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INSIGHT

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Post-attachment resistance to *Striga hermonthica* in finger millet (*Eleusine coracana*)

Josephine S. Kunguni[1,2,3] | Willy Kibet[4] | Chrispus O. Oduori[5] | Mathews M. Dida[6] | Sylvester Anami[1] | Benjamin Kilian[7] | Josiah M. Mutuku[2] | Steve Runo[4] | Damaris A. Odeny[3]

[1]Jomo Kenyatta University of Agriculture and Technology, Institute for Biotechnology Research, Nairobi, Kenya

[2]Biosciences Eastern and Central Africa-International Livestock Research Institute (BecA-ILRI) Hub, Nairobi, Kenya

[3]The International Crops Research Institute for the Semi-Arid Tropics - Eastern and Southern Africa, Nairobi, Kenya

[4]Department of Biochemistry, Microbiology and Biotechnology, Kenyatta University, Nairobi, Kenya

[5]Kenya Agricultural and Livestock Research Organization, Crops Department, Sorghum and Millets Research, Kibos, Kenya

[6]Department of Crop and Soil Sciences School of Agriculture, Environment and Food Security, Maseno University, Maseno, Kenya

[7]Global Crop Diversity Trust, Bonn, Germany

Correspondence
Damaris A. Odeny, The International Crops Research Institute for the Semi-Arid Tropics - Eastern and Southern Africa, Nairobi, Kenya.
Email: damaris.odeny@icrisat.org

Steve Runo, Department of Biochemistry, Microbiology and Biotechnology, Kenyatta University, Nairobi, Kenya.
Email: runo.steve@ku.ac.ke

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Abstract

Finger millet is a highly nutritious and climate-resilient cereal crop. Despite its importance, finger millet productivity in East Africa trails other cereals due to several biotic and abiotic factors, including the parasitic weed, *Striga hermonthica*. *Striga* spp. are noxious parasitic weeds whose damage can result in 100% yield losses in sub-Saharan Africa. The objective of our study was to determine differences in post-attachment responses of a selection of genotypes. We germinated finger millet in Petri dishes, transferred them to rhizotrons and infected the roots with *Striga* that had been pre-conditioned for 7 days at 30°C and subsequently pre-germinated using GR24. Histological analysis was done on three distinct genotypes to determine the host–pathogen interactions. The attachment of *Striga* onto the host was observed 3 days after inoculation. LESK10, a wild genotype, and OKHALE1 (cultivated) consistently supported fewer *Striga* plants after inoculation, while GBK029646A, a cultivated finger millet, consistently supported the highest. Histological analysis recorded an incompatible reaction in both OKHALE1 and LESK10 and a compatible reaction in GBK029646A as early as 3 days after infection. Our results suggest the likely existence of novel resistance in crop wild relatives that will be valuable for developing durable resistance to *Striga* in elite finger millet varieties.

KEYWORDS
GR24, millet, parasitic plant, post-attachment resistance, rhizotrons, witchweed

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1 | INTRODUCTION

Finger millet (*Eleusine coracana* (L.) Gaertn subsp. *coracana*) is an important crop to smallholder farmers in Eastern and Southern Africa and southern parts of India. Finger millet is well adapted to semi-arid conditions and resilient to soil acidity and infertility that is emblematic of marginal lands where other cereal crops like rice (*Oryza sativa*) and maize (*Zea mays*) cannot survive (Mal et al., 2010). The high nutrient content and long post-harvest shelf-life with minor pest damage make it a desirable subsistence crop in sub-Saharan Africa (Onipe & Ramashia, 2022).

Despite its importance, finger millet continues to trail other cereals like maize, sorghum (*Sorghum bicolor*), rice and wheat (*Triticum aestivum*) in production, research and development. The low productivity is attributed to poor management practices, unpredictable market prices, limited improved varieties, biotic and abiotic factors (Nagaraj et al., 2013). *Striga hermonthica* is the most important weed in finger millet with average yield loss estimated at 0.99 tons per ha in Kenya (Mac Opiyo et al., 2010). *Striga* spp. are hemiparasites that belong to the family Orobanchaceae and occur mainly in Africa and Southeast Asia (Spallek et al., 2013).

