

Striga (*Striga Hermonthica* (Del.) Benth) Tolerance in Maseno EH11 and EH14 Hybrid Maize Varieties

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Abstract

Striga (*Striga hermonthica* (Del.) Benth) is an obligate root hemi-parasitic weed parasitizing maize (*Zea mays* L.) and other grasses causing significant losses. Two newly released hybrid maize varieties Maseno EH11 and EH14 have been bred for tolerance to Striga but their extent and mechanism of tolerance have not been elucidated. Field experiments were carried out in Western Kenya at Kibos, Nyahera and Maseno for two seasons under natural Striga infestation to determine their level of tolerance to Striga alongside a Striga susceptible PHB3253 variety and two local checks, H513 and H516. The new maize varieties were later grown in rhizotrons where the roots were infected with pre-germinated Striga seeds and histological studies carried out to determine the extent of Striga attachment at 9 days after infection. The field data included days to Striga emergence, Striga incidence and crop growth and yield. The number, length and biomass of attached Striga in the rhizotrons were determined. Data was subjected to ANOVA through the general linear model of SAS and means separated using LSD_{0.05}. Maseno EH14 took the longest time for Striga to emerge in the field, exhibited few Striga attachments across the seasons and had the highest 100-grain weight. Maseno EH14 also exhibited few and shorter Striga attachments in the rhizotrons. Histological analysis showed that most Striga haustoria were unable to penetrate the endodermis of Maseno EH14 while PHB3253 and Maseno EH11 had successful parasite-host xylem to xylem vascular connections although EH11 had few cases of tolerance response similar to EH14. From these findings, Maseno EH14 has Striga tolerance which could be attributed to mechanical processes occurring at the cell wall thus becoming a good source of genetic material for the development of sustainable management of Striga and could provide genes leading to development of maize varieties with host-based resistance.

Key words: *Maize, Striga, tolerance and infestation*

Introduction

Purple witchweed (*Striga hermonthica* (Del.) Benth) is an obligate root hemi-parasitic plant that attacks several cereal grains in the poaceae family especially maize (*Zea mays* L.) and sorghum (*Sorghum bicolor* (L.) Moench) and other native and exotic grasses throughout Africa (Berner *et al.*, 1995). It causes yield losses ranging from 20 – 80% although this could go up to 100% in susceptible cultivars under high levels of infestation (Teka, 2014). This translates to more than US \$ 7 billion annually affecting the livelihoods of more than 300 million people living in sub-Saharan Africa (Ejeta, 2007).

Maize (*Zea mays* L.) is an important cereal grain providing nearly half of human calorific requirements. It therefore has a big potential in terms of its large utilization as a food and animal feed source (Farnia and Mansouri, 2015). In Kenya, maize is the main staple food with the consumption estimated at 98 kg per person per year translating to 30 – 40 million bags per year, and accounts for 36% of all calories consumed (Nyoro *et al.*, 2004). It therefore forms an important component of household food security within the Kenyan farm families and any threat to maize is a serious threat to food security. Maize yields in Western Kenya average 2.5 t ha⁻¹ (Davenport *et al.*, 2018) against the world's average yield of 5.5 t ha⁻¹ (Adnan *et al.*, 2017). The low yields is majorly attributed to the parasitic *Striga* weed amongst other factors like declining soil fertility (Odeno *et al.*, 2001). Maize is exceptionally susceptible to *Striga* infestations, especially in marginal areas characterized by sub-optimal soil nitrogen conditions (Menkir *et al.*, 2012, Ejeta, 2007). The infestation level is more severe in areas with poor soil fertility, low rainfall, and lack of fertilizer use (Sauerborn *et al.*, 2003).

The management of *Striga* has become quite challenging owing to its production of large amounts of tiny seeds that persist in the soil for long periods (Yoneyama *et al.*, 2010, Rich and Ejeta, 2008 and Westerman *et al.*, 2018). This therefore calls for a combination of several management options in an integrated approach. The use of improved crop varieties with resistance to *Striga* is a feasible option, especially for the resource-poor farmers (Rich and Ejeta 2008). Kamara *et al.* 2020 also observed that the use of *Striga*-resistant maize varieties combined with the application of nitrogen fertilizer and rotation with soybean could increase the productivity of maize in *Striga* infested fields. This study was carried out to determine the relative performance in *Striga* tolerance and *Striga* tolerance mechanisms of Maseno EH14 which has been bred for *Striga* tolerance and Maseno EH11 which has been bred for tolerance to foliar diseases including maize streak virus, grey leaf spot and turicum leaf blight (Kephis 2020) but has related parents to Maseno EH14. The evaluation was done alongside PHB3253 which is a *Striga* susceptible maize variety (Yoneyama *et al.*, 2015) from Pioneer Hybrid Company (Kephis 2020), and two locally grown hybrid maize varieties from Kenya Seed Company namely H513 and H516 as the check varieties. This study was carried out in the field under natural *Striga* infestation and a non-infested field.

Materials and Methods

Field Experiments

Field trials were conducted in the short rains of 2020 (SR2020) and long rains of 2021 (LR2021) at two *Striga*-infested fields at KESREF – Kibos (-0.03861°S, 34.81596°E) and a farmer's field in Nyahera (0°35.977'N, 34°53.452'E) and a *Striga* free field at Maseno University (0°00'08S, 34°35'47E), all within Kisumu County of Kenya. The seeds of Maseno EH11 and EH14 hybrid maize varieties were obtained from Maseno University seed unit while the seeds of the check varieties (H513, H516, and PHB3253) were obtained from the local seed stockists. The experiments therefore consisted of the five maize varieties and the treatments were arranged in a Randomized Complete Block Design (RCBD) with three replications. Soil samples were collected from every experimental unit to characterize the initial *Striga* seed bank.

