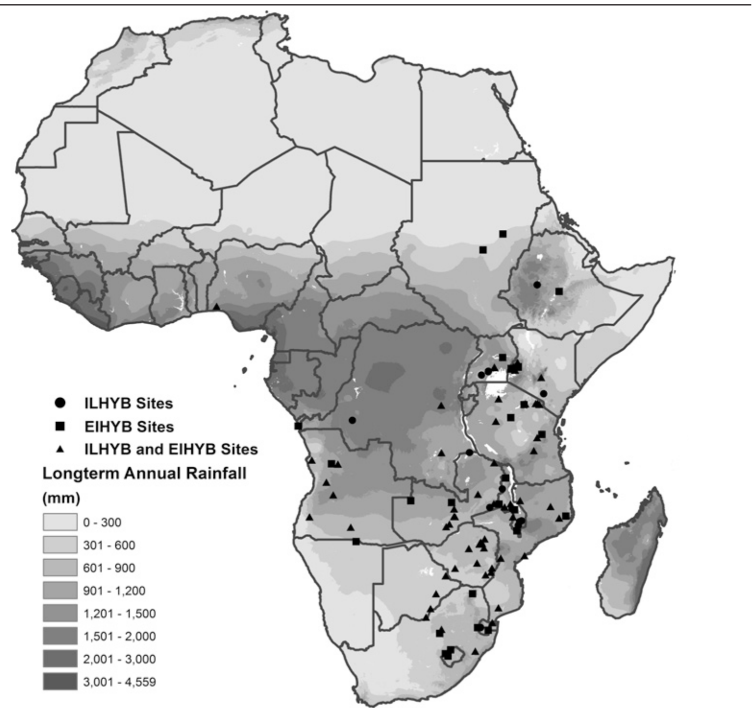
The study is based on data generated from 2001 to 2009 on the performance of 448 advanced maize hybrids, of which 219 were of early and 229 of later maturity (Table 1). The early maturity group was evaluated in 376 trials at 93 locations in 17 countries and the late maturity group in 328 trials at 84 locations in 14 countries in eastern and southern Africa. The trials were conducted by national agricultural research programs and private seed companies in collaboration with CIMMYT and are the last step in the breeding pipeline before national release testing in the countries within the region. New hybrids entered the trials annually and were tested for up to 3 yr, with some low yielding and disease susceptible or otherwise undesirable genotypes discarded each year. Therefore, there was no genotype in common across all 9 yr. Within each year, trials were balanced (i.e., the same hybrids were tested at all locations) but the number of hybrids in common in pairs of consecutive years varied between 6 and 31. Consequently, for the purposes of this study, only analyses within years were performed.

For selecting hybrids adapted to the random abiotic and low-N stress that most African farmers face, these regional trials evaluate hybrids for yield under optimal as well as low-N, managed drought, and random abiotic stress conditions. Trials conducted in

Table 1. Location of trials in Africa for the early (squares), late (circles), and both maturity groups (triangles) from 2001 to 2009 and distribution pattern of long-term annual rainfall (mm) interpolated according to Hijmans et al. (2005).

Year	N_{Gen}†	N_{Loc} (N_{Env})‡
Early maturity group		
2001	40	27 (37)
2002	30	44 (61)
2003	34	37 (52)
2004	23	32 (43)
2005	33	19 (25)
2006	33	29 (35)
2007	28	24 (30)
2008	62	43 (53)
2009	60	32 (40)
2001–2009	219	93 (376)
Late maturity group		
2001	42	26 (33)
2002	39	35 (51)
2003	46	33 (43)
2004	44	33 (41)
2005	48	19 (24)
2006	31	24 (32)
2007	42	22 (25)
2008	39	35 (43)
2009	37	30 (36)
2001–2009	229	84 (328)

Location of trials in Africa



†N_{Gen}, number of genotypes.

‡Number of locations (N_{Loc}) and number of environments constituting all location–trial combinations (N_{Env}, in parenthesis).

the rainy season as well as irrigated trials in the dry season (i.e., managed drought trials) were well fertilized unless they were purposely grown under low-N conditions. Well-fertilized trials conducted in the rainy season were grown under a wide range of conditions that were individually difficult to characterize for the occurrence of one particular stress. From 2001 to 2009 in total, 217 and 187 well-fertilized trials were conducted for the early and late maturity group, respectively. Those trials were categorized as having been subjected to random abiotic stress or optimal conditions based on the thresholds explained in the next section. Managed drought stress trials were conducted in the dry season, when stress was imposed at flowering and grain filling by stopping irrigation around 3 wk before anthesis until 4 wk after anthesis (Bänziger et al., 2000). For conducting low-N trials, the fields were depleted in N by growing unfertilized, nonleguminous crops and removing the crop biomass for several seasons before selecting genotypes in these fields. Low-N trials usually received no N fertilizer, but other fertilizer elements were applied according to recommended levels. At some locations, low-N trials were irrigated when drought occurred in the rainy season following details described in Bänziger et al. (2000, 2006). Out of the 376 trials evaluating early maturing materials, 22 were conducted under managed drought stress and 49 were conducted under low N. Of the 328 late-maturity trials, 24 were conducted under managed drought and 37 under low N.

Trials were laid out as α lattice designs with three replicates and plot size varying from 1.88 to 12.00 m^2. Trials included 23 to 62 hybrids and one to three local checks, with the number of genotypes being constant across locations within a given year. Ear yield was determined in tonnes per hectare adjusted to 10% moisture level assuming 80% shelling (Betrán et al., 2003). Days to anthesis were recorded when 50% of the plants had extruded at least one anther.

