


Grain yield performance and flowering synchrony of CIMMYT's tropical maize (*Zea mays* L.) parental inbred lines and single crosses

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Abstract Maize production constraints in sub-Saharan Africa (SSA) are being addressed by CIMMYT and partners through an array of projects, focusing on developing and evaluating parental inbred lines and single-crosses as well as formulating, evaluating and releasing high-yielding and stress resilient hybrids adapted to different agro-ecologies. The objectives of the present study were to (1) evaluate the grain yield performance of parental elite inbred lines developed over the years, and single crosses; and (2) ascertain the flowering synchrony among inbred lines and single-cross hybrid parents. Parental inbred lines and single-crosses were evaluated at seven locations in two

countries in 2014. Combined analysis of variance revealed differences ($P < 0.01$) among genotypes for grain yield (GY) and among different years/era of release of the inbred lines. The improvement in GY of inbred lines was estimated to be 1.4 % per year. Under irrigated conditions GY of some single-cross hybrids was over 16 t ha^{-1} . Some single-cross and inbred line parents showed acceptable flowering synchrony, good producibility, and stable performance across testing environments, suggesting that these have high potential for seed production. Further research is needed to determine the physiological and morphological characteristics that contributed to the GY improvement in the parental inbred lines. Information generated from this study will enhance the use of CIMMYT's tropical mid-altitude parental germplasm by breeders working in both private and public breeding programs for developing and deploying high-yielding maize hybrids for the benefit of small-scale farmers in SSA.

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Abbreviations

AMMI	Additive main effects and multiplicative interaction
CIMMYT	International Maize and Wheat Improvement Center
CML	CIMMYT maize line
COGS	Cost of goods sold

DH	Doubled haploid
ESA	Eastern and southern Africa
$G \times E$	Genotype \times environment interaction
GGE	Genotype main effect plus genotype \times environment interaction
GY	Grain yield
IPCA	Interaction principal component
SSA	Sub-Saharan Africa
TWC	Three-way cross

Introduction

Maize (*Zea mays* L.) is a major food crop in sub-Saharan Africa (SSA) with consumption averaging about 72 kg per capita (FAOSTAT 2014). However, smallholders in SSA who depend on maize for their income and livelihoods continue to grapple with several constraints including drought, poor soil fertility, emergence of new pests and diseases, lack of access to quality seed, degradation of soil and water resources, poor purchasing capacity and many others (Shiferaw et al. 2011). Several collaborative projects/initiatives involving public and private sector partners are striving to address these constraints, with the aim of developing and deploying improved maize varieties with resilience to important abiotic and biotic stresses (Bänziger et al. 2006; Menkir et al. 2012; Beyene et al. 2013; Badu-Apraku et al. 2013; Edmeades 2013; Ndhlela et al. 2014; Makumbi et al. 2015). Stress-tolerant maize varieties have contributed to improved grain yield (GY) and maize production in several countries (Debelo 2012; FAOSTAT 2014), resulting in improved food security for the population. Availability of improved maize varieties has also spurred the growth of many small and medium sized seed companies in the region, with the number quadrupling between 1997 and 2007 (Langyintuo et al. 2010). Release and utilization of maize hybrids have increased significantly over the years (Langyintuo et al. 2010; Worku et al. 2012).

Among the different types of maize hybrids that have been developed by CIMMYT and partners for commercial production in East Africa, three-way cross (TWC) hybrids are predominant. This is mainly due to the relationship between cost of goods sold (COGS) and acceptable market price of seed. Three-way hybrids make use of higher yielding single-cross females, keeping the production costs lower. In contrast, single-cross hybrids are the primary type of

hybrid grown in the major maize producing countries of the world mainly due to their high productivity and uniformity as compared to other types of hybrids. Improvement in the productivity and vigor of seed parent inbred lines coupled with improved management practices over the years have enabled increased yield during seed production, thus encouraging single-cross hybrid production in temperate regions (Hallauer 1990; Duvick 2005; Fischer and Edmeades 2010; Wang et al. 2011; Lauer et al. 2012; Li et al. 2014).

Over the last three decades, CIMMYT has developed an array of Africa-adapted inbred lines with good combining ability and stress resilience; these have been used to develop an array of single, double, and three-way cross hybrids, as well as synthetic cultivars that are widely cultivated by farmers in SSA. Inbred lines used to form most of these varieties were developed using the pedigree breeding method. Doubled haploid (DH) technology is now being increasingly used in maize breeding at CIMMYT to improve genetic gains (Prasanna et al. 2012). In addition, molecular markers are routinely employed during inbred line development for important traits like maize streak virus (MSV) resistance and pro-vitamin A content (Semagn et al. 2015). Currently, elite inbred lines developed through both pedigree breeding and DH methods are used to develop various types of improved maize hybrids in East Africa. Basic and certified seed production for these hybrids is mostly carried out under rain-fed conditions in East Africa as very few companies have irrigation facilities for seed production.

Due to environmental variability in eastern and southern Africa (ESA), various abiotic stresses (drought, poor soil fertility conditions, heat, difference in temperature caused by altitudinal ranges) and biotic stresses (like northern corn leaf blight (*Exserohilum turcicum*), gray leaf spot (*Cercospora zea-maydis*), common leaf rust (*Puccinia sorghi*), MSV, maize lethal necrosis (MLN), *Striga*, and insect pests) are among the factors limiting maize productivity. Several studies have assessed genotype \times environment ($G \times E$) interaction of maize hybrids in ESA (Windhausen et al. 2012; Ndhlela et al. 2014; Makumbi et al. 2015) under different environments. Information on parental inbred line and single-cross seed yield under different environments and flowering synchrony between parents is important for successful seed production. Evaluation of inbred lines released in different eras will also shed light on the progress made over the years, which in turn can be

used to design new and more effective breeding strategies (Troyer and Wellin 2009). The objectives of the present study were to (1) evaluate the grain yield performance of parental elite inbred lines developed over the years and single crosses under different environments; and (2) ascertain the flowering synchrony among inbred lines and single-cross hybrid parents.