The maize seeds were sown at a spacing of 75cm×25cm with two seeds per hole and later thinned to one plant per hill giving four rows of maize plants each 4m in length. Tripple supper phosphate was applied during planting at the rate of 60 kg P₂O₅ ha⁻¹ and topdressed at 6th week after planting with Calcium Ammonium Nitrate at the rate of 60 kg N ha⁻¹. Weeding was done three weeks after

planting but before *Striga* emergence by hand hoeing and thereafter hand pulling was done to remove other weeds to facilitate observation of emerged *Striga* plants. Data was collected from the net plot area of 6 m² which consisted of two middle maize rows. The parameters observed included days to first *Striga* emergence which was recorded as the number of days from crop emergence to the date of the first observed emerged *Striga* in the respective experimental plots determined by observing a small whitish protrusion above the ground. *Striga* incidence was recorded at 8, 10 and 12 weeks after crop emergence (WAE) by counting the number of emerged *Striga* plants from the net plot area which were then expressed as plants m⁻¹. The data was log-transformed due to the high variability in numbers as a result of the differences between experimental units and the locations to normalize the variability. Maize growth and yield parameters included plant height which was recorded once as the distance from the base of the plant to the point of the first tassel branch. Days to tasseling were taken as the number of days from crop emergence to the date when 50% of the plants in the net plot had started tasseling. Maize grain yield was determined by shelling the grains from the dried cobs and getting the total grain weight using an electronic weighing balance and the moisture content was determined using a moisture meter. The yield was then adjusted to 12.5% moisture content and then converted to t ha⁻¹. The 100-seed weight was determined by randomly selecting 100 seeds from the dried shelled grains and weighing using an electronic weighing balance. The data collected was subjected to analysis of variance (ANOVA) using the General Linear Model procedure of Statistical Analysis Software (SAS v. 9.1, SAS Institute, Cary, NC, USA) to test if there were significant differences between the treatment means. The means were separated using the Least Significant Difference (LSD) method at 5% probability level. Correlation analysis was done to compare the relationships between the *Striga* parameters and the maize growth and yield components.

Rhizotron Studies

Maseno EH11, Maseno EH14, and the most *Striga* susceptible maize variety (PHB3253) from the field results were screened for post-attachment *Striga* response. The *Striga hermonthica* seeds collected in 2020 from maize growing fields in Kibos Kenya (-0.03861°S, 34.81596°E) were used for the study. The maize seeds were first germinated in 10 cm by 10 cm by 10 cm pots filled with vermiculite. At 7 days after planting, the maize seedlings were transferred to root observation chambers called rhizotrons (25 cm by 25 cm by 5 cm Perspex plates) as described by Mbuvi *et al.* (2017). The rhizotron chambers were lined with 25 cm by 5 cm by 5 cm foam strips at the bottom to absorb excess water and packed with vermiculite. A 50-micron thick mesh was then placed on top, the germinated maize seedlings were placed on the mesh, the chamber closed, and then wrapped with aluminum foil. The maize plants were then maintained in the glasshouse at 60% relative humidity and a 12-hour photoperiod. The day and night temperatures were set at 28°C and 24°C respectively. During growth on the rhizotrons, the plants were drip-irrigated with 25 ml of 40% Long Ashton nutrient solution. After 10 days on the rhizotrons, the maize seedlings with well developed roots were infected with 25 mg of pre-germinated *Striga hermonthica* seeds per plant by aligning the *Striga* seeds along the maize roots with a soft paint brush. Five plants per maize variety were screened in a Completely Randomized Design with three replications.

The rhizotrons containing the infected maize roots were screened at 9 and 21 days after infection (DAI). At 9 DAI, the *Striga* seedlings attached on the maize roots were observed and documented using a Leica MZ7F stereomicroscope fitted with a DFC320FX camera (Leico, Germany). At 21 DAI, all the *Striga* plants attached to the maize roots were harvested, placed on 90-mm petri plates, and photographed to be screened for post-attachment response and to establish the effects of the

host plants on the parasite development. The number and length of the *Striga* seedlings parasitizing each host plant were determined from the photographs using the image analysis software ImageJ, v. 1.45 (<http://rsb.info.nih.gov/ij/>) according to Mbuvi *et al.* (2017). The *Striga* seedlings were then harvested, oven-dried at 45°C for seven days and weighed according to Mutinda *et al.* (2018) to determine the total *Striga* biomass attached on the maize roots. The data collected on *Striga* numbers, length, and total biomass was subjected to analysis of variance (ANOVA) using the General Linear Model procedure of Statistical Analysis Software (SAS v. 9.1, SAS Institute, Cary, NC, USA). The means were separated using the Least Significant Difference (LSD) method at 5% probability level and presented as box plots generated in R software.