Categorization of Well-Fertilized Trials into Optimal and Random Abiotic Stress Trials

From 2001 to 2009 an average of 11 and 15 well-fertilized trials conducted in the rainy season were categorized by the local trial coordinator at harvest as having been affected by drought stress for the early and the late maturity group, respectively. However, some of these trials were not low yielding, and some low-yielding trials were not reported as having experienced stress. A mean yield of 3 t ha^{-1} and a correlation coefficient of 0.10 between grain yield and anthesis data on a plot basis were therefore used as thresholds to categorize well-fertilized trials as either optimal or random abiotic stress conditions. The rationale for this was that trials with a mean grain yield <3 t ha^{-1} were stressed. A negative correlation between grain yield and anthesis date is usually observed in managed drought trials and may be observed under low-N stress whereas in high-yield, optimally managed trials, this correlation is usually moderately or strongly positive. Therefore, trials conducted in the rainy season were classified as having experienced random abiotic stress conditions when the trial mean was <3 t ha^{-1} and the correlation coefficient between grain yield and anthesis date was <0.10. All other trials were treated as having experienced optimal conditions, including those with a trial mean <3 t ha^{-1} but a correlation coefficient between grain yield and anthesis date >0.10, assuming that low yields were due to biotic stress rather than drought or low N availability.

Definition of Target and Test Environments

In the analysis of the regional trials, random abiotic stress and optimal conditions are usually not separated and considered as one target environment. However, since the main purpose of our study was to determine how best to predict hybrid performance under random abiotic stress, we considered random abiotic stress to be a target environment and optimal, managed drought, and managed low-N stress to be test environments for genotypes adapted to random abiotic stress. Because most farmers in southern Africa apply little or no N fertilizer, we also considered low-N trials to represent a breeding target. To select genotypes adapted to random abiotic stress and low-N conditions, test locations assigned to these two growing conditions were considered to be a random sample of both target environments. While CIMMYT locations were sampled each year, those of some regional collaborators changed over time. We compared the predicted efficiency of direct selection for yield under random abiotic stress with indirect selection under optimal, managed drought, and low-N conditions. The predicted efficiency of direct selection under low-N conditions was also compared with that of indirect selection under optimal, managed drought, and random abiotic stress conditions.

Statistical Analysis

For estimating the mean and repeatability (w^2) of grain yield in each trial, an α lattice analysis of variance was employed using a mixed-model approach. First, a single-trial analysis for grain yield was conducted based on the α lattice design; trials with $w^2 < 0.15$ were excluded from the combined analysis. For each test environment (optimal, managed drought, random abiotic stress, and low N) the variance components and H of grain yield were calculated in an analysis over trials within each year using the model

$$y_{ijklm} = \mu + g_i + e_j + ge_{ij} + r_k(e_j) + b_l[re]_{kj} + \varepsilon_{jklm}, \qquad [1]$$

where μ denotes the overall mean, g_i the genetic effect of genotype i, e_j the effect of trial j, ge_{ij} the interaction between genotype i and trial j, $r_k(e_j)$ the effect of the replication k nested in the trial j, $b_l[re]_{kj}$ the incomplete block l nested in the replication k and trial j, and ε_{jklm} the residual effect of the plot m nested in block l, replication k, and trial j. If the genotypes were tested in only one trial per test environment in a given year, the genotype × trial variance (σ^2_{ge}) was not estimated. While the adjusted genotype means in each test environment were calculated by considering the genotype as fixed, all factors were considered as random effects for estimating the variance components in the combined analysis over trials for each test environment. Significance of grain yield differences under optimal versus stress conditions was tested by applying the Welch Two Sample t test. Variance components were expressed for the genotypic variance (σ^2_g), σ^2_{ge}, and the residual variance due to plot error (σ^2_ε) as a percentage of the total phenotypic variance ($\sigma^2_p = \sigma^2_g + \sigma^2_{ge} + \sigma^2_\varepsilon$) according to Hallauer et al. (2010). In each type of test environment (optimal conditions, random abiotic stress, managed drought, or low N), H of grain yield was calculated as

$$H = \sigma^2_g / [\sigma^2_g + (\sigma^2_{ge}/e) + (\sigma^2_\varepsilon/er)], \qquad [2]$$

where e denotes the number of environments constituting all location–trial combinations and r the number of field replicates. Because the number of trials in each test environment class differed greatly (optimal trials were the most frequent followed in descending order by random abiotic stress, low-N, and managed drought trials), much of the variation in H observed among test environments was a result of differences in environmental replication. Therefore, H of each test environment was also predicted based on the variance components in each year but assuming testing in five trials. This provided an estimate of the precision of evaluation in each type of test environment unconfounded by differences in testing effort.

The adjusted genotype means from each test environment were used to calculate the genetic correlations among them for each year without including the local checks. Following Cooper et al. (1996), the genetic correlation was calculated as the ratio between the phenotypic correlation and the square roots of H of grain yield under direct and indirect selection. To avoid bias, the estimates of genotypic correlation were allowed to exceed the upper limit of 1 while they were restricted to ≤1 to get reasonable estimates of indirect selection. These correlation estimates were used along with H of grain yield to predict the relative efficiency of indirect selection (RE) for each pair of test environments assuming the same selection intensity under optimal and stress conditions as proposed by Falconer and Mackay (1996):

$$\mathrm{RE} = r_g(H_1/H_2)^{1/2}, \qquad [3]$$

where r_g is the genetic correlation between performance in the test and target environments and H_2 and H_1 are the H of grain yield in the target and test environments, respectively. The selection efficiency estimates were based on the whole data set as well as standardized for e = five trials. To provide an overall measure, the average and standard deviation of H, the genetic correlation, and the relative efficiency of indirect selection from 2001 to 2009 were calculated for each test environment. If only one trial was available for a particular test environment, this was not used for estimation of indirect selection efficiency because H estimates from single trials are biased upward by the genotype × trial interaction and could lead to unrealistically high estimates of the efficiency of indirect selection.

All statistical analyses were conducted using the R software (version 2.10.0; R Development Core Team, 2009). The variance components and adjusted means of grain yield were estimated using the ASReml package (Butler et al., 2007).

