

RESEARCH

Agronomic Performance and Genotype × Environment Interaction of Herbicide-Resistant Maize Varieties in Eastern Africa

Dan Makumbi,* Alpha Diallo, Fred Kanampiu, Stephen Mugo, and Haron Karaya

ABSTRACT

Striga hermonthica (Del.) Benth. and *Striga asiatica* (L.) Kuntze severely affect maize (*Zea mays* L.) production in sub-Saharan Africa. A single *Striga* plant produces a large number of seeds that form a bank of viable but dormant seed in the soil until they get a chemical signal from suitable maize host roots. Imidazolinone-resistant (IR) open-pollinated maize varieties (OPVs) developed for *Striga* control were tested in diverse environments in four countries of eastern Africa in 2004. The objective of the study was to assess the agronomic performance of IR maize and genotype × environment interactions (GE) for grain yield (GY) and the number of emerged *Striga* plants across 17 environments under *Striga*-infested and *Striga*-free conditions. In the combined analysis of variance across *Striga*-infested and *Striga*-free locations, mean squares for genotypes and GE were significant for most measured traits. The best IR maize variety (STR-VE-216) outyielded the *Striga*-tolerant and commercial genotypes by 113 and 89%, respectively, under *Striga*-infested conditions. IR OPVs supported significantly fewer emerged *Striga* plants relative to the check varieties. Under *Striga*-free conditions, IR OPVs showed GY advantage over commercial varieties. Under *Striga*-infested conditions genotypic variance (σ_G^2) was larger than genotype × location variance ($\sigma_{G \times L}^2$) for GY and number of emerged *Striga* plants at 12 wk after planting. The genetic correlations among locations under *Striga*-infested conditions were high (0.990), suggesting little GE between most environments used. Cluster analysis of genotypes under *Striga*-infested locations revealed two major groups that separated the IR OPVs from the check varieties. The outstanding performance of selected IR OPVs indicates that their use for *Striga* control would reduce the *Striga* seed bank while benefiting farmers with high GY.

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Abbreviations: AD, days to anthesis; AEC, average environment coordinate; ASI, anthesis–silking interval; EA, ear aspect; EPP, ears per plant; GE, genotype × environment interaction; GGE, genotype main effect plus genotype × environment interaction; GLS, gray leaf spot; GY, grain yield; HC, husk cover; IR, imidazolinone-resistant; MSV, maize streak virus; NID, normally and independently distributed; OPV, open-pollinated maize variety; PC, principal component; PH, plant height; SD, days to silking; SSA, sub-Saharan Africa; TLB, *turicum* leaf blight; WAP, weeks after planting.

STRIGA spp. are obligate parasitic plants commonly found in cereal-based agricultural systems in sub-Saharan Africa (SSA). *Striga hermonthica* (Del.) Benth. and *S. asiatica* (L.) Kuntze adversely affect grain production of cereal crops including maize (*Zea mays* L.), millet (*Pennisetum* spp), sorghum (*Sorghum bicolor* L. Moench), sugarcane (*Sacharum officinarum* L.), and upland rice (*Oryza sativa* L.) in SSA. These parasites currently infest up to 40% of cereal production area in SSA, causing substantial annual yield losses in small-holder farmers' fields (Ejeta, 2007). Grain yield of maize in SSA for the last two decades or more has remained at about 1.5 t ha⁻¹, well below the world average of 4.9 t ha⁻¹, partly due to *Striga* parasitism, among other factors. *Striga* produces large

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amounts of seed that stay dormant in soil for over 20 yr until triggered into germination by signals from potential host plants. Most *Striga*-infested areas in Africa have high levels of the *Striga* seeds in the soil due to years of neglect and mismanagement. Subsistence farmers in SSA are the most affected by *S. hermonthica* and can lose about 20 to 80% of their yields from *Striga* infestation (Ransom et al., 1990; Haussmann et al., 2000, Kim et al., 2002). Crop rotation and intercropping involving legumes (Carsky et al., 1994; Carsky et al., 2000; Khan et al., 2000; Oswald and Ransom, 2001), application of organic and inorganic fertilizers (Mumera and Below, 1993; Gacheru and Rao, 2001), and the use of *Striga*-resistant cultivars (Diallo et al., 1997, Kling et al., 2000; Badu-Apraku and Lum, 2007; Menkir et al., 2012b) can partially reduce the problem. However, no short-term control measure has been developed that subsistence farmers could use within their financial resources or that fits well into their traditional cropping systems. Thus, there is need for control measures that meet at least four criteria: (i) control *Striga* itself so that adequate crop yields can be achieved each cropping season, (ii) deplete the *Striga* seed bank in the soil, (iii) is cost-effective, and (iv) is compatible with existing small-holder cropping systems. Such *Striga* control options are needed as a stopgap control measures until crop varieties with adequate levels of genetic resistance become available (Kanampiu et al., 2001). One such *Striga* control measure is the use of herbicide-resistant maize.

The CIMMYT and partners have developed a seed-based technology for *Striga* control in maize. The technology involves coating of nontransgenic, imidazolinone-resistant (IR) maize seed with low doses of an acetolactate synthase-inhibiting herbicide, imazapyr (30 g a.i. ha⁻¹), for early *Striga* control before or during attachment to the maize roots (Abayo et al., 1998; Kanampiu et al., 2001). Development of herbicide-resistant maize started in 1996 at CIMMYT with incorporation of the IR gene into three CIMMYT maize inbred lines CML202, CML204, and CML206 through backcrossing using a temperate Pioneer hybrid PH3245-IR as the source of the IR gene (Kanampiu et al., 2003). These maize inbred lines were chosen because, at the time, they were among the most widely used in breeding programs in midaltitude areas of eastern and southern Africa. However, these inbred lines are extremely susceptible to *Striga*. An herbicide-resistant, single-cross hybrid (CML202-IR × CML204-IR) was developed and used as a source of the IR gene for introgression into other types of adapted tropical maize germplasm. Several IR maize varieties were developed and tested in artificially and naturally *Striga*-infested fields for *Striga* control in Kenya with promising varieties identified for wider testing in *Striga*-infested areas in eastern and central Africa (Diallo, unpublished data, 2004). Results showed that the use of IR maize varieties reduced the

Striga seed bank in the soil by over 80% in the 30-cm soil top layer and that imazapyr had no effects on intercropped legumes when sown at least 12 cm away from the treated maize seed (Kanampiu et al., 2002).

The performance of genotypes can vary from one environment to another, so genotypes that are superior in one environment may not be superior in other environments, resulting in genotype × environment interaction (GE). Presence of GE reduces the correlation between phenotype and genotype, making valid inferences more complicated in plant breeding (Comstock and Moll, 1963; Crossa, 1990; Kang, 1993; Annicchiarico, 1997; Epinat-Le Signor et al., 2001). At CIMMYT, regional trials are used to evaluate new maize germplasm in multiple environments (locations and years) because of differential genotypic responses in different environments. The objective of the multienvironment trials is to identify high yielding adapted varieties for release in the respective countries. Herbicide-resistant varieties, developed by CIMMYT, are tested in multienvironment trials across the *Striga* endemic areas of eastern and central Africa. Significant GE has been reported in CIMMYT maize regional trials (Setimela et al., 2005, 2007; Windhausen et al., 2012). Similarly, GEs have been reported in evaluation of maize and sorghum varieties for *Striga* control in SSA. In a study to evaluate maize varieties for resistance to *Striga*, Menkir et al. (2012a) reported significant cultivar × environment interactions for GY and the number of emerged *Striga* plants under *Striga*-infested and *Striga*-free conditions. In other studies (Menkir et al., 2012b; Badu-Apraku and Lum, 2007, 2010; Badu-Apraku et al., 2007), significant GEs have been reported for several traits in maize under *Striga* infestation. Also, Haussmann et al. (2001), reported significant GEs for sorghum GY, emerged *Striga* plants, and flowering traits in sorghum. In contrast, a study by Badu-Apraku and Lum (2007) revealed no significant GE for maize GY under *Striga* infestation. Genotype × environment interactions have been investigated through use of statistical tools such as the additive main effects and multiplicative interaction (AMMI) analysis (Gauch and Zobel, 1988; Crossa et al., 1990) and genotype main effect plus genotype × environment interaction (GGE) analysis (Yan et al., 2000). All these analytical methods provide an insight into the extent of GE present in a particular study. Genetic correlations can be used to quantify the importance of GE (Falconer, 1952) and have been used in GE studies (Eisen and Saxton, 1983; Cooper and DeLacy, 1994). Herbicide-resistant maize varieties developed by CIMMYT in Kenya have been tested in eastern, central, and southern Africa but the extent of GE has not been assessed. Therefore, the objectives of this study were to (i) evaluate the agronomic performance of herbicide-resistant OPVs for *Striga* control and (ii) assess GEs for GY and number of emerged *Striga* plants.

Table 1. Description of test locations used to evaluate 22 herbicide-resistant maize varieties and two commercial checks.

