RESEARCH

Gains in Maize Genetic Improvement in Eastern and Southern Africa: II. CIMMYT Open-Pollinated Variety Breeding Pipeline

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ABSTRACT

Open-pollinated varieties (OPVs) still represent a significant proportion of the maize (*Zea mays* L.) seed system in many countries of sub-Saharan Africa. The International Maize and Wheat Improvement Centre (CIMMYT) has been breeding improved maize varieties for the stress-prone environments experienced by most smallholder farmers in eastern and southern Africa for over 30 yr. Hybrid breeding is now the major focus of the CIMMYT breeding pipeline. However, OPVs are generated within the hybrid pipeline. This is the first study to document genetic gain for maize grain yield under both optimal and stress (random and managed drought, low nitrogen [N], and maize streak virus [MSV]) conditions within the CIMMYT eastern and southern African OPV breeding pipeline. Genetic gain was estimated using the slope of the regression on the year of OPV release in regional trials over a 12-yr period (1999–2011). Open-pollinated varieties were separated into two maturity groups, early (<70 d to anthesis) and intermediate-late (>70 d to anthesis). Genetic gain in the early maturity group under optimal conditions, random drought, low N, and MSV was 109.9, 29.2, 84.8, and 192.9 kg ha^{-1} yr^{-1}. In the intermediate-late maturity group, genetic gain under optimal conditions, random drought, low N, and MSV was 79.1, 42.3, 53.0 and 108.7 kg ha^{-1} yr^{-1}. No significant yield gains were made under managed drought stress for both maturity groups. Our results show continued improvement in OPVs for both yield potential and stress tolerance.

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Abbreviations: ASI, anthesis–silking interval; BLUE, best linear unbiased estimate; ESA, eastern and southern Africa; CIMMYT, International Maize and Wheat Improvement Centre; MSV, maize streak virus; OPV, open-pollinated variety; SSA, sub-Saharan Africa.

MAIZE (*Zea mays* L.) accounts for over 50% of the land area under cereal production in over 50% of the countries in sub-Saharan Africa (SSA). However, despite the importance of maize within the region, maize yields are among the lowest in the world. Maize yields in over 30 countries in SSA remain much lower than yields within the Corn Belt of the United States in 1926, before the introduction of hybrids (1.88 Mg ha^{-1}) (FAO, 2016). Maize in this region is grown under rainfed and low-input conditions. Drought is a recurrent feature within SSA agricultural areas (Rojas et al., 2011) and is a major cause of low yields and food insecurity (Cairns et al., 2013b). While increasing maize yields in farmers' fields in SSA is unlikely to be achieved with a single intervention, the development of drought-tolerant maize varieties will be an important component of the solution. Therefore, breeding for increased drought tolerance in maize has been the focus of intense

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research for over 30 yr in SSA (Fischer et al., 1982; Bänziger and Diallo, 2004; Bänziger et al., 2006; Cairns et al., 2012; Badu-Apraku and Fakorede, 2013).

Maize can be subdivided into three categories: hybrid, improved open-pollinated varieties (OPVs), and traditional OPVs known as landraces (Denning et al., 2009). Conventional hybrids are produced through crossing genetically diverse inbred lines. The resulting F_1 progeny exhibit hybrid vigor. The F_1 seed should not be replanted to produce the subsequent crop; the inbreeding resulting from such recycling usually reduces yield by at least 20% in the first recycling generation (Morris et al., 1999). In theory, yields should stabilize by the F_2, but empirical studies have shown yield reductions of almost 50% by the third recycling generation in eastern Africa (Japhether et al., 2006). Improved OPVs are multiple line synthetics and can often be recycled for up to 3 yr without a significant loss in yield, but they yield approximately 20 to 25% less than hybrids (Pixley and Bänziger, 2004). Maintaining OPVs without yield loss depends on their degree of isolation from pollen contamination by seed admixture with other varieties, conditions that are often difficult for smallholder farmers to control (Morris et al., 1999). Landraces are subject to similar types of degeneration.

Hybrids have been a key component in the success of maize genetic improvement in many regions of the world (Duvick, 2005). Although it has been almost 60 yr since the first hybrids were released in SSA, in many regions, hybrids are still not readily available or account for a small share of the seed system. In West Africa, OPVs represent 60% of the formal maize seed sector, with hybrid seed only available in Ghana and Nigeria (Tahirou et al., 2009). In eastern and southern Africa (ESA), OPVs account for approximately 17 and 18% of the formal maize seed sector (Langyintuo et al., 2010). However, these figures mask regional variation. For example OPVs account for <20% of the formal seed sector in Malawi, Zambia, and Zimbabwe, compared with 100% in Angola and 71% in Mozambique (Kassie et al., 2012). The continued prevalence of OPVs in SSA is related to many factors (Pixley, 2006). Farmers often cite higher seed prices and unavailability of hybrid seed compared with OPVs, while seed companies often favor OPVs over hybrids due to lack of knowledge or capacity for hybrid seed production, lower seed production costs compared with hybrid production, and low purchasing power of farmers in rural areas (Pixley and Bänziger, 2004). Thus, despite their lower yield potential, OPVs are likely to continue to account for a large component of the formal maize seed sector.

The International Maize and Wheat Improvement Centre (CIMMYT) maize breeding program for ESA started in Zimbabwe in 1985, later opening offices in Kenya and Ethiopia. Since its establishment, CIMMYT has bred OPVs for yield potential and abiotic and biotic stress tolerance. Presently, greater emphasis is placed on hybrid development, with OPVs largely a byproduct of the hybrid parental line development pipeline. The CIMMYT maize breeding program in ESA has been described by Masuka et al. (2017) and Setimela et al. (2012). The OPV breeding program is separated into two programs based on maturity; early maturity (<70 d to anthesis) and intermediate-late (>70 d to anthesis). New OPVs are created every few years by intermating elite inbred lines with high general combining ability for grain yield under optimal and stressed conditions. These are then tested in regional trials across ESA by partners in a phenotyping network coordinated by CIMMYT. The best-performing OPVs are selected from these regional trials by seed companies for release.

