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Maize Landraces are Less Affected by *Striga hermonthica* Relative to Hybrids in Western Kenya

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Production of maize in western Kenya is severely constrained by the parasitic weed striga. Although productivity of maize can be improved through adoption of improved varieties, adoption of such varieties remains low in the region, as the majority of smallholder farmers still grow unimproved open-pollinated varieties (landraces). The performance of two improved hybrid varieties was evaluated against six landraces in striga-infested soils in western Kenya. The varieties were planted in plots under natural striga infestation and were supplemented with pot experiments under artificial infestation. Striga emergence was lower in landraces than in the hybrid varieties in both field and pot experiments. Similarly, height of maize plants at harvest and grain yields were higher in the landraces than in the hybrids. After three continuous cropping seasons, in all treatments, striga seedbank density increased two to seven times. Seedbank increase was higher with hybrids and two of the landraces, 'Rachar' and 'Endere'. These results provide an insight into the potential role landraces could play in efforts toward an integrated management approach for striga in smallholder cropping systems. They also highlight the need to develop hybrid maize lines with local adaptation to biotic constraints, specifically striga.

Nomenclature: Striga, *Striga hermonthica* (Delile) Benth.; maize, *Zea mays* L., *Zea mays* L. 'Rachar', *Zea mays* L. 'Endere'.

Key Words: Food security, integrated control, smallholder farmers, striga, varietal resistance.

La producción de maíz en el oeste de Kenya está severamente limitada por la maleza parasítica *Striga hermonthica*. Aunque la productividad del maíz puede ser incrementada con la adopción de variedades mejoradas, la adopción de estas variedades sigue siendo baja en la región, ya que la mayoría de los pequeños productores todavía producen variedades no-mejoradas de polinización abierta (autóctonas). El desempeño de dos variedades mejoradas híbridas fue evaluado y comparado con seis variedades autóctonas en campos infestados con *S. hermonthica* en el oeste de Kenya. Las variedades fueron sembradas en parcelas con infestaciones naturales de *S. hermonthica* y en potes con infestaciones artificiales. La emergencia de *S. hermonthica* fue más baja con variedades autóctonas que con híbridos. Después de tres temporadas continuas de producción, la densidad del banco de semillas de *S. hermonthica* aumentó de dos a siete veces en todos los tratamientos. El aumento del banco de semillas fue mayor con variedades híbridas y con las autóctonas 'Rachar' y 'Endere'. Estos resultados brindan una idea del rol potencial que pueden jugar las variedades autóctonas en los esfuerzos para el manejo integrado de *S. hermonthica* en sistemas de cultivos de pequeños productores. Además, los resultados resaltan la necesidad de desarrollar líneas híbridas de maíz con adaptaciones a las limitaciones bióticas locales, especialmente *S. hermonthica*.

Maize is the world's most abundantly grown cereal crop, with an annual production of over 870 million metric tons (Cairns et al. 2013). It is the most important food and cash crop in sub-Saharan Africa (SSA) (FAO 2010), where it is mainly produced by smallholder farmers who have land holdings ranging from 0.5 to 3.0 ha (Byerlee and

Heisey 1997). Productivity increases, however, have not kept pace with increases in demand, largely due to biotic and abiotic constraints (Khan et al. 2014).

Among the most important yield-reducing factors in smallholder production systems in SSA is the obligate root parasite striga (Gressel et al. 2004). Although striga has long been a pest in traditional cropping systems, it did not cause serious yield losses because these production systems typically involved crop rotations, mixed cropping, and prolonged fallows (Van Ast et al. 2000). Practices such as crop rotation and prolonged fallows have since been replaced by continuous cereal cropping due to increased demand for food supplies and

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decreases in land sizes (Van Ast et al. 2000), with no corresponding investment in soil fertility management. Consequently, this has resulted in soil degradation and nutrient depletion, and a rapid increase in the extent and severity of infestation by striga (Parker and Riches 1993; Van Ast et al. 2000).

