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Effectiveness of selection at CIMMYT's main maize breeding sites in Mexico for performance at sites in Africa and vice versa

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With 6 tables

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Abstract

The exchange of elite breeding materials across regions is an important way in which multinational maize breeding programmes access new genetic variation, improve efficiency and reduce costs. Our objectives were to examine whether CIMMYT's breeding programmes for tropical and subtropical environments in Mexico and Eastern and Southern Africa (ESA) can effectively share materials. Sets of selected and unselected lines were evaluated for *per se* and testcross performance in multiple environments in Mexico and ESA for grain yield, days to anthesis and plant height. Genotypic correlations between performance in Mexico and ESA as testcross and line *per se* were high ($\geq$ 0.72) for all experiments, and indirect selection efficiency ranged from 67 to over 100% for all traits. Lines selected in ESA or Latin America performed equally well in each region, indicating selection was for broad rather than regional adaptation. Thus, breeding programmes of CIMMYT in both Mexico and ESA can benefit tremendously by exchanging breeding materials and test results, and elite selections from each region should be fast-tracked for evaluation in the other.

Key words: maize — breeding material exchange — regional adaptation — double haploids — genotypic correlation — indirect selection efficiency

Breeding programmes exchange materials across regions to obtain new genetic variability as well as immediately useful cultivars (Holland and Goodman 1995). In modern hybrid maize breeding, exchange of elite lines is preferred over other types of breeding materials because they permit rapid genetic gain (Troyer 1990, Holland 2004). Although exchange of early generation materials is possible, it is cost inefficient when compared with exchange of advanced generation materials. But the exchange of advanced generation materials for direct utilization requires assessing their adaptability in the new environment. In other words, the advanced materials must be broadly adapted to be promising for use in a new target population of environments. CIMMYT (Spanish acronym for International Maize and Wheat Improvement Center) has a multinational maize breeding programme where breeding materials developed in one target population of environments can be useful in another.

Since the 1970s, CIMMYT's maize breeding programme has been selecting maize varieties for high yield under managed low soil nitrogen, drought stress and non-stress conditions at its experimental stations in Mexico (Bolaños and Edmeades 1993, Bänziger et al. 1999, Zaidi et al. 2004). Products of this effort have been targeted at drought-affected countries in Eastern and Southern Africa (ESA). To enhance the efficiency of breeding for ESA, CIMMYT established experimental stations in Kenya and Zimbabwe in the 1990s and transferred most of its Africa-targeted breeding efforts there (Hassan et al. 2001).

The majority of germplasm used for breeding in ESA was initially selected for yield potential and drought tolerance in Mexico. This germplasm proved successful in the low- and midelevation subtropics of Africa after the introgression of resistances to diseases prevalent in the region (Bänziger et al. 2006, Weber et al. 2012). Meanwhile, CIMMYT's well-established breeding programmes in Kenya and Zimbabwe are now producing hybrids and open-pollinated varieties that may be useful for farmers in similar environments in Latin America. Although the transfer of breeding materials from ESA to Mexico and vice versa appears to be beneficial to both regions, the relationship between their agronomic performance in the two regions has not been formally studied.

CIMMYT's maize breeding programme can select genotypes with very broad adaptation within maize mega-environments because it has the capacity to evaluate germplasm in many countries on different continents through its network of collaborators (Windhausen et al. 2012). The predicted response in one region to selection in another is mainly determined by the genotypic correlation between the regions (Atlin et al. 2000a, Przystalski et al. 2008); a high genetic correlation between two regions indicates that there is little specific adaptation to individual regions and that elite germplasm selected in one region has a high potential to perform well in the other (Atlin et al. 2000b, Piepho and Möhring 2005). Consequently, the efficiency of a multinational maize breeding programme like that of CIMMYT can be improved by assessing the genotypic correlation between regions and whether there is specific adaptation to regions for the genotypes being tested. This information is useful in guiding the exchange of breeding materials between regions and in predicting the performance of selections in one region based on test results in another. In addition to the genotypic correlation between ESA and Mexico, the broad-sense heritability within each region determines the relative efficiency of indirect selection in one region for performance in the other (Falconer and Mackay 1996).