Materials and methods

Maize parental germplasm

Two different types of parental germplasm were evaluated in two separate trials. The first trial consisted of 124 maize inbred lines which were mainly developed for drought tolerance between 1996 and 2013 by CIMMYT (Supplementary Table 1). Thirty-four CIMMYT maize lines (CML) and 90 elite inbred lines also from CIMMYT were evaluated in this study. Inbred lines were categorized into five eras of release: pre-1996 (12 inbred lines), 1996–2000 (six inbred lines), 2001–2005 (27 inbred lines), 2006–2010 (34 inbred lines), and 2011–2013 (45 inbred lines) based on the year when the inbred line was first used to make elite hybrids for regional trials/national performance trials. The year of release for each inbred line is presented in Supplementary Table 1. These inbred lines are among the most widely used in the development of elite hybrids by CIMMYT and partners. The second trial consisted of 56 single-cross hybrids and five synthetics used as parents in the development of different types of maize hybrids in East Africa (Supplementary Table 2). The single-crosses were generated by crossing inbred lines within the same heterotic group or related inbred lines (11 B/B, 18 A/A and one AB/AB) to serve as single-cross parents in the formation of TWC hybrids. Single-cross parents formed from inbred lines from different heterotic groups (15 A/B, nine B/AB and two A/AB) were also part of this study (Supplementary Tables 1, 2). Five commercial hybrids (all TWC) were included in the single-cross parental trial as checks.

Experimental sites, experimental design, and trial management

Inbred line and single cross trials were evaluated at seven locations in Kenya and Uganda under irrigated

and rain-fed conditions (Table 1). The sites chosen for these trials are representative of the major maize production agro-ecologies in eastern Africa. These sites are also used by some of the major seed companies for seed production. Four locations (Bungoma, Thika, Namulonge, and Ngetta) represented the sub-humid lower mid-altitude; two locations (Chorlim and Elgon Downs) represented the sub-humid upper mid-altitude, while Kiboko represented the dry lower mid-altitude agro-ecology.

Genotypes in both trials were planted in an alpha (0,1) lattice design (Patterson and Williams 1976) with two replications at each location. Each replication of the inbred line trial had 31 blocks of 4 plots, while the single cross trial had 11 blocks of 6 plots. Plots consisted of two rows that were 4 m long with spacing of 0.75 and 0.25 m between rows and plants, respectively, giving a final plant density of 53,333 plants ha⁻¹ at all locations, except at Chorlim where a spacing of 0.75 and 0.2 m between rows and plants, respectively, giving a final plant density of 66,666 plants ha⁻¹. Trials at all locations were hand-planted with two seeds per hill and thinned at the 3-leaf stage. Planting dates at Elgon Downs, Thika, Chorlim, Kiboko, Bungoma, Namulonge and Ngetta were on 4, 30, 29, 9, 11, 8, and 17 April 2014 for both sets of trials, respectively. At each location the two trials were planted side by side with similar management regimes. The trials at Chorlim and Kiboko received supplemental water through sprinkler irrigation as needed while trials at other sites were entirely rain-fed. All trials were hand-harvested and dates varied by location. At Kiboko end plants in each plot were removed before harvesting while at the other locations all plants in a plot were harvested for grain yield data. Agronomic practices including fertilizer application and weed management were carried out as recommended at each location.

Data collection

Days to anthesis (AD) and silking (SD) were recorded for each plot when 50 % of the plants in the plot had shed pollen, and 50 % of the plants in the plot had emerged silks, respectively. Field weight was recorded from all ears harvested in each plot at all locations except at Kiboko where border plants were removed before harvesting, and a representative sample used to estimate moisture content for the plot using a moisture meter. Grain yield (t ha⁻¹) was calculated from field

Table 1 Description of testing locations used to evaluate inbred line and single cross parents in East Africa in 2014

Location	Elevation (m)	Latitude	Longitude	Temperature		Mean annual rainfall (mm)	Rainfall during 2014 growing season (mm)
				Min (°C)	Max (°C)		
Elgon Downs	1917	1°06'N	34°85'E	12.5	26.6	1260	858
Thika	1515	1°00'S	37°09'E	13.3	25.3	889	n/a ^a
Chorlim	1910	1°03'N	34°85'E	12.5	26.6	1260	858
Kiboko	976	2°20'S	37°72'E	16.5	28.6	530	57
Bungoma	1341	0°47'N	34°50'E	13.9	27.2	1221	968
Namulonge	1150	0°32'N	32°35'E	15.8	28.1	1200	n/a
Ngetta	1300	2°18'N	32°55'E	19.0	29.0	1483	n/a

^a Data not available

weight and grain moisture using an average shelling percentage of 80 % and adjusted to 12.5 % moisture content. To obtain the best estimate of relative maturity of the inbred lines and single crosses, growing degree days (GDD) were calculated (Gilmore and Rogers 1958). Kiboko flowering data were used to calculate GDD because meteorological data were available from the Kiboko Research Station, which is near the experimental site where both the single-cross and inbred line experiments were grown under optimum conditions. Thus, AD and SD were recorded under optimum conditions, without any obvious stress conditions. Then GDD for SD of single-cross parents and AD of the inbred line parents were calculated in degree Celsius (°C). The GDD was calculated according to the formula:

$$GDD = \sum_d \left[\frac{(T_{\min} + T_{\max})}{2} - T_b \right]$$

where T_{\min} and T_{\max} are the minimum and maximum daily temperature, respectively, and T_b is the base temperature, which was set to 10 °C. A base temperature of 10 °C was proposed for maize by Cross and Zuber (1972). While calculating GDD, the maximum daily temperature was set at 30 °C and the minimum daily temperature was set at 10 °C. Then we assessed the flowering synchrony of male inbred lines and single-cross seed parents for 98 TWC hybrids that were in the release process in Kenya, Tanzania and Uganda.

Statistical analyses

Analysis of variance (ANOVA) was conducted for both trials at each location except for the inbred line

trial at Elgon Downs which was discarded because of heavy damage caused by cut worms at an early stage. For each trial at each location, mixed model analysis in which genotypes were considered a fixed factor and replicates and incomplete blocks within replicates treated as random factors was carried using PROC MIXED of SAS (SAS Institute 2010) to generate lattice-adjusted genotype means. Analysis of variance across environments was carried out using PROC GLM of SAS (SAS Institute 2010) using raw data from each location to assess the differences among different eras of release of inbred lines and to assess the presence of $G \times E$. Then the mean yield across location for each inbred line was used for regression analysis to assess the progress made over the years. Simple linear correlation between GY and AD was carried out using PROC CORR of SAS.