Measuring genetic gain within breeding programs is essential to determine their effectiveness and establish a baseline that allows the outcomes of subsequent interventions on genetic improvement to be quantified. In temperate maize, the rate of breeding progress has been estimated at 73 kg ha^{-1} yr^{-1} for mild stress (Duvick, 1997), 146 kg ha^{-1} yr^{-1} when the stress was imposed at the flowering stage, and 76 kg ha^{-1} yr^{-1} when the stress was imposed during mid-grain-filling stage (Campos et al., 2004). Genetic gains in tropical maize under drought stress are not as well documented (Edmeades et al., 1999; Beyene et al., 2015). Genetic gains for grain yield in CIMMYT's ESA hybrid maize breeding program have been estimated at 109.4, 32.5, 22.7, 20.9, and 141.3 kg ha^{-1} yr^{-1} under optimal conditions, managed drought stress imposed by withholding irrigation during the dry season, random drought occurring naturally during the wet season, low nitrogen (N), and maize streak virus (MSV), respectively, during the period 2000 to 2010 (Masuka et al., 2017). In West and Central Africa, genetic gain has only been determined for OPVs. A genetic gain of 0.4% yr^{-1} for grain yield under optimal conditions was estimated for maize OPVs released between 1970 and 1999 in the Nigerian savannahs (Kamara et al., 2004). A more recent study estimated genetic gain for OPV grain yield at 40 kg ha^{-1} yr^{-1} (1% yr^{-1}) under optimal conditions and 14 kg ha^{-1} yr^{-1} under managed drought stress between 1988 and 2010 (Badu-Apraku et al., 2013, 2015).

The objective of this study was to estimate genetic gain for grain yield under optimal conditions, managed drought, and random stress-prone environments in the CIMMYT OPV development program in ESA. Although drought is one of the major causes of yield loss for maize in SSA, low yields are associated with several other abiotic and biotic stresses, including low-N stress and MSV. Genetic gain under these stresses was also assessed. A secondary aim of this study was to compare genetic gain within the CIMMYT OPV development program in ESA with its companion hybrid breeding program (Masuka et al., 2017).

MATERIALS AND METHODS

A total of 80 OPVs were selected from the CIMMYT ESA breeding program. The OPVs were selected based on their superior performance in regional trials in ESA between 1999 and 2011 (Vivek et al., 2001, 2002, 2003, 2004, 2005; Magorokosho et al., 2006, 2007, 2008, 2009, 2010; Makumbi, 2011). The germplasm was split into two maturity groups, early (43 OPVs) and intermediate-late (37 OPVs) (Table 1). The OPVs were selected for inclusion in the trial based on the year they were first evaluated in regional trials. For the early maturity group, the number of OPVs per year ranged from one in 2001 to eight in 2008 (no OPVs were included from 2005). For the intermediate-late maturity group, the number of OPVs ranged from one in 2000 and 2007 to seven in 2011 (with no OPVs included from 2001 and 2002). The different number of OPVs per year was due in part to problems with seed availability and multiplication. This also reflects the period of the breeding program when new experimental OPVs were not developed every year. Information on the pedigree and first year of entry in the regional trial of all OPVs is presented in Supplemental Table S1. The OPVs were developed using 8 to 16 synthetics. Each year 8 to 16 new elite lines within a heterotic group showing good combining ability and yield potential in trials are intermated amongst themselves for two generations to form a narrow-based synthetic. Synthetics from opposite heterotic groups are then crossed to form an F_1, which is advanced to F_2 through sib mating. The resultant broad-based population becomes a new OPV. Popular local OPVs 'Matuba' and 'Katumani' were used as checks for the early maturity group, while 'Hickory King' was used as a check for the intermediate-late maturity group (Machida et al., 2014).

Trial Management

Trials were planted at 17 locations across seven countries between 2010 and 2012. A summary of the locations and the treatments at each location is presented in Table 2.

Table 1. Summary of the number of open-pollinated varieties (OPVs) selected from each year used to evaluate genetic gains between the period 1999 to 2011 in the International Maize and Wheat Improvement Centre (CIMMYT) eastern and southern Africa OPV breeding program.

Year	Early	Intermediate-Late
1999	2	2
2000	3	1
2001	1	0
2002	2	0
2003	3	5
2004	6	3
2005	0	2
2006	6	3
2007	2	1
2008	8	6
2009	4	3
2010	2	3
2011	2	7
Check	2	1
Total	43	37

Experiments were planted using an α-lattice design, replicated twice in Harare, Kadoma, and Potchefstroom, and thrice at all other locations. Experiments were planted in two-row plots, in 5-m long rows with 25-cm interplant distance and 75 cm between rows, with a final plant density of 66,667 plants ha^{-1}. The OPVs were evaluated under five different environments: optimal conditions, managed and random drought, low-N stress, and MSV infestation. With the exception of low-N stress sites, all sites were optimally fertilized (160 kg N ha^{-1}) and recommended plant, weed, and insect control measures were followed. Optimal trials were planted during the main maize-growing seasons, irrigated at planting and germination, and then rain fed unless supplemental irrigation was required to avoid drought stress. Random drought stress trials were planted during the main growing season in drought-prone areas and relied entirely on rainfall throughout the growing season, with the exception of Chiredzi, where irrigation water was applied during planting and/or germination when necessary to ensure successful establishment of the trial. For managed drought stress, trials were planted during the dry season and irrigation was withheld approximately 2 wk prior to mid-anthesis. The amount of irrigation applied was not collected; however, pictures were sent of trials to indirectly monitor plant water status. The low-N trials were planted in sites that had been depleted of N for 10 and 4 seasons in Harare and Kiboko, respectively. The MSV trials were inoculated with MSV 10 to 14 d after planting using the *Cicadulina* vector following the procedure described by Tang and Bjarnason (1993). Maize streak virus symptoms were scored (as described below) 4 to 5 wk after inoculation, when symptoms were well developed, and in the early reproductive stage.

Measurements

The MSV disease scores were visually rated on a plot basis as the severity of disease symptoms using a 1 to 5 scale where 1 = no symptoms on leaves; 1.5 = very few streaks on leaves; 2 = light streaking on old leaves, gradually decreasing on young leaves; 2.5 = light streaking on old and young leaves; 3 = moderate streaks on old and young leaves; 3.5 = moderate streaks on old and young leaves and slight stunting; 4 = severe streaking on 60% of leaf area, with plants stunted; 4.5 = severe streaking on 75% of leaf area, with plants severely stunted; and 5 = severe streaking on 75% or more of the leaf area, with plants severely stunted, dying, or dead. Days to anthesis and silking were recorded when 50% of the plants had shed pollen and 50% of the plants had silks, respectively. The anthesis–silking interval (ASI) was calculated as days to silking − days to anthesis. At maturity, plant height was measured on two representative plants per plot (plants were still sufficiently intact for accurate height measurement at this time). All plants were hand harvested and grain yield measured. Grain weights were adjusted to 12.5% moisture content.

Statistical Analysis

Analyses of variance within and across locations were determined by the restricted maximum likelihood method using SAS 9.2 (SAS Institute, 2009). Variance components were determined by following linear mixed model:

$$Y_{ijrs} = \mu + G_i + E_j + GE_{ij} + R_{kj} + B_{sjk} + e_{ijks} \qquad [1]$$

Table 2. Summary of locations used in the study.