Histological Analysis

Root tissue at the point of the *Striga* haustoria attachment was dissected from the host plants at 9 DAI to determine the extent of parasite development within the host root cortex through sectioning. Five rhizotrons were sampled for each maize variety from which 3 attachments were collected from each rhizotron giving 15 samples for every variety. The tissues were fixed using Carnoy's fixative (4:1, ethanol:acetic acid) then dehydrated twice in 100% ethanol for 30 minutes before pre-infiltration in ethanol-Technovit solution (1:1) for 2 hours then in 100% Technovit solution for another 1 hour. The tissues were then incubated in fresh Technovit solution for 3 days at 4°C. For purposes of embedding, the samples were placed in Eppendorf lid molds containing Technovit-Hardener (1:15) and left to set. The embedded tissues were then mounted on wooden blocks using the Technovit 3040 kit according to the manufacturer's instructions. 5-micron thick sections were obtained using a Leica RM 2145 microtome (Leica, Germany) which were then transferred to microscope slides. They were stained using 0.1% toluidine blue O in 100 mM phosphate buffer at pH 7 for 2 minutes then washed in distilled water and dried at 65°C for 30 minutes on a hot plate. The sections were then mounted on glass slides and covered with slips using DePex (BDH, Poole, UK) before being observed and photographed using a Leica DM500 microscope mounted with a Leica ICC50 camera (Leica, Germany).

Results

The initial count of the *Striga* seed bank which was done before field evaluation across all the locations did not show any significant differences with respect to the maize varieties assigned to each experimental unit. The growing seasons did not have a significant effect on the days to *Striga* emergence (Table i). However, the locations significantly affected the days to *Striga* emergence ($P \leq 0.0001$) with Nyahera taking 42.9 days from crop emergence to *Striga* emergence while Kibos took 62.3 days. There was no *Striga* observed in the *Striga* free field. The maize varieties also significantly affected the duration of *Striga* emergence ($P \leq 0.01$) with the *Striga* susceptible maize variety, PHB3253 taking 47 days from crop emergence to the first observed *Striga* while the *Striga* tolerant maize variety, Maseno EH14 took 61.3 days (Table ii). Maseno EH11 did not differ significantly from Maseno EH14 and the local check varieties H513 and H516. The two local check varieties did not differ significantly from the *Striga* susceptible maize variety PHB3253.

The *Striga* counts were done at Kibos and Nyahera locations for the two seasons and the cumulative count per square metre was then computed by adding the counts of the three stages. The locations significantly affected the *Striga* incidence ($P \leq 0.0001$) right from 8 WAE to 12 WAE. The effect was also observed in the cumulative *Striga* count as shown in Table i. Nyahera had significantly higher *Striga* counts than Kibos from 8 WAE to 12 WAE with a cumulative count (CUMC) of 66.1 plants m^{-2} compared to 6.8 plants m^{-2} at Kibos (Fig. 1). Maize varieties

significantly influenced the *Striga* counts ($P \leq 0.0001$) from 8 WAE all through to 12 WAE (Table iii). The *Striga* susceptible maize variety PHB3253 had 12.8 *Striga* plants m^{-2} at 8 WAE which was not different from the local check varieties H513 and H516. Similarly, Maseno EH14 had 0.43 *Striga* plants m^{-2} which also did not differ significantly from the Maseno EH11 variety. The same trend was maintained all through to 12 WAE with the *Striga* susceptible maize variety PHB3253 having significantly higher *Striga* counts while Maseno EH14 and Maseno EH11 had significantly lower *Striga* counts (Table iii). The interaction of location and maize varieties significantly ($P \leq 0.0001$) affected the *Striga* counts in all three stages of counting as shown in Figure 2. While the *Striga* tolerant maize variety, Maseno EH14 and Maseno EH11 did not have significant differences in *Striga* counts at the two *Striga* infested locations, the *Striga* susceptible maize variety PHB3253 and the two local check varieties H513 and H516 had significantly higher counts in Nyahera than in Kibos.

The maize growth and yield parameters were evaluated across the seasons for both the *Striga* infested locations and the non-infested site (Maseno University research field). The effect of the locations was highly significant ($P \leq 0.0001$) on all the four parameters: plant height, days to tasseling, maize yield, and 100 seed weight (Table iv). The maize plants at Maseno took significantly higher number of days to tasseling at 66.7 days while Kibos took the lowest number of days to tasseling at 60.6 days (Table v). In terms of plant height, Kibos had the tallest plants at 225.95 cm although this did not significantly differ from the maize plants at Maseno. However, Nyahera had significantly shorter plants at 150.97 cm. Maseno which was the *Striga*-free location had significantly higher maize yields at 3.72 $t\ ha^{-1}$ although this did not significantly differ from the maize yield at Kibos. However, Nyahera had significantly lower maize yields at 2 $t\ ha^{-1}$. The highest significant grain weight in terms of 100 seed weight was 26.62 g at Kibos and the lowest was 19.37 g at Nyahera. The effect of maize varieties on the number of days from crop emergence to tasseling was highly significant ($P \leq 0.0001$) with the *Striga* tolerant maize variety, Maseno EH14 taking the highest number of days to tasseling across all the locations at 65.8 days while the local check varieties H516 and H513 took significantly shorter days to tasseling at 61.9 and 61 days respectively. There was however no significant difference between the *Striga* susceptible maize variety PHB3253 and the disease tolerant maize variety Maseno EH11 on their effect on the number of days to tasseling as shown in Table (vi).