Location	Country	Management	Latitude	Longitude	Elevation	Mean annual rainfall	Temperature	
							Min	Max
					m	mm	°C	
Kibos	Kenya	Artificial <i>Striga</i> infestation (2004A, 2004B) [†] and <i>Striga</i> free	0°2' S	34°48' E	1193	865	16.3	30.7
Alupe	Kenya	Artificial <i>Striga</i> infestation and <i>Striga</i> free (2004A, 2004B) [†]	0°30' N	34°7' E	1153	1400	15.8	28.6
Kiboswa	Kenya	Natural <i>Striga</i> infestation	0°1' S	34°44' E	1532	865	17.0	29.4
Nyahera	Kenya	Natural <i>Striga</i> infestation	0°1' S	34°44' E	1548	865	17.0	29.4
Vihiga	Kenya	Natural <i>Striga</i> infestation (2004A, 2004B) [†]	0°32' N	34°47' E	1629	1500	14.1	27.0
Bungoma	Kenya	<i>Striga</i> free (2004A, 2004B) [†]	0°33' N	34°33' E	1374	1600	11.4	25.4
Embu	Kenya	<i>Striga</i> free	0°30' S	37°27' E	1504	1200	13.9	24.6
Pawe	Ethiopia	Natural <i>Striga</i> infestation	11°09' N	36°03' E	1100	1577	16.6	33.4
Busia	Uganda	Natural <i>Striga</i> infestation	0°28' N	34°5' E	1180	1688	16.2	28.7
Wad Medani	Sudan	Artificial <i>Striga</i> infestation and <i>Striga</i> free	14°23' N	33°31' E	400	450	20.3	36.9

[†] Trials were conducted in two cropping seasons denoted as 2004A (first cropping season) and 2004B (second cropping season).

MATERIALS AND METHODS

Genetic Material

A breeding program was initiated in 2000 at CIMMYT in Kenya to introgress the gene for herbicide resistance into elite OPVs adapted to eastern and southern Africa. Twenty-two early and intermediate-maturing OPVs tolerant to maize streak virus (MSV), gray leaf spot (GLS) caused by *Cercospora zeae-maydis*, turcicum leaf blight (TLB) caused by *Exserohilum turcicum*, low nitrogen and drought stress that were developed under the Africa Maize Stress and the Southern Africa Drought and Low Soil Fertility projects were crossed to the herbicide-resistant single cross (CML202-IR × CML204-IR). The F₁ crosses were planted along with the elite OPVs (recurrent parents) for backcrossing. The F₁ plants were sprayed with imazapyr (15 g a.i. ha⁻¹) as 25% Arsenal (BASF Corp.) at the eight- to 10-leaf stage to identify homozygous plants (see details in Kanampiu et al., 2001). Three backcrosses were made before reconstituting the OPVs. During the formation of the BC₃F₁, a higher herbicide rate of 30 g imazapyr a.i. ha⁻¹ was applied as a spray, which is the optimum rate found to give maximum *Striga* control with minimum maize crop phytotoxicity (Kanampiu et al., 2001). Seed coating was found to be the best method of herbicide delivery during field evaluations of various herbicide formulations and was therefore adopted. The seed coating was achieved by mixing 54 g of 20% a.i. lindane and 26% a.i. thiram-containing commercial seed dressing powder (Murtano, Twiga Chemical Ind.) with 600 mL water and 30 g imazapyr to obtain a slurry (Kanampiu et al., 2001). The slurry was mixed thoroughly with maize seed before planting to give about 0.56 mg a.i. imazapyr seed⁻¹ (30 g a.i. ha⁻¹) of the herbicide-resistant maize, which was enough to plant a hectare of land. Twenty-two herbicide-resistant, open-pollinated varieties were selected for this study. Two commercial OPV checks, KSTP94, a *Striga*-tolerant variety, and WS202 and a local check were included in the trial. The seed of the two check varieties was treated with only the insecticide-fungicide powder Murtano.

Test Locations, *Striga* Infestation, and Experimental Design

The 22 IR OPVs, plus two commercial checks and a local check, were grown in trials planted in Kenya, Uganda, Ethiopia, and Sudan in 2004 under artificial *Striga* and natural *Striga* infestations, and *Striga*-free conditions (Table 1). Four trials were planted under artificial *Striga*-infestation at three locations (Alupe, Kibos, and Wed Medani), six trials under natural *Striga* infestation, and seven trials under *Striga*-free conditions. Under *Striga* infestation, plots were artificially infested with *Striga* seeds. The inoculum was prepared by mixing about 10 g *Striga* seeds (25% purity and 25% viability) thoroughly with 5 kg fine sand, which served as the carrier to allow uniform *Striga* infestation. The sand-*Striga* seed inoculum (20 g) containing approximately 3000 viable seeds was then added to each planting hole at a depth of 7 to 10 cm (directly below the maize) to ensure that each maize plant was exposed to *Striga* at germination. Two maize seeds were placed into the holes infested with sand-*Striga* seeds mixture and then covered with soil.

The experimental design was a five by five simple lattice with two replications at all locations. Each plot consisted of two maize rows spaced at 0.75 m apart and 0.25 m between plants within each row resulting in a population density of 53,333 plants ha⁻¹ at all locations. Standard agronomic and cultural practices were performed as recommended at each location.

Data Collection

Under both artificial and natural *Striga* infestation, the number of emerged *Striga* plants per maize plant at 8, 10, and 12 wk after planting (WAP) were recorded. The total number of *Striga* plants per plot was calculated and expressed as *Striga* plants m⁻². Days to anthesis (AD, days from planting to when 50% of the plants had shed pollen) and days to silking (SD, days from planting to when 50% of the plants had extruded silks) were recorded. Anthesis-silking interval (ASI) was determined as the difference between SD and AD. Plant height (PH, measured in centimeters as the distance from the base of the plant to the height of the first tassel branch), number of ears per plant (EPP, determined by dividing the total number of ears per plot

by the number of plants harvested per plot), poor husk cover (HC, obtained by dividing the number of ears with poor husk cover by the number of plants harvested per plot), ear aspect (EA, rated on a scale of 1 to 5, where 1 = nice uniform cobs with the preferred texture and 5 = cobs with the undesirable texture), and grain moisture under both *Striga*-free and *Striga*-infested conditions were also recorded. All ears harvested from each plot were weighed and representative samples of ears were shelled to determine percentage moisture using a Dickey Jones moisture meter at all locations. Grain yield (kg ha⁻¹) was calculated from ear weight and grain moisture assuming a shelling percentage of 80% and grain moisture content of 12.5%.

Statistical Analysis

Analysis of Variance

Analyses of variance were performed using PROC MIXED of SAS (SAS Institute, 2008) on data adjusted for maturity and number of plants harvested per plot. The random effects model was used to estimate the variance components while the fixed effects model was used to obtain the adjusted means. The basic two-way, fixed-effect linear model considers that the empirical response, y_{ijr} , of the i th level of factor τ ($i = 1, 2, \dots, I$), and the j th level of factor δ ($j = 1, 2, \dots, J$) with ($r = 1, 2, \dots, n$) replications in each of the $I \times J$ cells is expressed as:

$$y_{ijr} = \mu + \tau_i + \delta_j + (\tau\delta)_{ij} + \varepsilon_{ijr}$$

with the standard sum-to-zero restrictions on the parameters $\sum_i \tau_i = \sum_j \delta_j = \sum_{ij} (\tau\delta)_{ij} = 0$, where μ is the grand mean over all observations of both factors, τ_i is the additive effect of the i th level of factor τ , δ_j is the additive effect of the j th level of factor δ , $(\tau\delta)_{ij}$ is the nonadditive interaction of the i th level of factor τ in the j th level of factor δ , and ε_{ijr} is the error associated with τ_i and δ_j and assumed to be normally and independently distributed (NID) ($0, \sigma^2$) (where σ^2 is assumed to be either homogeneous or heterogeneous). For a complete random model, it is assumed that τ_i , δ_j , and $(\tau\delta)_{ij}$ are NID distributed with mean 0 and variances σ_τ^2 , σ_δ^2 , and $\sigma_{\tau\delta}^2$, respectively.

Estimates of genotypic (σ_G^2), location (σ_L^2), genotype \times location ($\sigma_{G \times L}^2$), and error variance (σ_E^2) were calculated using the PROC MIXED (option = REML) of SAS (SAS Institute, 2008). Across environments, ANOVA for each trait was conducted using PROC GLM of SAS (SAS Institute, 2008). In the across-environment analysis of variance, genotype effects were tested for significance using the corresponding interaction with the environment as the error term, while the GE was tested using the pooled error. A combination of location and *Striga*-infested or *Striga*-free treatment was considered an environment.

To assess consistency of maize variety performance across diverse growing conditions Kendall's (1962) coefficient of concordance (W statistic) was computed for each trait based on ranks of entry means recorded across *Striga*-infested locations, *Striga*-free locations, and across locations. Kendall's W statistic is expressed as:

$$W = \frac{12S}{p^2(n^3 - n) - pT}$$

in which S is a sum-of-squares statistic over the row sums of ranks, n is the number of varieties, p the number of locations, and T is a correction factor for tied ranks.

Heritability and Genetic Correlations

Broad-sense heritability (H) for individual trials was estimated according to Hallauer et al. (2010):

$$H = \frac{\sigma_G^2}{\sigma_G^2 + \left(\frac{\sigma_E^2}{r}\right)}$$

in which σ_G^2 is the genotypic variance, σ_E^2 is the error variance, and r the number of replications.

