Strategies to Subdivide a Target Population of Environments: Results from the CIMMYT-Led Maize Hybrid Testing Programs in Africa

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ABSTRACT
To develop stable and high-yielding maize (Zea mays L.) hybrids for a diverse target population of environments (TPE), breeders have to decide whether greater gains result from selection across the undivided TPE or within more homogeneous subregions. Currently, CIMMYT subdivides the TPE in eastern and southern Africa into climatic and geographic subregions. To study the extent of specific adaptation to these subregions and to determine whether selection within subregions results in greater gains than selection across the undivided TPE, yield data of 448 maize hybrids evaluated in 513 trials across 17 countries from 2001 to 2009 were used. The trials were grouped according to five subdivision systems into climate, altitude, geographic, country, and yield-level subregions. For the first four subdivision systems, genotype × subregion interaction was low, suggesting broad adaptation of maize hybrids across eastern and southern Africa. In contrast, genotype × yield-level interactions and moderate genotypic correlations between low- and high-yielding subregions were observed. Therefore, hybrid means should be estimated by stratifying the TPE considering the yield-level effect as fixed and appropriately weighting information from both subregions. This strategy was at least 10% better in terms of predicted gains than direct selection using only data from the low- or high-yielding subregion and should facilitate the identification of hybrids that perform well in both subregions.

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Abbreviations: BLUE, best linear unbiased estimation; H, broad-sense heritability; OPV, open-pollinated variety; REML, restricted maximum likelihood; TPE, target population of environments.

Maize is a major food crop in sub-Saharan Africa (FAO, 2011a). It is grown in a wide range of agroecologies and plays an important role in the farming systems and food security of the region (Langyintuo et al., 2008). Yield levels in eastern and southern Africa are considerably lower than the world average because maize crops are mostly grown under rain-fed conditions with little or no fertilizer or pesticide input and are often subject to abiotic and biotic stresses (Haussmann et al., 1998). Yields are also low because the adoption of hybrid maize seed is on average only 35% in sub-Saharan Africa (Langyintuo et al., 2008). The development of new, stable maize hybrids is an important way of increasing grain yield and food supply in Africa.

To develop stable and high-yielding maize hybrids, breeders must decide whether greater gains can be obtained by dividing the
The objectives of this study were therefore to determine whether selecting within climate, altitude, geographic, yield level, or country subregions was likely to increase rates of genetic gain. Data from more than 500 trials were used, covering the years 2001 to 2009, from the advanced regional hybrid testing network coordinated by CIMMYT in eastern and southern Africa. To test the benefit of subdivision, we estimated genotypic, genotype × subregion, and genotype × environment interaction variances in the undivided TPE and genotypic correlations among subregions. These parameter estimates were used to predict the efficiency of indirect selection across the undivided TPE relative to direct selection in each subregion.

MATERIALS AND METHODS

Genotypes and Experimental Design

The study is based on grain yield data of 448 elite maize hybrids collected in 17 countries in eastern and southern Africa. Between 2001 and 2009, 513 trials were conducted by national agricultural research programs and private seed companies in collaboration with CIMMYT to identify elite hybrids for the region. Each year, new hybrids were added to the trials and tested for up to 3 yr, with low-yielding and disease-susceptible or otherwise undesirable hybrids discarded annually. Thus, there was no hybrid in common across all 9 yr. Within each 3-yr interval, the number of hybrids in common was between 1 and 13. The hybrids were classified according to their maturity into early- (<3 t ha⁻¹) and late-flowering maturity groups (≥3 t ha⁻¹). Early-maturing hybrids were evaluated in 275 trials and late-maturing hybrids in 238 trials.

Trials were mainly conducted in the rainy season using α-lattice designs with three replicates and two-row plots, with plot size ranging from 1.88 to 12.00 m². Trials included 24 to 65 hybrids and one to three local checks, with the number of entries being constant in a given year. Trials were grown with irrigation in the dry season or under rain-fed conditions in the rainy season. Recommended quantities of fertilizers were applied. Weeds were controlled either by hand weeding or herbicide application, although weed control was imperfect in some trials. Ear yield was recorded in tonnes per hectare and adjusted to 10% moisture, and grain yield in tonnes per hectare was determined assuming 80% shelling percentage (Betrán et al., 2003).