Maize varieties also significantly affected the plant height ($P \leq 0.025$). Maseno EH14 and Maseno EH11 were taller plants at 207.56 cm and 207.89 cm, respectively however, their heights did not differ from the two local checks. The *Striga* susceptible maize variety PHB3253 was shorter among the rest at 185.17 cm although it also did not significantly differ from H516 and H513 (Table vi). The overall maize yield across the locations was not affected by the maize varieties but the yield trend per location was visibly different at Nyahera which had higher *Striga* counts (Fig 3). Maize varieties however, had significant effects ($P \leq 0.01$) on the 100 seed weight with the *Striga* tolerant maize variety Maseno EH14 having a significantly higher seed weight of 24.81 g although this did not significantly differ from Maseno EH11 and the local check variety H513. The *Striga* susceptible maize variety PHB3253 had a significantly lower seed weight across the locations at 21.39 g.

Correlation Analysis

The Pearson's correlation analysis revealed significant negative correlations between plant height and *Striga* count at 8 WAE ($r = -0.778^{**}$), *Striga* count at 10 WAE ($r = -0.7782^{**}$), *Striga* count

at 12 WAE ($r = -0.781^{**}$) and the cumulative *Striga* count ($r = -0.781^{**}$). There were also significant negative correlations between days to *Striga* emergence and *Striga* count at 8 WAE ($r = -0.8371^{**}$), *Striga* count at 10 WAE ($r = -0.8395^{**}$), *Striga* count at 12 WAE ($r = -0.8427^{**}$) and the cumulative *Striga* count ($r = -0.8429^{**}$). The other significant negative correlations included *Striga* count at 8 WAE and the total grain weight ($r = -0.7501^{**}$), *Striga* count at 8 WAE and 100 seed weight ($r = -0.7309^{*}$), *Striga* count at 10 WAE and total grain weight ($r = -0.7584^{**}$), *Striga* count at 10 WAE and 100 seed weight ($r = -0.7479^{**}$), *Striga* count at 12 WAE and grain weight ($r = -0.7444^{**}$), *Striga* count at 12 WAE and 100 seed weight ($r = -0.7478^{**}$), cumulative *Striga* count and grain weight ($r = -0.7526^{**}$) and cumulative *Striga* count and 100 seed weight ($r = -0.7466^{**}$) as shown in Table vii below. The notable significant positive correlations included days to *Striga* emergence and plant height ($r = 0.9334^{***}$), days to *Striga* emergence and total grain weight ($r = 0.8422^{**}$), days to *Striga* emergence and 100 seed weight ($r = 0.8793^{**}$), plant height and total grain weight ($r = 0.8612^{**}$), plant height and 100 seed weight ($r = 0.9533^{**}$) and finally the total grain weight and 100 seed weight ($r = 0.8941^{***}$)

Post-Attachment Response

Three main parameters used to determine the post-attachment response of the maize hybrids to *Striga* parasitism were the number of attached *Striga*, *Striga* length and the biomass of *Striga* attachments. Mutinda *et al.*, 2018 observed that *Striga* resistance is measured by the number of successful parasites infecting a host in the root observation chambers – rhizotrons where resistance response was characterized by fewer, smaller, and less biomass relative to a susceptible host. Our results indicated that Maseno EH14 suffered notably low infestation compared to EH11 and PHB3253 (Fig. 4). There were statistical differences ($P \leq 0.005$) in the number of *Striga* attachments with the susceptible variety PHB3253 having the highest mean number of attachments (55.3 ± 0.75) although this did not differ from Maseno EH11 (Fig. 5). Similarly, the length of the attached *Striga* seedlings in PHB3253 were longer (5.47 ± 0.04 mm) than those attached to Maseno EH14 (3.28 ± 0.22 mm) (Fig.6). The biomass of the attached *Striga* seedlings also showed significant differences ($P \leq 0.0001$) where PHB3253 had the highest *Striga* biomass (18.37 ± 0.32 mg), followed by EH11 (15.94 ± 0.62 mg) and a lower biomass for Maseno EH14 (5.18 ± 0.74 mg) (Fig. 7)

Discussion

Different maize varieties exhibit varied responses to *Striga* parasitism which is reflected in their growth and yield performances. Maseno EH14 and Maseno EH11 hybrid maize varieties both exhibited delayed emergence of *Striga* in the field with a significant difference of about two weeks from that of the *Striga* susceptible variety PHB3253 (Table ii). This could have been necessitated by resistance of the host's roots to *Striga* haustorial penetration leading to slow establishment of successful parasite-host relationship. Van Ast *et al.*, 2000 observed that slight differences in the disturbance of plant growth in the initial phases by parasite attachment have a large influence on the final level of yield reduction. After successful attachment, the developing *Striga* plants grow underground for 4 – 7 weeks prior to emergence (Berner *et al.* 1995) translating into 28 - 49 days. This therefore means that the susceptible variety PHB3253 with a mean days to *Striga* emergence of 47 had an immediate *Striga* attachment after maize seed germination. This therefore means that early attachment of *Striga* has a greater effect on the growth of its host compared to late attachments. This was further supported by the Pearson's correlation analysis which indicated a significant strong positive relationship between days to *Striga* emergence and maize yield and 100 seed weight (Table vii). Early or late *Striga* attachments translate to early or late *Striga* emergence

respectively. The early *Striga* emergence therefore impose a serious disturbance on the host's dry matter partitioning subsequently leading to a reduction in the maize yield.