Resistance to parasitic plants has been reported to occur either pre- or post-attachment to the host roots. Pre-attachment resistance occurs when the host plants produce low or less potent strigolactones (SLs) leading to poor or lack of germination of the parasite (Gobena et al., 2017). Pre-attachment resistance is determined by measuring the germination frequency and the radicle length of the parasitic plants upon exposure to the root exudates of the host plants (Mallu et al., 2021). Post-attachment resistance occurs when the host plant prevents the further development of already attached parasites (Fishman & Shirasu, 2021). A quick way to determine post-attachment resistance is to use rhizotrons and measure the mean number, lengths and total number of *Striga* seedlings attached to the host plant roots (Kavuluko et al., 2021; Mbuvi et al., 2017).

There are no previous reports on post-attachment screening of finger millet. The objective of our study was to establish post-attachment differences in the response of select finger millet genotypes to *Striga* infection.

2 | MATERIALS AND METHODS

2.1 | Plant material

We evaluated seven *Eleusine* genotypes (Table 1) against an isolate of *S. hermonthica* obtained from Alupe (Kenya) in 2011 that had been collected from finger millet fields using standard protocols (Kountche et al., 2019) and maintained at room temperature at the International Crops Research Institute for the Semi-Arid Tropics, Nairobi. The laboratory experiments were conducted at BecA-ILRI Hub (Kenya) and at the Plant Transformation Laboratory, Kenyatta University (Kenya).

2.2 | *Striga* seed conditioning and finger millet seed pre-germination

S. hermonthica seeds were surface sterilised in 20% commercial bleach (Orbit Products Africa Limited, Nairobi, Kenya), then thoroughly rinsed in sterile double distilled water. Clean *Striga* seeds were pre-conditioned as previously described by Mutuku et al. (2015). Finger millet seeds were surface sterilised in 10% commercial bleach, thoroughly rinsed with sterile double distilled water, followed by incubation in moist filter paper (Whatman® GF/C) in Petri dishes for 7 days at 26°C under 16-h light; 8-h dark cycles for growth. On the 8th day, the finger millet seedlings were transferred to the rhizotron dishes (10 × 12 cm square Petri dish containing rock wool and a 100 μm nylon mesh), which had the tops and bottoms perforated to allow shoot growth and draining of water from the growth medium. The rhizotrons were fertilised with one-half-strength MS medium (Mutuku et al., 2015) and covered with aluminium foil to prevent exposure of roots to light.

2.3 | *S. hermonthica* germination and infection

Pre-conditioned *Striga* seeds were induced for germination using 300 μL of 0.1 ppm solution of synthetic SL germination stimulant GR24 (Chiralix Nijmegen, the Netherlands) in 90 mm Petri dishes. The germination percentage of *Striga* seeds was determined using a Leica MZ7F stereomicroscope fitted with a DFC320FX camera (Leica, UK) by counting the numbers in each fibre-glass disc. Ten-day-old finger millet seedlings per replicate were infected with 10 germinated *Striga* seeds per root by placing the *Striga* seeds directly on the roots with a gentle brush. Subsequent observations were done according to Yoshida and Shirasu (2009). Each experiment was replicated four times. The number of *Striga* attached to the host plant and the subsequent progress in establishment in the host were recorded daily.

TABLE 1 The origin and sources of finger millet genotypes used in the study.

Genotype	Species	Origin	Received from
LESK10	*E. coracana* ssp. *africana*	Tanzania	Maseno University
MS6	*E. coracana* ssp. *africana*	Kenya	Maseno University
MS8	*E. coracana* ssp. *africana*	Kenya	Maseno University
OKHALE1	*E. coracana* ssp. *coracana*	Nepal	KALRO-Alupe
U15	*E. coracana* ssp. *coracana*	Uganda	KALRO-Alupe
P224	*E. coracana* ssp. *coracana*	Kenya	KALRO-Alupe
GBK029646A	*E. coracana* ssp. *coracana*	Kenya	KALRO-Alupe

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2.4 | Histological analysis

One wild and one cultivated genotype that least supported the establishment of *Striga* (likely resistant) and one genotype that supported the highest establishment of *Striga* (probably susceptible) were further selected for histological analysis. Roots of the three genotypes infected with *S. hermonthica* were randomly selected, dissected, and immediately processed for embedment and mounting as already described (Mbuvi et al., 2017). The mounted sections were observed and photographed using a Leica DM100 microscope fitted with a Leica MC190 HD camera (Leica, Germany).