Subdivision of the Target Population of Environments

Five different subdivision systems were used to stratify trials into less heterogeneous subregions to test for potential genotype × subregion interactions in the undivided TPE (Table 1). The subdivisions were defined according to (i) climatic and elevation differences modified after Bänziger et al. (2004, 2006), with division of trials into five subregions denoted A through E, (ii) altitude patterns modified after Setimela et al. (2005), in mid-altitude and lowland subregions, (iii) mean grain yield, with trials grouped into low- (<3 t ha⁻¹) and high-yielding (≥3 t ha⁻¹) subregions modified after Weber et al. (2012), (iv) geographic regions, in eastern (Ethiopia, Kenya,
Tanzania, Uganda, and Sudan) and southern Africa (Angola, Botswana, Democratic Republic of Congo, Lesotho, Malawi, Mozambique, Namibia, Nigeria, South Africa, Swaziland, Zambia, and Zimbabwe). Country and geographic subregions were contiguous areas whereas climate, yield level, and altitude subregions were noncontiguous areas. The information permitting climate and altitude subdivision was available only for those locations that were used regularly for hybrid evaluation. The whole data set was included in the yield-level and geographic subdivision. For the country subdivision, six countries, each with a maize production area >900,000 ha in 2009, were selected according to FAO (2011b) for inclusion in the analysis. Between 2006 and 2009 there were no trials in Angola. It should be noted that the yield-level subdivision differs in a fundamental way from the others in that trials cannot be allocated to low- and high-yielding subregions in advance (i.e., for optimally managed, rain-fed trials, we cannot predict with certainty which trials will yield more yielding subregions in advance (i.e., for optimally managed, rain-fed trials). For the analyses within the five subdivision systems, years were nested within subregions, following Atlin et al. (2000b), and (v) political country borders, in Angola, Malawi, Mozambique, Tanzania, Zambia, and Zimbabwe.

Country and geographic subregions were contiguous areas whereas climate, yield level, and altitude subregions were noncontiguous areas. The information permitting climate and altitude subdivision was available only for those locations that were used regularly for hybrid evaluation. The whole data set was included in the yield-level and geographic subdivision. For the country subdivision, six countries, each with a maize production area >900,000 ha in 2009, were selected according to FAO (2011b) for inclusion in the analysis. Between 2006 and 2009 there were no trials in Angola. It should be noted that the yield-level subdivision differs in a fundamental way from the others in that trials cannot be allocated to low- and high-yielding subregions in advance (i.e., for optimally managed, rain-fed trials, we cannot predict with certainty which trials will yield more or less than 3 t ha−1 in advance of planting). In contrast, trials could be allocated to the other subdivision systems before planting, meaning that genotype × subregion interaction variance in those could be exploited by breeding for specific adaptation.

General Description of Analyses

Variance components, broad-sense heritability (H) (Eq. [2]), genotypic correlations among subregions (Eq. [3]), and selection efficiency across the undivided TPE and each subregion (Eq. [6]) were estimated for plot data using the restricted maximum likelihood (REML) method. The estimation was conducted within seven overlapping 3-yr intervals from 2001 to 2009 because there was no hybrid in common across the 9 yr and to reflect the 3-yr testing cycle of hybrid evaluation. Local checks were excluded as they were not in common across trials. Arithmetic means and standard deviations of the seven 3-yr intervals were calculated for all parameter estimates to give an overall measure across 9 yr (2001 to 2009).

Variance Components and Broad-Sense Heritability
For the analyses within the five subdivision systems, years were nested within subregions, following Atlin et al. (2000b), because it is unlikely that a common year effect across an area as large as eastern and southern Africa exists. We tried to fit a model with trials nested within year–location combinations, but this led to singularities during REML iterations. Therefore, each year–location–trial combination was defined as a single environment. Environments were considered to be nested within years following Patterson (1997) and, consequently, a nested model instead of a factorial model was applied:

\[
Y_{ijklmn} = \mu + s_i + y(s)_{ij} + e(y)s_{k(i)} + r(eys)_{l} + b(yes)_{m(klj)} + g_{n(i)} + g_{n(i)} + g_{n(i)} + g_{n(i)} + g_{n(i)} + g_{n(i)} + e_{ijklmn}, \quad [1]
\]

in which \( \mu \) is the overall mean, \( s_i \) the effect of subregion \( i \), \( y(s)_{ij} \) the effect of the year \( j \) nested within subregion \( i \), \( e(y)s_{k(i)} \) the effect of the environment \( k \) nested within year \( j \) and subregion \( i \), \( r(eys)_{l} \) the effect of