The *Striga* counts exhibited locational differences with Nyahera having higher *Striga* counts than Kibos (Figure 1). However, the differences were only observed on the susceptible check varieties while Maseno EH11 and EH14 did not exhibit differences in *Striga* counts (Figure 2). This shows that these two maize varieties were able to outmaneuver *Striga* parasitism despite the level of infestation. This was reflected in the maize yield differences in the three locations (Figure 3). Both Maseno EH14 and EH11 exhibited significantly low *Striga* counts compared to the three check varieties (Table 3). This further implies that the apparent difficulty of the haustoria to penetrate the host's cell layers led to low *Striga* incidence in EH14 and EH11 maize varieties compared to the susceptible PHB3253 and the other two check varieties. The many *Striga* plants attached to the susceptible varieties at an early stage of their life cycle siphon water and nutrients from the hosts leading to exposure to nutrient stress. Exposing the host plants to nutrient stress leads to a decrease in growth rate and change in biomass partitioning and nutrient distribution as observed by Sun *et al.*, 2011. This explains the strong negative correlations between the *Striga* counts (8 WAE, 10 WAE, 12 WAE, CUMC) and the maize yield and 100 seed weight (Table vii).

The results from the rhizotron studies indicate that Maseno EH14 exhibits a post-attachment *Striga* resistance mechanism which is comparable to the observations of Mutinda *et al.*, 2018 with KSTP 94 maize variety. The few parasite seedlings indicate that the parasite is not able to effectively breach the host cell layers namely the epidermis, cortex, pericycle and endodermis to enable it form vascular connections to extract water and nutrients from the host. Small (short) parasite seedlings observed on Maseno EH14 (Fig. 6) indicate that even after successful penetration, the parasite is unable to effectively extract nutrients from the resistant host. This was further elucidated by histological analysis of the *Striga*-host interactions at the point of attachment at 9 days after infection to show the cells at the host-parasite interphase as indicated in Fig. 8. The results show that *Striga* was unable to effectively colonize the Maseno EH14 hybrid maize. Close-up microscopic images reveal that although the parasite had successfully attached on the host root, further advancement and penetration into the host was blocked (Figure 8Ai). A histological analysis of the transverse section at the parasite-host junction showed that parasite penetration was blocked at the endodermis. Rather than penetrate the cortex to make vascular connections with the host, the parasite infectious organ circled the endodermis and exited (Figure 8Aii). This resistance mechanism was observed in seven out of 10 sections made. A similar observation was made in Maseno EH11 (Figure 8Bi and Bii), albeit less frequently (2 out of 10). But in contrast, in PHB3253, *Striga* successfully invaded the host roots. A close-up image of *Striga* infecting PHB3253 show a well-developed haustorium that has advanced to reach the host's stele where xylem vessels are located. The parasite is also well developed and vegetative – a sign of good nourishment from the host (Figure 8Ci). A closer look at the parasite-host junction histologically reveals that the parasite in most cases, successfully penetrated the host cortex into the endodermis to form parasite-host xylem to xylem connections resulting into a successful parasite-host attachment (Figure 8Cii)

These results are in agreement with Mutinda *et al.* 2018 where *Striga* seedlings only managed to penetrate the host's tissues of an open pollinated maize variety KSTP 94 up to the cortex and did not go beyond the endodermis thereby failing to establish parasite-host xylem to xylem connections. Several possibilities can be advanced to explain this inability of the parasite to

effectively infect the host as described by Yoshida *et al.*, 2009 where three layers of host resistance occurring at the epidermis, cortex and endodermis are documented. The mechanism is attributed to cell wall thickening including lignification, secondary metabolites and programmed cell death at the interphase of the host and parasite. Amusan *et al.* 2008 also attributes the failure by the haustorium to penetrate the endodermis layer to other physiological and/or biochemical defense responses and a tough mechanical sclerenchyma tissue which might have acted as a barrier to haustorial penetration as observed in a maize inbred line ZD05. In many cases, this is the action of reinforcement of the cell wall by various processes such as carbohydrates, callose, xylan and secondary metabolites such as lignin. These results affirm the finding that Maseno EH14 exhibits some kind of resistance response against *Striga* parasitism. This is reminiscent of cell wall fortification as the most dominant mode of action for stopping invasion of the parasite as described by Mallu *et al.* 2021. The same can be said about Maseno EH11, although such response is weaker compared to Maseno EH14.

Conclusion

This study has shown that Maseno EH14 hybrid maize variety exhibits *Striga* tolerance which is attributable to post-attachment *Striga* limitation on haustorium growth and establishment. The mechanism could be linked to mechanical and/or chemical processes in the cortex thus becoming a good source of genetic material for the development of sustainable management of *Striga* and could provide genes leading to development of maize varieties with host-based resistance.

