Gains in Maize Genetic Improvement in Eastern and Southern Africa: I. CIMMYT Hybrid Breeding Pipeline

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ABSTRACT

Monitoring of genetic gain in crop genetic improvement programs is necessary to measure the efficiency of the program. Periodic measurement of genetic gain also allows the efficiency of new technologies incorporated into a program to be quantified. Genetic gain within the International Maize and Wheat Improvement Centre (CIMMYT) breeding program for eastern and southern Africa were estimated using time series of maize (*Zea mays* L.) hybrids. A total of 67 of the best-performing hybrids from regional trials from 2000 to 2010 were selected to form an era panel and evaluated in 32 trials in eight locations across six countries in eastern and southern Africa. Treatments included optimal management, managed and random drought stress, low-nitrogen (N) stress and maize streak virus (MSV) infestation. Genetic gain was estimated as the slope of the regression of grain yield on the year of hybrid release. Genetic gain under optimal conditions, managed drought, random drought, low N, and MSV were estimated to have increased by 109.4, 32.5, 22.7, 20.9 and 141.3 kg ha^{-1} yr^{-1}, respectively. These results are comparable with genetic gain in maize yields in other regions of the world. New technologies to further increase the rate of genetic gain in maize breeding for eastern and southern Africa are also discussed.

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Abbreviations: ASI, anthesis–silking interval; CIMMYT, International Maize and Wheat Improvement Center; DH, doubled haploid; ESA, eastern and southern Africa; GCA, general combining ability; MSV, maize streak virus; OPV, open–pollinated variety; QTLs, quantitative trait loci; SNP, single-nucleotide polymorphism; SSA, sub-Saharan Africa.

"Maize (*Zea mays* L.) is life" to many of sub-Saharan Africa's (SSA) most vulnerable people, occupying over 50% of land devoted to cereal production in over 50% of countries in this region (FAO, 2016). In eastern and southern Africa (ESA), maize accounts for 45% of the total calories and 43% of the total protein from cereals (Shiferaw et al., 2011). In contrast to most other regions of the world, where the private sector has driven maize yield gains, maize breeding in SSA is dominated by public research expenditure (Duvick and Cassman, 1999; Pardey and Beintema, 2001). The budgets of public sector research are low, while the share of agricultural gross domestic product invested in public sector research continues to decrease (Kremer and Zwane, 2005). Furthermore the seed sector is largely dominated by small and medium seed companies that often do not have adequate

breeding capacity and rely on national and international research institutes for new stress-tolerant and high-yielding maize hybrids (Langyintuo et al., 2010; Cairns et al., 2013a). Breaking the cycle of low maize yields and food insecurity will require considerable investments in agricultural research in SSA. Increasing maize yield in farmers' fields in SSA is unlikely to be achieved with a single intervention; however, improved high-yielding varieties, developed for rainfed areas in SSA, will be an important component of strategies to increase yield and mitigate the potential effects of climate variability and change on maize yield (Cairns et al., 2013a).

Breeding is essentially a numbers game; the larger the populations generated and screened and the more site–year combinations used for selection, the greater the probability of identifying superior variants (Araus and Cairns, 2014). The development of coordinated phenotyping networks was crucial for the success of the Green Revolution (Reynolds and Borlaug, 2006). Cooper et al. (2014) attributed the success of US maize breeding to large, interconnected breeding networks. In 1991, the Eastern India Rainfed Lowland Shuttle Breeding Network for rice (*Oryza sativa* L.) was formed (Collard et al., 2013) and is responsible for the release and development of many improved cultivars, including submergence-tolerant varieties (Ismail et al., 2013). Given the low investment in agricultural research in ESA, a coordinated phenotyping network enables maximum benefit of limited resources for maize improvement over a large geographical area by allowing breeders to extrapolate within similar agroclimatic zones (Hartkamp et al., 2000). The CIMMYT maize breeding program for ESA started in Zimbabwe in 1985, and by the late 1990s, a breeding network across 11 countries had been established (Bänziger and Diallo, 2004). By 2006, this network had expanded to 59 locations within these 11 countries, and the phenotyping capacity for managed drought screening increased from 6 to 35 ha (Magorokosho et al., 2010; Makumbi, 2011; Cairns et al., 2013a). This increase has enabled greater emphasis on increasing drought tolerance. The breeding strategy has been described by Bänziger et al. (2006). Briefly, parent lines were crossed and progenies advanced to F_3. Families are test-crossed to a single cross or broad base population tester and evaluated under managed drought stress, low N stress, and optimal conditions. The top 20% are advanced and evaluated in test-cross combinations with three testers from the opposite heterotic group under a minimum of two drought stress, two low-N stress, and five optimal environments. In addition, stage-three trials are evaluated in disease hotspots for maize streak virus (MSV), northern corn leaf blight [NCLB, caused by *Exserohilum turcicum* (Pass) K.J. Leonard and E.G. Suggs], and grey leaf spot [caused by *Cercospora zeae-maydis* (Tehon and E.Y. Daniels)]. A maximum of 75 hybrids are advanced to regional testing in ESA. Although hybrids are the main focus of the CIMMYT ESA maize breeding programs, open-pollinated varieties (OPVs) are developed as a byproduct. New hybrids are simultaneously selected for performance under optimal, low nitrogen, random, and managed drought stress conditions.

Genetic gains are usually estimated in era experiments (e.g., Tollenaar, 1989; Duvick, 2005), wherein varieties released in different years are evaluated in common field trials. Measured traits are then regressed on year of variety release. Genetic gain evaluation enables plant breeding organizations to measure and adjust breeding programs on the basis of their performance. To date, genetic gains in maize hybrid breeding in SSA has not been quantified. Badu–Apraku et al. (2013, 2015) estimated genetic gain in OPVs in West and Central Africa. Using 50 OPVs separated into three eras (1988–2000, 2001–2006, and 2007–2010), Badu-Apraku et al. (2013) estimated a genetic gain in grain yield of 1.3% yr^{-1} under optimal conditions and 1.1% yr^{-1} under managed drought stress. A second study estimated that grain yield under natural stress increased by 1.2% yr^{-1} (Badu-Apraku et al., 2015). The aim of this study was to estimate genetic gain in CIMMYT's maize breeding program in ESA during 2000 to 2010, with particular emphasis on gains in grain yield under drought stress. In many countries within ESA, OPVs still account for a large proportion of the market (with the exception of Zambia and Zimbabwe) (Langyintuo et al., 2010). A companion paper looks at genetic gain in OPVs in ESA over the same period (Masuka et al., 2016).