Statistical Analysis

Estimation of Mean Grain Yield in Individual Trials
Mean grain yield and repeatability were estimated for individual trials using an \( \alpha \)-lattice analysis of variance, treating all effects as random. Estimates of mean grain yield per trial were used to stratify trials into low- and high-yielding subregions as described above. Trial repeatability was based on entry means over three replicates in a single trial. All 513 trials included in the current study had a repeatability of grain yield >0.15.
the effect of replicate $l$ nested within environment $k$, year $j$, and subregion $i$, $g(y_{ijl})$ the effect of block $m$ nested within replicate $l$, environment $k$, year $j$, and subregion $i$, $g_{ij}$ the effect of genotype $n$, $g_{ij}$ the interactions between genotype $n$ and subregion $i$, $g_{ij}$ the interactions of genotype $n$ and environment $k$ nested within year $j$ and subregion $i$, and $e_{ijkm}$ the residual associated with a single plot. The subregion main effect was regarded as fixed to allow inferences to be made about specific subregions of the undivided TPE. All other effects were considered as random. It should be noted that when the purpose of hybrid testing is to predict future performance in farmers' fields, individual environments are best treated as random samples from the TPE.

For estimating $H$ of grain yield across the undivided TPE and in each subregion, variance components were calculated applying Eq. [1], but excluding the subregion effect and including the year and location effects representing individual trials, to facilitate convergence of REML estimates of hybrid effects. Broad-sense heritability was estimated according to Hallauer et al. (2010) across $e$ environments and $t$ replicates as follows:

$$H = \sigma^2_e / \left[ \sigma^2_e + (\sigma^2_g + \sigma^2_e) / e \right],$$  

[2]

in which $\sigma^2_e$, $\sigma^2_g$, and $\sigma^2_e$ are genotype, genotype × environment, and residual variance components, respectively. Estimation of $H$ based on Eq. [2] assumes balanced data whereas in the current dataset genotypes were tested in α-lattice designs involving incomplete blocks. The ad hoc estimation is justified if the block variance is smaller than $\sigma^2_e$ (Comstock and Moll, 1963) and $\sigma^2_e / e$ is small relative to $\sigma^2_g$ and $\sigma^2_g / e$ (Holland et al., 2003).

**Genotype Means**

There are four alternative approaches that can be used to predict genotype means in a targeted subregion: (i) direct selection based on local means estimated using only data from the targeted subregion, (ii) indirect selection based on local means estimated using only the data from the complementary subregion, (iii) indirect selection using all data to estimate a global mean, ignoring subdivision, and (iv) index selection based on local means estimated using all data and treating the subregion main effect as fixed. In the latter approach, different weights are given to the targeted subregion and its neighbors, depending on the similarity between subregions and the number of trials per subregion (Piepho and Möhring, 2005).

Based on best linear unbiased estimation (BLUE), hybrid means were derived using all data but ignoring subdivision (approach 3) and by using only the data from the targeted subregion (approach 1). Those estimates were used for estimating genotypic correlations and relative efficiencies of indirect selection. Equation [1] was applied treating all effects as random, except the genotype effect, excluding the subregion effect and combining the year and location effects as described above.

**Genotypic Correlations and Relative Efficiency of Indirect and Index Selection**

Under the assumed mixed model, genotype effects within subregions have a compound symmetry variance–covariance structure, in which genotypic variances are the same in each subregion, and genotypic covariances and correlations are the same for each pair of subregions. Based on a compound symmetry variance–covariance structure, the genotypic correlation among pairs of subregions as well as between the undivided TPE and subregion $s$ and $s'$ can be estimated by using the approach of Cooper and DeLacy (1994):

$$r_{g(s')} = r_{g(s')}/(H_i H_j)^{1/2},$$  

[3]

in which $r_{g(s')}$ is the phenotypic correlation coefficient between hybrid means estimated by using only the data from subregion $s$ or $s'$ and $H$ is the broad-sense heritability in subregion $s$ and $s'$. The genotypic correlations between the undivided TPE $t$ and subregions $s$ and $s'$ can be estimated similarly. Estimates of genotypic correlation exceeding 1 are presented but were restricted to ≤1 when estimating response to indirect selection.