Based on results of ANOVA indicating significant $G \times E$ for GY in the trials, Additive Main effects and Multiplicative Interaction (AMMI) analysis (Crossa et al. 1990) was used to assess $G \times E$ and stability of genotypes. The AMMI analysis uses principal component analysis (PCA) to decompose the multiplicative effects ($G \times E$) into a number of interaction principal component axes (IPCA). AMMI analysis was carried out using Genstat software version 15 (Payne et al. 2011). The AMMI model used was:

$$Y_{ge} = \mu + \alpha_g + \beta_e + \sum_n \lambda_n \gamma_{gn} \delta_{en} + \rho_{ge}$$

where Y_{ge} is the yield of genotype g in environment e , μ is the grand mean, α_g is the genotype deviation from the grand mean, β_e is the environment deviation, λ_n is the singular value for interaction principal component (IPC) n and correspondingly λ_n^2 is its eigen value, γ_{gn} is the eigen vector value for genotype g and component

n , δ_{en} is the eigen vector value for environment e and component n , with both eigen vectors scaled as unit vectors, and ρ_{ge} is the residual.

In addition, genotype and genotype by environment (GGE) biplot analysis (Yan and Tinker 2006) were conducted to assess relationships among testing environments, and relationships among parental materials and environments, using GGE software (Yan 2001). The GGE biplot shows the first two principal components (PC1 and PC2) derived from subjecting environment-centered yield data (the yield variation due to GGE) to singular value decomposition (Yan et al. 2000). The GGE biplot model used was:

$$Y_{ij} - Y_j = \lambda_1 \xi_{i1} \eta_{j1} + \lambda_2 \xi_{i2} \eta_{j2} + \epsilon_{ij}$$

in which Y_{ij} is the average yield of genotype i in environment j , Y_j is the average yield across all genotypes in environment j , λ_1 and λ_2 are the singular values for PC1 and PC2, respectively, ξ_{i1} and ξ_{i2} are the PC1 and PC2 scores, respectively, for genotype i , η_{j1} and η_{j2} are the PC1 and PC2 scores, respectively for environment j , ϵ_{ij} is the residual of the model associated with the genotype i in environment j . The data were not transformed (Transform = 0), not standardized (Scale = 0), and were environment centered (centering = 2).

Results

Comparison of different eras of release of CIMMYT inbred lines

Parental inbred lines evaluated in this experiment were elite CIMMYT inbred lines mainly developed between 1996 and 2013. ANOVA for GY showed highly significant differences ($P < 0.01$) among the different eras of release of parental inbred lines at individual locations (data not shown). Combined analysis of variance across locations revealed highly significant differences ($P < 0.01$) among the era of release of parental inbred lines for GY and AD (Table 2). The mean GY for the inbred lines was 2.7 t ha⁻¹ for the first two eras of release and 3.4 t ha⁻¹ for the fifth era of release (Fig. 1). The fifth era of release of inbred lines exhibited 23, 20, and 16 % yield advantage, respectively, over the first two, the third and fourth era of releases of inbred lines.

Although there was variation in GY within each era of inbred lines, the result of regression analysis showed, on average, GY increase of 39.3 kg ha⁻¹ year⁻¹ in this set of inbred lines (Fig. 2).

Days to anthesis across eras of release of inbred lines ranged from 75 (first era of release) to 73 (third era of release). Simple phenotypic correlation between mean GY and AD of parental inbred lines across the six testing locations was low, $r = 0.12$ ($P < 0.20$). However, the mean AD varied from 65 for G119 to 81 days for G40 (Supplementary Table 1) showing a wide range of maturities among this set of inbred lines. Mean AD at each location varied from 63 at Kiboko to 89 days at Chorlim (data not shown).

Growing degree days and flowering synchrony of the parental maize inbred lines and single crosses

Average GDD for silking of parental single-crosses was 794 while GDD to anthesis for inbred lines was 850 indicating that single-cross parents attained flowering earlier than the inbred line parents (Fig. 3). For example, G38 (CML444/CML536) flowered five days earlier than the average flowering time of the two parents, CML444 (G76, 65 days) and CML536 (G82, 69 days). A similar trend was observed for other single-crosses and their respective inbred line parents. GDD to silking for single-cross parents varied from 725 to 883, however, most inbred line male parents, were late in shedding pollen, as compared to the single cross seed parents, with GDD to anthesis varying from 747 for G119 to 955 for G124 (Figs. 3, 4). Most single-cross parents flowered earlier than the average of the inbred line male parents at Kiboko, revealing a

Table 2 Mean squares from combined ANOVA for grain yield and days to anthesis of different eras of release of inbred lines across six locations in East Africa in 2014

Source	df	Grain yield	Days to anthesis
Env	5	199.57**	16,045.76**
Rep (Env)	6	2.91*	16.25 ns
Era of release	4	27.45**	189.95**
Env × Era of release	20	2.21*	24.84 ns
Error	1452	1.26	17.77

*, ** Significant at $P < 0.05$ and $P < 0.01$, respectively

Fig. 1 Mean grain yield and days to anthesis of five eras of release of CIMMYT parental inbred lines tested at six locations in East Africa in 2014. LSD_(0.05) is 0.4 t ha⁻¹ and 1.5 days for grain yield and days to anthesis, respectively

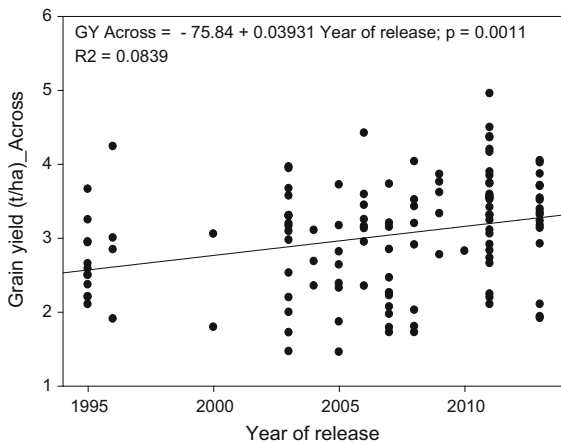
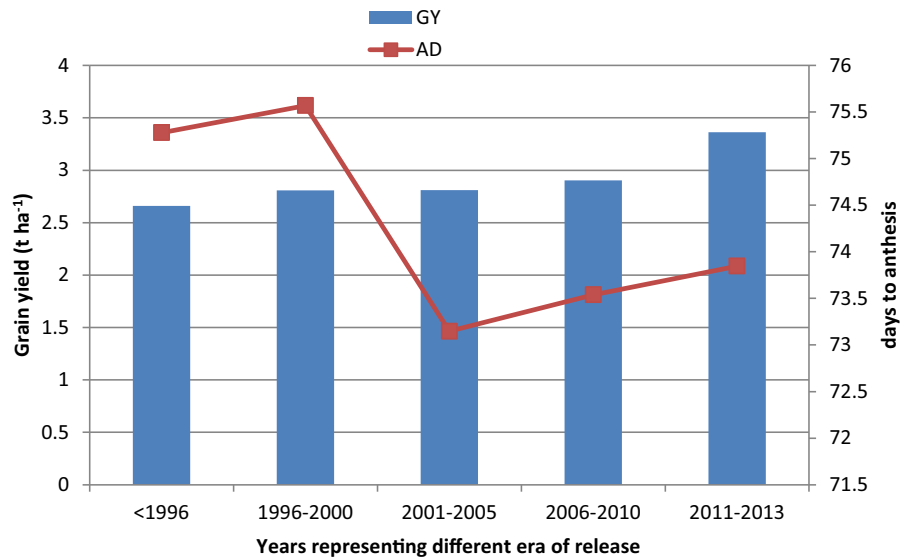