Broad-sense heritability for traits across environments was estimated using the variance components according to Hallauer et al. (2010) as:

$$H = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_{G \times L}^2}{E} + \frac{\sigma_E^2}{ER}}$$

in which σ_G^2 , $\sigma_{G \times L}^2$, and σ_E^2 are genotypic, genotype \times location, and residual variance components, respectively, E is the number of environments, and R is the number of replications.

Genotypic correlations (r_g) between locations were estimated according to Cooper et al. (1996) as:

$$r_g = \frac{r_{p(12)}}{(H_1 \times H_2)^{1/2}}$$

in which $r_{p(12)}$ is the phenotypic correlation between the traits measured in locations 1 and 2, H_1 and H_2 are the broad-sense heritabilities for the traits measured in locations 1 and 2, respectively. Cluster analysis using Ward's minimum variance method (Ward, 1963) was performed to group environments based on genetic correlations among the environments. The average linkage method was used to group varieties with similar reactions to *S. hermonthica*. The SAS procedure PROC CLUSTER was used for cluster analysis. The PROC TREE procedure of SAS was used to generate the dendrograms.

Genotype Main Effect Plus Genotype \times Environment Interaction Biplot Analysis

Adjusted GY from ANOVA was subjected to GGE biplot analysis to decompose the GE of each experiment (Yan et al., 2000; Yan, 2001) to investigate the stability of varieties in the various environments. 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:

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

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

Table 2. Grain yield, agronomic traits, and emerged *Striga* plants of 24 intermediate maturing maize varieties evaluated under *Striga*-infested conditions in eastern Africa, 2004.

Entry	Pedigree	Grain yield kg ha ⁻¹	AD [†] d	ASI [†]	PH [†] cm	EPP [†] no. of ears	HC [†] %	EA [†] 1–5 [‡]	Emerged <i>Striga</i> plants [†]			
									8 WAP	10 WAP	12 WAP	Per m ⁻² no. of plants
G1	STR-VE-200	860	67	2	131	0.9	16.7	3.5	2	5	6	1.6
G2	STR-VE-201	964	68	3	134	1.1	15.4	3.0	1	3	5	1.1
G3	STR-VE-202	813	68	3	139	0.9	12.9	2.9	1	3	3	0.9
G4	STR-VE-203	1706	72	3	140	0.8	8.2	2.4	1	6	6	1.7
G5	STR-VE-204	903	67	3	140	0.9	12.1	2.6	2	4	4	1.2
G6	STR-VE-205	1527	67	3	140	0.9	11.5	3.0	6	11	9	3.4
G7	STR-VE-206	2191	69	4	154	0.9	7.7	2.6	5	13	14	4.0
G8	STR-VE-207	1664	71	3	149	0.9	7.6	2.9	2	7	10	2.5
G9	STR-VE-208	2008	70	4	155	0.9	6.4	2.9	9	15	17	5.2
G10	STR-VE-209	2025	70	3	149	1.0	6.4	2.7	3	7	6	2.0
G11	STR-VE-210	1956	68	4	150	1.0	6.4	2.7	3	6	10	2.5
G12	STR-VE-211	1873	69	4	147	0.9	7.2	3.0	3	7	5	2.0
G13	STR-VE-212	2055	69	4	146	1.0	7.7	2.9	3	8	12	2.9
G14	STR-VE-213	1893	69	4	148	0.9	5.4	2.9	1	8	10	2.4
G15	STR-VE-214	1750	68	3	147	0.9	6.9	2.8	3	10	7	2.4
G16	STR-VE-215	1979	69	4	153	1.0	6.4	2.5	3	11	9	3.0
G17	STR-VE-216	2448	67	3	154	0.9	5.0	2.3	5	9	14	3.5
G18	STR-VE-217	2150	68	4	152	1.0	7.9	2.5	2	6	9	2.2
G19	STR-VE-218	1811	67	4	140	0.9	5.3	3.3	4	10	14	3.6
G20	STR-VE-219	1918	68	4	147	0.9	4.5	2.5	5	10	11	3.4
G21	STR-VE-220	1939	67	4	145	1.0	5.6	2.8	2	7	9	2.4
G22	STR-VE-221	1936	67	4	140	0.9	6.5	2.9	3	10	8	2.8
G23	KSTP94	1148	69	4	161	0.8	18.0	3.7	28	58	36	14.5
G24	WS202	1293	68	4	133	0.9	9.8	3.3	29	71	32	15.5
Mean		1698	68	3	145	0.9	8.6	2.9	7	15	13	4.3
Mean (test entries)		1744	68	3	146	0.9	8.2	2.8	3	8	9	2.6
LSD		545	2	NS [§]	13	0.1	8.5	0.6	19	38	12	7.5
Genotype		***	***	NS	***	**	*	***	***	***	***	***
Environment		***	***	***	*	***	***	***	*	***	***	***
Genotype × Environment		***	*	NS	***	***	***	*	***	***	***	**

* Significant at $P < 0.05$.

** Significant at $P < 0.01$.

*** Significant at $P < 0.001$.

[†] AD, days to anthesis; ASI, anthesis–silking interval; PH, plant height; EPP, ears per plant; HC, husk cover; EA, ear aspect; WAP, weeks after planting.

[‡] Ear aspect rating on a scale of 1 to 5, where 1 = nice uniform cobs with the preferred texture and 5 = cobs with the undesirable texture.

[§] NS, not significant.

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). The analyses were done using GGE biplot software (Yan, 2001).

RESULTS

ANOVA and GE under *Striga*-infested and *Striga*-free Conditions

This study was conducted in 10 locations (17 environments) in Kenya, Uganda, Ethiopia, and Sudan under both *Striga*-infested (10 environments) and *Striga*-free (seven environments) conditions. Combined analysis of

variance across *Striga*-infested conditions revealed that genotype, environment, and GE were significant for all traits except genotype and GE for ASI (Table 2). This implies that there were differences in performance among the varieties as well as differential response of the varieties at different locations. Under *Striga* infestation, mean GY across locations varied from 813 for STR-VE-202 to 2448 kg ha⁻¹ for STR-VE-216. The IR OPVs, on average, yielded 1744 kg ha⁻¹, while the yield of the two check entries averaged 1221 kg ha⁻¹. The best herbicide-resistant variety G17 (STR-VE-216) outyielded the *Striga*-tolerant check G23 (KSTP94) and commercial check G24 (WS202) by 113 and 89%, respectively (Table 2). Of the 22 IR OPVs tested, 73% had significantly higher GY than

Table 3. Grain yield and other agronomic traits of 24 intermediate maturing maize varieties evaluated under *Striga*-free conditions in eastern Africa, 2004.

Entry	Pedigree	Grain yield	AD [†]	ASI	PH	EPP	HC	EA
		kg ha ⁻¹	d		cm	no. of ears	%	1–5 [‡]
G1	STR-VE-200	1111	64	3	162	0.8	10.4	3.0
G2	STR-VE-201	1337	64	3	176	0.8	6.6	2.8
G3	STR-VE-202	1306	64	1	170	0.8	3.8	3.2
G4	STR-VE-203	1915	70	4	160	0.8	2.6	2.4
G5	STR-VE-204	1488	64	2	164	0.9	6.2	3.2
G6	STR-VE-205	1875	64	2	162	0.9	12.7	2.9
G7	STR-VE-206	2435	67	4	178	0.9	14.8	2.6
G8	STR-VE-207	2149	68	3	162	0.9	7.6	2.8
G9	STR-VE-208	2193	69	4	171	1.0	7.1	2.6
G10	STR-VE-209	2224	67	3	170	0.9	4.6	2.5
G11	STR-VE-210	2062	67	4	178	0.8	7.7	2.5
G12	STR-VE-211	2325	67	3	165	1.0	10.6	2.4
G13	STR-VE-212	2070	66	5	172	0.8	11.0	2.9
G14	STR-VE-213	2543	67	2	174	0.9	9.1	2.3
G15	STR-VE-214	1878	67	3	162	0.8	5.0	2.7
G16	STR-VE-215	2152	67	3	162	0.9	4.8	2.6
G17	STR-VE-216	2348	67	3	174	0.9	11.0	2.5
G18	STR-VE-217	2297	64	4	161	0.9	9.9	2.8
G19	STR-VE-218	2186	65	2	164	0.9	5.7	2.6
G20	STR-VE-219	2219	63	4	165	0.9	7.0	2.7
G21	STR-VE-220	2207	64	2	155	0.9	9.3	2.7
G22	STR-VE-221	2187	65	3	171	0.9	8.0	2.7
G23	KSTP94	2291	68	5	185	0.8	12.4	2.9
G24	WS202	1961	65	3	163	0.8	12.6	3.0
Mean		2060	66	3	168	0.9	8.4	2.7
Mean (test entries)		2022	66	3	167	0.9	8.0	2.7
LSD		606	3	2	NS [§]	NS	6.2	NS
Genotype		***	***	***	NS	NS	*	NS
Environment		***	***	***	*	***	**	***
Genotype × Environment		***	***	*	NS	NS	*	*

* Significant at $P < 0.05$.

** Significant at $P < 0.01$.

*** Significant at $p < 0.001$.

[†] AD, anthesis date; SD, silking date; ASI, anthesis–silking interval; PH, plant height; EPP, ears per plant; HC, husk cover; EA, ear aspect.

[‡] Ear aspect rating on a scale of 1 to 5, where 1 = nice uniform cobs with the preferred texture and 5 = cobs with the undesirable texture.