RESULTS

Trial Selection and Categorization into Optimal and Random Abiotic Stress Conditions

Averaged over the years 2001 to 2009, the phenotypic correlation between the trial w^2 and mean grain yield was around 0.4 (Fig. 1; $p < 0.001$) for both maturity groups. Around 12% of trials had w^2 of grain yield less than 0.15 and were therefore excluded. The exclusion of trials was more frequent under managed drought and random abiotic stress than under optimal and low-N conditions.

On average 29.7% of trials with $w^2 > 0.15$ conducted in the rainy season were categorized as random abiotic stress trials and the remaining as optimal trials by applying a threshold yield of 3 t ha^{-1} as well as a maximum correlation coefficient between grain yield and anthesis date of 0.10 (Fig. 2). In total, 74 out of 275 and 63 out of 238 well-fertilized trials were categorized as random abiotic stress trials for the early and late maturity group, respectively (Table 2). The

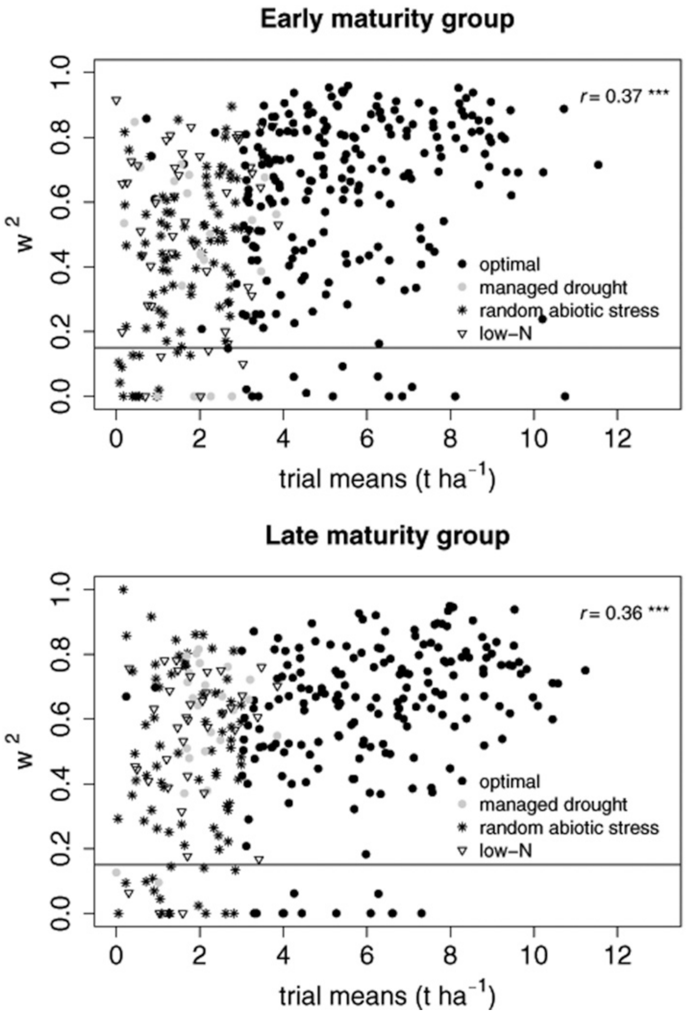


Figure 1. Relationship between trial means of grain yield and the repeatability (w^2) of grain yield in trials conducted from 2001 to 2009. ***Significant at the 0.001 probability level.

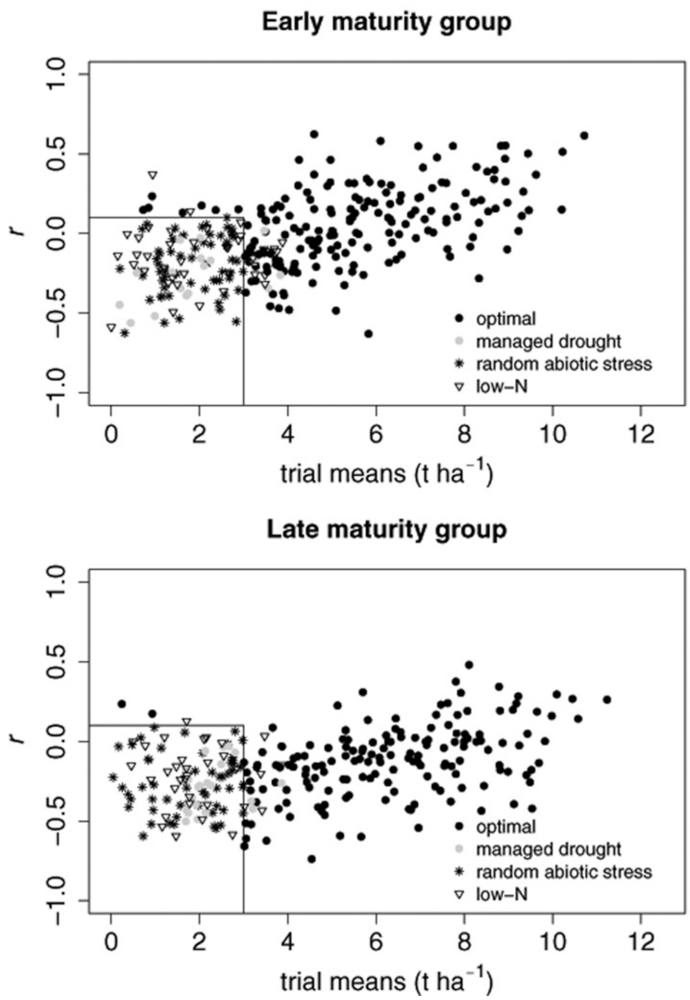


Figure 2. Relationship between trial means of grain yield and the correlation coefficient (r) between grain yield and anthesis date in trials conducted from 2001 to 2009.

random abiotic stress and optimal trials were spread across the same agro-ecological zones. However, random abiotic stress trials were more frequent in agro-ecological zones characterized as wet upper mid-altitude, dry mid-altitude, and dry lowland (Bänziger et al., 2006; data not shown). Eight trials with a mean grain yield of less than 3 t ha^{-1} were categorized as having been conducted under optimal conditions because the correlation coefficient between yield and anthesis date was larger than 0.10. These eight trials had a low to medium infection (score 1–3 out of 5) of gray leaf spot (*Cercospora zeae-maydis*), common rust (*Puccinia sorghi*), or turcicum leaf blight (*Setosphaeria turcica*) or a low to medium percentage (2 to 25%) of stem or root lodging, which might explain their low mean grain yield (detailed data not shown).