Fig. 2 Regression analysis of mean grain yield on year of release of tropical maize inbred lines in trials across six locations in Kenya and Uganda in 2014

potential synchronization problem in three-way cross hybrid formation if the parents are not selected to ensure good nicking. The difference between AD of the male inbred lines and SD of the female parent single-crosses in 98 selected elite TWC hybrids which were in variety release process in East Africa ranged from -2 days to 14 days. Of the 98 elite TWC hybrids 19, 34, 42, and three hybrids had -2 to 2 days, 3–5 days, 6–10 days, and 11–14 days difference between 50 % pollen shedding of the male inbred lines and 50 % silking of the female single-crosses, respectively (data not shown).

Productivity and $G \times E$ interaction of the parental maize inbred lines and single-crosses

ANOVA for GY at each location for the inbred line trial showed highly significant differences ($P < 0.01$) among inbred lines (data not shown). Combined ANOVA for GY also showed highly significant differences ($P < 0.01$) among the genotypes, environments, and $G \times E$ (Table 3). Presence of highly significant $G \times E$ effects indicates differential performance of inbred lines across testing locations. Partitioning of $G \times E$ using AMMI analysis showed that IPCA1, IPCA2 and IPCA3 were highly significant ($P < 0.01$) and explained 46, 19 and 14 % of the $G \times E$ sum of squares, respectively (Table 3). AMMI analysis for mean GY revealed that G36, G107, G123 and G58 were among the inbred line parents with GY above the mean and low IPCA scores indicating high relative stability and high GY across environments (Supplementary Table 1). Mean GY of inbred line parents across the six testing locations ranged from 1.5 for G110 to 4.9 t ha⁻¹ for G27 (Fig. 4). Mean GY across the testing locations and at each testing location for the 10 top yielding inbred line parents are presented in Table 4. Results showed that higher GY was recorded at Chorlim and Kiboko while the lowest GY was recorded at Thika (Table 4). Repeatability for GY of inbred lines ranged from 0.67 at Namulonge to 0.88 at Bungoma, and was 0.65 across locations (Table 4).

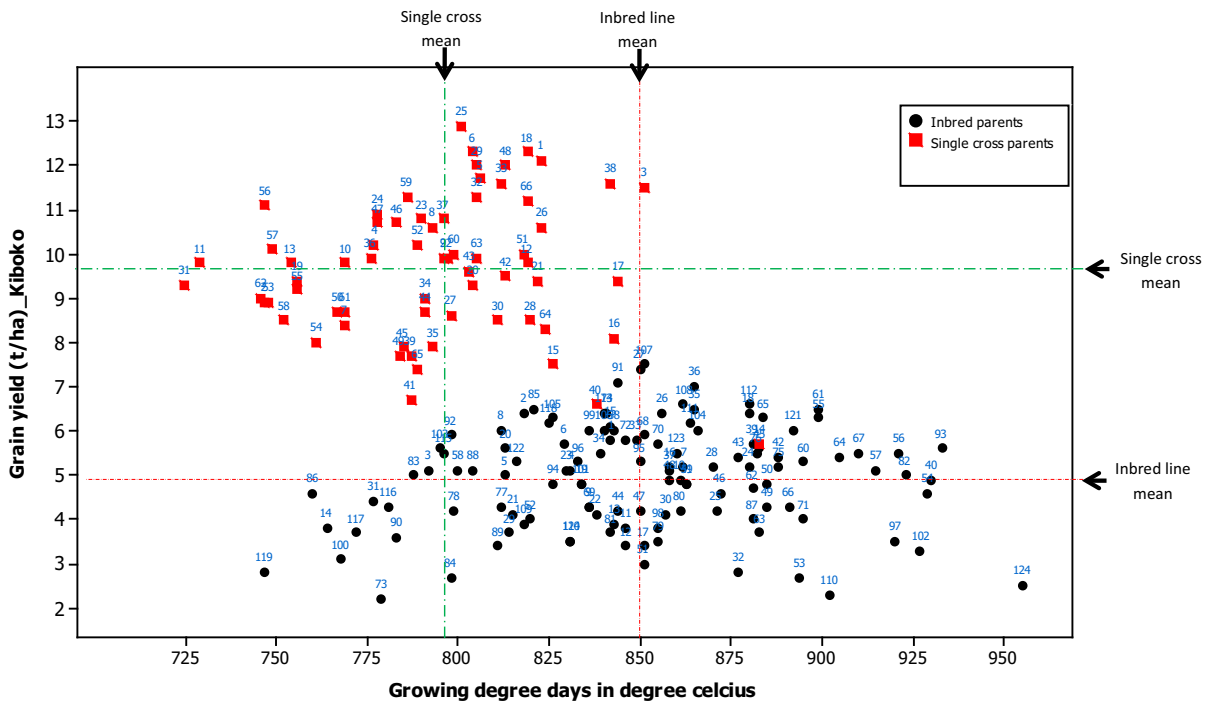


Fig. 3 Grain yield and growing degree days (anthesis for parental inbred lines, silking for parental single crosses) at Kiboko under irrigated conditions. Average GDD was 850 and

794 for inbreds and single-crosses, respectively. Average grain yield for inbred lines and single-crosses was 4.9 and 9.7 t ha⁻¹, respectively