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Tables and Figures

Table i: Mean Squares of *Striga* Emergence and Counts for the Maize Varieties

Source of Variation	Df	DTSE	C8WAE	C10WAE	C12WAE	CUMC
Location	1	5626.02***	2532.66***	6980.05***	9155.06***	52696.36***
Season	1	212.82	16.54	112.53	191.35	812.54
Replication	2	94.62	39.17	145.34	207.27*	999.22*
Variety	4	453.78**	400.99***	1321.06***	1833.39***	9812.08***
Location x Variety	4	123.23	315.32***	912.12***	1070.19***	6482.64***
Season x Variety	4	335.19*	15.87	45.1	30.17	235.51
Location x Season	1	170.02	31.08	130.45	215.95	1004.5
Location x Season x Variety	4	68.14	18.19	50.36	32.73	274.97

*P≤0.05, **P≤0.01, ***P≤0.001, Df-Degree of freedom, DTSE-Days to *Striga* Emergence from crop emergence, C8WAE-*Striga* count at 8 Weeks after Crop Emergence (WAE), C10WAE-*Striga* count at 10 WAE, C12WAE-*Striga* count at 12 WAE and CUMC-Cumulative *Striga* Count

Table ii: Effect of Maize varieties on the Days to *Striga* Emergence

Maize Variety	Mean Days to <i>Striga</i> Emergence
EH14	61.3a
EH11	56.8ab
H516	50.2bc
H513	47.9bc
PHB3253	47.0c
Mean	52.62
C.V (%)	21.37
LSD _{0.05}	9.29

Means followed by the same letter are not significantly different using Fisher's Least Significant Difference (LSD) test at P<0.05, C.V-Coefficient of Variation

Table iii: Mean *Striga* counts for the Maize varieties in the *Striga* infested locations across the seasons

Variety	8 WAE	10 WAE	12 WAE	Cumulative Count
Plants (Log ₁₀ X+001)				
PHB3253	12.78(2.04)a	24.45(2.72)a	29.67(3.03)a	66.89(3.71)a
H513	11.11(1.89)a	17.96(2.5)b	22.15(2.71)b	51.22(3.43)b
H516	10.44(1.77)a	19.24(2.29)ab	22.72(2.60)b	52.40(3.23)b
EH11	1.64(0.71)b	2.71(1.03)c	3.40(1.20)c	7.75(1.68)c
EH14	0.43(0.27)b	1.17(0.65)c	2.48(1.04)c	4.08(1.33)c
Mean	7.28(1.34)	13.1(1.84)	16.09(2.12)	36.47(2.68)
C.V (%)	59.54(21.35)	52.84(18.68)	44.37(16.36)	46.85(15.76)
LSD _{0.05}	3.58(0.24)	5.72(0.28)	5.89(0.29)	14.12(0.35)

Means followed by the same letter in a column are not significantly different using Fisher's Least Significant Difference (LSD) test at P<0.05, C.V-Coefficient of Variation, WAE-Weeks after crop Emergence

Table iv: Mean Squares of plant growth aspects for the maize varieties evaluated under natural *Striga* infestation

Source of Variation	Df	DTF	PHT	YIELD	SEEDWT
Location	3	295.54***	51950.01***	24.13***	417.38***
Season	1	9.34	7191.34***	2.51	1695.46***
Replication	2	1.91	271.56	2.63	34.91*
Variety	4	65.07***	1671.68*	0.73	40.70**
Location x Variety	8	17.53***	263.98	1.57	10.17
Season x Variety	4	3.09	414.52	1.59	9.53
Location x Season	2	86.54***	303.62	24.95**	169.03**
Location x Season x Variety	8	4.91	699.98	1.66	8.47

*P≤0.05, **P≤0.01, ***P≤0.001, Df-Degree of freedom, DTF-Days to tasseling, PHT-Plant height, YIELD - Grain yield in t ha⁻¹ and SEEDWT-100 Seed weight

Table v: Effect of Location on Days to tasseling, plant height, yield and 100 seed weight

Location	Days to Tasseling	Plant height (cm)	Yield (t/ha)	100 Seed weight (g)
Maseno	66.7a	219.73a	3.72a	24.47b
Nyahera	62.3b	150.97b	2.00b	19.37c
Kibos	60.6c	225.95a	3.31a	26.62a
Mean	63.2	198.88	3.01	23.49
C.V (%)	3.1	11.8	35.2	14.3
LSD _{0.05}	1.02	12.15	0.55	1.73

Means followed by the same letter in a column are not significantly different using Fisher's Least Significant Difference (LSD) test at P<0.05, C.V-Coefficient of Variation

Table vi: Effect of maize varieties on Days to tasseling, plant height and 100 seed weight across the three locations

Variety	Days to Tasseling	Plant height (cm)	100 Seed weight (g)
EH14	65.8a	207.56a	24.81a
EH11	64.2b	207.89a	24.29ab
PHB3253	62.9bc	185.17b	21.39c
H516	61.9cd	200.0ab	22.42bc
H513	61d	193.81ab	24.53ab
Mean	63.2	198.88	23.49
C.V (%)	3.1	11.8	14.3
LSD _{0.05}	1.3	15.69	1.42

Means followed by the same letter in the column are not significantly different using Fisher's Least Significant Difference (LSD) test at $P < 0.05$, C.V-Coefficient of Variation

Table vii: Pearson Correlation coefficients for the Striga and Crop Parameters of the Maize Varieties

Parameters	PHT	DTSE	C8WAE	C10WAE	C12WAE	CUMC	YIELD	SEEDWT
DTF	-0.2287	0.095	-0.1119	-0.1023	-0.0981	-0.1031	-0.0677	-0.1825
PHT		0.9334***	-0.778**	-0.7782**	-0.781**	-0.781**	0.8612**	0.9533**
DTSE			-0.8371**	-0.8395**	-0.8427**	-0.8429**	0.8422**	0.8793**
C8WAE				0.9934***	0.9937***	0.996***	-0.7501**	-0.7309*
C10WAE					0.9987***	0.9993***	-0.7584**	-0.7479**
C12WAE						0.9995***	-0.7444**	-0.7478**
CUMC							-0.7526**	-0.7466**
YIELD								0.8941***