Correlation coefficients between grain yield and anthesis date across trials and years were on average 0.09 and −0.11 under optimal, about −0.3 under managed drought and random abiotic stress, and −0.12 and −0.22 under low-N conditions for the early and late maturity group, respectively (Table 3).

Grain Yield under Optimal and Different Stress Conditions

Under optimal conditions the grain yield of the late maturity group (6.26 t ha^{-1}) was significantly higher than that of the early maturity group (5.53 t ha^{-1}, $p < 0.01$; Table 2). Relative to optimal conditions, the grain yield under low-N, managed drought, and random abiotic stress was reduced to about 2 t ha^{-1}, a reduction of 66 and 62% for the late and early maturity groups, respectively, with no significant differences between the two maturity groups.

Estimates of Variance Components and Broad-Sense Heritability of Grain Yield

Averaged across the years 2001 to 2009, σ_g^2 under optimal conditions accounted for 28.0% of the phenotypic variance for the early and 22.3% for the late maturity group (Table 2). Its contribution decreased under stress, with lowest values obtained under random abiotic stress conditions (~10.3%). Under low-N conditions σ_g^2 accounted for 19.0% of the phenotypic variance for the early and 15.7% for the late maturity group. Further, it was higher under

Table 2. Mean and standard deviation of maize grain yield, variance components, and broad-sense heritability (*H*) of grain yield under optimal, managed drought, random abiotic stress, and low-N conditions from 2001 to 2009 as well as predictions of *H* assuming testing in five trials (in italics).

Test environment	N_{Gen}†	N_C†	N_{Env}†	Grain yield (t ha⁻¹)	Variance components‡			*H* (whole set)	Predicted *H* (N_{Env} = 5)
					σ^2_g	σ^2_{ge}	σ^2_ε		
Early maturity group									
Optimal	219	17	201 (217)	5.53 ± 0.61	28.02 ± 11.14	24.17 ± 8.24	47.81 ± 13.95	0.92 ± 0.04	0.85 ± 0.07
Managed drought	210	5	17 (22)	2.29 ± 0.96	14.39 ± 9.30	14.58 ± 4.17	71.04 ± 8.08	0.44 ± 0.21	0.52 ± 0.21
Random abiotic stress	204	13	74 (88)	1.85 ± 0.22	10.29 ± 8.32	23.37 ± 11.76	66.34 ± 14.75	0.55 ± 0.22	0.49 ± 0.22
Low N	219	6	44 (49)	2.04 ± 0.59	19.01 ± 10.66	23.86 ± 11.30	57.13 ± 14.18	0.63 ± 0.21	0.63 ± 0.20
Late maturity group									
Optimal	229	14	175 (187)	6.26 ± 0.39	22.26 ± 4.50	22.41 ± 7.11	55.34 ± 7.85	0.91 ± 0.03	0.68 ± 0.06
Managed drought	216	5	22 (24)	2.11 ± 0.35	17.57 ± 9.43	15.72 ± 8.33	66.70 ± 13.52	0.56 ± 0.19	0.49 ± 0.16
Random abiotic stress	229	10	63 (80)	1.73 ± 0.42	10.28 ± 7.28	18.25 ± 6.39	71.47 ± 11.23	0.61 ± 0.19	0.38 ± 0.16
Low N	220	6	34 (37)	1.82 ± 0.53	15.69 ± 6.95	15.35 ± 4.77	68.95 ± 8.84	0.62 ± 0.14	0.49 ± 0.12

†Total number of genotypes (N_{Gen}), countries (N_C), and environments constituting all location–trial combinations (N_{Env}). The total number of environments excluding and including (in parenthesis) those with repeatability (w^2) < 0.15 is given.

‡Variance components expressed as percentage of the phenotypic variance including the genotype (σ^2_g), the genotype × environment (σ^2_{ge}), and the residual variance (σ^2_ε).

Table 3. Mean, standard deviation, minimum, and maximum of the correlation coefficient between grain yield and anthesis date in trials conducted from 2001 to 2009 for the early and the late maturity group.

Test environment	Mean	Min.	Max.
Early maturity group			
Optimal	0.09 ± 0.25	−0.63	0.62
Managed drought	−0.28 ± 0.15	−0.56	0.02
Random abiotic stress	−0.20 ± 0.17	−0.63	0.10
Low N	−0.12 ± 0.18	−0.59	0.37
Late maturity group			
Optimal	−0.11 ± 0.23	−0.74	0.48
Managed drought	−0.29 ± 0.14	−0.50	−0.03
Random abiotic stress	−0.26 ± 0.18	−0.60	0.09
Low N	−0.22 ± 0.19	−0.59	0.13

managed drought than under random abiotic stress conditions for both maturity groups.

On average, σ^2_{ge} under optimal conditions was less than σ^2_g for the early (24.2%) and comparable for the late maturity group (22.4%). Under stress, the contribution of σ^2_{ge} increased, with the highest estimate observed under random abiotic stress conditions wherein it was twice as large as σ^2_g for both maturity groups. The large σ^2_{ge} in the random abiotic stress trials is likely due to the variable type, timing, and intensity of stress across trials. The proportion of the phenotypic variance explained by σ^2_{ge} did not differ much between maturity groups under optimal and managed drought conditions while it was considerably higher for the early than for the late maturity group under random abiotic stress and low-N conditions. In all test environments ε was the largest variance component but it was lowest under optimal conditions at 47.8 to 55.3% of the phenotypic variance while it ranged between 57.1 and 71.5% of the phenotypic variance under stress.