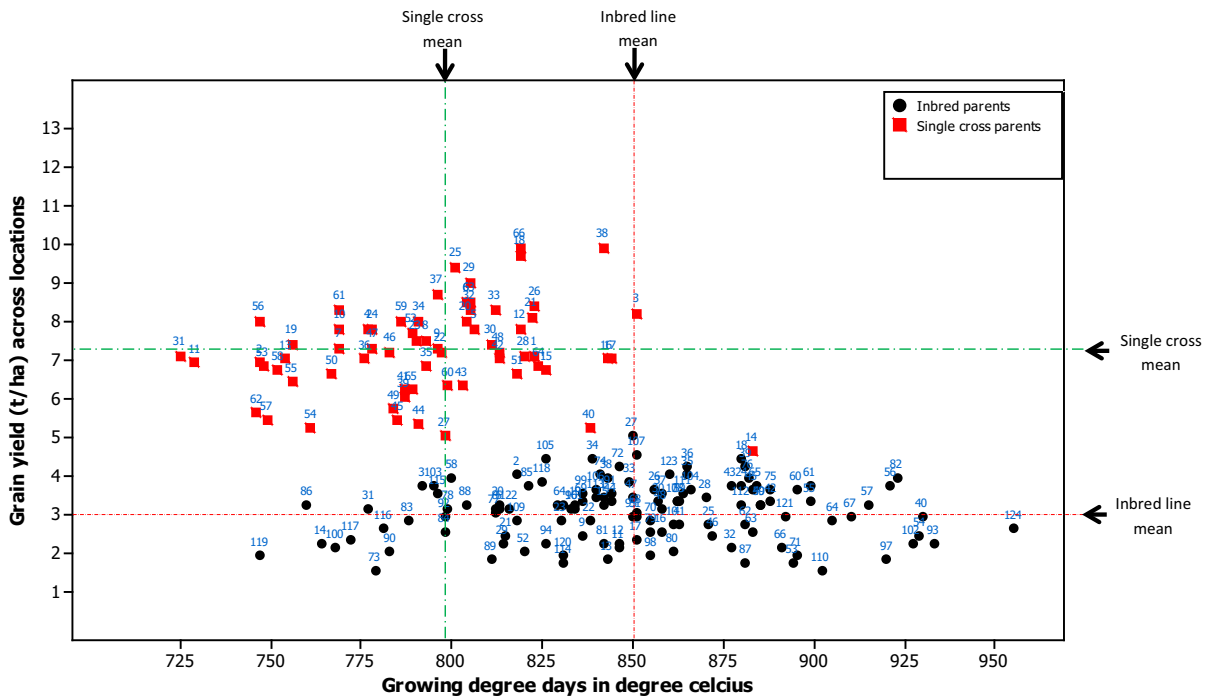


Fig. 4 Grain yield (across locations) and growing degree days (anthesis for parental inbred lines, silking for parental single crosses recorded at Kiboko). Average GDD was 850 and

794 for inbreds and single-crosses, respectively; average grain yield across locations for inbred lines and single-crosses was 3.0 and 7.2 t ha⁻¹, respectively

Table 3 Combined ANOVA and AMMI analysis for grain yield (t ha^{-1}) of 124 parental inbred lines and 66 parental single-crosses evaluated at seven locations in East Africa in 2014

Source	Inbred lines			Single-crosses		
	df	Mean squares	Percentage explained	df	Mean squares	Percentage explained
Genotypes	123	6.64**		65	18.36**	
Environments	5	417.68**		6	638.10**	
G X E Interaction	615	1.31**	100	390	3.29**	100
IPCA1	127	2.92**	46	70	9.86**	54
IPCA2	125	1.25**	19	68	3.07**	16
IPCA3	123	0.94**	14	66	2.06**	11
Residual	240	0.67**	20	186	1.33 ns	19
Error	738	0.51		454	1.41	

** Significant at $P < 0.01$

ANOVA for GY of single-cross parents at each location showed highly significant differences ($P < 0.01$) among single cross parents (data not shown). Combined ANOVA showed highly significant differences ($P < 0.01$) among genotypes, environments and $G \times E$ (Table 3). Significant $G \times E$ suggests inconsistency of the performance of single-cross parents across testing locations. Partitioning of $G \times E$ through AMMI analysis showed that axes IPCA1, IPCA2, and IPCA3 were highly significant ($P < 0.01$) with each explaining 54, 16, and 11 % of the $G \times E$ sum of squares, respectively (Table 3). GY of single-cross parents ranged from 2.2 to 6.4 t ha^{-1} at Thika (low yielding location) (data not shown) and 4.0–18.4 t ha^{-1} at Chorlim (high yielding location) (Supplementary Table 2). The highest yielding single-cross parent G38 out-yielded the best synthetic parent G42, used in commercial variety cross hybrid by 39 % across locations (Table 5). Mean GY of single-cross parents across testing locations ranged from 4.8 (G14) to 9.9 t ha^{-1} (G38) (Fig. 4; Supplementary Table 2). Repeatability for GY of parental-crosses ranged from 0.63 at Ngetta to 0.86 at Chorlim, and was 0.66 across locations (Table 5).

AMMI analysis showed differences among single-cross parents in stability of GY across locations. G6, G24, G26 and G56 were among the single-cross parents with GY above the mean GY and low IPCA scores, indicating high relative stability with reasonable GY (Supplementary Table 2). All the synthetics (G39, G40, G41, G42, and G49) and the TWC

commercial checks (G62, G64, and G65) yielded below the mean GY but had low IPCA scores indicating their relative stability across locations. Recently developed TWC hybrids G63 and G66 yielded above the mean (Fig. 4).

GGE biplot analysis explained 77.3 % (60.8 and 16.5 % for PC1 and PC2, respectively) of the total variation in GY for inbred line parents across locations (Fig. 5). The polygon view of the GGE showed inbred line parents with relatively better performance at each location. The perpendicular line drawn to each side of the polygon from the biplot origin divided the biplot into six sectors for the inbred line trial. The six testing locations of the inbred line parents were placed into two sectors. Chorlim, the upper mid-altitude testing site, was placed in one sector while the remaining lower mid-altitude testing locations were placed together in the other sector. The genotype at the vertex in each sector was the winning genotype for the locations in that sector. Based on this, inbred line G18 was the best at the upper mid-altitude testing location (Chorlim) while G27 was the highest yielding across the lower mid-altitude testing locations. Results showed that the highest yielding genotypes at the upper mid-altitude testing location were different from the best genotypes at lower mid-altitude testing locations suggesting cross-over interactions for some genotypes.