Selection gain ($R$) was predicted for direct (approach 1) and indirect selection (approaches 2 and 3; Falconer and Mackay, 1996) using the results of the variance component analysis with an assumed selection intensity of $i = 1.755$:

$$R = i H \sigma^2_e,$$  

[4]

Gain from index selection (approach 4) was predicted for subregions $s$ and $s'$ with an assumed selection intensity of $i = 1.755$ following Wricke and Weber (1986). Response to selection in both subregions ($s$ and $s'$), defined as $R = (R_s, R_s')$, can be expressed as

$$R = ib(G/b Ph)^{1/2},$$  

[5]

Smith (1936) and Hazel (1943) showed that the unknown index weights ($b$) can be derived by multiplying the inverse of the phenotypic variance–covariance matrix ($P$), the genotypic variance–covariance matrix ($G$), and the economic weights of each trait. The economic weight of the targeted region was 1 and of the complementary subregion 0 to optimize recommendations for farmers in each subregion.

The efficiency of indirect selection in subregion $s'$ relative to direct selection in the targeted subregion $s$ can be expressed as

$$CR_{s'/s} = \frac{D R_{s'} / D R_s}{r_{g(s')}/(H_i H_j)^{1/2}},$$  

[6]

in which $CR_{s'/s}$ is the predicted correlated response in subregion $s$ to selection in subregion $s'$ and $DR$ is the predicted direct response to selection in subregion $s$. The efficiency of indirect selection in the undivided TPE $t$, ignoring subdivision, relative to direct selection in subregion $s$ and $s'$ can be estimated accordingly. Further, we calculated the predicted ratio between index selection and direct selection response. Estimates >1 indicate that indirect or index selection is predicted to be more efficient than direct selection.

The compound symmetry variance–covariance structure mentioned before assumes a very simplistic model. The assumption of variance homogeneity was rejected by performing a likelihood-ratio test. Optimally, variance components and genotypic correlations should therefore have been estimated by using an unstructured variance–covariance structure for the subregion effect appearing in every nested effect or by a low-rank approximation thereof using a factor-analytic model (Piepho, 1997). This was not possible, however, because the high number of parameters and the very unbalanced nature of the data sets led to singularities and/or convergence problems. Consequently, a compound symmetry variance–covariance
was about twice as large for the climate, in the yield-level (\(\sigma^2_{\text{gs}}\)) was the second largest variance component (Table 2), genotype × environment (\(\sigma^2_{\text{geys}}\)) was relatively small (0.02 \(\sigma^2\)), genotype × subregion (\(\sigma^2_{\text{gs}}\)), genotype × year (\(\sigma^2_{\text{gy}}\)), and residual variance (\(\sigma^2_{\text{\epsilon}}\)), the variance of hybrid means the ASYREML software package version 3 was used (Butler et al., 2009).

RESULTS

Estimates of Variance Components and Broad-Sense Heritability

Mean grain yields over the 9 yr for early- and late-maturing hybrids were 4.5 and 5.0 t ha\(^{-1}\), respectively. From 2001 to 2009, \(\sigma^2_{\text{g}}\) was about twice as large for the climate, altitude, geographic, and country subdivision (0.15 to 0.23; Table 2) as for the yield-level subdivision (0.09 to 0.12) in both maturity groups. The lower \(\sigma^2_{\text{g}}\) in the yield-level subdivision tended to be associated with a higher genotype × subregion variance component (\(\sigma^2_{\text{gs}}\)) (0.05 to 0.07) whereas \(\sigma^2_{\text{g}}\) was close to 0 for the other subdivision systems. This indicated that only the yield-level subdivision explained a large proportion of genotype × environment interactions. For all subdivision systems, the genotype × year variance component (\(\sigma^2_{\text{gy}}\)) was relatively small (0.02 to 0.08) whereas the genotype × environment variance component (\(\sigma^2_{\text{geys}}\)) was the second largest variance component (0.23 to 0.33). Because \(\sigma^2_{\text{gs}}\) and \(\sigma^2_{\text{gy}}\) were considerably larger than \(\sigma^2_{\text{g}}\) and \(\sigma^2_{\text{geys}}\), the variance of hybrid means was more influenced by local field conditions and trial-to-trial variation than by differences in hybrid ranking among locations, subregions, and years.