2.5 | Statistical analysis

Means of germination frequency were subjected to analysis of variance in R version 4.3.1 followed by mean separation using Tukey's LSD test. Results were displayed in bar graphs using the ggplot2 package (Wickham, 2016).

3 | RESULTS

3.1 | *Striga* germination and establishment on finger millet roots

We observed significant differences in *Striga* growth and development across the seven genotypes at 6 and 9 days after infection (DAI) (Table 2). Wild accessions supported fewer numbers of *Striga* than the cultivated genotypes (Figure 1). LESK10, a wild genotype, consistently supported fewer (10% and 20%) *Striga* plants at all stages (6, 9 and 15 DAI), while GBK029646A, a cultivated finger millet, consistently supported the most (50% of the inoculated *Striga* plants) numbers (Figure 2). The most resistant cultivated genotype tested was OKHALE1 (Figure 1). Based on these results, all downstream analysis was done with the most resistant wild (LESK10), the most resistant cultivated (OKHALE1) and the most susceptible (GBK029646A).

We observed the attachment of *Striga* to the root systems of LESK10, OKHALE1 and GBK029646A genotypes at 3 DAI (Figure 2A). At 9 DAI, the attached *Striga* was either initiating leaf development, or had fully developed leaf pairs (Figure 2B). The vigorous vegetative growth of the parasite on the roots of GBK029646A was an indicator of susceptibility (Figure 2).

TABLE 2 Mean squares of *Striga* growth and development in the host within 15 days of inoculation.

		Mean sum of squares		
SOV	df	6 DAI	9 DAI	15 DAI
Rep	1	0.071	1.786*	4.571
Genotype	6	6.762**	4.413***	1.524
Residuals	13	0.969	0.375	1.187

Abbreviations: df, degrees of freedom; DAI, days after infection; SOV, source of variation.
*$p < 0.05$; **$p < 0.01$; ***$p < 0.001$.

3.2 | Histological analysis

Differences in the interactions of *S. hermonthica* and various finger millet genotypes were also observed at the cellular level (Figure 3). In OKHALE1 and LESK10, we recorded a successful penetration of *Striga* through the host cortex that did not result in a host–parasite xylem bridge due to the failure by the parasite to penetrate the endodermis (Figure 3). However, a compatible reaction was observed in GBK029646A as early as 3 DAI, with *S. hermonthica* haustorium establishing vascular connections and penetrating through the cortex and endodermis (Figure 3Cii). Well-developed hyaline bodies were observed in GBK0294696A (Figure 3Cii) while there was no progression to the cortex of LESK10 (Figure 3Bii) and OKHALE1 (Figure 3Aii) at 3 DAI.

4 | DISCUSSION

In the current study, we have identified post-attachment resistance against *S. hermonthica*. Previous *Striga*–host interaction activities have focused on other cereals (Mbuvi et al., 2017), making our study the first of its kind in finger millet. Post-attachment screening methods are a