Country	Site	Coordinates	Elevation	Treatments
		° lat, long	m above sea level	
Kenya	Embu	–0.503, 37.457	1492	Optimal
	Kakamega	0.270, 34.740	1526	Optimal
	Kiboko	–2.250, 37.730	990	Managed drought stress, low-nitrogen stress
Malawi	Chitedzi	–13.980, 33.630	1140	Optimal
South Africa	Potchefstroom	–24.483, 30.417	100	Random drought stress
Tanzania	Arusha	–3.387, 36.683	1415	Random drought stress
	Weruweru	–3.400, 37.300	1400	Random drought stress
Uganda	Bulindi	1.476, 31.441	1182	Optimal, managed drought stress
	Serere	1.500, 33.393	1065	Optimal, random drought stress
Zambia	Golden Valley Research Center	–14.170, 28.370	1173	Optimal
	Nanga Irrigation Research Center	–15.757, 27.920	978	Optimal
Zimbabwe	Agricultural Research Trust (ART)	–16.275, 31.184	1556	Optimal
	Chiredzi	–20.350, 32.330	443	Managed drought stress, random drought stress
	Chisumbanje	–20.768, 32.339	443	Managed drought stress
	Kadoma	–18.320, 30.900	1325	Random drought stress
	Harare	–17.800, 31.050	1498	Optimal, low-nitrogen stress, maize streak virus
	Save Valley	–20.350, 32.330	443	Managed drought stress

where Y_{ijrs} was the phenotypic performance of the *i*th genotype at the *j*th environment in the *r*th replication of the *s*th incomplete block, μ was an intercept term, G_i was the genetic effect of the *i*th genotype, E_j was the effect of the *j*th environment, GE_{ij} is the interaction effect of *i*th genotype and the *j*th environment, r_{kj} was the effect of the *k*th replication at the *j*th environment, b_{sjk} was the effect of the *s*th incomplete block in the *k*th replication at the *j*th environment, and e_{ijks} was the residual. Environments and replications were treated as fixed effects and the other effects as random. In addition, best linear unbiased estimates (BLUEs) were estimated by assuming genotypes as fixed effects.

Repeatability was estimated as $r^2 = \sigma_g^2 / (\sigma_g^2 + \sigma_{g\times e}^2 / e + \sigma_e^2 / re)$ where σ_g^2 is the genotypic variance, $\sigma_{g\times e}^2$ is the genotype × environment, σ_e^2 is the residual variance, *e* is the number of environments, and *r* is the number of replicates per environment. One trial with repeatability of <0.10 was removed from all analyses and is not presented.

To estimate genetic gain grain yield was regressed against year of release using the linear mixed effects model:

$$Y_{klmno} = \mu + \text{location}_k + \text{year of release}_l + (\text{location} \times \text{year of release})_{kl} + \text{genotype}_m(\text{year of release}_l) + \text{location} \times \text{genotype}_{km}(\text{year of release}_l) + \text{rRep}_n(\text{location}_k) + \text{block}_o(\text{rep} \times \text{location}_{nk}) + \varepsilon_{klmno}$$

where Y_{klmno} = grain yield in the *k*th location in the *l*th year of release for the *m*th genotype in the *n*th replication in the *o*th incomplete block, μ is the general mean, location_k is the fixed effects of the locations ($k = 1,2,\ldots.,K$), year of release_l is the fixed effects of the year of release ($l = 1,2,\ldots.,L$), $(\text{location} \times \text{year of release})_{kl}$ is the fixed effects of the *k*th location × *l*th year of release interaction, $\text{genotype}_m(\text{year of release}_l)$ is the effects of the genotype nested in the year of release, $\text{location} \times \text{genotype}_{km}(\text{year of release}_l)$ is the interaction effect of the *k*th location by the *m*th genotype nested in the year of release, $\text{rep}_n(\text{location}_k)$ is the random effects of the replicates within locations ($r = 1,2,\ldots.,P$) with mean zero and variance $\sigma^2\text{rep}_n(\text{location}_k)$, $\text{block}_o(\text{rep} \times \text{location}_{nk})$ is the random effects of the blocks within replicates within locations ($o = 1,2,\ldots.,F$) with mean zero and variance $\sigma^2\text{block}_o(\text{rep} \times \text{location}_{nk})$, and ε_{klmno} is the random residual assumed to be independently and identically normal distributed with mean zero and variance σ^2_ε.

Trials with a repeatability of <0.20 were removed from the combined analysis. Similarly, yield level was also used to identify trials that were subsequently removed before the combined analysis. Optimal trials with yields <4 Mg ha^{-1} were removed prior to the combined analysis. Abiotic stress trials with yields >4 Mg ha^{-1} were reassigned as optimal for the combined analysis (Setimela et al., 2012). Trials that were removed are not presented.

RESULTS

Selection of Trials for Combined Analysis

A total of 14 trials (20%) were removed or reassigned prior to the combined analysis due to low repeatability (<0.20) or nontarget yield levels (see Statistical Analysis, above). Three trials (one early and two intermediate-late maturity groups) under low-N stress were removed, as mean yields were >3 Mg ha^{-1}. For managed drought stress, two trials from the early maturity group were removed prior to the combined analysis due to low repeatability and also grain yield >4 Mg ha^{-1}. One trial was removed from the MSV set (early maturity group) due to low repeatability. Three optimal trials (two early and one intermediate-late maturity) with yields <4 Mg ha^{-1} were reassigned as random drought stress. One optimal trial (intermediate-late maturity group) was removed for low repeatability. Four random drought trials (one early and three intermediate-late maturity) were removed prior to combined analysis for low repeatability.

Grain Yield, Phenology, and Plant Height

Grain yield under optimal conditions ranged from 4.31 to 9.35 Mg ha^{-1} in the early maturity group and 4.63 to 9.50

Mg ha^{-1} in the intermediate-late maturity group (Table 3). Under managed drought stress, grain yield ranged from 1.61 to 3.59 Mg ha^{-1} in the early maturity group and 1.11 to 3.63 Mg ha^{-1} in the intermediate-late group (Table 4). Grain yield under random drought stress ranged from 1.42 to 3.78 Mg ha^{-1} in the early maturity group and 1.08 to 2.65 Mg ha^{-1} in the intermediate-late maturity group (Table 5). Grain yield under low-N stress ranged from 1.87 to 3.55 Mg ha^{-1} for the early group and 2.68 to 3.62 Mg ha^{-1} for the intermediate-late group (Table 6). Under MSV stress, only one trial was analyzed for the early group, and grain yield was 3.95 Mg ha^{-1} (Table 7). For the intermediate-late group, grain yield ranged from 4.71 to 6.04 Mg ha^{-1}. The mean number of days to anthesis varied widely between trials under optimal conditions. In the early maturity group, the range between trials was over 4 wk, while for the intermediate-late group, the range of days to anthesis was just over 3 wk. In general, ASI was larger under managed drought stress than random drought stress. Under random drought stress, only two trials out of five had an average ASI of greater than one. Trial means for plant height under optimal conditions ranged from 156 to 235 cm in the early maturity group and 177 to 270 cm in the intermediate-late maturity group. Plant height under managed drought stress ranged from 171 to 201 cm in the early maturity group and 185 to 208 cm in the intermediate-late maturity group. Under random stress, plant height ranged from 132 to 226 cm in the early maturity group. In intermediate-late maturity group under random stress, plant height ranged from 121 to 233 cm. Plant height under low N ranged from 156 to 170 cm in the early maturity group and 170 to 187 cm in the intermediate-late maturity group.