Genotypic Correlations and Relative Efficiency of Indirect and Index Selection

Genotypic correlations and relative efficiency of indirect and index selection relative to direct selection were estimated based on BLUEs solely for the yield-level subdivision because lower \(\sigma^2_{\text{g}}\) in the other subdivision systems indicated that genotypic correlations between subregions are high and subdivision of the TPE will not increase selection gain. The predicted selection gain due to direct selection in subregion \(s\) (approach 1) was compared with that of indirect selection in the complementary subregion \(s'\) (approach 2), the undivided TPE \(t\) (approach 3), and index selection (approach 4).

The genotypic variance in the low-yielding subregion was only 10% of that in the high-yielding subregion (Table 3). This difference was primarily caused by the lower absolute value of grain yield in the low- relative to the high-yielding subregion. In the undivided TPE, \(H\) of grain yield was 0.97 for both maturity groups. In the high-yielding subregion, \(H\) was nearly as high as in the undivided TPE whereas it ranged from 0.74 to 0.81 in the low-yielding subregion. Even when \(H\) was estimated assuming equal testing effort, it was larger in the high- than in the low-yielding subregion, primarily because of lower genotypic variance in the latter subregion (data not shown) relative to other sources of variation affecting hybrid means.

Genotypic correlations between low- and high-yielding subregions (\(r_{\text{gs}}\)) were on average 0.81 for the early maturity group and 0.69 for the late maturity group. Therefore, genotypic performance in one subregion explained a maximum of 66% of the performance in the complementary subregion. Furthermore, this indicated that genotypic rank changes occurred between them and that only a few hybrids had a good performance in both. In the 3-yr intervals between 2003 and 2006 the predicted relative efficiency of indirect selection in the high-yielding subregion for performance in the low-yield subregion was >1. Averaged over all 3-yr sets, indirect selection in one subregion \(s'\) for performance in the complementary subregion \(s\) was predicted to be less efficient (0.64–0.93; Table 3) than direct selection. This was also the case when estimates of \(H\) were predicted for testing in 50 environments (data not shown).

Genotypic correlations between hybrid means estimated using only data from the low-yielding subregion and means estimated by using all available trials but ignoring subdivision (\(r_{\text{gs}}\)) were between 0.76 and 0.87 (Table 3). In the 3-yr intervals between 2003 and 2007, the predicted relative efficiency of indirect selection in the undivided TPE for the performance in the low-yield subregion was >1 for the early maturity group because \(H\) in the low-yielding subregion was small relative to that in the undivided TPE. In all other 3-yr intervals, direct selection was predicted to be more efficient. Averaged
Table 3. Mean and standard deviation of the efficiency of indirect relative to direct selection. Three different approaches were applied to predict performance in the low- (LYS) and high-yielding subregion (HYS) based on the genotypic variance ($\sigma^2_g$), broad-sense heritability ($H$), and genotypic correlation ($r_{gs}$).

<table>
<thead>
<tr>
<th>Parameters†</th>
<th>Indirect selection in $s'$ (approach 2)</th>
<th>Indirect selection in $t$ (approach 3)</th>
<th>Index selection (approach 4)‡</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\sigma^2_g$</td>
<td>0.93 ± 0.06</td>
<td>1.01 ± 0.11</td>
<td>1.31 ± 0.15</td>
</tr>
<tr>
<td>H</td>
<td>0.70 ± 0.09</td>
<td>1.00 ± 0.00</td>
<td>1.17 ± 0.05</td>
</tr>
<tr>
<td>$r_{gs}$</td>
<td>0.76 ± 0.08</td>
<td>0.83 ± 0.08</td>
<td>1.14 ± 0.05</td>
</tr>
<tr>
<td>$r_{gt}$</td>
<td>0.64 ± 0.11</td>
<td>1.00 ± 0.00</td>
<td>1.10 ± 0.05</td>
</tr>
</tbody>
</table>

†The economic weight of the targeted region was 1 and of the complementary subregion 0 to make optimal recommendations for farmers in each subregion.

Early maturity group
- LYS: 0.02 ± 0.01, 0.74 ± 0.13, 0.81 ± 0.05, 0.87 ± 0.05
- HYS: 0.35 ± 0.14, 0.97 ± 0.02, 1.03 ± 0.02

Late maturity group
- LYS: 0.04 ± 0.01, 0.81 ± 0.07, 0.69 ± 0.09, 0.76 ± 0.10
- HYS: 0.36 ± 0.11, 0.97 ± 0.01, 1.02 ± 0.01