[§] NS, not significant.

the *Striga*-tolerant check across locations. The number of emerged *Striga* plants varied from 1 to 9, 3 to 15, and 3 to 17 at 8 WAP, 10 WAP, and 12 WAP, respectively, for the IR OPVs, while the checks had an average of 29 and 65 emerged *Striga* plants at 8 WAP and 10 WAP, respectively (Table 2). All IR OPVs supported a significantly lower number of emerged *Striga* plants compared with the two check varieties (Table 2). The best IR OPVs, in terms of emerged *Striga* plants, had 96 and 95% less emerged *Striga* plants at 8 WAP and 10 WAP, respectively, compared with the *Striga*-tolerant check. The best IR OPV in terms of GY (STR-VE-216) had 82 and 84% less emerged *Striga* plants at 8 WAP and 10 WAP, respectively, compared with the *Striga*-tolerant check. The IR OPVs supported significantly lower number of emerged *Striga* plants m⁻² compared with the two checks.

Combined analysis of variance across *Striga*-free conditions revealed significant differences among the OPVs for GY, AD, ASI, and HC but not PH, EPP, and EA, while GE was significant for all traits except PH and EPP (Table 3). Across *Striga*-free conditions, 68% of the IR OPVs had equal or higher GY compared with the commercial check (WS202) and were of similar maturity (Table 3). Five IR OPVs performed similar to or better than the *Striga*-tolerant check KSTP94. Assessment of consistency of the relative rankings of the variety means revealed significant ($P < 0.0001$) *W* for all traits under *Striga*-infested locations except ASI (Table 4). Under *Striga*-free conditions and across all test locations, *W* was significant ($P < 0.0001$) for GY and AD (Table 4).

Table 4. Kendall's coefficient of concordance (W) for maize varieties evaluated at 16 locations in eastern Africa.

Trait	Number of locations	W	Probability
Across <i>Striga</i> -infested locations			
Grain yield	9	0.482	<0.0001
Days to anthesis	9	0.407	<0.0001
Anthesis–silking interval	9	0.121	0.3499
<i>Striga</i> plants 8 WAP†	10	0.441	<0.0001
<i>Striga</i> plants 10 WAP	10	0.404	<0.0001
<i>Striga</i> plants 12 WAP	10	0.356	<0.0001
<i>Striga</i> plants m ⁻²	10	0.385	<0.0001
Across <i>Striga</i> -free locations			
Grain yield	6	0.405	<0.0001
Days to anthesis	6	0.431	<0.0001
Anthesis–silking interval	6	0.127	0.0107
Across all locations			
Grain yield	15	0.403	<0.0001
Days to anthesis	14	0.411	<0.0001
Anthesis–silking interval	14	0.135	0.0008

† WAP, weeks after planting.

Genetic Variances and Heritability under Different Conditions

Estimates of genotypic (σ_G^2), location (σ_L^2), genotype \times location ($\sigma_{G \times L}^2$) variances across *Striga*-infested, *Striga*-free, and all locations are presented in Table 5. Genotypic variance estimates were significant ($P < 0.05$) or highly significant ($P < 0.01$) for all traits across *Striga*-infested locations except ASI and HC. Under *Striga*-infested and *Striga*-free conditions, and across locations, σ_G^2 was smaller than σ_L^2 for all traits except EA across locations. The ratio of σ_L^2 to σ_G^2 was larger for GY under *Striga*-free conditions (19.5) compared with *Striga*-infested conditions (2.7). The ratio of σ_L^2 to σ_G^2 for the emerged *Striga* plants at 8 WAP, 10 WAP, and 12 WAP and *Striga* plant m⁻² ranged from 1.2 to 1.7. Under *Striga*-infested conditions σ_G^2 was larger than $\sigma_{G \times L}^2$ for GY, AD, PH, EA, and emerged *Striga* plants at 12 WAP but smaller than $\sigma_{G \times L}^2$ for HC, emerged *Striga* plants 8 WAP, 10 WAP, and emerged *Striga* plants m⁻². Under both *Striga*-infested and *Striga*-free conditions, the error

Table 5. Estimates of genotypic (σ_G^2), location (σ_L^2), genotype \times location ($\sigma_{G \times L}^2$), error (σ_E^2) variance components, and broad-sense heritability (H) of grain yield and other agronomic traits under *Striga*-infested conditions, *Striga*-free conditions, and across environments.

	σ_G^2	σ_L^2	$\sigma_{G \times L}^2$	σ_E^2	H
Across <i>Striga</i> -infested locations†					
Grain yield	0.19 \pm 0.07**	0.51 \pm 0.28*	0.14 \pm 0.04***	0.41 \pm 0.04***	0.84
Days to anthesis	1.33 \pm 0.47**	41.65 \pm 20.88*	0.21 \pm 0.37	5.08 \pm 0.48***	0.83
Anthesis–silking interval	0.00 \pm 0.00	9.12 \pm 4.61*	0.00 \pm 0.00	5.18 \pm 0.35***	0.05
Plant height	37.51 \pm 17.70*	257.48 \pm 141.60*	21.21 \pm 25.93	326.16 \pm 32.65***	0.64
Ears per plant	0.00 \pm 0.00	0.01 \pm 0.01*	0.01 \pm 0.00***	0.02 \pm 0.00***	0.54
Ear aspect	0.12 \pm 0.05**	0.18 \pm 0.10*	0.07 \pm 0.05*	0.65 \pm 0.06***	0.74
Husk cover	4.91 \pm 4.11	40.76 \pm 24.98*	41.94 \pm 9.43***	40.04 \pm 5.02***	0.35
STR8WAP	0.70 \pm 0.41*	0.85 \pm 0.53*	5.12 \pm 0.67***	3.28 \pm 0.30***	0.53
STR10WAP	3.03 \pm 1.68*	5.32 \pm 3.02*	24.24 \pm 2.63***	5.88 \pm 0.53***	0.54
STR12WAP	1.64 \pm 0.55**	2.82 \pm 1.38*	0.52 \pm 0.34	4.53 \pm 0.41***	0.87
STRSQM	16.99 \pm 7.05**	22.47 \pm 11.98*	56.05 \pm 7.19***	34.00 \pm 3.04***	0.70
Across <i>Striga</i> -free conditions					
Grain yield	0.11 \pm 0.05*	2.15 \pm 1.37	0.20 \pm 0.04***	0.26 \pm 0.03***	0.70
Days to anthesis	2.14 \pm 1.03*	46.85 \pm 33.32	2.61 \pm 1.13*	8.54 \pm 1.08***	0.61
Anthesis–silking interval	0.41 \pm 0.23*	1.45 \pm 1.08	0.77 \pm 0.30**	2.20 \pm 0.28***	0.53
Plant height	10.61 \pm 15.84	2671.80 \pm 2676.55	0.00 \pm 0.00	247.02 \pm 31.50***	0.20
Ears per plant	0.00 \pm 0.00	0.01 \pm 0.01*	0.00 \pm 0.00	0.03 \pm 0.00***	0.37
Ear aspect	0.01 \pm 0.01	0.44 \pm 0.32	0.08 \pm 0.04*	0.31 \pm 0.04***	0.26
Husk cover	3.70 \pm 2.69	48.51 \pm 40.30	0.00 \pm 0.00	43.06 \pm 4.64 ***	0.50
Across locations					
Grain yield	0.15 \pm 0.05**	1.12 \pm 0.44**	0.17 \pm 0.03***	0.35 \pm 0.03***	0.87
Days to anthesis	1.61 \pm 0.55**	41.49 \pm 16.34**	1.08 \pm 0.41**	0.31 \pm 0.48***	0.85
Anthesis–silking interval	0.12 \pm 0.08	6.09 \pm 2.42**	0.03 \pm 0.24	4.37 \pm 0.33***	0.44
Plant height	30.07 \pm 13.01*	825.33 \pm 372.00*	3.50 \pm 20.01	316.32 \pm 26.99***	0.68
Ears per plant	0.00 \pm 0.00	0.01 \pm 0.00**	0.00 \pm 0.00	0.02 \pm 0.00***	0.47
Ear aspect	0.07 \pm 0.03**	0.07 \pm 0.03**	0.09 \pm 0.03**	0.53 \pm 0.04***	0.74
Husk cover	3.34 \pm 2.16	33.70 \pm 18.11*	21.90 \pm 5.61***	44.45 \pm 4.39***	0.45

* Significant at $P < 0.05$.

** Significant at $P < 0.01$.

*** Significant at $P < 0.001$.

† STR8WAP, emerged *Striga* plants 8 wk after planting (WAP); STR10WAP, emerged *Striga* plants 10WAP; STR12WAP, emerged *Striga* plants 12WAP; STRSQM, *Striga* plants m⁻².

Table 6. Genetic (upper triangle) and phenotypic (lower triangle) correlations for grain yield and emerged *Striga* plants 12 wk after planting among *Striga*-infested locations.