MATERIALS AND METHODS
Germplasm
An era panel was assembled from hybrids selected by national programs and seed companies in consecutive years from 2000 to 2010. Hybrids and their parental lines originated from the CIMMYT breeding programs in ESA. A total of 67 hybrids were selected from the CIMMYT ESA maize breeding pipe-line. Hybrids were selected based on superior performance in regional trials within ESA between 2000 and 2010 (Vivek et al., 2001, 2002, 2003, 2004, 2005; Magorokosho et al., 2006, 2007, 2008, 2009, 2010; Makumbi, 2011). Hybrids are organized by the year they were first present in regional trials. The number of hybrids per year ranged from two in 2002 and 2003 to 10 in 2004 (Supplemental Table S1). Seed availability and multiplication challenges contributed to the imbalance of entries from each year. Several hybrids have the same female, independent of year of release. Information on the pedigree and first year of entry in the regional trials of all hybrids is presented in Supplemental Table S1. Three popular commercial hybrids, SC513 (released in 1997), SC635 (released in 2003), and SC727 (released in 2010), were used as checks. Thus, in all trials, a total of 70 hybrids were used.

Trial Management
A total of 32 trials were planted from 2011 to 2013 in eight locations across six countries in ESA. A summary of locations is presented in Table 1.

Table 1. Summary of trial locations.

Country	Location	Coordinates	Elevation
			m above sea level
Kenya	Kakamega	0.270, 34.740	1526
	Kiboko	−2.250, 37.730	990
Malawi	Chitedzi	−13.980, 33.630	1140
South Africa	Potchefstroom	−24.483, 30.417	100
Uganda	Bulindi	1.476, 31.441	1182
	Serere	1.500, 33.393	1065
Zambia	Golden Valley Research Trust	−14.170, 28.370	1173
	Nanga Irrigation Research Centre	−15.757, 27.920	978
Zimbabwe	Agricultural Research Trust (ART)	−17.716, 31.716	1516
	Chiredzi	20.350, 32.330	443
	Kadoma	−18.320, 30.900	1325
	Harare	−17.800, 31.050	1498

Experiments were planted in an α-lattice design (with 14 blocks of five), replicated twice in Harare under low-N stress and three times in all other locations. Experiments were planted in two-row plots (with the exception of Kiboko in 2012, with only one-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}. With the exception of low-N stress sites, all sites were optimally fertilized based on local recommendations and received recommended weed and insect control measures. Optimal trials were planted during the main maize growing seasons, irrigated twice at planting and emergence, and supplemental irrigation was applied as needed to avoid drought stress. For random drought stress, trials were planted in drought-prone locations, with irrigation supplied only at planting and emergence. For managed drought stress, irrigation was withheld approximately 2 wk prior to midtrial anthesis. Rescue irrigation was only applied to avoid total crop loss when required. Low-N trials were planted on sites that had been depleted for 10 and 4 seasons in Harare and Kiboko, respectively. Depletion was achieved by applying no N fertilizer to plots and removing stover from the field after grain was harvested. Trials under MSV were inoculated with MSV 10 to 14 d after planting using the *Cicadulina* spp. Vector, following the procedure described by Tang and Bjarnason (1993). Maize streak virus was scored twice, at least 4 to 5 wk after inoculation, when symptoms were well developed and the crop was at the early reproductive stage.

Measurements

Maize streak virus 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, plants stunted; 4.5 = severe streaking on 75% of leaf area, plants severely stunted; 5 = severe streaking on 75% or more of the leaf area, plants severely stunted, dying or dead. Days to anthesis and silking were recorded when 50% of the plants were shedding pollen and 50% of the plants had silks emerged. The anthesis–silking interval (ASI)

was calculated as days to silking − days to anthesis. At maturity, plant height was measured on five representative plants per plot using a ruler. All plants were hand harvested and shelled grain weight was measured. Grain weights were adjusted to 12.5% moisture content and 80% shelling percentage to calculate grain yield.

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:

$$Y_{ijrs} = \mu + G_i + E_j + GE_{ij} + r_{kj} + B_{sjk} + e_{ijks}$$

where Y_{ijrs} was the phenotypic performance of the ith genotype at the jth environment in the rth replication of the sth incomplete block, μ was an intercept term, G_i was the genetic effect of the ith genotype, E_j was the effect of the jth environment, GE_{ij} is the interaction effect of ith genotype and the jth environment, r_{kj} was the effect of the kth replication at the jth environment, b_{sjk} was the effect of the sth incomplete block in the kth replication at the jth environment, and e_{ijks} was the residual. Environments and replications were treated as fixed effects and the other effects as random. In addition, BLUEs (Best Linear Unbiased Estimates) 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 less than 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:

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

where Y_{klmno} was grain yield in the kth location in the lth year of release for the mth genotype in the nth replication in the oth incomplete block, μ is the general mean, location_k is the fixed effects of the locations ($k = 1, 2, ..., K$), year of release$_l$ is the fixed effects of the year of release ($l = 1, 2, ..., L$), (location × year of release)$_{kl}$ is the fixed effects of the kth location × lth year of release interaction, genotype$_m$(year of release$_l$) is the effects of the genotype nested in the year of release, location × genotype$_{km}$(year of release$_l$) is the interaction effect of the kth location by the mth genotype nested in the year of release, rep$_n$(location$_k$) is the random effects of the replicates within locations ($r = 1, 2, ..., P$) with a mean zero and variance $\sigma^2\text{rep}_n(\text{location}_k)$, block$_o$(rep × location$_{nk}$) is the random effects of the blocks within replicates within locations ($o = 1, 2, ..., F$) with a mean 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 normally distributed with a mean zero and variance σ_ε^2.