Infestation by striga is more prevalent in low-input cropping systems with poor soil fertility (Sauerborn 1991), and can result in maize yield losses of up to 100%, depending on the level of susceptibility of the host genotype (Berner et al. 1995). These losses are estimated to be more than US\$7 billion in SSA annually (Berner et al. 1995), and affect livelihoods of approximately 100 million people (Kanampiu et al. 2002). Although a number of approaches have been developed for management of striga, including the imazapyr-resistant mutant maize (Kanampiu et al. 2003), effective control of the parasite remains elusive due to poor adoption of such approaches (Oswald 2005). This is further complicated by the high reproductive rate and seed longevity of the parasite, combined with a complicated mode of parasitism that occurs underground (Midega et al. 2014).

Striga is dependent on its host for survival, and its lifecycle is closely linked to that of its host (Hausmann et al. 2000). Striga seeds, once preconditioned, will only germinate in the presence of germination stimulants, usually exuded by roots of host, and some nonhost, plants (Pickett et al. 2010). Subsequent developmental and physiological events, including haustorial root formation, development, and attachment, as well as further growth and development of the parasite, also depend on signals and resources from the host plant (Ejeta et al. 2000). Generally the effects of striga on plant production are attributed to two damage mechanisms: directly through the role of the parasite as an additional sink for organic carbon, inorganic solutes, and water, and indirectly through the phytotoxic effects of the parasite on the host (Van Ast et al. 2000).

A considerable amount of research has been devoted to the improvement of maize through conventional breeding, leading to production and release of a number of improved hybrid varieties with higher grain yield potential in Kenya. Use of these hybrid varieties might increase total household income due to their potential for higher productiv-

ity (Mathenge et al. 2012). Although productivity of maize can be improved through adoption of such hybrid varieties, emerging evidence indicates that adoption of such varieties remains low among growers (Smale and Olwande 2014). The majority of smallholder farmers in most parts of SSA still rely on unimproved, open-pollinated varieties (OPVs) for their plantings (Aquino et al. 2001). Such OPVs, also known as landraces, are locally grown and are the result of farmer selection and management over many generations (Bellon et al. 2006). However, it is posited that under limiting conditions, such as striga-infested soils, landraces may be as productive as or more productive than hybrid varieties (Schroeder et al. 2013). Therefore as part of our continuing efforts to address constraints to maize production in the region, we evaluated performance of hybrid maize varieties in relation to farmers' landraces in striga-infested soils.

Materials and Methods

These studies were conducted at the field site of the International Centre of Insect Physiology and Ecology, Thomas Odhiambo Campus, at Mbita Point (0.42°S, 34.20°E), on the eastern shores of Lake Victoria in western Kenya, a region where striga is a serious limitation to maize production (Khan et al. 2008a). The studies were conducted between the long (March to August) and short (September to December) rainy seasons of 2012 and long rainy season of 2013. The experimental site receives approximately 900 mm of rainfall per year, with a mean annual temperature of 27 °C, and is located at an elevation of approximately 1,200 m above sea level.

Treatments (maize varieties) were laid out in 5-m by 6-m plots arranged in a completely randomized design with four replications, and were separated by a 2-m buffer space. Treatments comprised six smallholder farmers' landraces of maize commonly grown in western Kenya (known by local names as 'Mochore', 'Endere', 'Nyamula', 'Sefensi', 'Rachar', and 'Jowi') and two hybrid varieties 'WH504' (Western Seed Company, Kitale, Kenya) and 'PH4' (Kenya Seed Company). Three seeds of each variety were planted at 75 cm between and 30 cm within rows. Two weeks after emergence (WAE), maize plants were thinned to one plant per hill. Each plot received di-ammonium phosphate (DAP) (18–46–

0) at planting at the rate of 60 kg ha⁻¹ and calcium ammonium nitrate (CAN, 26% N) after thinning of maize at the rate of 60 kg ha⁻¹, the recommended rates of these fertilizers (Mucheru-Muna et al. 2014). Plots were kept weed-free by hand-weeding, except for striga, throughout the growing season.

Striga infestation was determined 8 and 12 WAE of maize, when 40 maize plants were randomly selected from within the middle rows in each plot and the number of striga plants visible above ground was determined from within a radius of 15 cm from each plant.

At maize physiological maturity, the height of 40 randomly selected maize plants was measured. All maize plants were then harvested and grain yields were converted to t ha⁻¹ after drying to 12% moisture content.