	Alupe	Pawe	Busia	Kibos1	Wad Medani	Kibos2	Kiboswa	Vihiga	Nyahera	Vihiga2
Grain yield										
Alupe	1	0.042ns	0.077ns†	0.990**	0.637**	0.791**	0.936**	0.990**	0.719**	
Pawe	0.018ns	1	0.990**	0.416ns	0.547**	0.628**	0.727**	-0.990**	0.990**	
Busia	0.050ns	0.496**	1	0.261ns	0.537**	0.288ns	0.374*	0.990**	0.862**	
Kibos1	0.825**	0.207ns	0.195ns	1	0.769**	0.710**	0.948**	-0.990**	0.828**	
Wad Medani	0.461**	0.237ns	0.350ns	0.633**	1	0.513**	0.977**	0.990**	0.982**	
Kibos2	0.551**	0.262ns	0.181ns	0.562**	0.355*	1	0.990**	0.990**	0.852**	
Kiboswa	0.705**	0.328ns	0.254ns	0.812**	0.732**	0.731**	1	0.990**	0.834**	
Vihiga	0.003ns	-0.032ns	0.323ns	-0.010ns	0.120ns	0.138ns	0.113ns	1	0.990**	
Nyahera	0.434*	0.366ns	0.469**	0.569**	0.590**	0.493**	0.521**	0.220ns	1	
EmergEd <i>Striga</i> plants 12 wk after planting										
Alupe	1	0.228ns	0.007ns	0.846**	0.990**	0.969**	0.843**	0.990**	0.990**	0.990**
Kibos1	0.673**	0.488**	0.990**	1	0.990**	0.537**	0.990**	0.990**	0.697**	0.990**
Pawe	0.138ns	1	0.990**	0.296ns	-0.990**	0.464**	0.593**	0.382*	0.472**	0.790**
Busia	0.001ns	0.127ns	1	0.164ns	0.990**	-0.814**	0.428*	0.774**	-0.446*	0.990**
Kibos2	0.836**	0.306ns	-0.109ns	0.466**	-0.990**	1	0.706**	0.768**	0.969**	0.990**
Wad Medani	0.151ns	-0.242ns	0.035ns	0.233ns	1	-0.055ns	0.990**	0.990**	0.990**	0.990**
Kiboswa	0.700**	0.375*	0.055ns	0.894**	0.236ns	0.640**	1	0.990**	0.822**	0.990**
Nyahera	0.910**	0.317ns	-0.061ns	0.616**	0.056ns	0.930**	0.760**	0.864**	1	0.990**
Vihiga	0.877**	0.228ns	0.094ns	0.862**	0.238ns	0.655**	0.813**	1	0.751**	0.990**
Vihiga2	0.669**	0.235ns	0.089ns	0.846**	0.512**	0.426**	0.824**	0.828**	0.611**	1

* Significant at $P < 0.05$.

** Significant at $P < 0.01$.

† ns, not significant.

variance (σ_E^2) was larger than σ_G^2 for all traits. The results show that $\sigma_{G \times L}^2$ accounted for 11, 51, 63, 5 and 43% of the total variation for GY, emerged *Striga* plants at 8 WAP, 10 WAP, and 12 WAP, and emerged *Striga* plants m^{-2} , respectively, under *Striga*-infested conditions. Under *Striga*-free conditions, σ_L^2 accounted for 79, 78, 91, 52, and 51% of the total variation for GY, AD, PH, EA, and HC, respectively. Broad-sense heritability for GY was 0.84, 0.70, and 0.87 under *Striga*-infested, *Striga*-free conditions, and across locations, respectively (Table 5). Broad-sense heritability ranged from 0.05 (ASI) to 0.83 (AD) for agronomic traits under *Striga* infestation and 0.20 (PH) to 0.61 (AD) under *Striga*-free conditions. Broad-sense heritability was moderate for emerged *Striga* plants 8 WAP (0.53) and 10 WAP (0.54) and high for emerged *Striga* plants 12 WAP (0.87) and *Striga* plants m^{-2} (0.70).

Genetic Correlations Among Test Locations

The genetic correlations for GY among locations ranged from -0.990 (between Pawe and Vihiga and between Kibos and Vihiga) to 0.990 for 10 pairs of locations under *Striga*-infested conditions (Table 6). Two of the locations with a high negative genetic correlation were located in different countries (Pawe in Ethiopia and Vihiga in Kenya), but both were under natural *Striga* infestation. However, Pawe had moderate to strong genetic correlations with other locations under natural *Striga* infestation

in Kenya. The other locations that had a negative genetic correlation were both in Kenya but were under different *Striga* infestation regimes. The two locations under artificial *Striga* infestation (Alupe and Kibos) showed a strong positive genetic correlation of 0.990 (Table 6). The phenotypic correlations between locations for GY varied from -0.032 between Pawe and Vihiga to 0.825 between Alupe and Kibos (Table 6). Both Alupe and Kibos were under artificial *Striga* infestation. One location in Kenya (Nyahera) had positive significant phenotypic correlations with all other locations except Pawe and Vihiga. For emerged *Striga* plants 12 WAP, the genetic correlations ranged from -0.990 for two pairs of locations (Pawe-Wad Medani and Kibos2-Wad Medani) to 0.990 for 20 pairs of locations (Table 6). Pawe and Wad Medani were under different *Striga* infestation regimes, but Kibos2 and Wad Medani were both under artificial *Striga* infestation. The Vihiga2 location had significant positive genetic correlation with all the other locations used in this study. The phenotypic correlations ranged from -0.242 between Pawe and Wad Medani to 0.930 between Kibos and Nyahera (Table 6). The Vihiga2 location had significant positive phenotypic correlation with all the other locations except Pawe and Busia. Under *Striga*-free conditions the genetic correlations for GY between locations ranged from -0.990 between Alupe2 and Wad Medani to 0.990 for 14 pairs of locations (Table 7). Alupe had significant positive genetic

Table 7. Genetic (upper triangle) and phenotypic (lower triangle) correlations for grain yield among *Striga*-free locations.

	Alupe1	Bungoma1	Bungoma2	Embu	Alupe2	Kibos	Wad Medani
Alupe1	1	0.990**	0.990**	0.990**	0.990**	0.990**	0.990**
Bungoma1	0.469*	1	0.083ns†	0.990**	0.990**	0.216ns	0.990**
Bungoma2	0.187ns	0.060ns	1	0.229ns	0.737**	0.990**	0.990**
Embu	0.595**	0.809**	0.179ns	1	0.990**	0.317ns	0.990**
Alupe2	0.432*	0.447**	0.197ns	0.554**	1	0.405ns	-0.990**
Kibos	0.160ns	0.160ns	0.761**	0.257ns	0.112ns	1	0.990**
Wad Medani	0.140ns	0.146ns	0.412*	0.162ns	-0.152ns	0.271ns	1

* Significant at $P < 0.05$.** Significant at $P < 0.01$.

† ns, not significant.

Table 8. Genetic correlations for grain yield under *Striga*-infested and *Striga*-free conditions.

	Alupe1 [†] (<i>Striga</i> -free)	Alupe2 [‡] (<i>Striga</i> -free)
Alupe (<i>Striga</i> -infested)	0.990**	-0.059ns [§]
	Kibos (<i>Striga</i> -free)	
Kibos1 [†] (<i>Striga</i> -infested)	0.988**	
Kibos2 [‡] (<i>Striga</i> -infested)	0.731**	
	Wad Medani (<i>Striga</i> -free)	
Wad Medani (<i>Striga</i> -infested)	0.990**	

** Significant at $P < 0.01$.

† Alupe1 and Kibos1 refer to trials conducted in 2004A cropping season.

‡ Alupe2 and Kibos2 refer to trials conducted in 2004B cropping season.

§ ns, not significant.

correlations with all other locations. The phenotypic correlations varied from -0.152 to 0.809 for GY between locations under *Striga*-free conditions. The genetic correlations for GY between *Striga*-infested and *Striga*-free conditions at the same location were high and positive except between Alupe and Alupe2 (Table 8).

The genetic correlations between locations for GY and emerged *Striga* plants m^{-2} were used for cluster analysis to classify the environments under *Striga* infestation. Clustering based on genetic correlation for GY revealed three major clusters. Cluster I consisted of six locations that were separated into three subclusters (Fig. 1). Subcluster I consisted of locations under artificial *Striga* infestation and natural *Striga* infestation in Kenya. The second subcluster had two locations (one each in Kenya and Ethiopia). The third subcluster had one location (Busia) in Uganda. Cluster II consisted of one location (Vihiga) in Kenya. Cluster III consisted of two locations that were under artificial *Striga* infestation. Clustering based on emerged *Striga* plants m^{-2} revealed three major clusters. Cluster I consisted of locations that were under artificial *Striga* infestation and natural *Striga* infestation in Kenya and Ethiopia (Fig. 2). Cluster II consisted of five locations, four of which were in Kenya and one in Sudan. Cluster III consisted of one location in Uganda.

Cluster analysis of the genotypes based on agronomic traits (GY, AD, ASI, PH, EPP, HC, and EA) and emerged *Striga* plants m^{-2} across *Striga*-infested locations revealed

two major clusters. Cluster I consisted of the herbicide-resistant varieties that were grouped into four subgroups, while Cluster II consisted of the two check entries (Fig. 3). Subgroup I had mostly low-yielding maize varieties (4 out of 5), but these varieties supported a lower number of *Striga* plants. On the other hand, subgroup IV consisted of high-yielding varieties, but these supported a relatively higher number of *Striga* plants (Fig. 3). Cluster analysis based on agronomic traits and emerged *Striga* plants m^{-2} across all locations revealed a similar pattern to that based on clustering emerged *Striga* plants m^{-2} and agronomic traits across *Striga*-infested locations. Two major clusters were obtained that clearly separated the herbicide-resistant varieties and check entries (Fig. 4). The herbicide-resistant varieties in cluster I were grouped into five subgroups, with subgroup I consisting of mostly low-yielding varieties that supported fewer *Striga* plants.