Ten trials were removed due to low repeatability for grain yield (<0.20). In general, repeatability for trials under optimal conditions was high in both maturity groups, with 80% of included optimal trials having repeatability >0.50. Almost 70% of drought trials (managed and random) and low-N stress trials had repeatability >0.50. For MSV, two of the three trials had a repeatability >0.50.

Genetic Gain under Contrasting Environments

Under optimal conditions, yield increased at 109.9 and 79.1 kg ha^{-1} yr^{-1} for the early and intermediate-late maturity groups, respectively (Fig. 1a and 2a). Under managed drought stress, the observed rates of increase in grain yield of 24.0 and 15.2 kg ha^{-1} yr^{-1} for the early and

Table 3. Summary of mean, range, and repeatability (*h*) of grain yield, anthesis date, and plant height in optimal trials conducted in Kenya, Malawi, Uganda, Zambia, and Zimbabwe.

		Grain yield			Anthesis date			Plant height		
Location	**Country**	**Mean**	**Range**	***h***	**Mean**	**Range**	***h***	**Mean**	**Range**	***h***
			Mg ha^{-1}			d			cm	
Early maturity										
Harare	Zimbabwe	6.74	4.45–9.38	0.79	67.6	59.0–77.0	0.93	200.6	175.0–227.5	0.50
Embu	Kenya	6.12	4.87–7.25	0.74	66.7	58.9–78.0	0.98	—	—	—
Kakamega	Kenya	6.50	4.12–9.26	0.76	71.0	60.0–81.7	0.86	217.3	186.1–248.9	0.34
ART	Zimbabwe	9.35	7.07–11.48	0.77	63.9	57.7–74.7	0.97	250.2	205.0–310.0	0.62
Chitedzi	Malawi	4.31	2.96–5.46	0.75	47.0	42.0–52.3	0.88	156.0	138.1–173.7	0.72
Nanga	Zambia	6.15	5.70–6.72	0.37	53.1	48.3–60.3	0.95	218.5	191.1–257.3	0.61
Golden Valley	Zambia	4.50	3.48–5.54	0.52	67.4	61.8–75.7	0.87	200.5	174.6–241.5	0.68
Harare	Zimbabwe	5.50	4.69–6.04	0.33	—	—	—	—	—	—
Harare	Zimbabwe	6.00	3.60–8.24	0.77	73.4	68.2–80.7	0.83	189.6	165.0–225.0	0.58
Bulindi	Uganda	7.04	5.25–8.81	0.71	51.8	45.8–63.7	0.89	—	—	—
Harare	Zimbabwe	7.93	5.50–10.49	0.82	57.0	47.0–68.0	0.97	162.6	184.9–232.3	0.30
ART	Zimbabwe	8.84	7.55–10.16	0.51	67.1	62.7–75.8	0.96	234.7	209.9–270.4	0.61
Combined		6.58	4.66–8.13	0.93	63.5	58.0–72.6	0.98	208.8	191.9–234.5	0.89
Intermediate-late maturity										
Harare	Zimbabwe	6.86	4.94–8.07	0.55	70.8	66.2–75.2	0.37	—	—	—
Embu	Kenya	7.86	6.97–8.32	0.46	72.2	66.3–77.0	0.93	—	—	—
Kakamega	Kenya	5.99	2.97–7.81	0.85	75.2	69.5–80.0	0.84	253.1	231.7–276.7	0.20
Serere	Uganda	7.01	4.62–8.25	0.68	60.5	57.3–63.3	0.63	—	—	—
ART	Zimbabwe	9.01	8.02–9.67	0.47	71.5	67.5–75.8	0.76	269.5	232.7–316.0	0.44
Chitedzi	Malawi	6.66	4.67–8.81	0.76	68.8	65.0–72.1	0.77	—	—	—
Nanga	Zambia	6.36	4.72–7.31	0.63	83.8	81.0–88.8	0.77	224.3	198.3–255.0	0.10
Harare	Zimbabwe	6.29	4.26–7.35	0.62	70.5	66.9–74.0	0.68	—	—	—
Bulindi	Uganda	4.63	3.39–5.18	0.64	65.8	62.7–69.3	0.79	177.1	160.8–200.3	0.28
Harare	Zimbabwe	8.68	7.23–9.65	0.62	76.1	72.0–80.0	0.74	242.0	216.0–270.0	0.27
ART	Zimbabwe	9.50	8.80–10.01	0.37	72.6	66.7–76.8	0.80	—	—	—
Combined		6.45	4.56–7.11	0.91	70.3	65.9–73.4	0.95	189.7	182.4–199.5	0.40

Table 4. Summary of mean, range, and repeatability (*h*) of grain yield, anthesis date, anthesis–silking interval (ASI), and plant height in managed drought stress trials conducted in Kenya, Uganda, and Zimbabwe.

		Grain yield			Anthesis date			ASI			Plant height		
Location	Country	Mean	Range	*h*	Mean	Range	*h*	Mean	Range	*h*	Mean	Range	*h*
		Mg ha^{-1}			d			d			cm		
Early maturity													
Chiredzi	Zimbabwe	1.61	0.33–3.08	0.51	96.8	84.6–109.6	0.98	2.78	−8.30–8.78	0.11	200.6	177.2–226.4	0.39
Chisumbanje	Zimbabwe	3.59	1.11–5.11	0.80	101.2	91.7–110.3	0.93	1.95	−1.95–8.68	0.57	174.4	158.5–192.7	0.18
Save Valley	Zimbabwe	2.14	0.57–3.02	0.66	90.4	79.0–99.6	0.98	1.29	−1.30–12.33	0.85	170.7	155.0–192.9	0.60
Kiboko	Kenya	2.79	1.15–4.15	0.85	98.5	90.4–105.9	0.98	3.21	0–8.61	0.80	182.6	167.3–204.6	0.64
Combined		2.53	2.00–2.85	0.52	96.7	87.2–105.9	0.98	2.31	0.54–6.70	0.74	182.1	171.8–190.7	0.62
Intermediate-late maturity													
Chiredzi	Zimbabwe	4.29	3.27–5.01	0.34	96.8	88.0–102.3	0.85	–	–	–	219.4	193.4–237.1	0.52
		3.63	1.99–4.84	0.79	99.2	91.3–106.9	0.92	2.58	0–6.00	0.55	201.0	176.7–233.3	0.48
Bulindi	Uganda	3.20	1.87–4.61	0.53	89.3	81.3–95.0	0.86	2.90	0.31–8.58	0.79	208.0	187.4–245.4	0.50
Kiboko	Kenya	1.41	0.55–2.47	0.28	–	–	–	–	–	–	–	–	–
Chiredzi	Zimbabwe	1.11	0.14–1.63	0.72	58.0	48.9–66.7	0.65	7.51	2.33–17.67	0.46	185.0	144.2–218.6	0.51
Chiredzi	Zimbabwe	4.10	2.26–5.11	0.33	88.0	81.2–93.8	0.89	–	–	–	–	–	–
Combined		2.96	2.50–3.28	0.64	93.6	87.1–98.2	0.89	4.33	3.42–6.45	0.40	201.1	191.3–210.1	0.58

Table 5. Summary of mean, range, and repeatability (*h*) of grain yield, anthesis date, anthesis–silking interval (ASI), and plant height in random drought stress trials conducted in South Africa, Tanzania, Uganda, and Zimbabwe.