RESULTS
Grain Yield, Phenology, and Plant Height

Mean grain yield under well-watered conditions ranged from 4.35 to 10.80 Mg ha^{-1} (t ha^{-1}) (Table 2). The range of trial means for grain yield was high under managed

Table 2. 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.

Location	Country	Year	Grain yield Mean	Range	H	Anthesis date Mean	Range	H	Plant height Mean	Range	H
			—— Mg ha⁻¹ ——			—— d ——			——— cm ———		
Kakamega	Kenya	2013	9.60	3.54–13.53	0.74	76.1	66.7–82.7	0.94	254.1	221.9–288.0	0.76
Chitedze	Malawi	2012	10.80	4.65–16.91	0.76	70.5	64.8–77.9	0.90			
Bulindi	Uganda	2012	7.76	4.66–11.80	0.65	62.7	58.7–68.2	0.89	222.4	191.1–248.4	0.57
Serere	Uganda	2012	8.12	5.59–11.71	0.45	60.1	53.7–65.3	0.86	204.7	167.4–233.9	0.48
Golden Valley	Zambia	2012	4.35	3.13–5.67	0.39	70.7	66.2–75.6	0.79	207.8	179.9–244.5	0.45
Nanga	Zambia	2012	6.76	4.05–9.08	0.66	85.2	77.6–88.9	0.95			
Harare	Zimbabwe	2012a	7.45	3.68–11.16	0.47	74.3	60.5–71.5	0.80	212.2	177.4–249.8	0.54
Harare	Zimbabwe	2012b	6.85	2.91–9.78	0.60	72.1	64.2–76.0	0.86	201.0	171.5–234.3	0.65
Harare	Zimbabwe	2012c	7.07	3.59–10.15	0.59	75.2	67.9–80.3	0.90	203.3	173.2–243.9	0.63
Harare	Zimbabwe	2013	9.56	5.02–12.72	0.80	78.4	72.5–83.9	0.92	246.4	209.0–297.0	0.87
ART	Zimbabwe	2012	10.70	7.35–17.22	0.67	70.4	62.0–76.1	0.95	286.9	242.7–323.9	0.79
ART	Zimbabwe	2013	9.46	6.30–11.75	0.35	73.0	65.9–79.4	0.91	264.2	227.0–307.2	0.70
Chiredzi	Zimbabwe	2012	4.98	3.37–6.06	0.33	90.1	80.3–95.9	0.92	200.6	165.1–243.2	0.48
Bulindi†	Uganda	2012	2.39	1.29–3.59	0.65	64.3	57.3–69.0	0.89			
Combined			7.54		0.95	71.5		0.70	209.1		

† Removed from combined analysis due to low yield.

drought stress, ranging from 0.89 to 5.23 Mg ha⁻¹ (Table 3). Under random drought stress the range of trial means for grain yield ranged from 1.88 to 3.98 Mg ha⁻¹. Mean grain yield under low–N stress ranged from 2.36 to 5.92 Mg ha⁻¹ (Table 4). Mean grain yield under MSV ranged from 5.21 to 7.21 Mg ha⁻¹ (Table 5). The range in ASI was large under managed drought stress, reflecting the range in levels of drought stress. The anthesis–silking interval was less than four in all managed and random drought stress trials, with the exception of the managed drought stress trial in Chiredzi 2012. The range of mean days to anthesis date among well-watered trials was 30 d. Within trials, the range of mean anthesis date ranged from 9.5 (Golden Valley) to 16 d (Kakamega). Under managed drought stress, the range of mean days to

anthesis within trials was significantly shorter in Chiredzi in 2012 (planted in August) and Kiboko, reflecting the higher temperatures during the growing season compared with the trials in Chiredzi in 2013 (planted in May and July).

For optimal trials, the repeatability of grain yield in individual trials ranged from 0.33 (Chiredzi 2012) to 0.80 (Harare 2013). Repeatability was high (>0.60) in two-thirds of trials. In the combined analysis, repeatability for grain yield was 0.95. Under drought stress, repeatability of grain yield in individual trials ranged from 0.18 (Chiredzi 2012) to 0.64 (Kiboko 2012) under managed drought stress and from 0.21 (Chiredzi 2013a) to 0.47 (Kadoma 2013) under random drought stress. In the combined analysis, repeatability was 0.55 and 0.53 under managed and random drought stress,

Table 3. Summary of mean, range, and repeatability (H) of grain yield, anthesis date, anthesis–silking interval (ASI), and plant height in managed and random drought stress trials conducted in Kenya, South Africa, and Zimbabwe.

Location	Country	Year	Grain yield Mean	Range	H	Anthesis date Mean	Range	H	ASI Mean	Range	H	Plant height Mean	Range	H
			—— Mg ha⁻¹ ——			—— d ——			—— d ——			—— cm ——		
						Managed drought stress								
Chiredzi	Zimbabwe	2012	0.89	0.18–1.42	0.18	63.8	53.6–71.7	0.88	7.9	1.5–18.0	0.48	162.4	135.9–185.1	0.30
Kiboko	Kenya	2012	4.19	2.21–6.14	0.64	68.4	62.0–74.1	0.94	2.30	0.3–8.1	0.64	208.1	186.4–223.6	0.79
Chiredzi	Zimbabwe	2013a	5.23	2.81–6.98	0.63	92.9	84.3–101.5	0.96	2.1	−0.9–5.4	0.49	226.2	201.7–252.7	0.51
Chiredzi	Zimbabwe	2013b	2.24	2.76–7.55	0.47	94.1	85.0–105.5	0.92	2.9	−2.1–13.7	0.45	216.7	189.3–243.2	0.58
	Combined		3.95		0.55	75.7		0.95	4.0		0.45	203.4		0.70
						Random drought stress								
Chiredzi	Zimbabwe	2012	3.03	1.65–4.22	0.32	75.1	70.1–79.3	0.85	1.19	−7.89–5.13	0.34	203.5	151.2–234.8	0.13
Kadoma	Zimbabwe	2012	3.98	1.81–4.48	0.34	62.8	56.8–67.7	0.68	0.33	−1.56–4.69	0.59	181.4	145.3–220.5	0.34
Potchef-stroom	South Africa	2012	3.23	1.01–5.79	0.33	73.6	68.9–80.1	0.42	0.61	−2.40–5.68	0.34	233.3	208.2–276.7	
Kadoma	Zimbabwe	2013	1.88	0.92–2.90	0.42	64.9	58.7–68.4	0.70	3.06	−1.50–5.75	0.31	179.6	148.4–231.1	0.06
Kadoma	Zimbabwe	2013	1.83	1.12–2.67	0.47	64.4	58.4–70.1	0.75	0.18	−1.66–2.70	−	183.3	151.6–212.8	0.40
Chiredzi	Zimbabwe	2013a	3.41	2.35–4.47	0.21	59.0	50.9–64.6	0.69	0.44	−1.41–4.51	0.75	224.2	203.6–252.2	0.47
Chiredzi	Zimbabwe	2013b	3.59	2.20–4.85	0.27	59.5	53.8–63.2	0.94	2.42	−0.08–5.84	0.61	220.6	168.8–284.1	0.34
Combined			2.80		0.53	65.8		0.93	0.50		0.69	192.1		0.75