The main purpose of this study was to determine whether selecting maize inbreds based on test results from Mexico would be efficient in identifying superior genotypes for ESA and vice versa. To this end, we estimated, in both selected and unselected materials, the genotype x region interaction and genetic correlations across the regions, as well as broad-sense heritability within regions, to predict gains in each region from selection in the other. We also compared the performance of lines selected in Mexico and Africa with respect to their performance in each region. The results were used to develop recommendations on the stage at which an exchange of materials might be most efficient.

Materials and Methods

Plant materials: A total of 655 maize lines was evaluated, 375 lines as testcrosses and 280 as lines *per se*, in three experiments at three CIMMYT sites in Mexico (Agua Fria, El Batan and Tlaltizapan) and four sites in ESA (Kiboko and Kakamega in Kenya and Chisumbanje and Harare in Zimbabwe).

Experiment 1 comprised 259 unselected double haploid (DH) lines. The DH lines were produced from diallel crosses among 10 inbreds developed by CIMMYT for yield potential and drought tolerance. A detailed description of the parent lines as well as the method of producing the DH lines is presented in Kebede et al. (2011). In winter 2010, the D_1 generation of the DH lines was evaluated visually for uniformity in plant height and other traits, and heterogeneous lines discarded. In the same season, testcross seed of the DH lines with a single-cross tester (CML195/DRB-F2-60-1-1-1-B) was produced. Testcrosses were evaluated at CIMMYT stations in Mexico (Agua Fria and Tilaltizapan) and ESA (Kiboko and Chisumbanje) in 2010 (Table 1).

Experiment 2 comprised a sample of 116 advanced inbred lines developed by the CIMMYT maize breeding programmes in Africa and Latin America using conventional pedigree breeding. Of the 116 inbred lines, 85 were developed in Latin America (Mexico and Colombia) and 31 were developed in ESA. The inbreds were developed on the basis of selection for line *per se* and testcross performance for yield potential as well as tolerance to drought and low soil nitrogen. Testcrosses of these inbreds with the broadly adapted tester CML539 were produced during the 2010 winter season in Mexico and evaluated in Mexico (Agua Fria and Tilaltizapan) and ESA (Kiboko and Kakamega) in 2011 (Table 1). The test materials and testers in Exp. 1 and Exp. 2 originated from different genetic backgrounds.

Experiment 3 was composed of 280 maize lines developed by the different breeding programmes of CIMMYT in Africa and Latin America, of which 50 lines were developed in Africa and 230 lines were developed in Latin America (Mexico and Colombia) where 21 of the Latin American developed lines were in common with Exp. 2. These materials were selected based on their line *per se* and testcross performance for grain yield under optimum, drought and low soil nitrogen stress conditions. Details of the inbreds tested in this experiment can be found elsewhere (Cairns et al. 2013, Kebede et al. 2013). The line *per se* performance trial was conducted for three years in Mexico and two years in ESA (Table 1).

Experimental conditions: All the experimental locations used in Mexico and ESA represent the tropical and subtropical zones and are characterized for their agro-ecological conditions in Supplement Table 1. Test sites in Mexico were Agua Fria, El Batan and Tlaltizapan. Agua Fria is a humid low-altitude site on the Gulf of Mexico coast, and El Batan and Tlaltizapan are dry high- and midaltitude sites in central Mexico, respectively. The test sites in ESA were Kiboko, Kakamega, Chisumbanje and Harare. Kiboko is dry midaltitude site, while Kakamega is a wet midaltitude site in Kenya. Chisumbanje and Harare are dry low- and midaltitude sites in Zimbabwe, respectively. Exp. 1 and Exp. 2 had all locations in common except Chisumbanje, where only Exp. 1 was grown, and Kakamega, where only Exp. 2 was tested. Exp. 3 had Agua Fria as a common location with the other two experiments. Two trials for Exp. 1 were planted at Kiboko in adjacent irrigated fields under mild drought stress and well-watered conditions. All other trials were conducted under rainfed conditions.