A screen-house experiment was conducted to determine whether postgermination growth differed among varieties. The six landraces and two hybrid varieties were planted in 5-L plastic pots (20 cm diam and 20 cm deep) filled with autoclaved soil to which DAP had been added at the rate of 60 kg ha⁻¹. There were 10 plastic pots for each treatment, and the experiment was repeated. The soil in each pot was inoculated artificially using a spatula with approximately 3,000 seeds of striga, and emergence of striga was measured at 2-wk intervals, starting from the fourth WAE of maize.

In the field studies, striga seedbank density analysis was conducted using methodologies adapted from Vanlauwe et al. (2008). Soils were sampled to estimate the striga seedbank density. Preplant soil sampling was conducted in March 2012, the first season, by collecting five soil cores (5-cm diam and 15-cm depth) from each plot using a systematic “W” sampling pattern and combining them into a representative composite sample. A subsample of 250 g was used for elutriating striga seeds in the soil, as described by Eplee (1976) and Ndung’u et al. (1993). Here, the 250 g of soil was placed in an elutriator overflowing into three sieves of different mesh sizes (850, 250, and 90 mm). Tap water was passed through the base of the elutriator and lifted the lighter soil fraction through a spout and onto the meshes. Striga seeds were captured on the 90-mm mesh while coarse materials were trapped on the larger mesh sieves and dispersed finer minerals were washed through the sieves. The sample on the 90-mm sieve was recovered by washing into a 500-

ml glass burette column containing a potassium carbonate (K₂CO₃) solution with a specific density of 1.8 g cm⁻³. When tap water was applied to the column, striga seeds were retained in the K₂CO₃-water interface. The K₂CO₃ was then drained away through the burette and the seeds drained from the K₂CO₃-water interface onto a 90-mm nylon cloth before being counted using a binocular microscope. Soil samples were taken again at the end of the long rainy season of 2013 (August 2013) and analyzed for striga seedbank density.

Striga count data at 12 WAE of maize were utilized for analysis since the number of emerged striga peaked at 12 WAE. However, for the pot culture experiment, striga count data at 6 WAE of maize were used for analyses since this was the peak emergence period. Striga counts were log transformed [$\log_{10}(x + 1)$] prior to analysis to normalize the data and stabilize the variance. To avoid possible bias in estimates due to correlated errors in the striga counts repeatedly collected from the same experimental plots, a generalized least squares model was used to examine the effect of treatments and season (time) on log transformed striga counts. ANOVA was performed to examine the effects of treatments and seasons, and their interactions, on plant height, maize yield, and striga seed counts. Tukey’s honestly significant difference test was used to separate treatment means. Additionally, a two-way *t* test was used to assess overall differences between landrace and hybrid groups, and within-treatment effects on striga seed counts, at the beginning and end of the field experiment. All data analyses were conducted in R version 3.1.1 statistical software (R Development Core Team 2014), with significance level set at $\alpha = 0.05$ for all analyses.

Results and Discussion

Due to significant treatment by season interaction, data are presented by seasons. Striga emergence was reduced in landrace varieties compared to two hybrid varieties ($P < 0.0001$; Figure 1). Overall, striga counts were about four times higher with the hybrid maize varieties than with the landraces. Among the landraces, seasonal striga counts at peak emergence were not different among treatments, but ranged from 57 to 253. However,