Genotype Main Effect Plus Genotype × Environment Interaction Biplot Analysis of Performance and Stability

The GGE biplot analysis was used to identify the best entries at each location and assess the stability of the entries. The polygon view of the GGE biplot based on GY explained 82% (69.3 and 12.7% for PC1 and PC2, respectively) of the total variation across the *Striga*-infested locations (Fig. 5). The results revealed seven sectors with the nine locations falling into one of the two sectors. The vertex varieties were G17 (STR-VE-216), G10 (STR-VE-209), G23 (KSTP94), G2 (STR-VE-201), G1 (STR-VE-200), G19 (STR-VE-218), and G13 (STR-VE-212). The vertex cultivar in each sector represents the highest yielding cultivar in the location that fell within that particular sector (Yan et al., 2000). Variety G17 (STR-VE-216) was the vertex entry in the sector where eight of the nine locations fell, indicating that this herbicide-resistant variety was the highest yielding entry in these locations under both natural and artificial *Striga* infestation. Varieties G19 (STR-VE-218), G13 (STR-VE-212), G10 (STR-VE-209), G23 (KSTP94), G2 (STR-VE-201), and G1 (STR-VE-200) did not have any location falling in the sectors where they were located, suggesting that these varieties were low

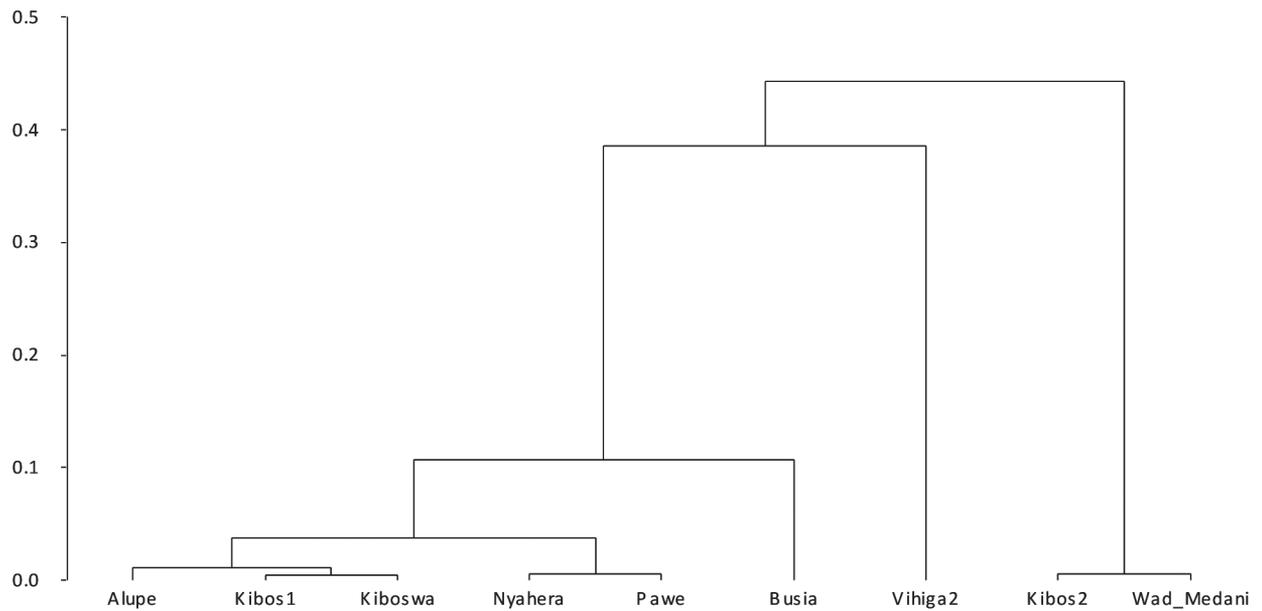


Figure 1. Dendrogram of nine *Striga*-infested locations based on grain yield.

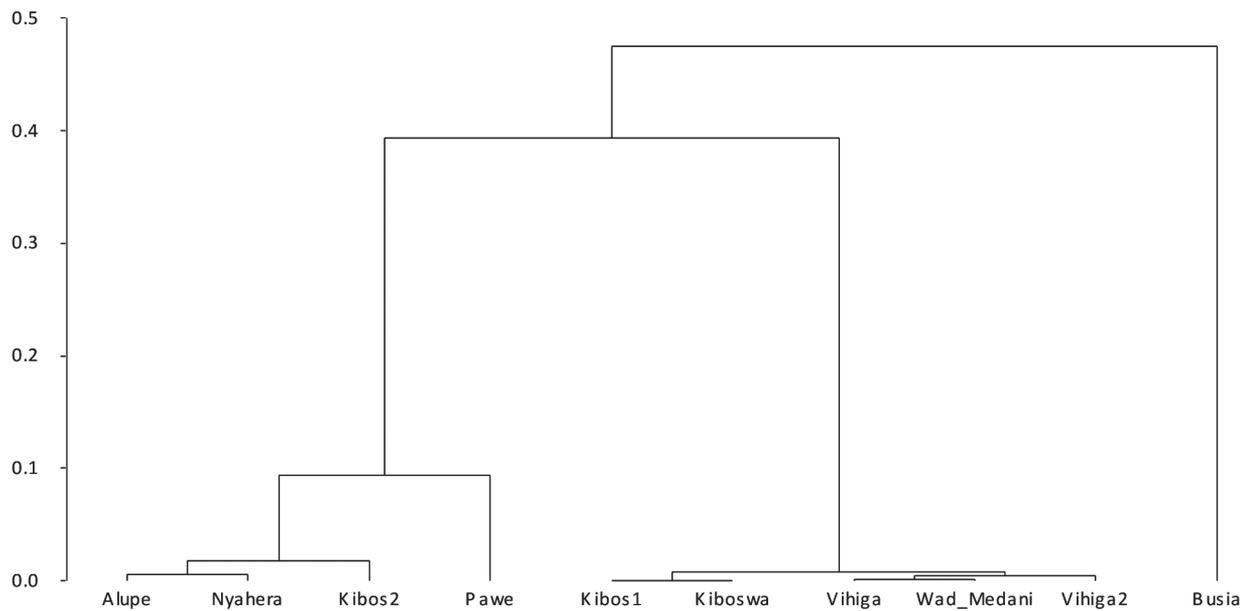


Figure 2. Dendrogram of 10 *Striga*-infested environments based on number of emerged *Striga* plants m^{-2} .

yielding in some or all of the locations. Fifteen varieties fell within the polygon, indicating that they were less responsive than the vertex cultivars. The mean vs. stability view biplot was used to assess stability of the 24 varieties across the nine *Striga*-infested locations. This biplot accounted for 82% of the variation in GY (Fig. 6). In this biplot, the axis of the average environment coordinate (AEC) abscissa, or average environment axis, is the single-arrowed line that passes through the biplot origin and the average environment, which is at the center of the small circle. The axis of the AEC ordinate is the double-arrowed line that passes through the biplot origin and is perpendicular to the AEC abscissa (Yan et al., 2007). The

cultivars were ranked along the average environment axis, with the arrow pointing to a greater value based on mean performance across all locations. The seven top ranking varieties according to their projections onto the average environment axis were G17 (STR-VE-216), G22 (STR-VE-221), G18 (STR-VE-217), G10 (STR-VE-209), G9 (STR-VE-208), G7 (STR-VE-206), and G13 (STR-VE-212). In this analysis, the stability of the cultivars is measured by their projection onto the AEC ordinate. Varieties G20 (STR-VE-219), G12 (STR-VE-211), G8 (STR-VE-207), G22 (STR-VE-221), G1 (STR-VE-200), and G3 (STR-VE-202) were the most stable because of their short projection onto the AEC ordinate. On the other hand,

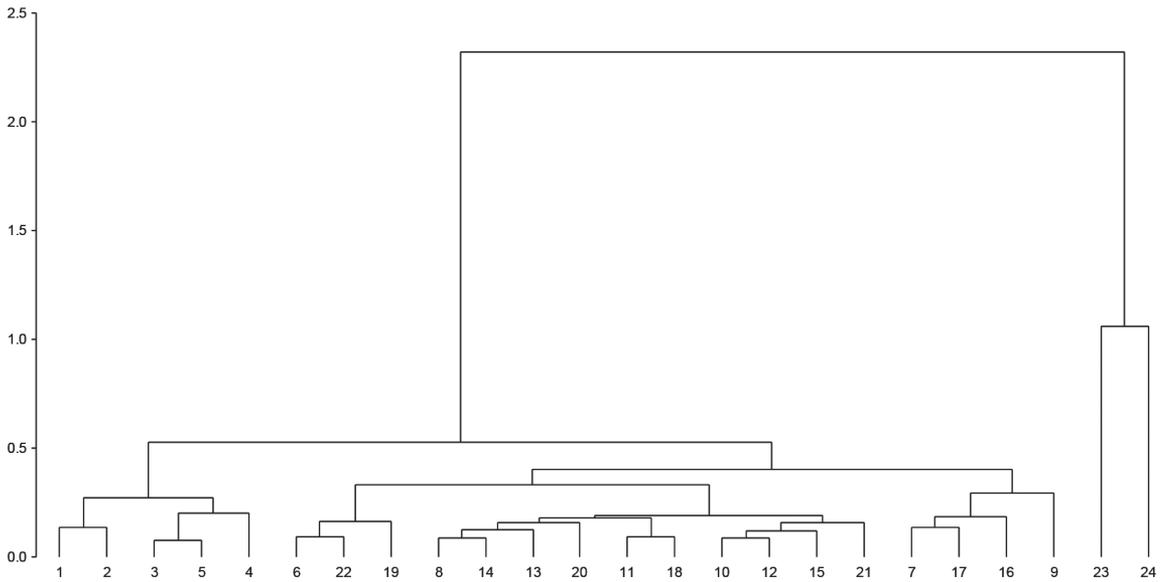


Figure 3. Dendrogram of 24 open-pollinated varieties based on agronomic traits (GY, AD, ASI, PH, EPP, HC, and EA) and number of emerged *Striga* plants m^{-2} under *Striga* infestation using the average linkage method.