Across all 3-yr intervals, the efficiency of indirect selection in the undivided TPE for performance in the low-yielding subregion was predicted to be between 0.83 and 1.01 for both maturity groups (Table 3). Indirect selection in the undivided TPE was predicted to be as efficient as direct selection in the high-yielding subregion when restricting the genotypic correlation to ≤1. Estimates of genotypic correlations between the undivided TPE and the high-yielding subregion slightly exceeded 1 (i) whether they were derived from Eq. [3], (ii) if the genetic covariance between the undivided TPE and the high-yielding subregion was estimated directly by subtracting the environmental covariance from the phenotypic covariance (Falconer and Mackay, 1996), (iii) when $H$ was predicted for $n = 50$ environments, or (iv) estimated on the basis of the genotypic variance and the variance of best linear unbiased predictions (Holland et al., 2003; Piepho and Möhring, 2007; data not shown).

The ratio of the response to index selection and direct selection in the low-yielding subregion was predicted to be between 1.10 and 1.31, assuming that the economic weight of the targeted region was 1 and of the complementary subregion 0 (Table 3). Consequently, selection based on all available data using a model considering the yield-level effect as fixed and the genotype × yield-level effect as random would be at least 10% better than direct selection using only data from the low- or high-yielding subregion.

**DISCUSSION**

**Variance Components of Maize Grain Yield in Eastern and Southern Africa**

Genotypic variance is a prerequisite for improvement of maize hybrids. Some hybrid testing programs try to increase genotypic variance by subdividing a TPE into several less heterogeneous subregions, in effect converting genotype × subregion interaction variance into genotypic variance. Optimal subregion delineation, in breeding terms, should maximize genetic gains for the testing resources available (Atlin et al., 2000a). The International Maize and Wheat Improvement Center currently divides its hybrid testing programs into eastern and southern African subregions. If a TPE is subdivided, it is implicitly assumed that significant genotype × subregion interaction exists, a hypothesis that should be verified. Examination of variance components can provide initial information about the magnitude and practical importance of genotype × subregion interactions.

Variance components of maize grain yield were estimated for five different subdivision systems, assuming homogeneous variances. For the climate, altitude, geographic, and country subdivisions, $\sigma^2_g$ was small relative to $\sigma^2_t$ in both maturity groups. This indicated that there was little specific adaptation to the respective subregions and that simultaneous selection for a wide range of environments is possible and may be cost-effective. Even though locations were grouped according to their similarity in earlier studies using cluster analysis and geographic information system data (Bänziger et al., 2004, 2006), genotype × subregion interaction variance based on these groupings was small, indicating that the patterns of genotype × environment interaction on which the subdivisions were based included substantial noise, and do not recur. These results clearly show that adaptation of elite maize hybrids across eastern and southern Africa is very broad, a finding that is in accordance with commercial maize breeding practice in the region; several OPVs and hybrids are used from the Limpopo region of northern South Africa to the mid-elevation regions of Ethiopia. Hence, for maximizing genetic gains, treating climate, altitude, geographic, and country subregions as separate TPEs is not useful if data-based groupings tend not to recur and no region-specific farming practices or locally important quality traits must be considered. Subdividing the TPE according to locations (i.e., Harare and Nairobi) would also not be appropriate as the testing effort in the resulting subregions would be very low and this subdivision system probably accounts for very little or no genotype × subregion interaction variance. Furthermore, the yields at a certain location vary from year to year, which means that trials may be categorized as low yielding in one and as high yielding in another year. This
also may imply low correlation among those trials, even though they are conducted at the same location.

Predicted gains obtainable via selection for specific adaptation to different agroecologies might have been slightly underestimated because (i) genotypes were already selected for wide adaptation in previous breeding stages and (ii) information permitting subdivision was only available for those locations that were regularly used for hybrid evaluation. However, the consistent adoption of the best CIMMYT and commercial hybrids across subregions in eastern and southern Africa is strong support for the overall finding of little local or specific adaptation. Reporting hybrid means separately for each subregion, in addition to the undivided TPE, can provide confidence in the range of adaptation of the selected hybrids.

In the yield-level subdivision $\sigma^2_{y_i}$ was relatively large (~60% of $\sigma^2_{g}$ for both maturity groups). Because of the fact that $\sigma^2_{p}$ was nearly as high as $\sigma^2_{g}$, it is likely that some hybrids do not perform well under both low- and high-yield subregions and that their performance in each must be considered in making selection decisions. The underlying environmental factors reducing yields in the low-yielding subregion may be multifold, including various combinations of abiotic and biotic stresses (Weber et al., 2012). It may be of interest to research the relative importance of each of those stresses. Nevertheless, it should be noted that maize yields in farmers’ fields are usually not decreased by one particular stress at a certain plant growth stage but rather by a combination of different stresses occurring at the same or at different plant growth stages. As such, selection of genotypes in low- and high-yielding environments may be optimal to serve farmers’ needs.