Table 4. Summary of mean, range, and repeatability (*H*) of grain yield, anthesis date, anthesis–silking interval (ASI), and plant height in low-N stress trials conducted in Kenya and Zimbabwe.

Location	Country	Year	Grain yield Mean	Range	*H*	Anthesis date Mean	Range	*H*	ASI Mean	Range	*H*	Plant height Mean	Range	*H*
			——— Mg ha⁻¹ ———			——— d ———			——— d ———			——— cm ———		
Harare	Zimbabwe	2012	2.36	1.21–3.65	0.62	77.6	68.5–84.9	0.92	1.58	–1.70–5.42	0.53	152.6	136.7–179.3	0.62
Kiboko	Kenya	2012	5.92	3.03–7.73	0.62	67.0	59.2–75.1	0.94	2.06	–0.28–5.08	0.38	181.3	151.6–211.4	0.61
Harare	Zimbabwe	2013a	2.66	1.37–3.75	0.20	72.8	65.0–77.9	0.94	3.36	0.90–6.74	0.55	169.4	120.9–200.1	0.20
Harare	Zimbabwe	2013b	4.15	2.75–6.23	0.11	72.6	64.1–79.5	0.92	2.78	0.07–5.16	0.27	181.1	149.5–206.2	0.11
Kiboko	Kenya	2013	3.59	2.73–4.80	0.52	61.5	53.0–66.2	0.94	1.80	–1.40–3.90	0.49	180.3	155.1–210.1	0.78
Combined			3.77		0.69	72.4		0.95	2.14		0.60	171.0		0.40

Table 5. Summary of mean, range, and repeatability (*H*) of grain yield, anthesis–silking interval (ASI), and visual scores of maize streak virus (MSV) and northern corn leaf blight (NCLB) in trials conducted in Kenya and Zimbabwe.

Location	Country	Year	Grain yield Mean	Range	*H*	ASI Mean	Range	*H*	MSV Mean	Range	*H*	NCLB Mean	Range	*H*
			——— Mg ha⁻¹ ———			——— d ———			——— 1–9 ———			——— 1–9 ———		
Harare	Zimbabwe	2012	5.21	1.44–7.21	0.79	–0.1	–2.0–3.0	0.51	1.98	1.42–2.90	0.73	2.09	1.56–2.77	0.69
Harare	Zimbabwe	2013a	7.21	1.87–10.51	0.72	0.6	–2.0–2.0	0.37	2.40	1.90–3.80	0.50	3.01	1.76–4.11	0.77
Harare	Zimbabwe	2013b	6.93	1.12–11.18	0.92	0.5	–3.0–3.0	0.41	2.50	1.60–3.80	0.59	2.66	1.48–3.48	0.75
Combined			6.45		0.82	0.3		0.72	2.20		0.67	2.60		0.77

respectively. For low-N stress trials, repeatability of grain yield ranged from 0.11 (Harare 2012) to 0.62 (Kiboko 2012). Under MSV, repeatability of grain yield in individual trials ranged from 0.72 (Harare 2013a) to 0.92 (Harare 2013b). For abiotic stress trials, repeatability of grain yield was higher than that of ASI for both managed and random drought stress and low-N stress. Similarly, under MSV, repeatability of grain yield was higher than that of ASI.

Genetic Gain for Grain Yield under Optimal, Drought, Low-Nitrogen, and Biotic (MSV) Stresses

Under optimal conditions, the rate of yield progress measured was 109.4 kg ha⁻¹ yr⁻¹ (Fig. 1a). Under managed and random drought stress, a rate of yield progress of 32.5 and 22.7 kg ha⁻¹ yr⁻¹ was reported, respectively (Fig. 1b and 1c). For low-N environments, a rate of yield progress of 20.9 kg ha⁻¹ yr⁻¹ was observed. Finally, for MSV environments, a rate of 141.3 kg ha⁻¹ yr⁻¹ was observed (Fig. 1e). No significant change in anthesis date was observed under any treatments (Table 6). The anthesis–silking interval was significantly reduced under optimal, managed drought, low-nitrogen, and MSV stresses, although the change was less than 1 d under all treatments. There was a small-yet-significant increase in the number of ears per plant under managed drought stress and MSV. The score for MSV decreased by 0.03 over the 10-yr period.