All trials were laid out in an alpha-lattice (0, 1) design (Patterson and Williams 1976) with two replications for the testcross experiments (Exp. 1 and Exp. 2) and with three replications for the line *per se* experiment (Exp. 3). Single-row plots were used for all trials. Plots for Exp. 1 and Exp. 2 were 4.5 m in length, with 0.75 m between rows in Tlaltizapan and Agua Fria and a final plant density of 5.3 plants/m^2. Plots in Kiboko and Kakamega were 4 m long, with 0.75 m between rows with final plant density of 6.7 plants per m^2. Plot size in the Chisumbanje trial was 4 m in length with 1 m between rows and final plant density of 3.3 plants per m^2. Exp. 3 had plot size of 2 m in length, with 0.75 m between rows and plant density of 6.7 plants in Agua Fria and El Batan, whereas in Kakamega and Harare, plot size and planting density were similar with testcross trials conducted in Kenya.

Standard agronomic practices were followed at all locations. Application of nitrogen, phosphorous and potassium fertilizer was based on the recommended amount for each location. Before planting, seeds were treated with a mixture of chemicals to control fungal diseases and insect pests. In the field, appropriate weed, disease and pest control measures were taken. For the managed drought experiment in Kiboko, drought stress was imposed by withholding irrigation from 4 to 5 weeks before flowering until harvest (Bänziger et al. 2000).

Days to anthesis were determined as the number of days after planting when 50% of plants in the plot shed pollen. Plant height was measured in centimetres as the distance from the base of the plant to the height of the first tassel branch and calculated from the average of five competitive plants in each plot. Harvesting was carried out by hand, and grain moisture was measured from a sample of shelled grain at the time of harvest. Grain yield was calculated from ear weight and grain moisture assuming a shelling percentage of 80% and final adjusted moisture content of 12.5%.

Statistical analysis: Considering Mexico and ESA as two different regions, data were analysed for each region separately using the model

$$Y_{jklm} = \mu + e_j + r(e)_{k(j)} + b(re)_{l(kj)} + g_m + ge_{mj} + \varepsilon_{jklm} \qquad (1)$$

where μ is the overall mean, e_j the effect of environment j, $r\ (e)_{k(j)}$ the effect of replicate k within environment j, $b(re)_{l(kj)}$ the effect of block l

Table 1: Description of trials conducted in each experiment, location and years of evaluation

Exp.	No. of genotypes	Evaluation	No. of trials	Number of locations				Evaluation years	
				Mexico		ESA		Mexico	ESA
1	259	Testcross	5	2	Agua Fria Tlaltizapan	2	Kiboko[1] Chisumbanje	2010	2010
2	116	Testcross	4	2	Agua Fria Tlaltizapan	2	Kiboko Kakamega	2011	2011
3	280	Line *per se*	10	2	Agua Fria El Batan	2	Kakamega Harare	2009, 2010, 2011	2009, 2010

[1] One additional trial was conducted under mild drought stress conditions in Kiboko.

within replicate k and environment j, g_m the effect of genotype m, ge_{mj} the effect of interaction between genotype m and environment j and ε_{jklm} the plot error.

Treating each location by year combination as an environment, variance components for genotypes $\left(\sigma_g^2\right)$, genotype × environment interaction $\left(\sigma_{ge}^2\right)$ and the experimental error $\left(\sigma_\varepsilon^2\right)$ for testcross performance of the lines in Exp. 1 and 2 in each region were estimated by the SAS PROC MIXED procedure (SAS Institute 2001), using the restricted maximum-likelihood option. All factors were considered random.