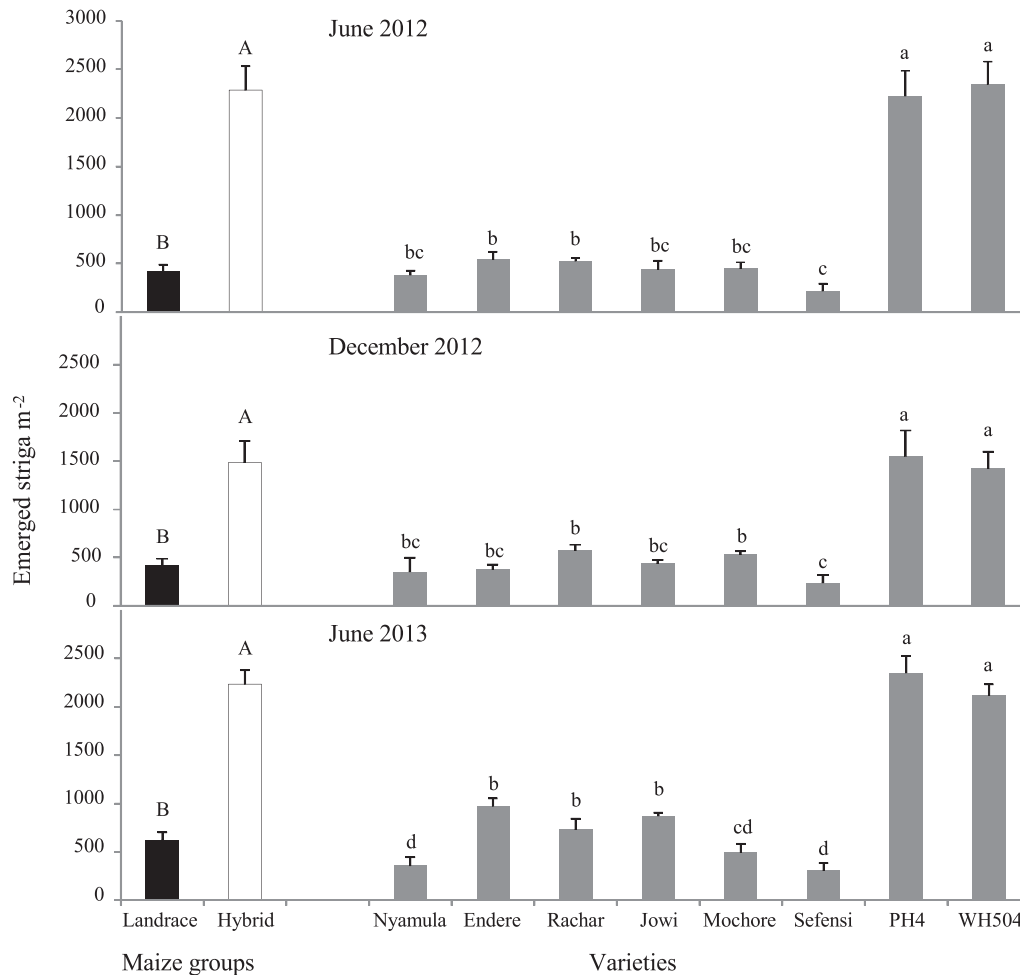


Figure 1. Striga emergence in response to different maize varieties during June 2012, December 2012, and June 2013 in western Kenya. Varieties with different lowercase letters were statistically different based on Tukey's honestly significant difference ($P < 0.05$), and maize groups (landrace and hybrid) with different capital letters were statistically different based on a t test ($P < 0.05$). Error bars represent SEM.

these counts ranged from 370 to 612 with the hybrids WH504 and PH4.

Results from the pot culture experiments showed that there were higher striga counts with hybrids than with landraces ($P < 0.0001$), except with Endere and Rachar (Figure 2). The reduced emergence of striga in soils planted with the landraces in the current study implies reduced germination of striga or reduced attachment of germinated striga to roots of the host plant, or both. Because striga is an obligate parasite, interactions between striga and its host plant plays a crucial role in survival of the parasite; if this interaction was disrupted, it may be a beneficial approach for integrated management of this parasite. Differences in production of striga germination stimulants are known to occur between crop cultivars (Hess et al.

1992), and may be the cause for reduced striga emergence in the landraces in the current study. This needs to be determined, in addition to testing more landraces and hybrids in different agroecosystems that may present challenges in terms of striga severity, biotypes, and virulence.

Across seasons harvest height was greater for landraces than for hybrid varieties ($P < 0.0001$; Figure 3). These heights, however, did not differ among the landraces, where they ranged between 123 cm and 153 cm. However, plant height of the two hybrid varieties was consistently below 100 cm.