DISCUSSION
Genetic Gain in the Eastern and Southern Africa Breeding Pipeline

Over the past 10 yr, genetic gain in grain yield in the CIMMYT ESA hybrid maize breeding program was estimated at 109.4, 32.5, 22.7, 20.9, and 141.3 kg ha⁻¹ yr⁻¹

under optimal, managed drought, random drought, low-N, and MSV-infested research conditions, respectively. Yield gain under managed drought stress was lower than under random drought stress. While random drought stress more accurately simulates drought experienced by smallholder farmers, managed drought stress trials are less expensive to carry out and easier to maintain at higher repeatability (Bänziger et al., 2000). These results suggest that genetic gain is not being made in both managed and random drought treatments at an equivalent rate. Genetic gain in grain yield per year in this study was higher than reported in West and Central Africa by Badu-Apraku et al. (2013, 2015); 109.4 compared with 40 kg ha⁻¹ yr⁻¹ under optimal conditions and 32.5 kg ha⁻¹ yr⁻¹ for managed drought and 22.7 kg ha⁻¹ yr⁻¹ for random drought stress compared with 13.5 kg ha⁻¹ yr⁻¹, reflecting the higher yields levels of this study. At the end of the study period (2010), yield under optimal conditions in West and Central Africa was 3.96 compared with the 7.54 Mg ha⁻¹ observed in this study. Similarly under drought stress, Badu-Apraku et al. (2015) reported average grain yield was 1.61 Mg ha⁻¹ (representing a 60% reduction in grain yield) compared with the 3.95 Mg ha⁻¹ under managed drought stress (representing a 48% reduction in grain yield) or 2.80 Mg ha⁻¹ under random drought stress (representing a 63% reduction in grain yield) reported here. These results are also comparable with genetic gain estimates in other regions of the world. Under high input conditions, gain for maize grain yield has been estimated at 94.7 kg ha⁻¹ yr⁻¹ in China (Ci et al., 2011), 132 kg ha⁻¹ yr⁻¹ in Argentina (Luque et al., 2006), 80 kg ha⁻¹ yr⁻¹ in Canada (Bruulsema et al., 2000), and 65 to 75 kg ha⁻¹ yr⁻¹ in the United States (Duvick, 2005). Under drought stress, the rate of genetic gain in the United States was estimated

at 73 kg ha^{-1} yr^{-1} for mild drought stress (Duvick, 1997), 146 kg ha^{-1} yr^{-1} when drought stress was imposed at the flowering stage, and 76 kg ha^{-1} yr^{-1} when drought stress was imposed during mid-grain-filling stage (Campos et al., 2004). In tropical maize, Edmeades et al. (1999) previously estimated a genetic gain of 144 kg ha^{-1} yr^{-1} under flowering stage drought stress in a recurrent selection program.

Masuka et al. (2016) estimated genetic gain within the CIMMYT OPV breeding pipeline in ESA. In general, OPV yield gain under abiotic stress in the CIMMYT ESA breeding program was higher than that for hybrids. This study evaluated 67 hybrids used to represent different years; however, only 33 females were unique to these hybrids, with 13 females used more than once in the composition of hybrids. One female was in the background of 10 hybrids selected to represent 2007 to 2010, while another female was in the background of six hybrids selected to represent 2001, 2004, and 2005. The replacement of females in the CIMMYT breeding program is considerably slower than the replacement of males (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. Thus, this study is not a true breeding program assessment, as conducted by Edmeades et al. (1999) and Beyene et al. (2015), where genetic gains within populations

Table 6. Significant changes in secondary traits (ears per plant, anthesis date, anthesis–silking interval, plant height, and maize streak virus [MSV] score) identified by plotting traits against the year of entry of the best performing hybrids from regional trials between 2000 and 2010.

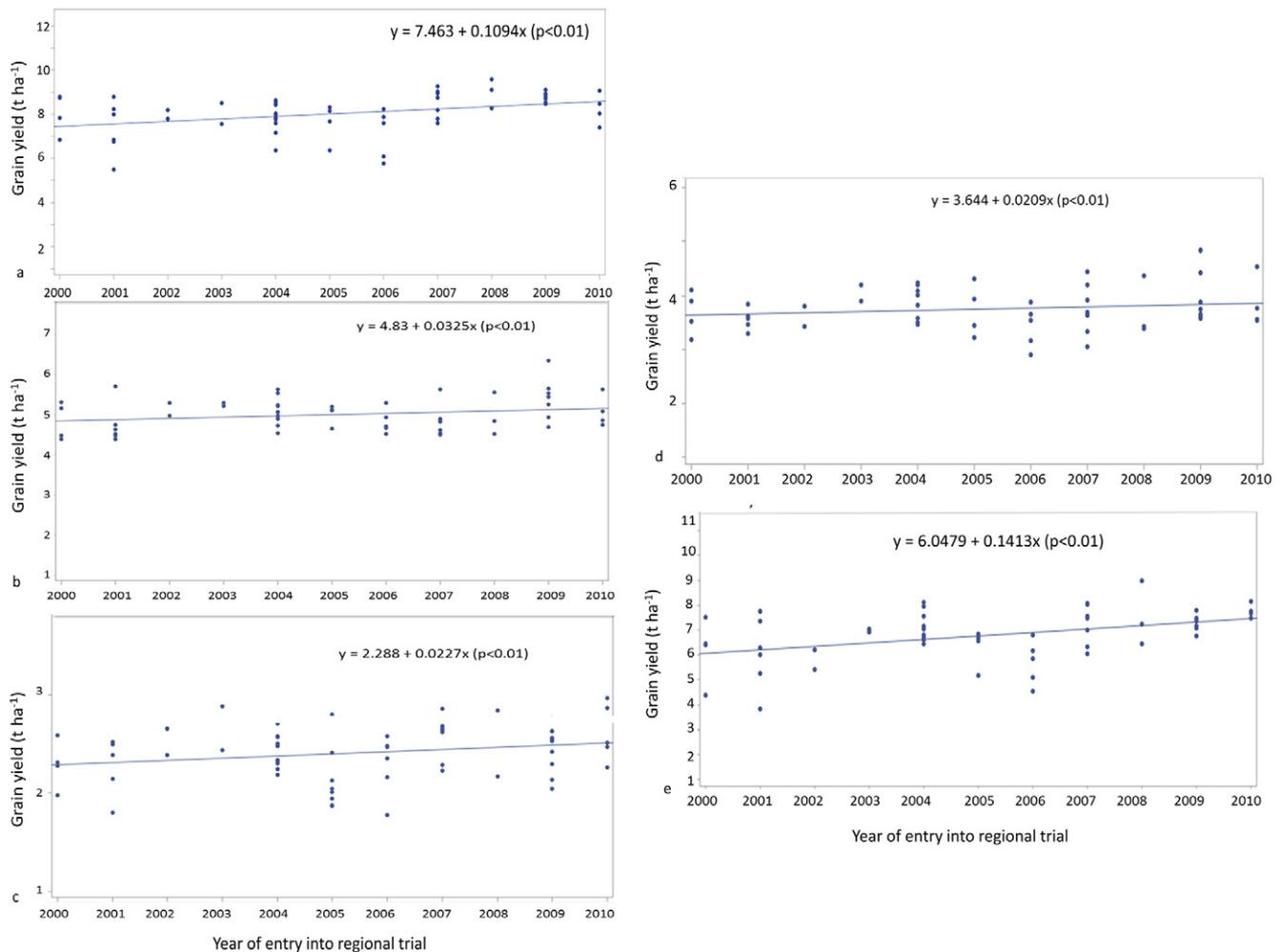| | | Drought | | Low-N | |
	Optimal	Managed	Random	stress	MSV
Ears per plant	ns†	+0.01	ns	ns	+0.01
Anthesis date	ns	ns	ns	ns	ns
Anthesis–silking interval	−0.08	−0.08	ns	−0.08	−0.06
Plant height	ns	ns	ns	ns	ns
MSV score	−	−	−	−	−0.03