Averaged across 2001 to 2009, *H* of grain yield was highest under optimal conditions (~0.9) and lower under stress (0.44–0.63) for both maturity groups when no adjustment was made for the number of trials per test environment type. When estimated assuming testing in five trials, *H* was predicted to be highest under optimal and lowest under random abiotic stress conditions for both maturity groups. Managed drought trials had lower predicted *H* than low-N trials in the early maturity group whereas they had similar *H* in the late maturity group.

Estimated Genetic Correlations and Relative Efficiency of Indirect Selection

The genetic correlation of grain yield under random abiotic stress with yield in optimal or managed stress conditions varied around 0.9 for the early and 0.8 for the late maturity group (Table 4). The performance under random abiotic stress conditions was most strongly correlated with that under low-N conditions (~1) for both maturity groups. Similarly high estimates were observed between random abiotic stress and optimal conditions (0.83–0.86). The genetic correlation between random abiotic stress and managed drought was high for the early maturity group (0.88) whereas it was lower for the late maturity group (0.78). Moderate estimates of genetic correlation of low N with managed drought and optimal conditions (0.69–0.79) were observed for both maturity groups.

The predicted efficiency of indirect selection for genotypes adapted to random abiotic stress varied between 0.70 and 1.12 in the early and between 0.83 and 0.96 in the late maturity group based on the whole data set. In the early maturity group indirect selection under optimal and low-N conditions was predicted to be more efficient (~1.1) than direct selection under random abiotic stress conditions. For the late maturity group indirect selection under low-N conditions was predicted to be as efficient as direct selection under random abiotic stress and slightly more efficient than indirect selection under optimal conditions. When the predictions were standardized for testing in five trials,

Table 4. Mean and standard deviation of the estimates of genetic correlation and efficiency of selection under optimal, managed drought, random abiotic stress, and low-N conditions for genotypes adapted to random abiotic stress and low-N stress based on the whole data set and standardized for testing in five trials (number of environments [N_{Env}] = 5) from 2001 to 2009.

	Target environment					
	Genetic correlation		Selection efficiency†			
			Random abiotic stress		Low N	
Test environment	Random abiotic stress	Low N	Whole set	N_{Env} = 5	Whole set	N_{Env} = 5
Early maturity group						
Optimal	0.86 ± 0.33	0.69 ± 0.20	1.12 ± 0.49	1.24 ± 0.46	0.84 ± 0.17	0.83 ± 0.18
Managed drought	0.88 ± 0.76	0.73 ± 0.40	0.70 ± 0.67	0.79 ± 0.71	0.52 ± 0.24	0.52 ± 0.24
Random abiotic stress	1	0.98 ± 0.19	1	1	0.79 ± 0.12	0.76 ± 0.14
Low N	0.98 ± 0.19	1	1.09 ± 0.33	1.19 ± 0.35	1	1
Late maturity group						
Optimal	0.83 ± 0.19	0.77 ± 0.32	0.91 ± 0.20	1.02 ± 0.24	0.76 ± 0.53	0.73 ± 0.50
Managed drought	0.78 ± 0.30	0.79 ± 0.10	0.83 ± 0.38	0.91 ± 0.35	0.65 ± 0.33	0.63 ± 0.34
Random abiotic stress	1	0.95 ± 0.20	1	1	0.88 ± 0.27	0.83 ± 0.22
Low N	0.95 ± 0.20	1	0.96 ± 0.29	1.10 ± 0.28	1	1

†Selection efficiency was based on genotypic correlation estimates restricted to ≤1.

indirect selection under optimal or low-N conditions was predicted to be more efficient than direct selection under random abiotic stress conditions for both maturity groups. In contrast, indirect selection under managed drought conditions was less efficient than direct selection under random abiotic stress conditions for both maturity groups based both on the whole data set and standardized for five trials. With respect to low-N conditions, direct selection was on average more efficient than indirect selection under optimal, managed drought, or random abiotic stress conditions. The estimates of genetic correlation and selection efficiency did not change significantly when all well-fertilized trials with <3 t ha^{-1} were considered as random abiotic stress trials, regardless of the correlation between grain yield and anthesis date (data not shown).

DISCUSSION

Mean, Variance Components, and Broad-Sense Heritability of Grain Yield under Optimal and Stress Conditions

A positive and significant although weak Pearson correlation between w^2 and the trial means of grain yield indicated decreased w^2 under stress, as also reported by other authors (Blum, 1988; Bolaños and Edmeades, 1996; Monneveux et al., 2008).

The gap between grain yield potential (4.5 to 7.0 t ha^{-1}) and actual grain yield (0.6 to 2.5 t ha^{-1}) under drought or low-N conditions in Africa was reported to be around 4 t ha^{-1} (Pingali and Pandey, 2001). Therefore, the observed grain yield of about 2 t ha^{-1} under stress in these trials is representative of the actual grain yield in farmers' fields (Table 2). The early maturity group had a higher yield than the late maturity group under stress, as also observed by Bolaños and Edmeades (1996). The usage of uniform but arbitrary thresholds based on grain yield (3 t ha^{-1}) and the correlation coefficient between grain yield and anthesis date (0.10) across maturity groups was appropriate because (i) the grain yield of the two maturity groups did not differ significantly under stress and (ii) the correlation coefficient between grain yield and anthesis date was at maximum 0.02 under managed drought and about 0.1 under low-N conditions. While Ceccarelli et al. (1992, 1998) and Gallais et al. (2008) categorized experiments based on the grain yield level alone, the inclusion of a threshold correlation coefficient prevented at least some trials, the low grain yield of which may have been mainly due to biotic stress, from being incorrectly categorized as affected by abiotic stresses such as targeted in this study. When applying these thresholds, on average 30% of trials conducted in the rainy season were classified as having experienced random abiotic stress conditions. The percentage of random abiotic stress is likely to have been underestimated, because severely stressed trials may often not been harvested. These results emphasize the importance of breeding stress tolerant cultivars for farmers in eastern and southern Africa.