* $P \leq 0.05$, ** $P \leq 0.01$, *** $P \leq 0.001$, DTF-Days to tasseling, PHT-Plant height, DTSE-Days to *Striga* Emergence from crop emergence, C8WAE-*Striga* count at 8 Weeks after Crop Emergence (WAE), C10WAE-*Striga* count at 10 WAE, C12WAE-*Striga* count at 12 WAE and CUMC-Cumulative *Striga* Count, YIELD-Total Grain Weight and SEEDWT- 100 Seed Weight

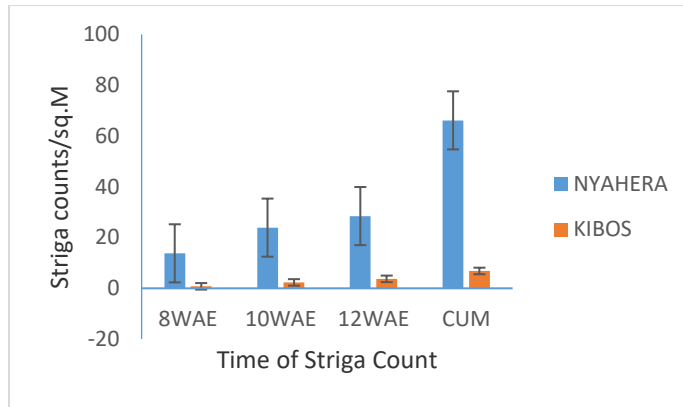


Fig. 1: *Striga* incidence for the Locations across the seasons

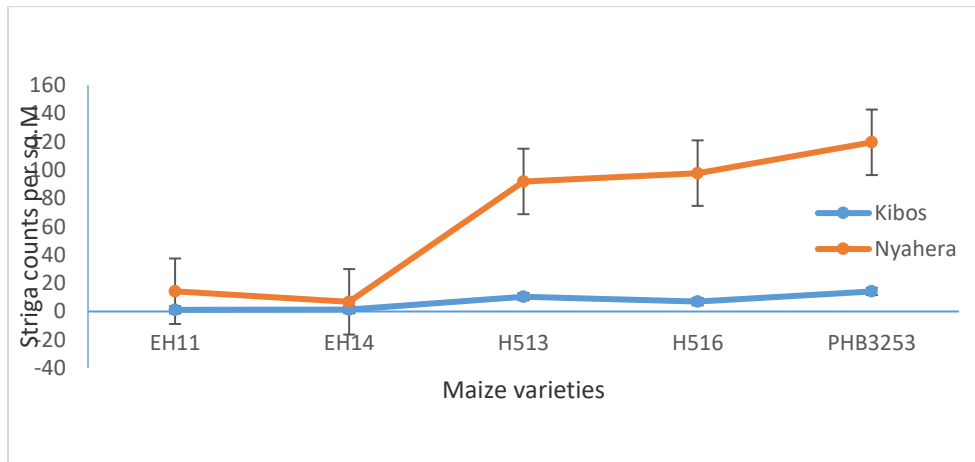


Fig. 2: The influence of location by variety interaction on cumulative *Striga* count in Kibos and Nyahera

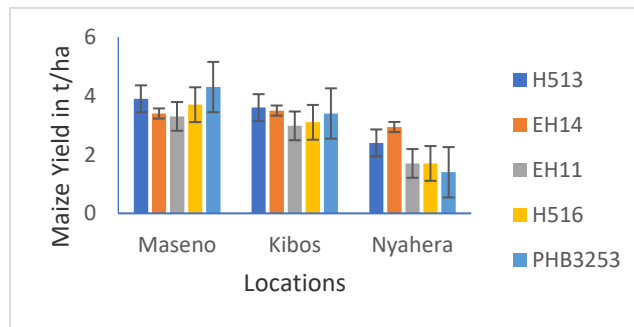


Fig 3: Average maize yield per Location



Fig. 4: *Striga hermonthica* seedlings growing on the roots of maize varieties screened on rhizotrons 21 days after infection with pre-germinated *Striga hermonthica* seeds. Plate A is Maseno EH14 characterized by fewer and smaller attachments; B and C are EH11 and PHB3253 respectively with relatively many attachments of *Striga* seedlings

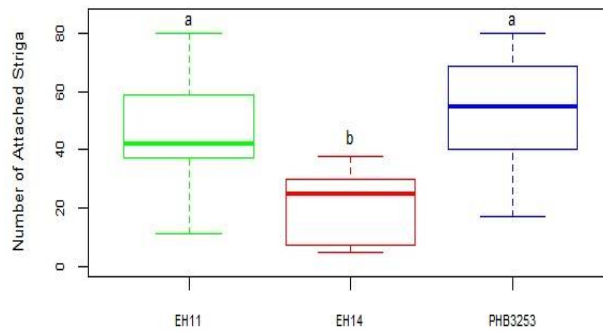


Fig. 5 Number of *Striga* attachments on roots of EH11, EH14 and PHB3253 maize varieties. Box plots with same letters are not statistically different ($P < 0.05$)