† ns, not significant.

Fig. 1. Grain yield plotted against year of entry of the best performing hybrids from regional trials between 2000 and 2010 under (a) optimal conditions, (b) managed drought stress, (c) random drought stress, (d) low N stress, and (e) maize streak virus (MSV).

were established. In this study, although all varieties were selected based on yield, they were also selected for a wider range of reasons (e.g., yield potential, performance under abiotic stress, hybrid producibility, and disease resistance). Selection gains may have been higher if breeders did not have to make trade-off decisions associated with traits valued by seed companies (such as hybrid producibility) and farmers (such as cooking characteristics).

Gain for grain yield under both stress and optimal conditions was not associated with a change in maturity (estimated through days to anthesis), suggesting that yield gain was not a function of an increase in the length of the photosynthetic period associated with increased maturity, but rather a direct increase in tolerance to stress and/or an increase in overall yield potential. Increased flowering synchrony is one of the major changes associated with yield gain under flowering stage drought stress (Edmeades et al., 1999). In this study, reduced ASI was associated with yield gain under managed drought stress, low-N stress, and optimal conditions. Increased flowering synchrony has previously been associated with increased grain yield under optimal, drought, and low–N stress (Bolaños and Edmeades, 1993a; Bänziger et al., 2002; Cairns et al., 2012b). During eight cycles of full-sib recurrent selection in a Tuxpeno–Sequia population, grain yield increased by 94 to 125 kg ha^{-1} cycle^{-1} under flowering stage drought stress (Bolaños and Edmeades, 1993a). This increase in grain yield under stress was associated with a reduction of ASI, an increase in harvest index, and an increase in the number of ears and kernels per plant (Bolaños and Edmeades, 1993a, 1993b). Physiological changes associated with increased grain yield were not estimated in this study. Further work is required to identify key drivers of yield gain.

Maize streak virus is one of the most important disease threats to maize production in SSA (Martin and Shepherd, 2009; Nair et al., 2015). Many CIMMYT ESA breeding lines are derived from materials developed in Mexico, where MSV does not exist. Genetic gain for grain yield was highest under MSV inoculation. Since the visual disease scores have not changed appreciably over the 10-yr period, it is hypothesized that yield gain under optimal conditions is a significant influence on this observed trend. However, it is also plausible that not all yield-impacting effects of MSV infection may be captured by the visual rating scale, and it is likely that continued selection for grain yield within a wide area testing network, predominantly within endemic MSV areas, has also led to selection for favorable alleles that do not necessarily contribute to an improved visual score. The analogous condition exists for grain yield itself. Barrenness might be a useful visual indicator to predict grain yield until the entire germplasm pool has improved to the point where barrenness becomes uninformative. At this point, yield gain continues, even though the visible indicator has become irrelevant. Since all hybrids from 2000 onward have relatively low MSV visual scores, it is plausible that the large-effect genes for MSV were accumulated rapidly during the 1990s, while ongoing selection pressure for yield in MSV endemic areas has enabled continued improvement in the germplasm pool for MSV resistance, even after the visual score rating has become less useful. Increased seed movement and/or climate change may produce new combinations of pathogen and vector species and the potential for new hybrid pathogens (Garrett et al., 2011). An example of this is maize lethal necrosis (MLN), a devastating viral disease caused by a combination of maize chlorotic mottle virus (MCMV) and sugarcane mosaic virus (SCMV) or any other cereal virus of the *Potyviridae* family. In 2011, the first outbreak of MLN in Africa was reported in Kenya and spread to Tanzania, Uganda, Rwanda, the Democratic Republic of Congo, and Ethiopia (Wangai et al., 2012). In 2013, losses to Kenyan maize production as a result of MLN were estimated at 0.5 million Mg, or 22% of the average production before the outbreak of the disease (2.3 million Mg), with a value estimated at US$187 million (De Groote et al., 2016). Screening of commercial hybrids in ESA revealed high levels of susceptibility to MLN (Semagn et al., 2015). As the disease continues to spread, it is crucial that breeding for increased tolerance to MLN is incorporated into maize breeding programs within SSA. Demonstrated yield gain under MSV infection provides a benchmark for response to emerging biotic stresses.

Potential to Increase Genetic Gain in the Eastern and Southern Africa Breeding Pipeline

Although yield gain was comparable with gain in other regions of the world, absolute yield in experimental conditions is still lower than in 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. Maize yields in SSA are currently the lowest in the world (Cairns et al., 2012a). Nearly 30% of maize-growing countries in SSA have national maize yield averages <1 Mg ha^{-1}, and over 50% of countries are below 1.5 Mg ha^{-1}. Assuming a constant linear increase at current yield gain trends, maize yield will reach 3 Mg ha^{-1} in 17 yr under random drought stress in experimental conditions. Accelerated gain in both favorable and unfavorable environments is required to further drive maize yield higher in SSA. Genetic gain within a breeding program can be increased in a number of ways, including (i) increasing the size of the breeding program to enable higher selection intensity, (ii) ensuring adequate genetic variation, (iii) increasing accuracy of selection (higher repeatability), and (iv) acceleration of breeding cycles.