As proposed by Chapman and Edmeades (1999) and Bänziger et al. (2000), the genotypes were evaluated under managed stress conditions so that the genetic variation for tolerance was revealed to a greater extent than normally observed in trials conducted under sporadic random abiotic stress. The genetic variation (expressed as percentage of the phenotypic variance) was indeed much larger under managed drought and low-N conditions than under random abiotic stress conditions, where drought and low-N stresses may occur at various plant developmental stages and in different combinations.

Under optimal, low-N, and managed drought conditions σ^2_{ge} was lower than or comparable to σ^2_g (Table 2). Under random abiotic stress conditions σ^2_{ge} was around twice as high as σ^2_g. Therefore, under optimal, managed drought, and low-N conditions genotypes responded similarly across diverse environments while the evaluation under random abiotic stress conditions resulted in more genotypic rank changes among trials; these rank changes seem more likely to be noise than to be associated with some repeatable subsets of trials within the random abiotic stress environment. Regarding the fact that the genotypes were tested across 68 to 79 random abiotic stress environments, σ^2_{ge} as a proportion of the phenotypic variance (18–23%) seems rather low compared to that reported in maize for a sample of two low-N environments in France (21%; Gallais et al., 2008) and in barley (*Hordeum vulgare* L.) for a sample of five optimal environments in Alberta, Canada (54%; Anbessa et al., 2010).

Under optimal conditions, H of grain yield was highest due to a high σ^2_g, extensive testing effort, and relatively low σ^2_{ge} and σ^2_ε. As σ^2_g under managed drought conditions was larger than under random abiotic stress conditions, H estimates of grain yield in both conditions were comparable even though the genotypes were evaluated at a larger number of environments under random conditions. Under low-N conditions, H and σ^2_g of grain yield were medium to high. Reasonably high estimates of H were obtained when standardized for testing in five trials under stress. However, in the actual data set, in some years only one managed drought trial remained after excluding those with w^2 of grain yield less than 0.15. As H of grain yield is a direct function of the number of trials, H under managed drought conditions was low. The number of managed drought trials could be increased by including more locations with high H of grain yield (e.g., Chiredzi in Zimbabwe; data not shown). The payoff of this investment is discussed in the next section with regard to the relative efficiency of indirect selection of genotypes adapted to random abiotic stress under managed drought conditions. It is impossible to ensure a specific number of trials under random abiotic stress each year because its occurrence is unpredictable. However, more trials could be conducted in locations with a high occurrence of random abiotic stress, such as Arusha in Tanzania and Makaholi in Zimbabwe.

Genetic Correlations for Grain Yield among Optimal, Low-N, Managed Drought, and Random Abiotic Stress Environments

Somewhat unexpectedly, genetic correlations of the random abiotic stress target environment with the low-N test environment were slightly higher than with either the optimal or managed drought test environments. This result seems to indicate that, although the random abiotic stress trials received optimal levels of fertilization, the availability of N was reduced due to drought or other factors such as inadequate weed control. It also indicates that, in this large series of rainfed trials, low N availability was a more important cause of low yield than drought per se at the flowering and grain-filling stages. Genetic correlations of yield in the low-N target environment with the optimal and managed drought test environments were 0.69 to 0.79, indicating that screening in these test environments was not highly predictive of yield under low-N conditions and that screening of elite hybrids in low-N trials is critical to the ability to identify hybrids suitable for production in minimally fertilized fields and adapted to random abiotic stress in southern Africa. It should be noted that estimates of genotypic correlations exceeded 1 in some years, a frequent occurrence due to sampling error (Atlin, 2003).

Utility of Managed Drought, Low-N Stress, or Optimal Conditions for Selecting Genotypes Adapted to Random Abiotic and Low-N Stress in Southern Africa

Indirect selection under low-N or optimal conditions was observed to be more efficient than direct selection under random abiotic stress conditions for both maturity groups when the estimates were standardized for testing in five trials. Because indirect selection under optimal or low-N conditions implies a possibility of discarding some genotypes that may be high yielding under random abiotic stress conditions (Ceccarelli et al., 1992), a combined evaluation across low-N, optimal, and random abiotic stress conditions might be of advantage, as suggested by Bänziger et al. (2006). Indirect selection under managed drought conditions was only moderately predictive of grain yield under random abiotic stress conditions, which is in contrast to the results of Venuprasad et al. (2007) in rice. For the random abiotic stress environment, greater gains were predicted for direct selection as well as for indirect selection under optimal or low-N conditions than under managed drought. These results indicate that managed drought screening results should be weighed somewhat less heavily in selection decisions than results from the other test environments. The lower efficiency of selection for genotypes adapted to random abiotic stress under managed drought compared to that resulting from direct selection or from indirect selection under low-N or optimal conditions may partly be the result of (i) the type of stress occurring, (ii) the occurrence of drought stress under random abiotic stress conditions at phenological stages other than flowering and grain filling (Byrne et al., 1995; Van Oosterom et al., 2006), (iii) the conduct of trials in the dry season, which might not be predictive of genotype performance in the rainy season due to differences in temperature, daylength, and biotic stress pressure, and (iv) the effective selection against genotypes susceptible to drought stress at anthesis in previous breeding stages. In contrast, low-N trials are conducted in the same season as random abiotic stress trials and are subject to the same climatic conditions. Further, both test environments showed similar relationships between grain yield and anthesis date, because plants facing drought might also be N stressed due to restricted N uptake and vice versa.