All the landrace varieties had higher grain yields than the hybrid varieties ($P < 0.05$; Figure 4), except in 2013 when grain yields were not different between the hybrids and most of the landraces. Maize grain yields ranged between 1.7 t ha^{-1} and

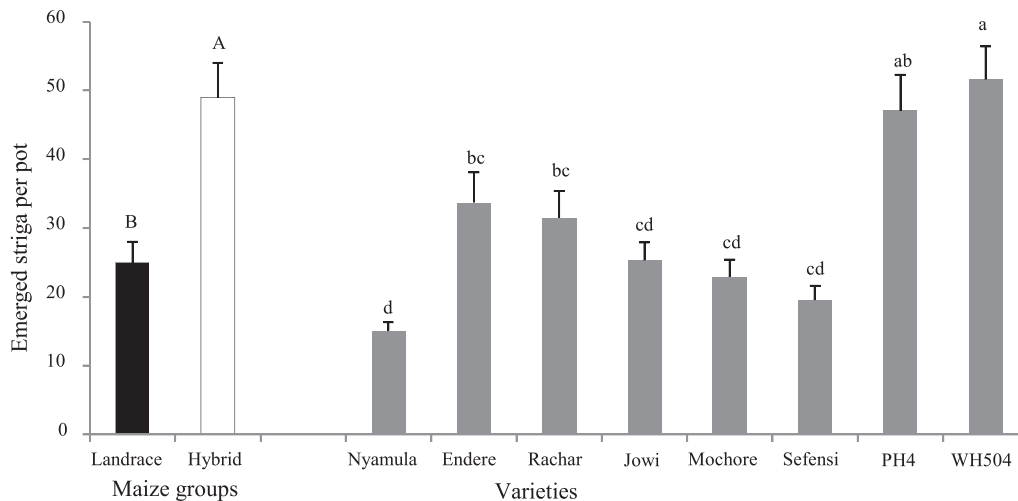


Figure 2. Striga emergence in response to different maize varieties in the pot culture experiment. Varieties with different lowercase letters were statistically different based on Tukey's honestly significant difference ($P < 0.05$), and maize groups (landrace and hybrid) with different capital letters were statistically different based on a t test ($P < 0.05$). Error bars represent SEM.