Increasing the Size of the Testing Network to Enable Higher Selection Intensity

A key component of the success of plant breeding in the past century has been the increased scale of field testing

(Cooper et al., 2014). The recent AquaMax hybrids of Pioneer Dupont were tested on almost 11,000 on-farm trials before their release in 2014 (Gaffney et al., 2015). The maize seed sector in SSA is dominated by small- and medium-sized companies with limited breeding capacity and geographic scope (Langyintuo et al., 2010). National breeding programs face financial constraints and often operate on a small scale within a relatively small geographic region, but adaptation zones for maize hybrids in Africa are large and usually include many countries (Windhausen et al., 2012). As a result, information generated from variety trials in one country is relevant to others in the region. The large-scale, regional testing network coordinated by CIMMYT, in collaboration with African national programs and seed companies, allows for more robust estimates of phenotypic performance, faster development of broadly adapted varieties, and maximized benefits of limited resources for crop genetic improvement in SSA over a large geographical area by allowing breeders to extrapolate within similar agroclimatic zones (Hartkamp et al., 2000). Furthermore under climate change projections, target environments for breeding products may change and new traits may increase in importance (Sonder et al., 2016). Genetic gains under abiotic stress in this study reflect the impact of phenotyping capacity, with the lowest gains made under low-N stress, which had the smallest area available for screening. Prior to 2009, the lowest phenotyping capacity in the CIMMYT ESA breeding pipeline was for low-N stress, with less than 10 ha of N-depleted land available for screening in ESA (Magorokosho et al., 2010). The low-N phenotyping capacity has recently been expanded, with sites in 10 countries on 48 ha of N-depleted land (Das et al., 2016). Drought phenotyping capacity has increased since 2006, with managed drought screening capacity increasing from 6 to 35 ha (Magorokosho et al., 2010; Makumbi, 2011; Cairns et al., 2013a). Although the newest hybrids in this study entered into regional trials in 2010, they were developed in 2006, and thus this study does not reflect the impact of recent expansion of maize breeding effort.

The ability to expand phenotyping capacity will, ultimately, always be limited. Molecular technologies offer the ability to expand the size of a breeding program and selection intensity without increasing phenotyping requirements. Genotypic information can be used to preselect germplasm prior to the phenotyping stages, and the capability to increase this untested layer will allow the total number of lines within a breeding program to be expanded (Cooper et al., 2014). Validated trait-linked markers for abiotic stress remain largely elusive in maize. Extensive mapping studies using both biparental and association mapping panels have identified many small-effect quantitative trait loci (QTLs) (e.g., Almeida et al., 2012, 2014). Meta-analysis of QTLs reduced the number of QTLs for grain yield to 59

(Semagn et al., 2013). However, only a few meta QTL were detected across well-watered and drought stress conditions and/or multiple genetic backgrounds, with each explaining a very small proportion of the phenotypic variance. Similarly for low N, many small-effect genomic regions, which are unlikely to be suitable for marker-assisted backcrossing, have been identified (Coque and Gallais, 2006; Semagn et al., 2015). By contrast, trait-linked markers are now either at the validation stage or are being deployed for key diseases in SSA. A major QTL (*msv1*) for MSV resistance on chromosome 1 has been identified in several populations (Welz et al., 1998; Pernet et al., 1999; Nair et al., 2015). Subsequent fine mapping of *msv1* identified three single-nucleotide polymorphisms (SNPs) within a haplotype block with an accuracy of 0.94 in predicting the disease reaction in a collection of breeding lines with known responses to MSV infection. High-throughput KASP (Kompetitive Allele Specific Polymerase Chain Reaction) assays have been developed for these three SNPs to enable routine marker screening in the breeding pipeline for MSV resistance. In the last year, 30,000 double haploid lines from the CIMMYT ESA breeding program were screened for the favorable haplotypes at *msv1* prior to advancing to field screening (Nair et al., 2015). Breeder-ready markers for northern corn leaf blight, grey leaf spot, and MLN are currently in the validation stage. Four promising haplotypes for northern corn leaf blight, accounting for 22% of the phenotypic variation, are currently being tested (S. Nair, unpublished data, 2016). For grey leaf spot, 16 promising genomic regions have been identified, representing 32 SNPs. For MLN, 24 SNPs of medium effect have been identified and validated using a combination of genomewide association analysis (GWAS), genomic selection, and association mapping (Gowda et al., 2015). Application of these markers to screen for tolerant material before expensive multilocation field testing is initiated will allow resources for yield testing to be focused on materials with acceptable levels of disease resistance, effectively increasing selection intensity for yield and, we hope, increasing the rate of genetic gains.

Increasing Functional Genetic Variation

The multilocation testcross characterization of large sets of inbreds from tropical maize programs worldwide allowed the systematic identification of the best drought and low-N donors (Cairns et al., 2013b; Das et al., 2016). The top 10 testcrosses yielded at least 0.65 Mg ha^{-1} more under drought stress than the current key line used in drought breeding (CML444) crossed to the broadly adapted tester CML539 (Cairns et al., 2013b). Under low N stress, the top 10 testcrosses (crossed to the broadly adapted tester CML539) yielded at least 1 Mg ha^{-1} more than lines previously considered to be low-N tolerant (including CML504 and CZL02012) under severe low-N stress (Das et al., 2016). Donors for both drought and low-N stress

have been incorporated into the CIMMYT ESA maize stress breeding pipeline. A number of important MLN–tolerant lines from Latin America and Asia are also being incorporated into the CIMMYT breeding effort to accelerate genetic gain for maize yield under MLN pressure (B. Das, unpublished data, 2016). The CIMMYT ESA breeding program is also actively seeking to diversify the germplasm base through the use of temperate lines. The CIMMYT is utilizing temperate maize lines with expired intellectual proprietary protection (off–PVP) as sources of yield potential and stress resilience. Since these lines have unfavorable haplotypes at the *msv1* locus (Semagn et al., 2015) and do not carry resistance loci for important MLN QTL, there are opportunities to enrich breeding populations involving off–PVP materials through the deployment of markers for disease tolerance in ESA.