To assess the presence or absence of specific adaptation to a region, combined analyses of variance were performed adopting the model employed by Windhausen et al. (2012), where environments were nested within regions:

$$\begin{aligned} Y_{ijklm} = \mu + s_i + e(s)_{j(i)} + r(es)_{k(ji)} + b(res)_{l(kji)} \\ + g_m + gs_{mi} + ge(s)_{mj(i)} + \varepsilon_{ijklm} \end{aligned} \tag{2}$$

where s_i is the effect of region i, $e(s)_{j(i)}$ the effect of environment j nested within region i, $r(es)_{k(ji)}$ the effect of replicate k nested within environment j and region i, $b(res)_{l(kji)}$ the effect of block l nested within replicate k, environment j and region i, gs_{mi} the effect of interaction between genotype m and region i, $ge(s)_{mj(i)}$ the effect of the interaction between genotype m × environment j nested within region i and ε_{ijklm} the plot error. The region effect was considered as fixed and all others as random.

The effect of the programme in which a line originated in the selected lines (Exp. 2 and Exp. 3) was estimated using the model

$$\begin{aligned} Y_{ijklm} = \mu + e_i + r(e)_{j(i)} + b(re)_{k(ji)} + o_l + g(o)_{m(l)} \\ + eo_{il} + ge(o)_{mi(l)} + \varepsilon_{ijklm} \end{aligned} \tag{3}$$

where o_l is the effect of origin l, $g(o)_{m(l)}$ the effect of genotype m within origin l, eo_{il} the effect of the interaction between environment i and origin l, $ge(o)_{mi(l)}$ the effect of the interaction between genotype m and environment i within origin l and ε_{ijklm} the effect of the plot error. The origin effect was fixed, while all the other main and interaction effects were considered random. This analysis was conducted separately for trials in ESA and Mexico.

Broad-sense heritability (H) for E environments and R replicates was estimated using the variance components estimated using equation (1) according to Hallauer et al. (2010):

$$H = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{ge}^2}{E} + \frac{\sigma_\varepsilon^2}{ER}} \tag{4}$$

Genotype means for grain yield in each region were estimated based on equation 1 with genotypes considered fixed effects and locations random. These estimates were used to calculate phenotypic and genotypic correlations as well as indirect selection efficiencies for grain yield across regions. Genotypic correlations between Mexico and ESA for all traits were estimated using the formula of Cooper et al. (1996) as:

$$r_{g(i,i*)} = \frac{r_{p(i,i*)}}{\sqrt{H_i \times H_{i*}}} \tag{5}$$

where $r_{p(i,i*)}$ is the phenotypic correlation between means estimated in the two regions i and $i*$ and H_i and H_{i*} are the broad-sense heritability values for each of the corresponding regions.

Indirect selection efficiency (ISE), which is the ratio of (i) the predicted correlated response in region $i*$ to indirect selection in region i to (ii) the predicted direct response to selection in region i under the assumption of the same selection intensity for both direct and indirect selection, was estimated according to Falconer and Mackay (1996):

$$\mathrm{ISE} = \frac{r_{g(i,i*)} \times \sqrt{H_{i*}}}{\sqrt{H_i}} \times 100. \tag{6}$$

Results

Grain yield for testcrosses of unselected lines (Exp. 1) showed similar means and ranges in Mexico and ESA (Table 2). By comparison, testcrosses of selected lines (Exp. 2) had higher mean grain yield in ESA (7.75 t/ha) than in Mexico (6.16 t/ha). The line *per se* trial of selected lines (Exp. 3) had higher mean grain yield in Mexico (1.79 t/ha) than in ESA (1.55 t/ha). Mexican trials were earlier flowering and taller than trials in ESA in testcross experiments (Exp. 1 and Exp. 2), while for the line *per se* experiment (Exp. 3), the ESA trials were earlier but shorter than Mexican trials.