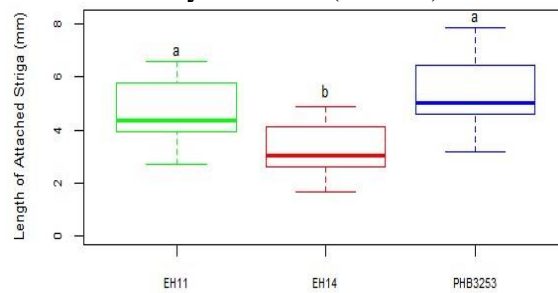


Fig. 6 *Striga* length (mm) on roots of EH11, EH14 and PHB3253 maize varieties. Box plots with same letters are not statistically different ($P < 0.05$)

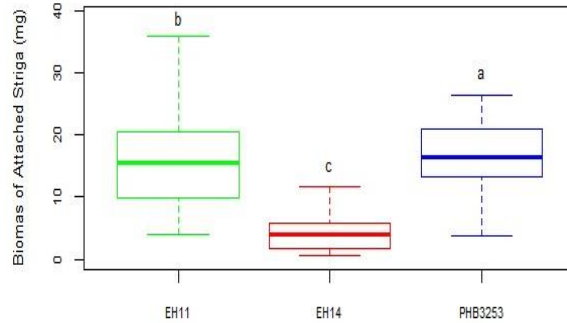


Fig. 7 *Striga* biomass (mg) on roots of EH11, EH14 and PHB3253 maize varieties. Box plots with same letters are not statistically different ($P < 0.05$)

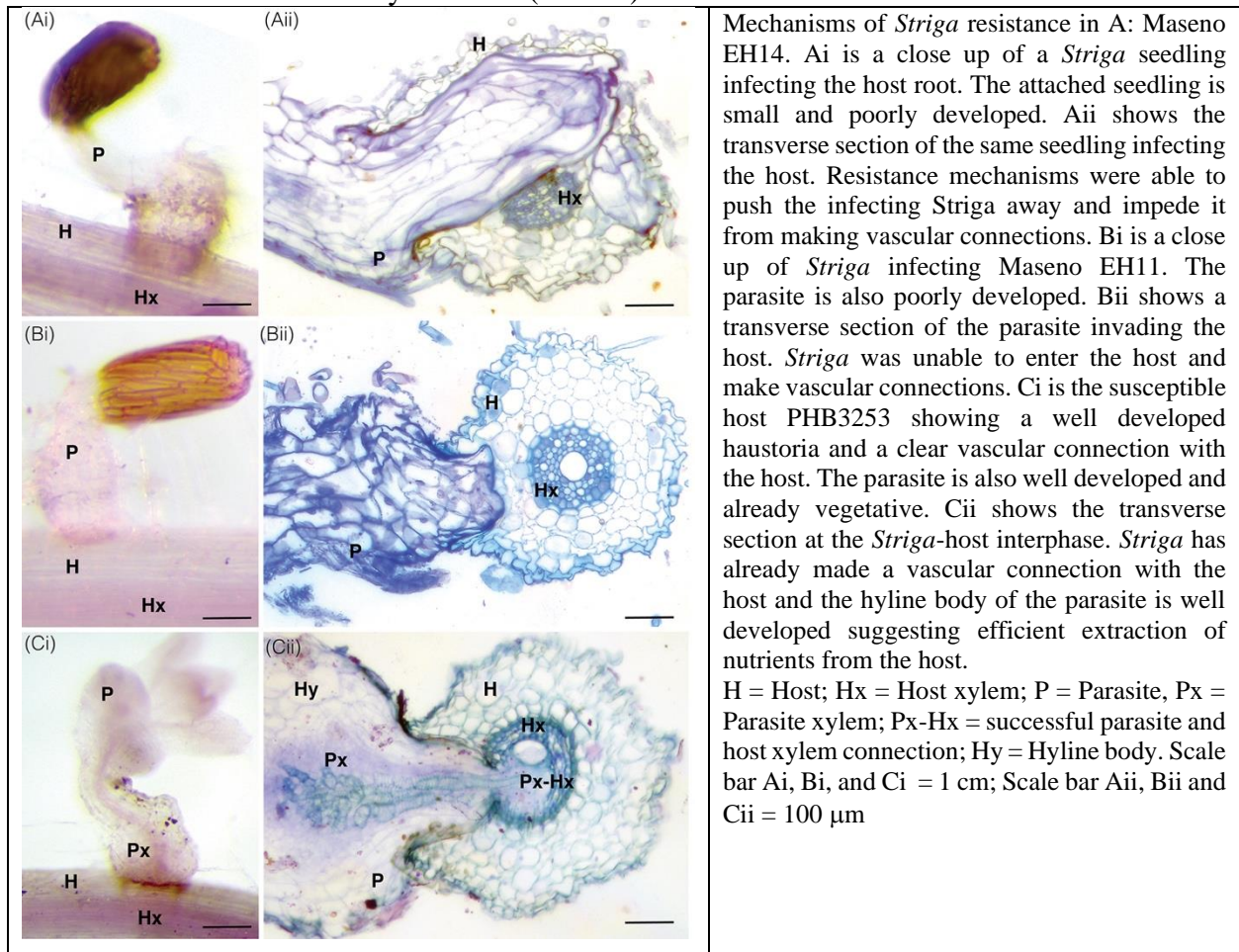


Fig 8: *Striga*-host interactions at the point of attachment at 9 DAI