For single-cross parents, the GGE biplot model explained 77.1 % (65.5 and 11.6 % for PC1 and PC2, respectively) of the total variation in GY (Fig. 6). The

Table 4 Grain yield of top 10 and lowest 10 yielding parental inbred lines at six and across testing locations in East Africa in 2014

Entry	Era of release	Testing locations (t ha ⁻¹)						Across
		Thika	Chorlim	Kiboko	Bungoma	Namulonge	Ngetta	
Top								
G27	5	1.6	7.1	7.9	4.5	5.6	3.3	4.9
G107	5	2.6	5.1	7.5	2.9	5.7	2.9	4.5
G18	4	2.3	8.9	6.5	1.6	4.4	2.9	4.4
G105	5	1.5	6.7	6.5	4.0	4.4	3.3	4.4
G34	5	1.3	7.3	5.5	3.6	4.9	3.5	4.4
G72	2	2.4	6.6	5.8	2.2	5.0	3.6	4.2
G39	5	1.4	6.8	5.9	2.1	5.0	2.8	4.2
G36	5	2.8	4.8	7.3	3.7	4.3	2.2	4.2
G35	5	1.9	6.5	6.4	3.6	3.3	2.3	4.0
G2	4	2.7	6.1	6.8	3.2	4.2	1.5	4.0
Lowest								
G71	2	0.9	1.5	4.0	0.8	2.4	1.8	1.9
G98	3	1.0	1.2	3.6	0.9	2.9	1.2	1.9
G89	4	1.3	2.0	3.5	0.4	2.2	1.2	1.8
G97	2	1.0	2.1	3.4	0.7	2.7	0.9	1.8
G13	4	1.1	1.9	4.0	0.2	2.2	1.1	1.8
G53	4	1.2	2.4	2.8	0.4	1.9	1.4	1.7
G87	4	1.1	1.9	3.9	1.0	1.4	0.7	1.7
G114	3	1.7	1.1	3.2	1.1	1.9	0.7	1.7
G73	3	0.6	1.7	2.1	0.9	2.6	0.7	1.5
G110	3	0.7	1.3	2.2	0.7	2.4	1.1	1.5
Mean		1.8	4.1	4.3	1.7	3.2	1.9	3.0
LSD _(0.05)		1.0	2.3	1.1	1.0	1.5	1.1	1.3
Repeatability		0.73	0.74	0.87	0.88	0.67	0.74	0.65

polygon view of the GGE biplot showed seven sectors, with two upper mid-altitude testing locations (Chorlim and Elgon Downs) falling into one sector while the rest of the locations were in another sector (Fig. 6). The phenotypic correlation between GY of the two sites, Chorlim and Elgon Downs, was moderately strong ($r = 0.62$, $P < 0.01$). In the single-cross parental trial entries G66 and G38 were the best at Chorlim. Genotypes G18 followed by G25 were among the best at the other testing locations.

Discussion

The present study evaluated across location grain yield performance of inbred lines developed over an 18 year period (1996–2013) and single-cross hybrids, and

investigated flowering synchrony of male parental inbred lines and single-cross seed parents.

Progress in improving grain yield of parental inbred lines

In this study the most recently released inbred lines exhibited 23 % yield advantage over the first and second eras of released inbred lines indicating that improvements in productivity of Africa-adapted maize lines have been made over the years. The improvement in GY of inbred lines, on average, was estimated to be 1.4 % per year, or 39.3 kg ha⁻¹ year⁻¹. GY improvement in tropical maize inbred lines is lower than the 2 % per year (Troyer 2006) or 6 % per breeding cycle (Mikel 2008) that was reported for temperate maize inbred lines. The lower yield

Table 5 Grain yield of top ten yielding parental single-crosses, three commercial checks, and two best parental synthetics at seven and across testing locations in East Africa in 2014

Entry	Testing locations (t ha ⁻¹)							
	Elgon Downs	Thika	Chorlim	Kiboko	Bungoma	Namulonge	Ngetta	Across
G38	9.1	6.3	17.8	11.9	7.7	9.6	6.7	9.9
G18	7.8	5.5	18.4	12.6	6.7	8.8	8.2	9.7
G25	8.1	6.4	16.0	13.6	6.6	9.0	5.9	9.4
G29	7.2	5.4	15.7	12.2	6.7	9.0	6.8	9.0
G37	9.6	4.6	16.9	10.7	7.1	7.0	4.9	8.7
G6	7.0	3.5	12.6	13.0	7.4	7.6	8.6	8.5
G26	8.7	6.2	11.8	10.7	6.1	9.1	5.9	8.4
G61	8.8	4.3	14.8	8.6	5.3	9.6	6.8	8.3
G33	7.3	5.8	14.2	11.5	7.5	6.2	5.6	8.3
G32	9.7	5.4	13.3	11.6	5.4	7.6	5.2	8.3
64 (check)	6.7	4.5	10.9	8.5	5.9	7.0	3.8	6.8
63 (check)	9.0	5.0	13.2	9.8	7.0	9.1	6.5	8.5
66 (check)	9.6	6.2	17.6	11.3	8.9	10.1	5.8	9.9
41 (synthetic)	7.5	3.6	9.9	6.4	4.5	7.1	4.6	6.2
42 (synthetic)	7.4	4.1	9.9	9.5	4.4	9.2	4.8	7.0
Mean yield	6.8	4.7	11	9.7	5.5	7.9	5.1	7.2
LSD _(0.05)	1.8	1.8	2.9	2	2.1	1.7	2.3	2.1
Repeatability	0.76	0.67	0.86	0.85	0.76	0.65	0.63	0.66

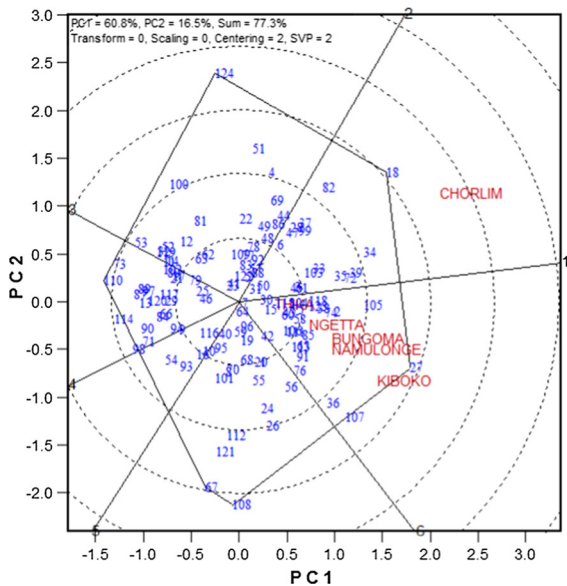


Fig. 5 A which-won-where biplot of grain yield of 124 maize inbred lines evaluated across six locations in 2014