For the analysis within regions, genotypic variances (σ_g^2) were similar in Mexico and ESA in both testcross experiments for all traits (Table 2). Apart from grain yield in ESA, σ_g^2 was consistently smaller in Exp. 2, which consisted of highly selected lines, than in Exp. 1. In line *per se* experiments, σ_g^2 for grain yield was twice as large in ESA as in Mexico and higher in Mexico than in ESA for days to anthesis and plant height. Estimates of σ_{ge}^2 were smaller than σ_g^2 for both regions and all experiments for anthesis date and plant height but higher for grain yield. Broad-sense heritability estimates (H) were high for days to anthesis and medium to high for the other traits. Estimates of H were consistently higher for the unselected lines in Exp. 1 than for the selected materials in Exp. 2 and generally higher in Mexico for all experiments than in ESA except for days to anthesis in Exp. 1.

Genotypic correlations [$r_{g(i,i*)}$] between testcross means in Mexico and ESA were equal to or exceeded 0.85 for all traits in Exp. 1 and were 1.0 for days to anthesis and plant height in Exp. 2 and greater than or equal to 0.72 for all traits in Exp. 3 (Table 2). Indirect selection efficiency for grain yield in Mexico based on selection in ESA exceeded 98% in both unselected (Exp. 1) and selected (Exp. 2) lines, which could be due to the use of broadly adapted testers but was also reasonably high ($\geq$78%) for selected lines evaluated *per se* (Exp. 3). By comparison, ISE for grain yield in ESA based on selection in Mexico was nearly 80% in Exp. 1 and exceeded this value in Exp. 2, while it was the lowest in Exp. 3, at 67%. Estimates of ISE for the other traits also ranged between nearly 80 and 110%. Days to anthesis and plant height had ISE values greater than 88% in both directions for all experiments.

For the combined analysis across regions, genotype × region interaction variance (σ_{gs}^2) for grain yield was not significant in either of the testcross experiments as well as in the line *per se* experiment and was small in comparison with the genotypic variance across both regions and the genotype × environment interaction variance nested within regions ($\sigma_{ge(s)}^2$) (Table 3). For days to anthesis and plant height, estimates of σ_{gs}^2 were zero in Exp. 2 and negligible in Exp. 3 but significant ($P < 0.05$) in Exp. 1. Plant height in Exp. 1 was the only trait for which σ_{gs}^2 exceeded $\sigma_{ge(s)}^2$.

Testcross yield of Exp. 2 lines selected in Latin America did not significantly differ from performance of ESA-selected lines, either in Mexico or in ESA (Table 4). Similarly, grain yield of Exp. 3 lines selected in Latin America did not significantly differ from performance of lines selected in ESA in Latin America. However, there was nearly 1 t/ha difference in performance of

Table 2: Means ($\bar{X}$), estimates of genotypic (σ^2_g), genotype × environment interaction (σ^2_{ge}) and error (σ^2_ε) variance components as well as heritability (*H*) for grain yield, days to anthesis and plant height of testcrosses of unselected lines (Exp. 1) and selected lines (Exp. 2) and line *per se* of selected lines (Exp. 3) evaluated in multiple environments in two regions (Mexico *vs.* Eastern and Southern Africa (ESA)). Genotypic correlations of all means ($r_{g(i,i^*)}$) between both regions and indirect selection efficiency (ISE) when selecting on the basis of results from the other region are also shown