The second largest variance component of grain yield was $\sigma^2_{g(p)}$, resulting from random changes in the relative performance of genotypes from environment to environment and year to year, which is consistent with results of other studies (Cooper et al., 1999; Atlin et al., 2000a; Setimela et al., 2005). The contribution of $\sigma^2_{g(p)}$ and $\sigma^2_{g}$ to the variance of entry means could be decreased with increasing testing effort plus good field technique and trial designs. Unlike $\sigma^2_{g(p)}$ and $\sigma^2_{g}$, $\sigma^2_{g(r)}$ was low, as also reported for grain yield of maize in India (Atlin et al., 2011) and rice (Oryza sativa L.) in Thailand (Cooper et al., 1999). However, $\sigma^2_{g(r)}$ could have been imprecisely estimated because it was based on a maximum of 13 common hybrids. To estimate $\sigma^2_{g(r)}$ and breeding progress across time with more accuracy, it would be worthwhile to use long-term checks that are retained in the trials across many years.

**Efficiency of Direct Selection Versus Indirect and Index Selection**

Applying classical results from selection theory (Falconer and Mackay, 1996) to the problem considered here, relative efficiency of indirect selection compared with direct selection depends on $H$ of grain yield in and genotypic correlation between the selection environments. Examination of Eq. [6] shows that indirect selection will be more efficient than direct selection if $H$ in the indirect selection environment is higher than that in the direct selection environment and if genotypic correlation between both selection environments is high (Atlin et al., 2000a). Broad-sense heritability is proportional to testing effort. Often, a decrease of $H$ is observed with decreasing environmental mean yield (Bänziger et al., 1997; Mandal et al., 2010; Weber et al., 2012). In the current study, $H$ of grain yield was considerably larger in the undivided TPE and in the high-yielding subregion than in the low-yielding subregion based on the actual testing effort (Table 3) and on hypothetical testing in 50 environments (data not shown). Therefore, even if the number of low-yielding trials is equal to the number of trials in the undivided TPE or in the high-yielding subregion, precision of the corresponding hybrid means will be lower.

Genotypic correlations between the low- and high-yielding subregions were moderate (Table 3). This indicated that substantial genotypic rank changes between the two subregions occurred. Therefore, selection based on means estimated across the undivided TPE may fail to achieve the goal of CIMMYT to select maize hybrids that are both high yielding and optimal for farmers in low-yielding, stress-prone environments. Furthermore, the product of the genotypic correlation and $\sqrt{H}$ in the high-yielding subregion was smaller than $\sqrt{H}$ in the low-yielding subregion. Consequently, direct selection in the low-yielding subregion was predicted to be more efficient than indirect selection in the high-yielding subregion and vice versa (Table 3). These results indicate that hybrid means should be reported separately for the low- and high-yielding subregions to identify those that perform well in each, which is in accordance with the results of Mandal et al. (2010) and Venuprasad et al. (2008).

Specific adaptation to either low- or high-yielding subregions may have been more important than for the other subdivision systems because yield differences between subregions were much larger for this subdivision system, and mean yield differences have been negatively associated with genotypic correlation in performance across environments (Bänziger et al., 1997). Furthermore, it was reported that early-maturing hybrids performed better in low-yielding trials whereas late-maturing hybrids performed better in high-yielding trials because they needed more water and N to complete their life cycle (Diallo, 1996; Weber et al., 2012). Therefore, different physiological mechanisms and genes responsible for high relative grain yield in low- and high-yielding production environments might lead to the relatively low genotypic correlation between them. In the current study, a small portion of the improved performance of certain hybrids in low-yielding environments appeared to be the result...
of early flowering. In both the early and late maturity groups the highest yielding hybrids in the low-yielding environments flowered on average between 1.4 and 1.6 d earlier than the highest yielding hybrids in the high-yielding environments (data not shown).