Direct selection under low-N conditions was more efficient than any form of indirect selection due to a medium to high H under low-N conditions, as also observed by other authors (Lafitte and Edmeades, 1994; Bänziger et al., 1997; Mandal et al., 2010), and a relatively low genetic correlation with yield under optimal or managed drought conditions. Bänziger et al. (1999) found that selection under managed drought conditions increased grain yield across a wide range of N stress levels, as would be expected given the positive genetic correlation observed between yield under drought and low N in this study, but they did not compare this with gains from direct selection under low N. In the current study direct selection under low-N conditions proved to be effective and the results suggested that investment in a larger number of low-N trials will increase selection efficiency in the countries and locations wherein random abiotic stress occurs frequently. The availability of low-N tolerant maize genotypes would especially help resource-poor farmers, who often apply little or no fertilizer.

Recommendations for Selection of Broadly Adapted Maize Genotypes

Farmers' fields in southern Africa are rarely characterized by only one abiotic stress; therefore, for a variety to become popular among farmers, it must combine tolerance to random abiotic stress, including drought and low-N stress, with high grain yield potential under favorable conditions (Bänziger et al., 1999; Kumar et al., 2008). The identification of broadly adapted genotypes can be achieved by combining selection under random abiotic stress, optimal, and/or low-N conditions. Selection based on combined analysis across stress and nonstress environments was recommended above a genetic correlation of 0.65 (Presterl et al., 2003) and if σ^2_{ge} in the combined analysis is either not large relative to σ^2_g or does not involve crossover interactions (Atlin et al., 2000).

When combining performance data generated in different test environments, appropriate weights for those test environments should be given, because their *H* and correlation with performance in the target environments may be different. Selection indices that give substantial weight to grain yield under managed stress have proven highly effective in improving drought tolerance in maize (Edmeades et al., 1999; Monneveux et al., 2006). However, too much weight placed on test environments with low *H* relative to the weight on those with high *H* can potentially reduce selection gains in both environments. Some form of selection index giving appropriate weights, based on *H* and genetic correlations, to data from optimal, random abiotic stress, low-N, and managed drought environments is likely needed to maximize gains in stress-prone southern African maize production environments. The frequency of occurrence of random abiotic stress or low-N stress could be considered as the economic weight for construction of such an index. The impact of different economic weights, genetic correlations, and *H* on the overall selection gain as well as target environment-specific selection gain warrants further research.

CONCLUSIONS

In this study, selection under optimal and low-N conditions was predicted to be more efficient for selecting advanced maize hybrids that perform well under random abiotic stress conditions in eastern and southern Africa than either direct selection under random abiotic stress or indirect selection under managed drought conditions, indicating that N stress may have been more important than reproductive-stage drought stress in this set of low-yielding trials, which is likely to be representative of conditions on-farm in southern Africa. The results imply that somewhat higher weight should be given to optimal and low-N screening results than to managed drought screening results, which may be more effective in eliminating hybrids that perform very poorly under drought stress at the reproductive and grain-filling stages than in predicting performance under random abiotic stress. A selection index approach taking into account *H* in the selection and target environments, the correlations between them, and the frequency of occurrence of stress should be developed to assist in assigning appropriate weights that will maximize gains from selection in providing cultivars for farmers in stress-prone maize production environments in southern Africa.

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References

Anbessa, Y., P. Juskiw, A. Good, J. Nyachiro, and J. Helm. 2010. Selection efficiency across environments in improvement of barley yield for moderately low nitrogen environments. Crop Sci. 50:451–457.

Atlin, G. 2003. Breeding to improve yield under adverse environments: Direct selection for grain yield. p. 13–22. *In* K.S. Fischer, R. Lafitte, S. Fukai, G. Atlin, and B. Hardy (ed.) Breeding rice for drought-prone environments. International Rice Research Institute, Los Baños, Philippines.

Atlin, G.N., and K.J. Frey. 1990. Selecting oat lines for yield in low-productivity environments. Crop Sci. 30:556–561.

Atlin, G.N., K.B. McRae, and X. Lu. 2000. Genotype × region interaction for two-row barley yield in Canada. Crop Sci. 40:1–6.

Bänziger, M., F. Betran, and H. Lafitte. 1997. Efficiency of high-nitrogen selection environments for improving maize for low-nitrogen target environments. Crop Sci. 37:1103–1109.

Bänziger, M., G.O. Edmeades, D. Beck, and M. Bellon. 2000. Breeding for drought and nitrogen stress tolerance in maize: From theory to practice. CIMMYT, Mexico D.F., Mexico.

Bänziger, M., G.O. Edmeades, and H.R. Lafitte. 1999. Selection for drought tolerance increases maize yields across a range of nitrogen levels. Crop Sci. 39:1035–1040.

Bänziger, M., P.S. Setimela, D. Hodson, and B. Vivek. 2006. Breeding for improved abiotic stress tolerance in maize adapted to southern Africa. Agric. Water Manage. 80:212–224.

Betrán, F.J., M. Bänziger, and D.L. Beck. 1997. Relationship between line and topcross performance under drought and non stressed conditions in tropical maize. p. 383–387. *In* G.O. Edmeades, M. Bänziger, H.R. Mickelson, and C.B. Peña-Validivia (ed.) Developing drought- and low N-tolerant maize. Proceedings of a Symp., El Batan, Mexico. 25–29 Mar. 1996. CIMMYT, Mexico, D.F., Mexico.

Betrán, F.J., D. Beck, M. Bänziger, and G.O. Edmeades. 2003. Secondary traits in parental inbreds and hybrids under stress and non-stress environments in tropical maize. Field Crops Res. 83:51–65.

Blum, A. 1988. Plant breeding for stress environments. CRC Press, Boca Raton, FL.

Bolaños, J., and G.O. Edmeades. 1996. The importance of the anthesis-silking interval in breeding for drought tolerance in tropical maize. Field Crops Res. 48:65–80.