	Grain yield (t/ha)		Days to anthesis (d)		Plant height (cm)	
Statistics	Mexico	ESA	Mexico	ESA	Mexico	ESA
Experiment 1 (N = 259 unselected lines)						
$\bar{X}$	3.85	3.61	57.43	67.26	236.63	216.98
σ^2_g	0.47 ± 0.06	0.35 ± 0.06	4.27 ± 0.42	5.13 ± 0.48	114.64 ± 13.48	98.88 ± 13.23
σ^2_{ge}	0.18 ± 0.04	0.42 ± 0.06	0.44 ± 0.11	0.09 ± 0.10	12.52 ± 7.14	0.00 ± 0.00
σ^2_ε	0.68 ± 0.03	0.81 ± 0.05	1.89 ± 0.09	2.04 ± 0.12	150.27 ± 6.93	264.43 ± 11.77
H	0.73	0.56	0.90	0.93	0.82	0.69
$r_{g(i,i^*)}$	0.92		0.95		0.85	
ISE (%)	105.6	81.0	93.9	96.9	93.0	78.4
Experiment 2 (N = 116 selected lines)						
$\bar{X}$	6.16	7.75	66.72	71.09	214.31	195.19
σ^2_g	0.42 ± 0.14	0.42 ± 0.18	3.27 ± 0.51	2.58 ± 0.51	75.24 ± 17.95	56.97 ± 16.80
σ^2_{ge}	0.71 ± 0.14	0.73 ± 0.20	0.33 ± 0.16	0.32 ± 0.34	34.51 ± 14.91	43.48 ± 16.07
σ^2_ε	0.55 ± 0.07	1.33 ± 0.15	1.26 ± 0.15	3.37 ± 0.37	112.43 ± 12.80	107.93 ± 12.48
H	0.46	0.38	0.87	0.72	0.62	0.54
$r_{g(i,i^*)}$	0.89		1.00		1.00	
ISE (%)	97.9	80.2	110.0	90.9	107.6	93.0
Experiment 3 (N = 280 selected lines)						
$\bar{X}$	1.79	1.55	93.18	79.64	142.70	129.08
σ^2_g	0.13 ± 0.02	0.29 ± 0.04	16.66 ± 1.59	8.80 ± 0.89	217.18 ± 21.31	172.56 ± 19.56
σ^2_{ge}	0.25 ± 0.02	0.63 ± 0.04	8.01 ± 0.44	3.02 ± 0.28	98.07 ± 6.89	34.73 ± 9.74
σ^2_ε	0.27 ± 0.01	0.35 ± 0.01	5.71 ± 0.17	3.72 ± 0.15	146.33 ± 4.48	237.91 ± 10.76
H	0.70	0.61	0.91	0.89	0.88	0.82
$r_{g(i,i^*)}$	0.72		0.92		0.92	
ISE (%)	77.5	67.2	92.7	90.9	94.9	88.3

Table 3: Estimates of genotypic (σ^2_g), genotype × region interaction (σ^2_{gs}), genotype × environment interaction nested within region ($\sigma^2_{ge(s)}$) and error (σ^2_ε) variance components for grain yield, days to anthesis and plant height of testcrosses of unselected lines (Exp. 1) and selected lines (Exp. 2) and line *per se* of selected lines (Exp. 3) evaluated in multiple environments in two regions (Mexico *vs.* Eastern and Southern Africa (ESA))

Statistics	Grain yield (t/ha)	Days to anthesis (days)	Plant height (cm)
Experiment 1 (N = 259 unselected lines)			
σ^2_g	0.40 ± 0.05	4.62 ± 0.42	99.31 ± 10.59
σ^2_{gs}	0.02 ± 0.03	0.14 ± 0.06	12.39 ± 4.39
$\sigma^2_{ge(s)}$	0.30 ± 0.05	0.26 ± 0.10	6.41 ± 6.42
σ^2_ε	0.72 ± 0.03	1.94 ± 0.07	152.33 ± 5.55
Experiment 2 (N = 116 selected lines)			
σ^2_g	0.38 ± 0.09	3.10 ± 0.46	75.86 ± 13.33
σ^2_{gs}	0.04 ± 0.10	0.00 ± 0.00	0.00 ± 0.00
$\sigma^2_{ge(s)}$	0.74 ± 0.15	0.28 ± 0.11	30.00 ± 11.63
σ^2_ε	0.90 ± 0.07	2.23 ± 0.15	109.44 ± 8.75
Experiment 3 (N = 280 selected lines)			
σ^2_g	0.17 ± 0.02	13.00 ± 1.19	196.03 ± 18.42
σ^2_{gs}	0.07 ± 0.01	0.97 ± 0.25	8.34 ± 4.93
$\sigma^2_{ge(s)}$	0.39 ± 0.02	6.10 ± 0.27	79.38 ± 5.31
σ^2_ε	0.30 ± 0.01	5.02 ± 0.12	175.53 ± 4.44

ESA developed lines as compared to Latin American developed lines in ESA.