		Grain yield			Anthesis date			ASI			Plant height		
Location	Country	Mean	Range	*h*	Mean	Range	*h*	Mean	Range	*h*	Mean	Range	*h*
		Mg ha^{-1}			d			d			cm		
Early maturity													
Chiredzi	Zimbabwe	2.38	1.40–3.12	0.35	65.1	61.2–70.6	0.94	0.81	−1.33–3.67	0.46	215.6	188.8–240.6	0.52
Kadoma	Zimbabwe	1.42	0.35–2.66	0.57	58.7	50.7–69.2	0.76	3.26	0.14–8.47	0.35	132.4	69.8–169.3	0.48
Serere	Uganda	3.78	1.23–5.42	0.72	60.1	53.0–67.4	0.90	0.66	−3.60–5.20	0.55	157.7	131.8–185.5	0.69
Weruweru	Tanzania	2.51	1.65–3.43	0.39	62.6	59.1–67.1	0.78	3.07	−0.35–4.00	0.06	226.1	200.6–253.5	0
Potchefstroom	South Africa	2.64	1.03–4.35	0.67	71.4	69.5–76.5	0.76	0.48	−1.00–2.50	0.20	216.4	190.0–255.0	0.20
Kadoma	Zimbabwe	2.36	1.39–3.03	0.14	63.0	58.5–69.0	0.84	3.41	0.50–7.50	0.53	167.1	139.2–204.9	0.45
Combined		2.17	1.64–2.56	0.62	64.5	52.6–71.1	0.92	2.00	0–7.00	0.48	182.9	187.2–239.0	0.67
Intermediate-late maturity													
Chiredzi	Zimbabwe	2.59	1.36–3.41	0.61	68.6	64.7–71.6	0.78	0.93	−2.33–4.00	0.39	232.7	217.2–249.5	0.26
Arusha	Tanzania	1.08	0.39–2.02	0.64	91.8	80.3–95.3	0.99	3.84	2.64–4.68	0.12	121.2	97.7–143.3	0
Potchefstroom	South Africa	2.65	0.51–4.32	0.68	–	–	–	–	–	–	–	–	–
Combined		2.62	2.05–3.02	0.47	68.6	64.7–71.6	0.78	0.93	−2.33–4.00	0.39	232.7	217.2–249.5	0.26

Table 6. Summary of mean, range, and repeatability (*h*) of grain yield, anthesis date, anthesis–silking interval (ASI), and plant height in low-nitrogen-stress trials conducted in Kenya and Zimbabwe.

		Grain yield			Anthesis date			ASI			Plant height		
Location	Country	Mean	Range	*h*	Mean	Range	*h*	Mean	Range	*h*	Mean	Range	*h*
		Mg ha^{-1}			d			d			cm		
Early maturity													
Harare	Zimbabwe	1.87	0.86–3.16	0.52	69.3	62.5–79.5	0.93	3.58	1.18–6.97	0.52	155.8	127.5–176.4	0.67
Harare	Zimbabwe	3.53	1.28–6.08	0.84	71.3	61.5–83.9	0.98	4.03	0.37–7.51	0.63	169.9	144.4–198.1	0.67
Kiboko	Kenya	3.55	2.47–4.27	0.69	69.0	64.1–76.0	0.95	1.61	−1.02–3.40	0.38	163.4	137.2–189.2	0.78
Combined		2.98	2.16–3.73	0.67	69.9	63.5–78.7	0.91	3.08	2.40–3.91	0.42	163.1	149.1–178.3	0.82
Intermediate-late maturity													
Harare	Zimbabwe	2.68	1.05–3.63	0.84	73.5	70.8–76.4	0.79	1.20	0.30–2.10	0.18	186.7	162.4–219.4	0.29
Kiboko	Kenya	3.47	2.10–4.45	0.55	61.5	56.7–65.4	0.91	1.92	1.00–4.67	0.44	184.5	164.5–202.2	0.72
Harare	Zimbabwe	3.62	1.76–4.99	0.69	77.1	70.9–85.0	0.88	3.87	−1.00–6.33	0.20	170.1	157.1–186.2	0.51
Combined		3.26	2.28–3.75	0.72	70.7	67.5–74.0	0.82	2.33	2.00–2.60	0.17	180.4	173.4–188.5	0.54

Table 7. Summary of mean, range, and repeatability (*h*) of grain yield, anthesis date, anthesis–silking interval (ASI), and plant height in maize streak virus (MSV) stress trials conducted in Zimbabwe.

		Grain yield			Anthesis date			ASI			Plant height		
Location	Country	Mean	Range	*h*	Mean	Range	*h*	Mean	Range	*h*	Mean	Range	*h*
		—— Mg ha^{-1} ——			——— d ———			——— d ———			——— cm ———		
Early maturity													
Harare	Zimbabwe	3.95	0.73–6.87	0.92	63.4	64.0–77.4	0.93	0.03	–1.67–1.33	0.48	–	–	–
Intermediate-late maturity													
Harare	Zimbabwe	4.71	1.54–6.97	0.87	74.7	69.4–78.3	0.77	0.30	–0.99–1.66	0.32	2.24	1.50–2.83	0.27
Harare	Zimbabwe	6.04	2.69–8.07	0.47	73.2	67.8–76.5	0.48	–	–	–	4.79	2.37–7.06	0.19
Combined		5.37	3.01–6.32	0.76	73.9	70.1–76.2	0.78	0.58	0.48–0.70	0.13	2.14	1.75–2.85	0