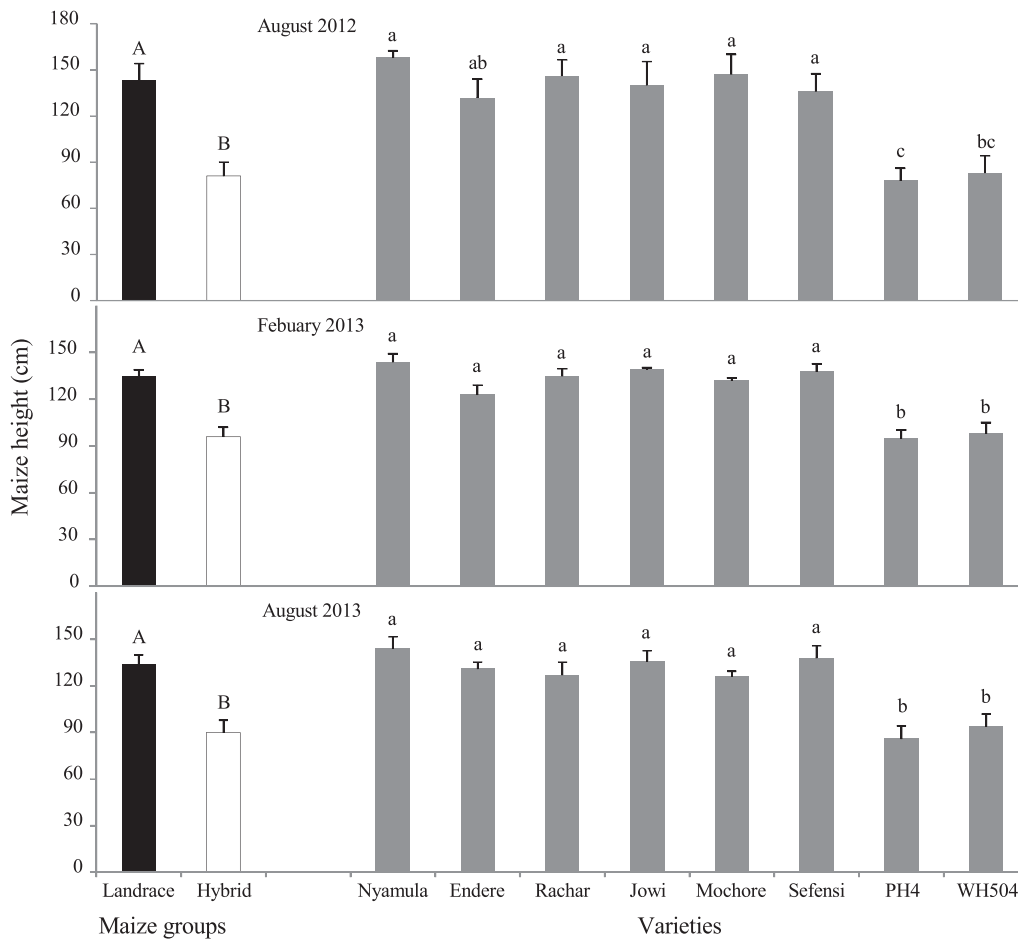


Figure 3. Plant height of different maize varieties at harvest in August 2012, February 2012, and August 2013 in western Kenya. Varieties with different lowercase letters were statistically different based on Tukey's honestly significant difference ($P < 0.05$), and maize groups (landrace and hybrid) with different capital letters were statistically different based on a t test ($P < 0.05$). Error bars represent SEM.

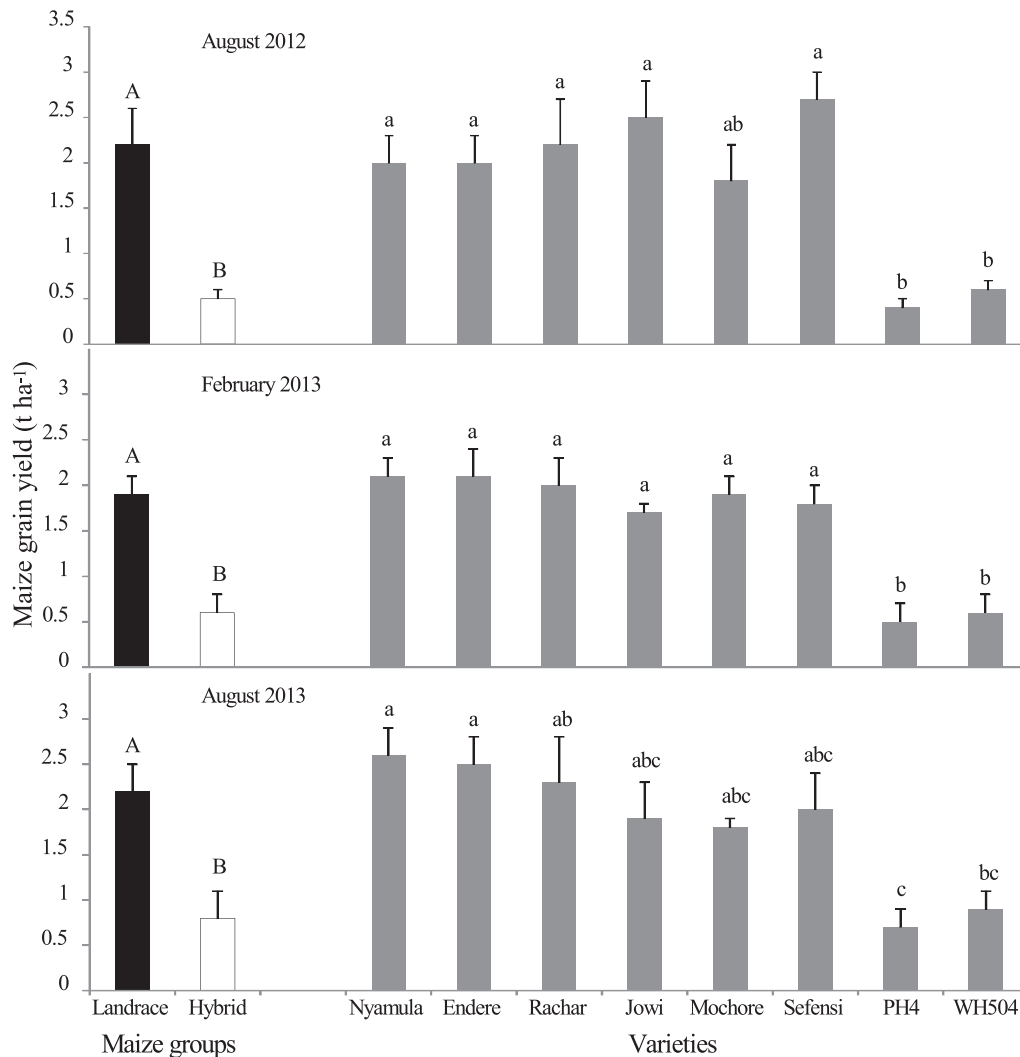


Figure 4. Grain yields of different maize varieties at harvest in August 2012, February 2012, and August 2013 in western Kenya. Varieties with different lowercase letters were statistically different based on Tukey's honestly significant difference ($P < 0.05$), and maize groups (landrace and hybrid) with different capital letters were statistically different based on a t test ($P < 0.05$). Error bars represent SEM.