Discussion

Exchanging breeding materials between regions within a multinational breeding programme is a highly effective approach to increasing genetic variability and gains, if the elite germplasm developed in one region also performs well in the other region and if the ranks of genotypes are highly correlated among regions. If this is the case, breeders can take advantage of the elite germplasm developed in one region and use it in the other region by immediately incorporating elite lines from other regions in replicated yield testing. Thus, our research focused on determining the efficiency of selecting materials in Mexico for use in ESA and vice versa. Furthermore, we considered the breeding stage at which germplasm exchange between these two regions is likely to be most efficient. To this end, we examined the predicted effectiveness of selection in one region in generating selection gain in the other region with testcrosses of unselected lines (Exp. 1) and selected lines (Exp. 2) originating from genetically different backgrounds and employing different testers. To reduce bias from using broadly adapted testers, we also evaluated line *per se* performance of selected lines (Exp. 3) over multiple years.

Performance level of the germplasm in Mexico and ESA and regional adaptation

We investigated the importance of regional adaptation by partitioning the genotype × environment interaction variance across all environments in both regions into the genotype × region interaction variance σ^2_{gs} and the genotype × environment interaction variance within regions $\sigma^2_{ge(s)}$. Because estimates of σ^2_{gs} were only about 5% of the magnitude of $\sigma^2_{ge(s)}$ for grain yield in Exp. 1 and 2 and 0 for days to anthesis and plant height in Exp. 2, there was little indication for specific adaptation to one of the regions. Although σ^2_{gs} for lines *per se* was higher than for testcrosses, it was still 15% or less as a proportion of total genotype × environment interaction variance, indicative of limited specific

Table 4: Mean estimates of grain yield, days to anthesis and plant height for advanced lines evaluated as testcross (Exp. 2) and as line *per se* (Exp. 3) and selected in Latin America *vs* Africa

	Performance in Mexico			Performance in ESA		
Origin	Grain yield (t/ha)	Days to anthesis (days)	Plant height (cm)	Grain yield (t/ha)	Days to anthesis (days)	Plant height (cm)
Africa						
Testcross	6.03 ± 0.41	67.38 ± 12.18	212.15 ± 14.82	7.85 ± 0.34	71.65 ± 10.43	195.62 ± 3.83
Line *per se*	1.03 ± 0.09	102.18 ± 2.39	142.19 ± 10.87	2.32 ± 0.51	80.16 ± 4.72	132.07 ± 8.88
Latin America						
Testcross	6.20 ± 0.39	66.50 ± 12.17	215.17 ± 14.74	7.72 ± 0.31	70.89 ± 10.43	195.03 ± 3.51
Line *per se*	0.83 ± 0.07	102.04 ± 2.29	144.66 ± 10.66	1.41 ± 0.50	79.54 ± 4.70	128.30 ± 8.63

adaptation to regions. σ^2_{gs} explained a substantial proportion of the total genotype × environment interaction variance only for days to anthesis and plant height in Exp. 1, which might be due to the fact that the unselected lines in Exp. 1 were developed in Mexico only, while the lines in Exp. 2 had been selected based on their performance in Mexico as well as in ESA. Consequently, regional adaptation to Mexico or ESA was rather unimportant for both unselected and selected materials.