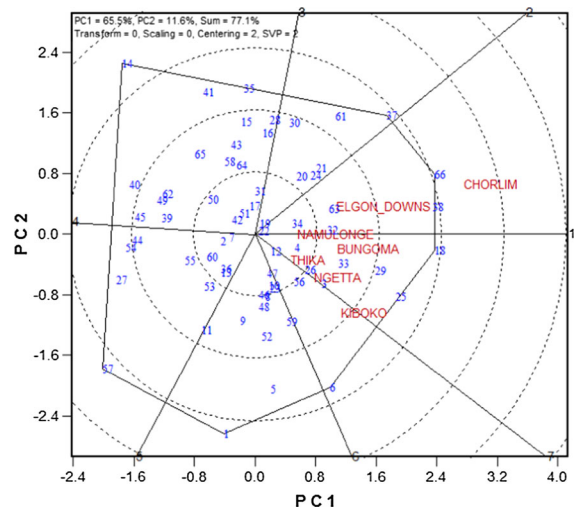


Fig. 6 A which-won-where biplot of grain yield of 66 parental single-cross hybrids and synthetics, and commercial hybrids evaluated across seven locations in 2014

improvement rate in CIMMYT's tropical maize inbred lines is probably due to the germplasm used for the development of the inbred lines as well as the smaller scope of resources invested in tropical maize improvement in Africa. Maize breeding at CIMMYT initially entailed population improvement but later switched to hybrid development in the 1980s (Pandey and Gardner 1992). Yield improvement in temperate maize has been attributed to increased grain filling period, changes in morphology and better tolerance to biotic and abiotic stresses (Duvick 2005; Fischer and Edmeades 2010; Lauer et al. 2012; Egli 2015). In Argentina, genetic gains were attributed to improved kernel number, enhanced post-silking biomass production, and enhanced biomass allocation to reproductive sink (Luque et al. 2006). In tropical maize, Gasura et al. (2013) attributed GY improvement in early maturing maize hybrids to better grain filling rate and effective grain filling duration. Field studies at CIMMYT also showed that early biomass production prior to anthesis and the ability to maintain a high biomass throughout the growing cycle are important traits for GY in diverse tropical maize inbred lines under drought and well-watered conditions, respectively (Cairns et al. 2012). Further studies may be needed under different plant densities using inbred lines developed over time to understand physiological and morphological changes which may have contributed to yield improvements in tropical maize inbred lines.

Grain yield improvement in the parental materials from 2006 to 2013 was relatively high, 2.3 % per year, compared to the previous years. This may be due to use of better source populations, elite inbred line recycling, and/or the recent use of DH technology for the development of maize inbred lines by CIMMYT maize breeders which enabled them to develop large number of fixed inbred lines within short period of time, as compared to pedigree method, and select for traits of interest (Prasanna et al. 2012; Beyene et al. 2013). In this study, 75 % of the most recent era of inbred lines were DH lines, reflecting the increased use of DH technology for inbred line development at CIMMYT. Troyer and Wellin (2009) argued that identification of stress-tolerant and productive inbred lines increased the rate of commercial hybrid yield gains in temperate maize. Smith (2007) indicated that future genetic gain in maize improvement depends on the deployment of useful genetic diversity. A study of

450 inbred lines used widely by maize breeders in SSA (Semagn et al. 2012) revealed large genetic distances among the inbred lines. Maintenance of genetic diversity in new tropical maize inbred lines and monitoring genetic diversity will be important for ensuring long term genetic gain. High grain yield recorded in this study was not associated with increase in flowering time. AD was generally reduced over time, indicating that yield improvement in tropical maize has been achieved without lengthening the growing cycle. Similarly, yield improvement achieved in temperate maize from 1930–2001 was achieved without substantial changes in flowering date (Duvick 2005).

Productivity and flowering synchronization of the parental maize materials

Highly productive inbred line parents are the foundation for the development of successful commercial hybrid production. Trials evaluated at Kiboko and Chorlim under optimum management with supplemental irrigation enabled estimation of yield potential of these inbred lines. The high station soil fertility conditions, low disease pressure (data not shown) and other environmental conditions at the two locations as compared to other testing locations might have also contributed for better GY of the inbred lines at Kiboko and Chorlim. Duvick and Cassman (1999) recommended the use of optimum testing environments to evaluate yield potential of temperate maize inbred lines. The average GY of the top yielding 10 inbred lines was 4.3 t ha⁻¹ across locations. GY of temperate inbred lines where single-cross hybrids are commercially grown widely has been reported to be in the range of 6 t ha⁻¹, under unstressed conditions (Duvick 2005; Troyer and Wellin 2009; Wang et al. 2011; Lauer et al. 2012; Li et al. 2014). Intensive breeding efforts and use of diverse germplasm over time has contributed to productivity improvement of temperate inbred lines (Smith 2007). The current study indicates that there has been progress in improving the productivity of tropical maize inbred lines in SSA over the last two decades. Further progress will be required to enable large-scale commercial production of single-cross hybrids. Increased productivity of tropical maize inbred lines can be achieved by recycling elite inbred lines and through utilization of temperate germplasm in breeding populations. Some of the top yielding

inbred lines identified in this study with $GY > 4.5 \text{ t ha}^{-1}$ (Fig. 4), may offer a starting point to transition from primarily TWC hybrids to single-cross hybrids in SSA.