Table 1. Change of striga seed bank density (mean \pm SEM) from the beginning (March 2012) to the end of the experiment (August 2013). Striga seed bank density increased in plots planted with PH4, WH504, Rachar, and Endere ($P < 0.05$).

Variety	March 2012	August 2013	P value
Nyamula	44.7 \pm 23.9	148.7 \pm 115.8	0.50
Endere	19.0 \pm 6.5	84.5 \pm 15.2	0.01
Rachar	13.0 \pm 7.5	81.2 \pm 7.1	0.01
Jowi	42.2 \pm 18.1	130.7 \pm 46.7	0.11
Mochore	41.2 \pm 33.6	93.7 \pm 20.5	0.07
Sefensi	32.7 \pm 22.1	70.5 \pm 34.3	0.23
PH4	30.0 \pm 19.9	202 \pm 49.5	0.01
WH504	21.0 \pm 7.3	147.2 \pm 55.7	0.01

2.7 t ha⁻¹ with the landraces, and consistently averaged below 1 t ha⁻¹ with the hybrid varieties, ranging between 0.4 t ha⁻¹ and 0.9 t ha⁻¹. Previous studies have shown that when striga is controlled, these hybrids yield about 4t ha⁻¹ and grow to about 180 cm tall (Khan et al. 2008a). Results of the current study thus indicate that an increase in striga emergence, reduction in maize plant height, and reduction in yield occurred with the hybrid varieties compared to the landrace varieties.

After three continuous cropping seasons, an increase in the striga seedbank densities occurred when PH4, WH504, Rachar, or Endere were planted ($P = 0.01$, t test) (Table 1). Striga

emergence is dependent upon seedbank and soil health. Analysis of striga seedbank in the study site indicated that the number of striga seeds did not differ between treatments at the beginning of the field experiment. An effective management approach for striga should aim, among other things, to reduce and eventually deplete the soil seedbank. The increase in seedbank density when planted to hybrid varieties and the landraces Rachar or Endere might have been influenced by the higher number of emerged striga in these treatments. An effective and sustainable management program for depleting the striga seedbank, such as use of *Desmodium* spp. (Khan et al. 2008b), is thus an important component of an integrated management approach for the parasite.

It is noteworthy that while improved maize varieties possess desirable traits for higher productivity, they seem to lack useful traits that are innate in the landraces, such as local adaptation to constraints such as striga. Furthermore, artificial selection of crop plants for increased yield and quality has been shown to negatively influence resistance to pathogens and pests in a number of crops, including maize (Chen et al. 2015; Tamiru et al. 2011). Results of the present study suggest that farmers select landraces for their adaptability, especially in striga-infested areas. Additionally, the landraces are easy to multiply and therefore affordable and readily available (Aquino et al. 2001).

In conclusion, the current study showed reduced striga emergence under landraces relative to hybrids. Therefore, these varieties could play an important role in integrated management programs for striga in smallholder systems in the region. Generally, maize landraces represent a large gene pool for crop improvement, but despite the potential for local adaptations there are few instances where local African varieties have been used in the development of modern varieties for African markets. There is an accumulating body of evidence showing existence of innate defenses in these varieties against some of the biotic constraints affecting maize production in smallholder cropping systems in the continent. It is therefore necessary to conserve the varieties that are adaptable to the local conditions for use in maize breeding programs. Additionally, it is important to consider participation of farmers in the research and product development, in order to harness the value of farmers' local knowledge, interests, and goals

(Bellon 2001). Further studies are necessary to elucidate defense mechanism (or mechanisms) employed by the landraces responsible for reduced striga infestation to allow for exploitation of the mechanism in an integrated management approach for the noxious weed in smallholder cereal farming systems in striga-endemic areas of western Kenya and beyond.

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