When subdividing the TPE according to yield levels, the effect of reduced testing effort in the resulting subregions has to be taken into account. The testing effort in the low-yielding subregion was reduced by about 70% relative to that in the undivided TPE whereas it was reduced by about 30% in the high-yielding subregion. The relative proportion of low-yielding environments in these regional trials might have been lower than in the TPE because trials were grown with recommended quantities of fertilizers and weed control whereas maize hybrids are mostly grown with little or no fertilizer or pesticide input on-farm in the TPE. Furthermore, identifying genotypes adapted to low-yielding and drought-prone production environments from rain-fed testing only is difficult because the number of low-yielding trials per year is difficult to predict and the stress resulting in low yields is uncontrolled. For these reasons, the CIMMYT breeding pipeline relies heavily on managed stress screens conducted under drought and low-N conditions to generate low-yield environments via the application of stress timing and levels that are thought to be representative of those occurring in farmers’ fields (Bänziger et al., 2000; Weber et al., 2012).

Indirect selection based on all data but ignoring subdivision according to yield levels was in most cases less efficient than direct selection based on means estimated by using only the data from the targeted subregion (Table 3). The disadvantage of estimating hybrid means ignoring subdivision is that, effectively, much greater weight is given to high- than to low-yielding subregions. This may explain why crop varieties bred primarily under high-yielding conditions sometimes failed to have an impact in low-yielding production environments (Atlin and Frey, 1990; Ceccarelli et al., 1992; Simmonds, 1991; Atlin et al., 2001).

Index selection was generally more efficient than direct selection in low- or high-yielding subregions (approach 4 in Table 3). Especially for the low-yielding subregion, predicted gains from indirect selection were highest when stratifying the TPE considering the yield-level effect as fixed, thereby using information from both subregions, appropriately weighted, in estimating hybrid effects within each. It follows from the theory of mixed models that this approach minimized prediction error and maximized gain from selection (Piepho and Möhring, 2005; Table 3). Therefore, the application of this approach is optimal to estimate genotype means for low- and high-yielding subregions, which is in agreement with the results of Przystalski et al. (2008) for organic and nonorganic production environments.

Selection Strategy for Hybrids Adapted to Both Low- and High-Yielding Environments

Precision of hybrid mean estimates and response to selection can be maximized by stratifying the TPE into subregions, using all available information, and weighting the subregions based on their relevance to the targeted subregion (Piepho and Möhring, 2005). The extent to which the information from neighboring subregions is exploited depends on H in the neighboring subregions and on the genotypic correlation to the subregion of interest.

Estimating hybrid means based on Eq. [1] considering the yield-level effect as fixed and the genotype × yield-level effect as random (approach 4) constitutes an advance over using information from only one subregion (approach 1 and 2) and ignoring subdivision and genotypic correlation between subregions (approach 3). Approach 4 is rarely used in the analysis of cultivar trial data (for an exception, see Przystalski et al. [2008]) but is expected to always result in selection response that equals or exceeds the response from direct selection.

The flexible subdivision of the eastern and southern African TPE into yield levels might be optimal to exploit specific adaption but also to identify hybrids that are broadly adapted to both the low- and high-yielding subregions. This is an important goal for CIMMYT maize hybrid testing programs, which serve both resource-poor farmers in highly unfavorable areas as well as small farmers in more productive regions who invest substantially in inputs.

CONCLUSIONS

The existence of genotype × environment interactions in the undivided TPE may indicate that subdivision is necessary. However, it is not always true that small differences between environments require specifically adapted hybrids or that selection response can be increased by dividing the TPE. Whether to select across the undivided TPE or separately in several subregions has to be validated for each hybrid testing program individually. The current study showed that maize hybrids are very broadly adapted to different agroecologies across eastern and southern Africa and that the subdivision of the broad TPE into climate, altitude, geographic, and country subregions was identifying little or no specific adaptation within the early- and late-maturing hybrid groups used in this study. In contrast, means need to be estimated for the low- and high-yielding subregions separately to identify hybrids adapted to both subregions because genotype × subregion interaction variances were large relative to genotypic variance and genotypic correlations between subregions were relatively low, indicating that genotypic rank changes between low- and high-yielding subregions occurred. As a consequence, the CIMMYT maize hybrid testing programs will now report hybrid means separately for low- and high-yielding subregions, estimating these
means using all available data. The yield-level effect will be considered as fixed and correlation between subregions as correlated random genotype effects nested within subregions. With this strategy, it is possible to identify hybrids that perform well in both low- and high-yielding subregions, and that will therefore efficiently serve African smallholders in a broad range of environments.

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