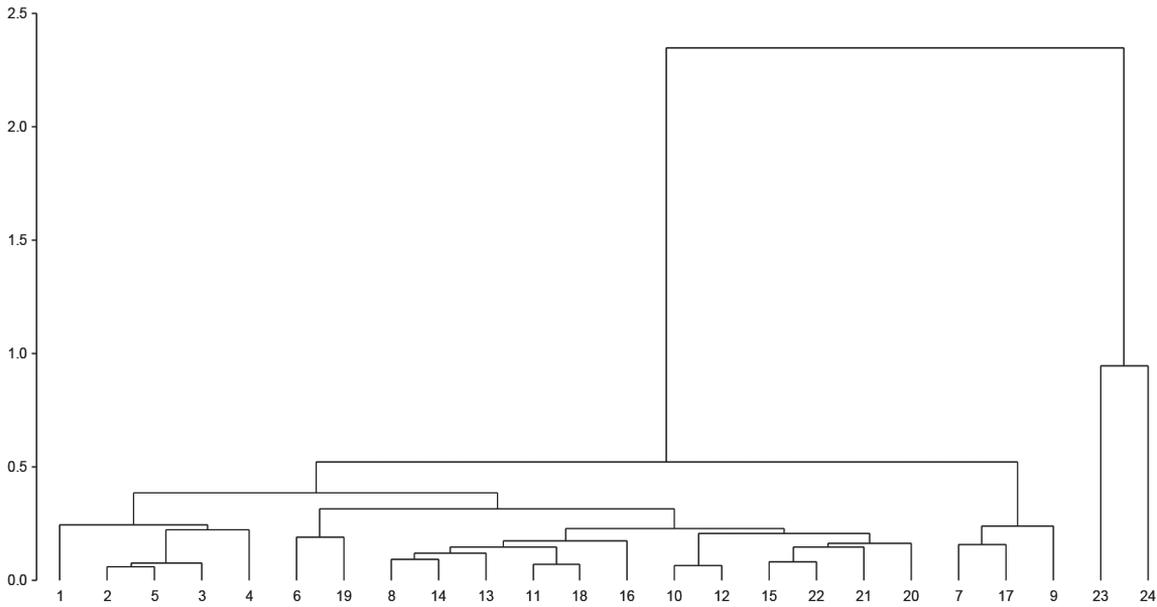


Figure 4. Dendrogram of 24 open-pollinated varieties based on agronomic traits (GY, AD, ASI, PH, EPP, HC, and EA) and number of emerged *Striga* plants m^{-2} across locations using the average linkage method.

Striga-tolerant variety KSTP94 was the most unstable because of the long projection onto the AEC ordinate.

DISCUSSION

This study examined the agronomic performance and genotype \times environment interactions of IR OPVs under *Striga*-infested and *Striga*-free conditions in eastern Africa. The IR OPVs used in this study were a conversion of OPVs developed for tolerance or resistance to some of the major biotic (MSV, GLS, and TLB) and abiotic (low nitrogen and drought stress) constraints in the midaltitude agroecology of eastern Africa. The present study revealed

highly significant genotypic differences for GY, emerged *Striga* plants, and other agronomic traits except ASI across *Striga*-infested locations. Under *Striga*-free conditions, highly significant genotypic differences were observed for GY, AD, and ASI. These results indicated differential performance of the varieties under *Striga*-infested and *Striga*-free conditions. Results showed a clear GY advantage of the IR OPVs over the checks entries. The best IR maize variety under *Striga* infestation was G17 (STR-VE-216) with a yield advantage of 89% over the commercial variety and 113% over the *Striga*-tolerant check across locations under *Striga* infestation. Similar findings were

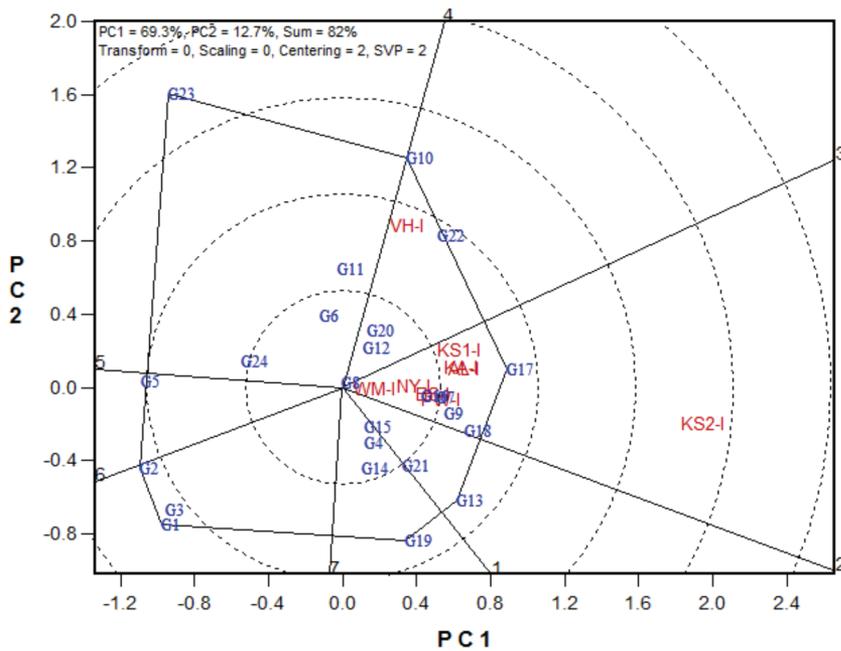


Figure 5. A which-won-where biplot of grain yield of 24 maize varieties evaluated across nine locations under *Striga*-infestation in 2004.

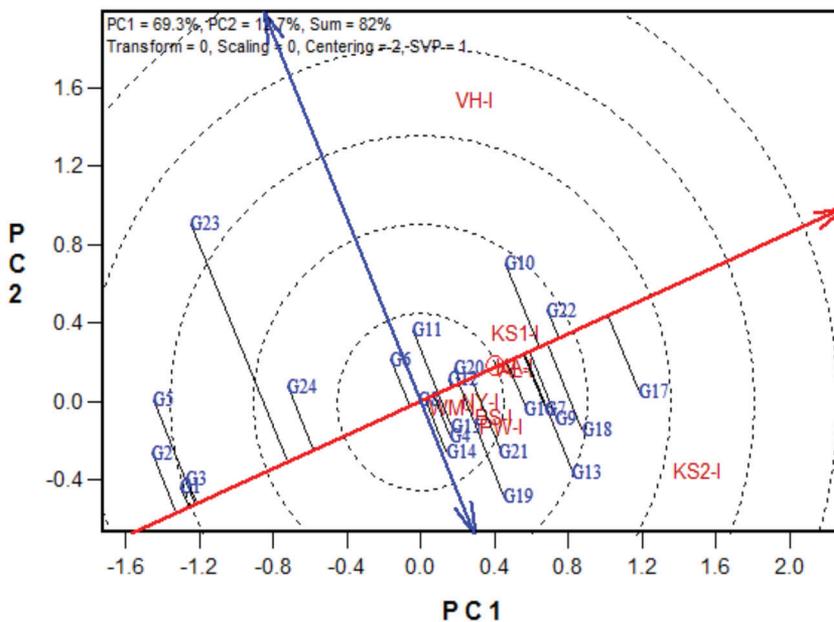


Figure 6. The mean vs. stability view of the genotype main effect plus genotype \times environment interaction biplot based on yield data of 24 maize varieties evaluated across nine locations under *Striga*-infestation in 2004.

reported by Menkir et al. (2010) for IR maize hybrids under *Striga* infestation in Nigeria. The best IR OPVs supported 77 and 76% less emerged *Striga* plants m^{-2} than the commercial and *Striga*-tolerant checks, respectively. Herbicide-resistant maize varieties have been reported to support a lower number of *Striga* plants in other studies (Kanampiu et al., 2003; Menkir et al., 2010). Use of IR maize varieties for *Striga* control would lead to fewer *Striga* plants maturing to set seed, and this will lead to fewer *Striga* seeds being added to the soil compared with commonly grown commercial varieties. This will ultimately

lead to reduced *Striga* seed bank in the soil. Across *Striga*-free conditions, the IR OPVs had equal or higher GY than the commercial check. These results suggest that the IR OPVs have the potential to do well in *Striga*-free areas. This study evaluated IR OPVs developed through a backcross program to incorporate herbicide resistance in OPVs adapted to the ecologies in eastern Africa. The resultant IR OPVs should therefore have good adaptation in *Striga*-free areas in the target ecologies as only herbicide resistance was added to the recurrent parent in the backcross program. Three of the IR OPVs used in this study

were registered for commercialization and are marketed for *Striga* control in Kenya and Tanzania.