One advantage of there being little or no specific regional adaptation of genotypes is that data generated from multilocation testing can be combined without strong effects on the ranking of genotypes; thus, it is possible to maximize selection for broadly adapted genotypes (Atlin et al. 2000a,b). A recent study of Windhausen et al. (2012) demonstrated that combining different regions into one large mega-environment for testing purposes could be very effective in selecting broadly adapted materials when there is no or minimum regional adaptation. Another advantage of low regional adaptation would be that it strongly supports the idea of exchanging breeding materials between Mexico and ESA.

Efficiency of direct versus indirect selection

An important parameter for assessing the prospects and limitations of exchanging breeding materials between regions and exploiting test results from one region to select the most promising hybrids for the other region is the genotypic correlation ($r_{g(i,i*)}$) between the regions. Moreover, comparing $r_{g(i,i*)}$ for unselected and selected materials is helpful in determining the optimum stage for exchanging germplasm between programmes. In accordance with the low importance of σ^2_{gs} relative to σ^2_g, the genotypic correlations ($r_{g(i,i*)}$) for testcross and line *per se* performance in Mexico and ESA were positive and high for all traits recorded in all three experiments. Besides $r_{g(i,i*)}$, the ISE is determined by the broad-sense heritability for each region (Falconer and Mackay 1996). For indirect selection to be more efficient than direct selection, the product of the square root of the heritability for the indirect selection region (H_{i*}) and the genotypic correlation between the direct and indirect selection regions ($r_{g(i,i*)}$) should be greater than the square root of the heritability of direct selection region (H_i) (Falconer and Mackay 1996, Hallauer et al. 2010). In our study, the Mexico region had consistently higher heritabilities for all traits and both experiments than the ESA region. Hence, indirect selection in Mexico for ESA was always higher than vice versa and exceeded 77% (Table 2). Nevertheless, ISE for indirect selection in the ESA region to improve performance in the Mexico region also exceeded 67%. These results indicate that selection in one region can be effective for generating gains in the other. This appraisal applies equally to both unselected and selected materials.

In Exp. 2 and Exp. 3, testcross and line *per se* yields of the lines selected in Africa and in Latin America were similar in both regions (Table 4). This indicates that the region, in which a line was selected, had little effect on its performance and that the lines in the other region are competitive in yield with those that were specifically developed in each one of the regions. These results support the finding that there is little local adaptation to Africa versus Mexico in elite subtropical germplasm and that elite lines from one region are promising materials for direct release or use as parents in the other.

Breeding implication

CIMMYT's maize breeding programmes in Mexico and ESA serve the tropical and subtropical environments. High estimates of $r_{g(i,i*)}$ and ISE, as well as little indication of specific adaptation of genotypes to the two regions in our study, suggest that selection of superior genotypes in Mexico should be highly effective for ESA and vice versa. Thus, exchange of elite, selected breeding materials from the later stages of the breeding programmes should be advantageous and cost-efficient; exchanging material at later stages reduces the number of genotypes that must be evaluated in each region. However, one must be aware that adaptive diseases differ between Mexico and ESA. In ESA, the most common adaptive disease is maize streak virus (MSV), for which sources of resistance have been identified and major QTL are being fine mapped for use in marker-assisted selection (G. Mahuku, personal communication). This could facilitate introgression of MSV resistance QTL into new materials from Mexico, making them immediately useful in ESA. In Mexico, the corn stunt complex and tar spot are the two main adaptive diseases. No molecular markers have yet been identified to support marker-assisted introgression of resistances against these diseases. However, moving germplasm from Africa to Latin America in CIMMYT's breeding programmes is likely to be easier than moving germplasm in the other direction, because the African germplasm used by breeding programmes in ESA was largely derived from Mexican sources within the last 30 years, and the frequency of alleles for resistance to these adaptive diseases likely remains high. Our results indicate that CIMMYT's breeding programmes in Africa could be an important source of elite materials for Latin American breeding programmes.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Description of experimental sites with annual average maximum and minimum temperatures and average annual rainfall.