The mean GY of the single-cross parents was better at Chorlim than at Kiboko. This suggests that the yield potential of the single-cross hybrids was better expressed under the milder temperatures of the upper mid-altitude at Chorlim compared to the relatively hot conditions of the lower mid-altitude at Kiboko. Some single-cross hybrids recorded over 16 t ha^{-1} at Chorlim, indicating that new single-cross females have high yield potential. In another study, GY over 15 t ha^{-1} was also reported for single-cross hybrids in Zimbabwe (Ndhlela et al. 2014). Yield at the upper mid-altitude location under supplement irrigation (over 16 t ha^{-1} for some single cross hybrids) is high compared to the yield potential estimate of 13 t ha^{-1} for upper mid-altitude areas (1600–2000 masl) of eastern Africa (Muchow et al. 1990) as cited in Fischer et al. (2014) and the 12 t ha^{-1} recorded by the world's first commercial single cross hybrid, SR52 in Zimbabwe in 1960s (Allison 1969) as cited in Fischer et al. (2014). However, the current yield potential recorded in East Africa is low compared with 25 t ha^{-1} yield estimates recorded in the Corn Belt of the USA where they grow single cross hybrids (Egli 2015). Also, current average farm yields recorded in some countries like Kenya ($<2 \text{ t ha}^{-1}$) are still very low compared to the global average maize yield of 5 t ha^{-1} indicating the need for further improvement of tropical maize. Higher plant density at Chorlim ($66,666 \text{ plants ha}^{-1}$) may have contributed to high GY recorded for both single-cross and inbred line parents at this location compared to other testing locations; although other environmental and management factors might have contributed to the high GY at Chorlim. Assessment of the effect of higher plant density in tropical maize hybrids has indicated that higher plant densities can lead to higher GY (Trachsel et al. 2016). Breeding for higher plant density stress tolerance in temperate maize has also led to increased sink size per unit area and hence higher GY (Egli 2015). Further investigation is required to ascertain the optimum planting density for increased GY of mid-altitude adapted stress tolerant maize hybrids under eastern Africa environments. In addition, in the current study single-cross hybrids developed at different eras were not considered. Only single-crosses

used as seed parent in elite TWC hybrids were studied under research station conditions. Therefore, further study under different plant density conditions on larger plots using single-cross hybrids developed over the years in SSA may be required to assess the improvements over the years.

Flowering synchrony between male and female parents of maize hybrids is an important driver for the COGS. Flowering synchrony improves kernel set and seed yield in maize (Cárcova et al. 2000). In this study 19 % of the 98 TWC hybrids would be produced with minimal synchronization problems as the female flowering of the single-cross parents and male flowering of the inbred line male parents nearly matched (-2 to 2 days). However, some of the inbred line parents flowered later than the parental single-crosses implying that seed production of 46 % of the TWC hybrids would require six or more days planting split between the male and female while 35 % need 3–5 days planting split between male and female parents. Female delay production splits are undesirable because the seed parent utilizes less of the available growing season resulting in lower potential yield and there is greater risk of missing flowering synchronization because of potential complications in planting the second parent at the optimal time due to weather or changing seed bed conditions. This risk increases with the duration of the planting split. Generally, same day plantings or female first planting is much preferred. The use of late or intermediate flowering parental inbred lines within a heterotic pattern to form parental single-crosses for use as females together with early flowering inbred lines from the opposite heterotic pattern as male parents is a strategy that can be used to form TWC hybrids with minimal flowering synchronization problems. CIMMYT breeders are increasingly emphasizing flowering synchronization of male inbred lines and single-cross seed parents when advancing new hybrids to national performance trials. Currently, single-crosses formed within heterotic groups (A/A, B/B and AB/AB) and across heterotic groups (A/B, A/AB and B/AB) are used as seed parents in different CIMMYT maize hybrids. However, targeting heterotic group B male inbred lines being 5–8 days earlier flowering than heterotic group A inbred lines used to make single-cross females and vice versa during TWC hybrid identification will be a good strategy to minimize synchronization problems and maximize seed yield from production fields.

G × E interaction of parental materials

Small and medium-sized seed companies in eastern Africa carry out production of commercial hybrids mainly in the lower and upper mid-altitude areas under irrigated and rain-fed conditions. In the current experiments, both G × E and yield of the parents of elite TWC, double-cross and variety cross hybrids developed by CIMMYT-Kenya was assessed under irrigated (Kiboko and Chorlim) and rain-fed (Elgon Downs, Bungoma, Thika, Namulonge and Ngetta) conditions in Kenya and Uganda in 2014. Kiboko and Chorlim, lower and upper mid-altitude sites, respectively, were the highest yielding environments for both single-cross and inbred line parents (Tables 4, 5). This suggests that all classes of seeds of these parental materials can be produced in the lower and upper mid-altitude of eastern Africa, even if the productivity level of each parental material may differ across sites. Although differences in soil fertility, uneven rainfall distribution, disease pressure and other environmental factors might have contributed for the yield difference among the testing locations, on average, the single-cross and inbred line parents had a yield advantage of 73 and 102 % under irrigated conditions (Kiboko and Chorlim) compared to rain-fed conditions (Bungoma, Thika, Elgon Downs, Namulonge, and Ngetta), respectively. This indicates that inbred lines were more susceptible to environmental stresses or that they needed more conducive environments to express their genetic potential as compared with single-cross parents. This result corroborates well-known effects of heterosis in enhancing stress tolerance of hybrids (e.g. Troyer and Wellin 2009).

The significance of G × E in both trials as assessed by ANOVA, AMMI and GGE plots indicates differences in performance for both single-cross and inbred line parents in different environments. AMMI biplots identified some stable single-cross and inbred line parents with reasonable GY across locations. However, selection of single-cross parents cannot rely only on the performance of the single-cross hybrids, but must also consider the performance of the TWC hybrids which are the final products for use in farmers' fields. The worst inbred line parents, with large G × E and very poor performance across locations, will certainly not be attractive to seed producers and can be omitted from future use in hybrid formation. GGE analysis also identified the better-performing parental

single-crosses and inbred lines at each testing site, which should be very helpful in site selection for seed production. Further validation, including multiple year evaluations are required to confidently group sites into similar seed production environments (Yan and Tinker 2006).

Conclusions

This study revealed that the productivity of CIMMYT's tropical maize inbred lines has improved over the last 18 years. The most recently released inbred lines had a 23, 20, and 16 % yield advantage over the first two, the third and fourth eras of inbred line releases, respectively, indicating that progress has been made in developing more productive tropical maize inbred lines in SSA. The mean GY of inbred lines has been increasing by 39.3 kg ha⁻¹ year⁻¹. Results also showed that there were single-cross and inbred line parents with good productivity and flowering synchrony, which could be suitable for seed production of TWC hybrids without requiring split-date plantings of male and female parents. The information generated in this study will enhance the exploitation of CIMMYT's tropical mid-altitude parental single-crosses and inbred lines by breeders working in both private and public breeding programs to develop high yielding maize hybrids for small scale farmers in SSA.

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