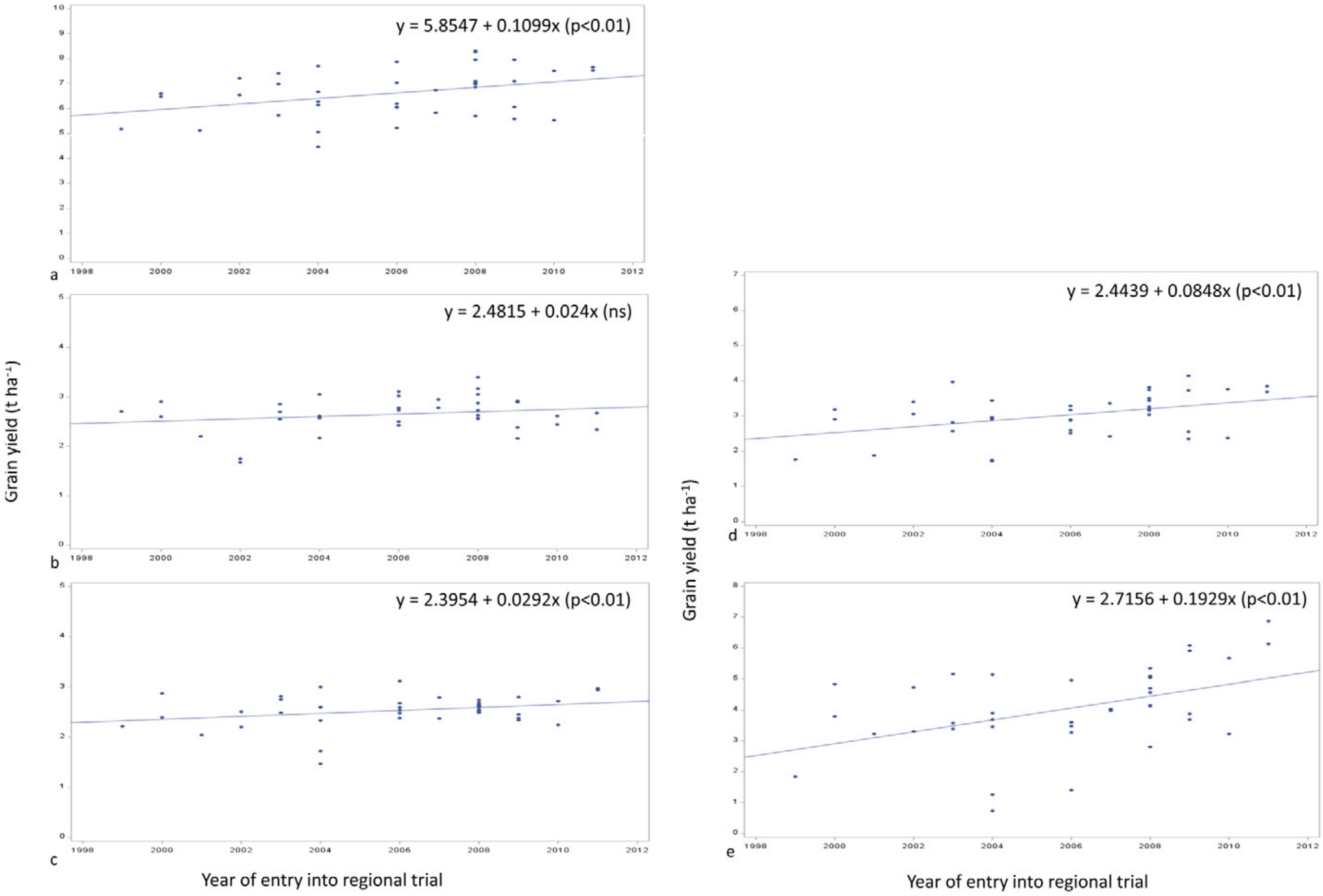

Fig. 1. Grain yield plotted against year of entry into regional trials of early open-pollinated varieties (OPVs) from regional trials between 1999 and 2011 under (a) optimal conditions, (b) managed drought stress, (c) random drought stress, (d) low-N stress, and (e) maize streak virus (MSV).

intermediate-late maturity groups, respectively, were not significantly different from zero. Under random drought-stress environments, grain yield increased at rates of 29.2 and 42.3 kg ha^{-1} yr^{-1} for the early and intermediate-late maturity groups, respectively (Fig. 1c and 2c). For low-N-stress environments, rates of 84.8 and 53.0 kg ha^{-1} yr^{-1} were observed for the early and intermediate-late maturity groups, respectively (Fig. 1d and 2d). Under MSV infection, rates of 192.9 and 108.7 kg ha^{-1} yr^{-1} were observed for the early and intermediate-late maturity groups, respectively (Fig. 1e and 2e). There were no significant changes in MSV scores over the 12-yr period for the early group (Fig. 3a). However, in the intermediate-late group, the MSV scores were reduced by 0.06 yr^{-1} (Fig. 3b). There were no significant changes in anthesis date, plant height, or ASI in the environments, except for a small (0.09 d yr^{-1}) but significant decrease in ASI under MSV infection in the early maturity group.

DISCUSSION

Genetic Gains in OPVs

Rates of genetic gains for grain yield did not differ among the two maturity groups. Gain under optimal conditions (109.9 and 79.1 kg ha^{-1} yr^{-1} for the early and intermediate-late maturity groups, respectively) were higher than recently reported for West and Central Africa, where