Butler, D.G., B.R. Cullis, A.R. Gilmour, and B.J. Gogel. 2007. Analysis of mixed models for S language environments. ASReml-R reference manual. Queensland Department of Primary Industries and Fisheries, Toowoomba, QLD, Australia.

Byrne, P.F., J. Bolanos, G.O. Edmeades, and D.L. Eaton. 1995. Gains from selection under drought versus multilocation testing in related tropical maize populations. Crop Sci. 35:63–69.

Ceccarelli, S., S. Grando, and J. Hamblin. 1992. Relationship between barley grain yield measured in low- and high-yielding environments. Euphytica 64:49–58.

Ceccarelli, S., S. Grando, and A. Impiglia. 1998. Choice of selection strategy in breeding barley for stress environments. Euphytica 103:307–318.

Chapman, S.C., and G.O. Edmeades. 1999. Selection improves drought tolerance in tropical maize populations: II. Direct and correlated responses among secondary traits. Crop Sci. 39:1315–1324.

Cooper, M., I.H. DeLacy, and K.E. Basford. 1996. Relationships among analytical methods used to analyse genotypic adaptation in multi-environment trials. p. 193–224. *In* M. Cooper and G.L. Hammer (ed.) Plant adaptation and crop improvement. CAB International, Wallingford, UK.

Edmeades, G.O., J. Bolaños, S.C. Chapman, H.R. Lafitte, and M. Bänziger. 1999. Selection improves drought tolerance in tropical maize populations: I. Gains in biomass, grain yield, harvest index. Crop Sci. 39:1306–1315.

Falconer, D.S., and T.F.C. Mackay. 1996. Introduction to quantitative genetics. Pearson Education Limited, Essex, England.

FAO. 2010. The state of food insecurity in the world. Addressing food insecurity in protracted crises. Available at http://www.fao.org/publications/sofi/en/ (verified 10 Dec. 2011). Food and Agriculture Organization of the United Nations, Rome, Italy.

FAO. 2011. Area of maize harvested (ha) in 2009, food supply (kcal/capita/day) and protein supply quantity (g/capita/day) in 2007. Available at http://faostat.fao.org/site/567/DesktopDefault.aspx?PageID=567#ancor (verified 7 Jan. 2012). Food and Agriculture Organization of the United Nations, Rome, Italy.

Gallais, A., M. Coque, and P. Bertin. 2008. Response to selection of a maize population for adaptation to high or low nitrogen fertilization. Maydica 53:21–28.

Hallauer, A.R., M.J. Carena, and J.B. Miranda Filho. 2010. Quantitative genetics in maize breeding. Iowa State Univ. Press, Ames, IA.

Hijmans, R.J., S.E. Cameron, J.L. Parra, P.G. Jones, and A. Jarvis. 2005. Very high resolution interpolated climate surfaces for global land areas. Int. J. Climatol. 25:1965–1978.

International Fertilizer Development Center (IFDC). 2010. Africa fertilizer situation. Available at http://www.ifdc.org/getdoc/5fee0591-47b9-4226-9338-cf43a980e15a/Fertilizer_Market-Related_Reports_(1) (verified 10 Dec. 2011). International Fertilizer Development Center, Muscle Shoals, AL.

Kumar, A., J. Bernier, S. Verulkar, H.R. Lafitte, and G.N. Atlin. 2008. Breeding for drought tolerance: Direct selection for yield, response to selection and use of drought-tolerant donors in upland and lowland-adapted populations. Field Crops Res. 107:221–231.

Lafitte, H.R., and G.O. Edmeades. 1994. Improvement for tolerance to low soil nitrogen in tropical maize. II. Grain yield, biomass production, and N accumulation. Field Crops Res. 39:15–25.

Mandal, N.P., P.K. Sinha, M. Variar, V.D. Shukla, P. Perraju, A. Mehta, A.R. Pathak, J.L. Dwivedi, S.P.S. Rathi, S. Bhandarkar, B.N. Singh, D.N. Singh, S. Panda, N.C. Mishra, Y.V. Singh, R. Pandya, M.K. Singh, R.B.S. Sanger, J.C. Bhatt, R.K. Sharma, A. Raman, A. Kumar, and G. Atlin. 2010. Implications of genotype×input interactions in breeding superior genotypes for favorable and unfavorable rainfed upland environments. Field Crops Res. 118:135–144.

Monneveux, P., C. Sánchez, D. Beck, and G.O. Edmeades. 2006. Drought tolerance improvement in tropical maize source populations: Evidence of progress. Crop Sci. 46:180–191.

Monneveux, P., C. Sanchez, and A. Tiessen. 2008. Future progress in drought tolerance in maize needs new secondary traits and cross combinations. J. Agric. Sci. 146:287–300.

Pingali, P.L., and S. Pandey. 2001. Meeting world maize needs: Technological opportunities and priorities for the public sector. p. 1–3. *In* P.L. Pingali (ed.) CIMMYT 1999–2000 world maize facts and trends. CIMMYT, Mexico D.F., Mexico.

Presterl, T., G. Seitz, M. Landbeck, E.M. Thiemt, W. Schmidt, and H.H. Geiger. 2003. Improving nitrogen-use efficiency in European maize: Estimation of quantitative genetic parameters. Crop Sci. 43:1259–1265.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Van Oosterom, E.J., E. Weltzien, O.P. Yadav, and F.R. Bidinger. 2006. Grain yield components of pearl millet under optimum conditions can be used to identify germplasm with adaptation to arid zones. Field Crops Res. 96:407–421.

Venuprasad, R., H.R. Lafitte, and G.N. Atlin. 2007. Response to direct selection for grain yield under drought stress in rice. Crop Sci. 47:285–293.

Williams, A.P., and C. Funk. 2011. A westward extension of the warm pool leads to a westward extension of the Walker circulation, drying eastern Africa. Clim. Dyn. 37:2417-2435.