Increased Repeatability

More accurate selection through increased repeatability increases selection response for the trait of interest. Recent combined analysis of the southern Africa regional trials of CIMMYT and partners and managed drought and low-N stress trials in ESA showed that the repeatability (H) of the managed stress trials in this study was lower than that of nonstress trials and that plot residual variance under abiotic stress was high (Weber et al., 2012; Cairns et al., 2013b; Das et al., 2016). In this study, the combined H was above 0.5 for all stress treatments; however, several trials had to be removed due to low H. These results highlight the need for measures to reduce the effects of field variability to increase the genetic signal–to–noise ratio and enable detection of real differences between lines. Reducing the size of the residual relative to the genetic component of variance and/or increasing replication would have a positive impact on repeatability levels and expected genetic gains (Cairns et al., 2012a; 2013b).

Doubled haploid (DH) technology provides another avenue to increase genetic variance (the variance among DH lines is higher than among the S_1 or S_2 lines usually used in early-generation testing schemes) and reduce breeding cycle times. Although early-generation testing schemes can be optimized to have shorter breeding cycle time, genetic drift during inbreeding and advancement results in lower realized heritability compared with DH. Doubled haploid allows completely homozygous lines to be rapidly developed from heterozygous parents in two seasons, enabling greater selection efficiency, since DH lines do not change from one testing season to the next. This, combined with higher between-entry variation compared with early-generation testing methods, improves overall realized heritability, resulting in higher genetic gain. Tropically adapted maize inducer lines with a haploid induction rate of up to 10% and a new marker system were recently developed (Prigge et

al., 2011; Chaikam et al., 2015). A DH facility was established in Kenya to allow the routine incorporation of DH into breeding programs in ESA (CIMMYT, 2014). The current haploid induction rate is 5.5%, with a production capacity of over 50,000 haploid lines per year (S. Bumagat, unpublished data, 2016). However, current costs (~US$30 line^{-1}) limit further utilization of this technology. Work is now underway to reduce DH production costs through (i) more efficient haploid induction, (ii) more efficient chromosome doubling, (iii) optimization of protocols to more closely reach production targets, and (iv) more efficient haploid discrimination systems.

Faster Breeding Cycles

Maize hybrid breeding begins by crossing two inbreds. Progeny are then advanced by either selfing or DH technology and evaluated in testcross trials to determine general combining ability (GCA). Testcross selection within a biparental cross is based on phenotypic information and requires one season of field trials (Hallauer, 1990). Genomic selection offers a faster way to predict GCA without phenotyping. Jacobson et al. (2014) successfully developed a GCA model for genomic selection within A × B crosses. The GCA model relies on information from previously phenotyped and genotyped crosses with inbreds A and B as one of the parents and can be used in advanced breeding programs that use elite inbreds as the parents of new breeding crosses. The ability to predict GCA has the potential to significantly reduce time and costs in inbred development and thus speed up breeding cycles.

Improved Decision Support Tools

The importance of data management and decision support tools has been undervalued in public breeding. With advancing technology, the volume and diversity of data increases, hence, improved data management and decision support tools are necessary to facilitate the meta-analysis of big data. Meta-analysis of over 20,000 CIMMYT regional trials in southern Africa showed a nonlinear relationship between warming and maize yields (Lobell et al., 2011). For each degree day above 30°C, maize yields were reduced by 1% under optimal rainfed conditions and by 1.7% under drought conditions. Breeding for heat stress was subsequently incorporated into the CIMMYT ESA breeding program (Cairns et al., 2013a). Over the course of this study, the CIMMYT maize breeding program has rolled out Fieldbook to partners as a data management system to improve data capture and subsequent analysis (Vivek et al., 2007).

CONCLUSIONS

This is the first study to quantify genetic gain from maize breeding in ESA. Yield gain is comparable with other maize stress breeding programs. Yield shows no indication of reaching a plateau under any of the treatments evaluated,

suggesting that further gain can be made under both optimal and stress environments. The lowest realized genetic gain was observed under low-N stress. Fertilizer use in SSA is very low compared with the rest of the world (less than 10 kg ha^{-1} compared with over 200 and 96 kg ha^{-1} in Asia and Europe, respectively), and fertilizer use in the region decreased between 1997 and 2007 (Kostandini et al., 2015). Many current commercial varieties have very low yields under low-N stress, and because farm-gate fertilizer prices are high in most of Africa relative to prices in other regions, N fertilizer application rates are likely to remain low for some years to come. Thus, there is an urgent need to increase genetic gain for yield under low fertility conditions. Yield gains under drought stress were moderately higher. Increased yield testing under low-N and drought conditions and the incorporation of new technologies and germplasm into the CIMMYT ESA breeding pipeline are likely to accelerate genetic gain for maize yield.

These results suggest that, although maize yields in some countries in ESA have declined or stagnated during this period (Ray et al., 2012), this was not due to a lack of genetic progress, but rather to the slow rate of dissemination of new hybrids in the region. Hybrid turnover is very slow in ESA; for example, despite the development of many new drought and low-N tolerant hybrids from CIMMYT's maize program in Kenya, the age of hybrids in farmers' fields averaged over 14 yr (Smale and Olawande, 2014); by contrast, the average commercial life of a maize hybrid in the US Corn Belt is approximately 4 yr (S. Eathington, personal communication, 2014). The rapid development, dissemination, and adoption of drought-tolerant maize has the potential to generate between US$362 million to US$590 million over a 7-yr period, through both yield gains and an increase in yield stability (Kostandini et al., 2013). A similar *ex ante* study showed that low-N-tolerant maize has the potential to deliver a total of US$586 million in gross benefits, with US$136 million and US$100 million of benefits to producers in Kenya and South Africa (Kostandini et al., 2015). However the impact of stress-tolerant maize on both total production and production variability within ESA is dependent on increased varietal turnover by the seed sector and adoption of new varieties by farmers (Cairns et al., 2013a).

Conflict of Interest
The authors declare there is no conflict of interest.

Supplemental Material Available
Supplemental material for this article is available online.

Acknowledgments

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