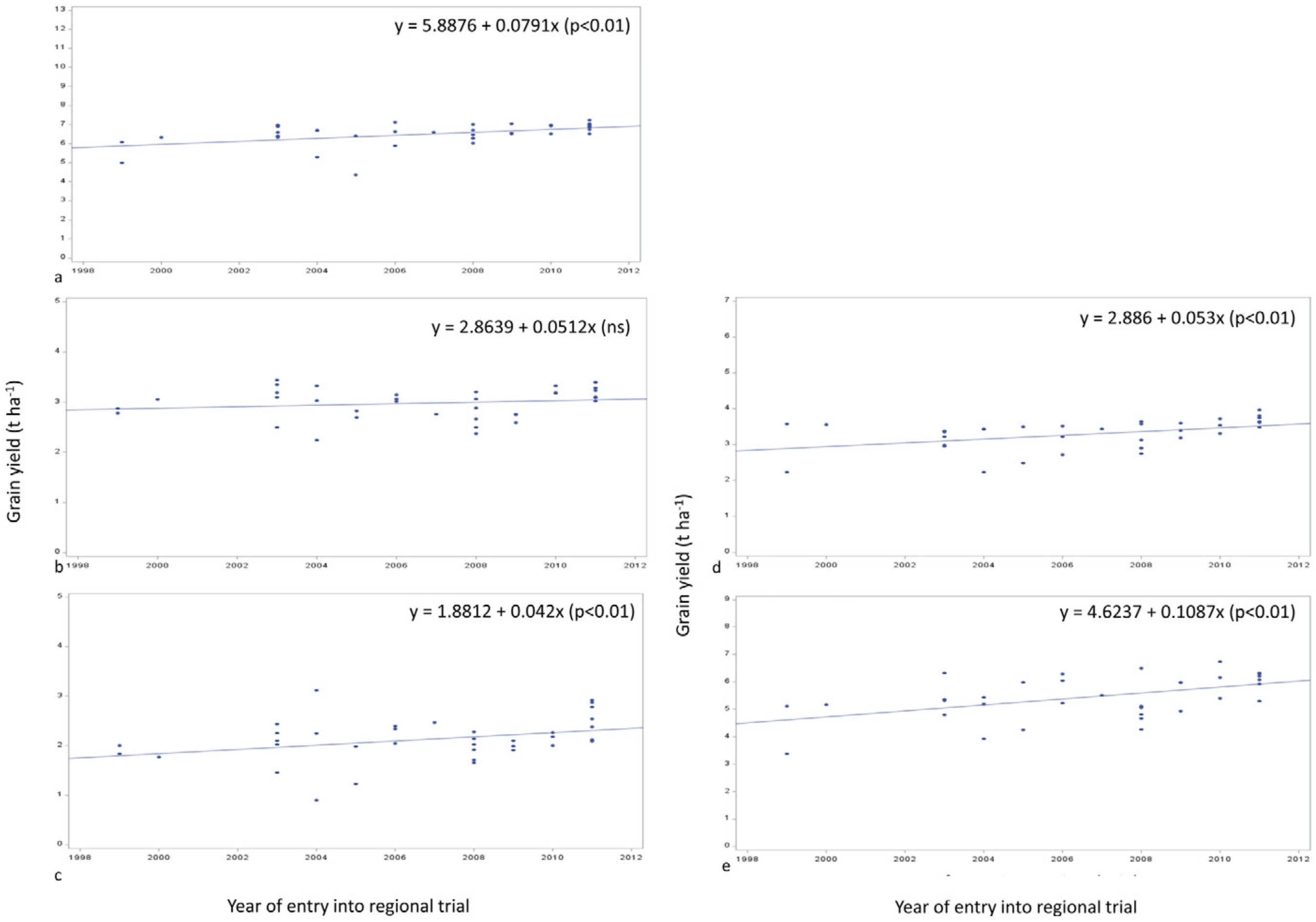

Fig. 2. Grain yield plotted against year of entry into regional trials of intermediate-late open-pollinated varieties (OPVs) from regional trials between 1999 and 2011 under (a) optimal conditions, (b) managed drought stress, (c) random drought stress, (d) low-N stress and (e) maize streak virus (MSV).

genetic gains of 40 kg ha^{-1} yr^{-1} were estimated for early-maturing OPVs (Badu-Apraku et al., 2013, 2015). Under managed drought stress, a genetic gain of 30 kg ha^{-1} yr^{-1} was achieved in West Africa, while in this study, there was no significant genetic gain in yield under managed drought stress. In general, OPV yield gains under abiotic stress in the CIMMYT ESA breeding program was higher than those for hybrids (Masuka et al., 2017); under random drought stress, a genetic gain in grain yield of 22.7 kg ha^{-1} yr^{-1} was achieved in the hybrid breeding pipeline compared with 29.2 kg ha^{-1} yr^{-1} for the early-maturing and 42.3 kg ha^{-1} yr^{-1} for intermediate-late-maturing OPV populations. Similarly, under low-N stress, a genetic gain in grain yield of 20.9 kg ha^{-1} yr^{-1} was observed in the hybrid breeding pipeline compared with 84.8 kg ha^{-1} yr^{-1} for early-maturing and 53.0 kg ha^{-1} yr^{-1} for intermediate-late-maturing OPV populations. Although greater genetic gains were observed under MSV in both the early and intermediate-late maturity OPVs compared with the hybrids, this result may lack robustness because only one location was used for the early OPVs (a second site was removed due to low repeatability). Yields under random stress were higher for the early OPV population than for the intermediate-late population. Maturity groups (early and intermediate-late) in the CIMMYT OPV breeding pipeline are handled as separate breeding programs, with different breeders and germplasm, and this is likely to account for early-maturing OPVs have higher yields than later-maturing OPVs. Yield gains under drought and low-N stress have previously been associated with an increase in flowering synchrony (a reduction in ASI) (Lafitte and Edmeades, 1994; Bolaños and Edmeades, 1996). Although there was no significant change in ASI, grain yield was negatively related to this trait, implying that ASI was not optimized in these OPVs and could be selected for to increase genetic gain. Yield progress was not associated with changes in plant height or days to flowering. A similar study looking at genetic gain in grain yield OPVs in West and Central Africa also found no significant change in ASI (Badu-Apraku et al., 2014). Yield progress was found to be associated with changes in ear per plant and days to anthesis.

Hybrid breeding is the main focus of the CIMMYT ESA breeding pipeline and OPV development is a byproduct of this program. Thus, by corollary, genetic gain for grain yield may have been expected to be lower in the