Results revealed consistency of ranking for GY across *Striga*-infested and *Striga*-free environments among the IR OPVs, suggesting stable performance of the IR OPVs across environments. Consistent performance of *Striga*-resistant varieties in contrasting environments was reported by Menkir et al. (2012b), who attributed this to the presence of polygenic resistance in the germplasm used. Consistency of performance could also mean that the *S. hermonthica* populations were similar in the diverse environments used in the present study.

The results of the present study revealed highly significant GE effects for all traits except ASI under *Striga* infestation, and PH and EPP under *Striga*-free conditions. These results suggested that the IR maize varieties performed differently at the various locations in eastern Africa. Representative locations where *Striga* is a problem were used in Kenya, Uganda, Ethiopia, and Sudan. These locations had different climatic and soil conditions and these might have led to the variable performance of the varieties. Results revealed that σ_G^2 was smaller than $\sigma_{G \times L}^2$ for EPP, HC, emerged *Striga* plants at 8WAP and 10 WAP, and *Striga* plants m^{-2} under *Striga* infestation, and for GY, AD, ASI, and EA under *Striga*-free conditions, probably due to the diverse environments used in this study (Comstock and Moll, 1963; Allard and Bradshaw, 1964). Results indicated that σ_L^2 explained 79% of the total variation for GY under *Striga*-free conditions. Similar results were reported for GY of early maturing maize hybrids grown in France (Epinat-Le Signor et al., 2001). In this study, $\sigma_{G \times L}^2$ was the major source of variation for emerged *Striga* plants 8 WAP, 10 WAP, *Striga* plants m^{-2} , and HC. The large $\sigma_{G \times L}^2$ component for these traits might have resulted in low to moderate broad-sense heritabilities.

Broad-sense heritability is an estimate of the upper boundary of narrow-sense heritability (Robinson, 1963). The moderate broad-sense heritability for emerged *Striga* plants at 8 WAP and 10 WAP ($H = 0.53$ and 0.54 , respectively) in this study suggested that the actual heritability estimates might be lower (Falconer and Mackay, 1996), which may lead to low genetic gain from selection for these two traits under *Striga* infestation. The number of emerged *Striga* plants at 12 WAP had the highest broad-sense heritability estimates among the *Striga* parameters, suggesting that actual heritability estimates might be high (Falconer and Mackay, 1996), which might lead to higher genetic gain when selecting for this trait. The broad-sense heritability estimate for emerged *Striga* plants m^{-2} was 0.70 while that for GY was 0.84 under *Striga* infestation. The high broad-sense heritability estimates for GY and emerged *Striga* plants 12 WAP were partly due to low $\sigma_{G \times L}^2$ for these two traits. The broad-sense heritability estimates for these two traits are lower than the values

reported in studies by Menkir et al. (2010, 2012b). The broad-sense heritability for emerged *Striga* plants m^{-2} is similar to that reported in sorghum by Haussmann et al. (2001). Evaluation of *Striga*-resistant maize varieties will have to be performed over locations and years for traits with low broad-sense heritability to obtain consistent varietal reactions compared with those traits with higher broad-sense heritability.

For a trait measured for the same genotype in different environments, indirect selection can be applied given information on the heritability and the genetic correlation for the trait in the two environments. In this study, the majority of the genetic correlations among locations were positive and highly significant for GY under both *Striga*-infested and *Striga*-free conditions and for emerged *Striga* plants at 12 WAP. The two main *Striga* breeding and evaluation locations in Kenya had strong positive genetic correlations with most of the other locations except Busia and Pawe for both GY and emerged *Striga* plants at 12 WAP. This indicates that germplasm selected at either of these two locations can be used at the other *Striga*-infested locations. The high genetic correlations also suggest that there is little GE for most pairs of environments used in this study. There were some low genetic correlations between some pairs of locations suggesting that these environments are very different (Falconer, 1952; Malla et al., 2010). This also indicates that GE has a strong influence (Falconer, 1952; Cooper and DeLacy, 1994) and different genetic systems operate in the two environments (Falconer, 1952; Eisen and Saxton, 1983). A weak genetic correlation ($r_g = 0.083$, $P > 0.10$) was obtained between evaluations performed in two cropping seasons at the same location (Bungoma1 and Bungoma2) probably due to differences in the rainfall pattern experienced during the two cropping seasons. Similar observations were made by Yang and Baker (1991) for wheat (*Triticum aestivum* L.) grown in temperate regions. The first cropping season (March–August) was characterized by higher rainfall compared with the second cropping season (September–December). As a result, some level of stress may have been experienced in late-maturing maize when planted during the second cropping season thus affecting performance of the crop. Genotype \times environment interactions are of importance where there are environmental extremes that induce stress conditions (Eisen and Saxton, 1983). The Busia location had low genetic correlations with other locations in this study. Burdon (1977) pointed out that locations with low genetic correlations between them should be treated separately, and based on this, these results suggested that Busia should be considered a unique environment for evaluations of genotypes for *Striga* resistance. Grain yield was highly correlated between *Striga*-free and *Striga*-infested conditions at the same location indicating that GY under both conditions is probably governed by the same set of

genes. These results are similar to those reported for GY in maize grown under organic and conventional production systems (Lorenzana and Bernardo, 2008) but are different from those of Bänziger et al. (1997) who reported that different sets of genes control maize GY under low- and high-nitrogen environments.

Genetic correlations can be used to evaluate similarities between locations. In this study, cluster analysis using genetic correlations based on GY revealed groups of locations under different *Striga* infestation regimes (artificial and natural). Malla et al. (2010) reported that locations used to evaluate wheat germplasm were not clustered according to geographical location. Results showed that Kibos and Wad Medani (both under artificial infestation) and Vihiga, a high-altitude location, were distinct from the rest of the locations. Results of clustering based on emerged *Striga* plants m^{-2} revealed that Busia was a different environment. The presence of locations that clustered separately suggested the presence of GE and the effect of different crop management practices. These results provided further support that the presence of GE was due to the low genetic correlations between some locations. In this study, clustering of the test varieties based on both agronomic traits and emerged *Striga* plants m^{-2} revealed two groups depending on the type of germplasm, with the IR OPVs clearly separated from the check varieties. This separation was due to the differences in the reaction of the two types of germplasm to *Striga* infestation. This finding is consistent with results of Menkir et al. (2012b) that showed that *Striga*-resistant hybrids were separated from *Striga*-tolerant hybrids but contrary to results of Badu-Apraku and Lum (2007) who reported that the clustering of inbred lines was independent of the genetic backgrounds of the genotypes. Within the IR OPVs, separation was based on both GY and the number of emerged *Striga* plants supported by the variety. Similar findings were reported by Menkir et al. (2012b). The availability of high-yielding IR OPVs that also supported a low number of *Striga* plants holds promise for farmers in *Striga* endemic areas of eastern Africa.

Use of GGE biplot analysis allowed us to obtain information on variety performance and stability. An ideal genotype should have both high mean grain yield and high stability within a megaenvironment (Yan and Tinker, 2006). The most stable varieties were all IR OPVs. Two of the most stable varieties, G1 (STR-VE-200) and G3 (STR-VE-202), were among the lowest yielding varieties. Among the most stable varieties only G22 (STR-VE-221) was high yielding, and, therefore, it has potential to be grown in a wide range of *Striga*-prone environments in eastern Africa because of its broad adaptation. Two of highest yielding varieties, G17 (STR-VE-216) and G18 (STR-VE-217), were not among the most stable, suggesting that these varieties may have specific adaptation to some of the *Striga*-prone environments. These results are consistent

with those of Badu-Apraku et al. (2012) who identified high yielding but unstable varieties in West Africa. Variety G23 (KSTP94), a *Striga*-tolerant check, exhibited the highest instability and also low yield potential across locations. The commercial check, G24 (WS202), was among the lowest yielding varieties in this study. The low yield of the *Striga*-tolerant variety and the commercial check was expected because they were evaluated in *Striga*-infested areas that are outside their range of adaptation (Eskridge et al., 1993). These two varieties had never been tested in Ethiopia and Sudan before this study.

CONCLUSIONS

A number of IR OPVs showed superiority in GY and other agronomic traits compared with non-IR maize varieties currently used by farmers under both *Striga*-infested and *Striga*-free conditions. These results suggest that adoption of the adapted IR OPVs by farmers in *Striga* endemic areas of eastern Africa would increase maize production and productivity. In addition to increased maize yield for farmers, IR maize technology for *Striga* control would also deplete the *Striga* seed bank in the soil. Imidazolinone-resistant maize will act as a stopgap measure to help African farmers in *Striga* endemic areas obtain good maize yields until maize varieties with adequate genetic resistance become available in eastern Africa. There appears to be little GE between most of the *Striga*-infested environments used in this study, but a few environments are unique and should be treated separately from others for *Striga* germplasm evaluation.

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