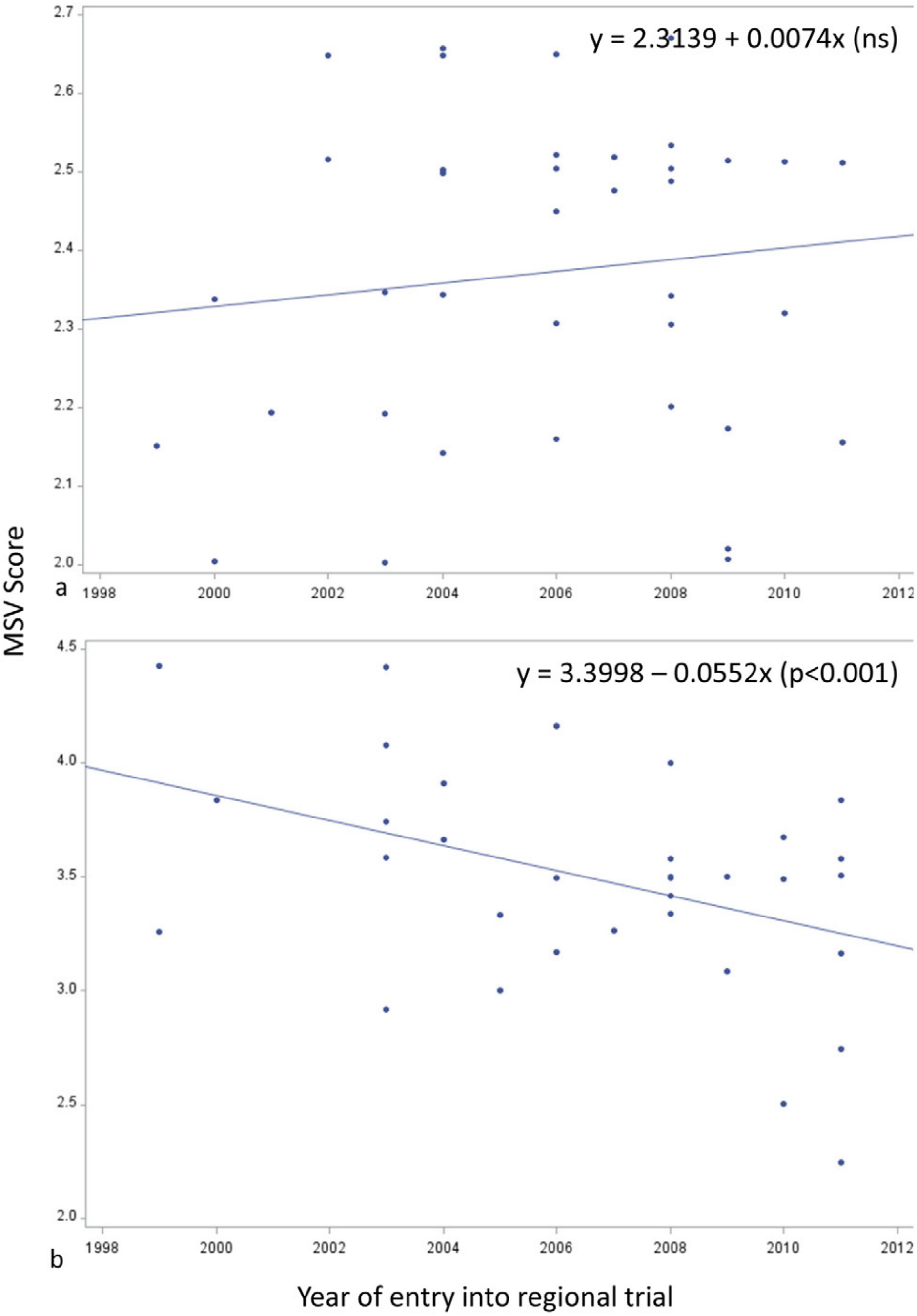

Fig. 3. Maize streak virus (MSV) score plotted against year of entry into regional trials of (a) early open-pollinated varieties (OPVs) and (b) intermediate-late OPVs from regional trials between 1999 and 2011.

OPV breeding program compared with the hybrid program, but this was not the case. In general, genetic gain in grain yield in the CIMMYT ESA OPVs was greater than observed for hybrids (Masuka et al., 2017). One possible reason for this is that, in general, the replacement of parental females inbreds of elite hybrids in the CIMMYT breeding program is considerably slower than the replacement of male parents of elite hybrids (for example, widely used females include CML395/CML444 and CML442/CML312, which are approximately 17 yr old; CML539/CML442, which is approximately 10 yr old; and CML536/CML312, which is approximately 4 yr old). New hybrids (generally three-way crosses reflecting the preference of seed companies) contain one or two parents, usually on the female side, that are older inbreds. By contrast, new OPVs are primarily derived from all new inbreds, taking advantage of the more rapid turnover of elite lines.

Genetic gain in the CIMMYT ESA hybrid maize breeding pipeline is comparable with gain in other regions of the world; however, absolute yield in experimental conditions is still lower than many regions, reflecting, in part, the yield potential of tropical maize, the severity of stresses experienced in the target environment, and the young age of the breeding program (Masuka et al., 2017). To accelerate genetic gain in the CIMMYT ESA hybrid breeding pipeline, a number of interventions are being undertaken, including expanding the size of the phenotyping network, increasing genetic variation, increasing the accuracy of selection, and accelerating breeding cycles (Cairns et al., 2013a, 2013b; Araus and Cairns, 2014; Beyene et al., 2015; Nair et al., 2015; Masuka et al., 2017). Hybrid and OPV development in the CIMMYT ESA breeding pipeline are intrinsically linked; all breeding is focused on hybrids, with OPV synthetic variety development just a byproduct of the hybrid breeding pipeline. Despite limited investment in OPV synthetic variety development (e.g., an offshoot of the hybrid pipeline, rather than a separate breeding program), genetic gain in grain yield significantly increased over the 10-yr period. These results indicate that, although OPV development is just a derivative of the hybrid breeding program rather than a separate breeding program itself, there was significant genetic gain in grain yield across different environments. This implies that there is no need to change the focus of the CIMMYT breeding pipeline from hybrid breeding to ensure that higher-yielding OPVs are developed. These results also infer that investments to increase genetic gain in grain yield within the hybrid breeding program should also benefit genetic gain within the OPV breeding program.

OPVs—an Option for Increased Food Security?

The CIMMYT hybrids yield >20% more than OPVs under optimal conditions (Pixley, 2006; Masuka et al., 2017). This yield advantage of hybrids over OPVs increased under abiotic stress, particularly for the early-maturing cultivars. Hybrids yielded almost 60 and 30% more under managed drought stress than early- and intermediate-late-maturing OPVs, respectively. Hybrids yielded almost 30% more than early maturity OPVs under random drought stress and low-N stress, and >60% more under MSV. Under random drought stress, hybrids yielded 30% more than early maturity OPVs. While the yield difference between new hybrids and OPVs under farmer-managed conditions in ESA is less, hybrids still outyield OPVs, particularly under very low-yielding conditions (Setimela et al., 2012). Earlier studies examining the profitability of hybrids and OPVs were based on old non-drought-tolerant maize varieties (Heisey et al., 1998; Pixley and Bänziger, 2004; Japhether et al., 2006). Substantial investment has been made in hybrid breeding at CIMMYT since 2006 (Cairns et al., 2013b), and yields have significantly increased under abiotic stress (Masuka et al., 2017; Setimela et al., 2012). Although there remains many barriers to the successful implementation of hybrids in many regions of SSA (Gaffney et al., 2016), together these results suggest that hybrids may be economically more viable than OPVs, despite initial investments. These results are in agreement with recent studies in Kenya and Zambia. The use of hybrid seed increased maize yields and annual income, reducing the depth of poverty (Jones et al., 2012; Mason and Smale, 2013; Mathenge et al., 2014). However, OPVs provide an option for resource-poor farmers who do not have access hybrid seeds. Furthermore in marginal areas where the risk of crop failure due to drought is high, farmers minimize the risk by not investing annually in inputs such as hybrid seed (Holden and Shiferaw, 2004). In on-farm trials, drought-tolerant OPVs were recently shown to offer a yield advantage over popular commercial hybrids (that were not developed for drought-prone environments) in southern Africa, although they yielded less than new drought-tolerant hybrids (Setimela et al., 2012).

Extensive breeding efforts have been made to increase maize yield in optimal and stress-prone environments in ESA (Bänziger and Diallo, 2004; Bänziger et al., 2006; Cairns et al., 2013a, 2013b). This is the first study to quantify genetic gain from OPV breeding effort in ESA. Although hybrid breeding is the main focus of the CIMMYT ESA breeding pipeline and OPV synthetic varietal development is a byproduct of this program, genetic gain in grain yield in the CIMMYT ESA OPVs was greater than gain observed for hybrids.

Conflict of Interest

The authors declare there to be no conflict of interest.

Supplemental Material Available

Supplemental material for this article is available online.

Acknowledgments

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