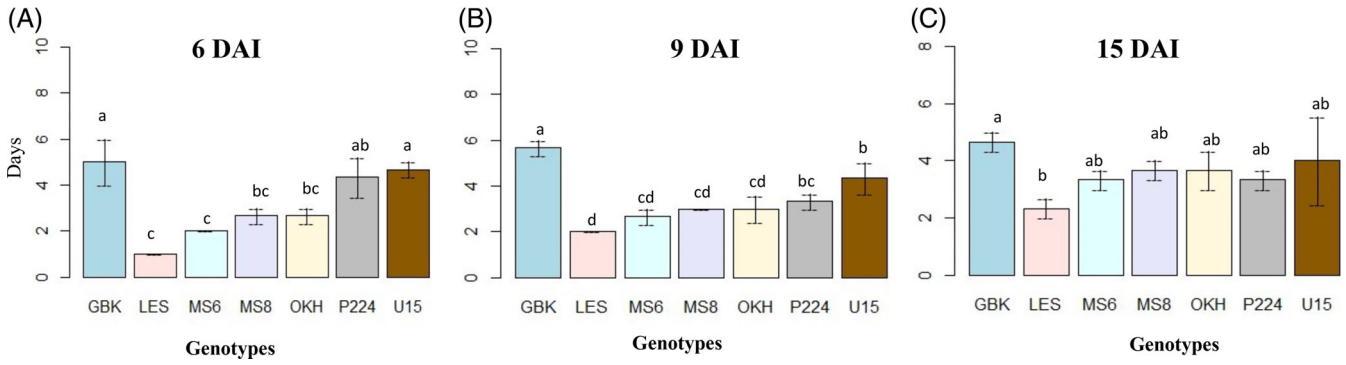

FIGURE 1 Differences and mean separation in *Striga* growth and development on finger millet genotypes at 6 (A), 9 (B), and 15 (C) DAI. The experiment was replicated four times with each replicate having 10 seedlings. Means across reps from each genotype were used to draw the charts. GBK-GBK029646A; LES-LESK10; OKH-OKHALE1.

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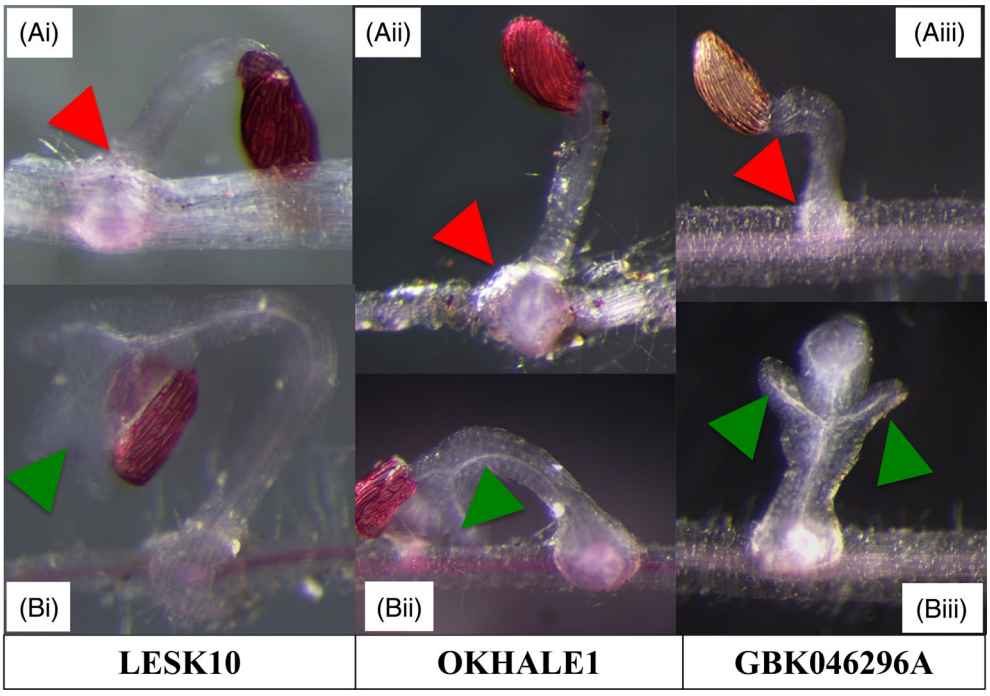

FIGURE 2 The attachment and establishment of *Striga* on the roots of different finger millet genotypes as observed under the microscope. (A) Attachment of finger millet at 3 DAI on LESK10 (Ai), OKHALE1 (Aii) and GBK029649A (Aiii).
(B) Establishment of finger millet on different genotypes can be seen at varying levels of leaf development at 9 DAI with the most susceptible (GBK046296A) supporting *Striga* with fully developed leaf pair (Biii), LESK10 (Bi) and OKHALE1 (Bii) only just initiating leaf development.

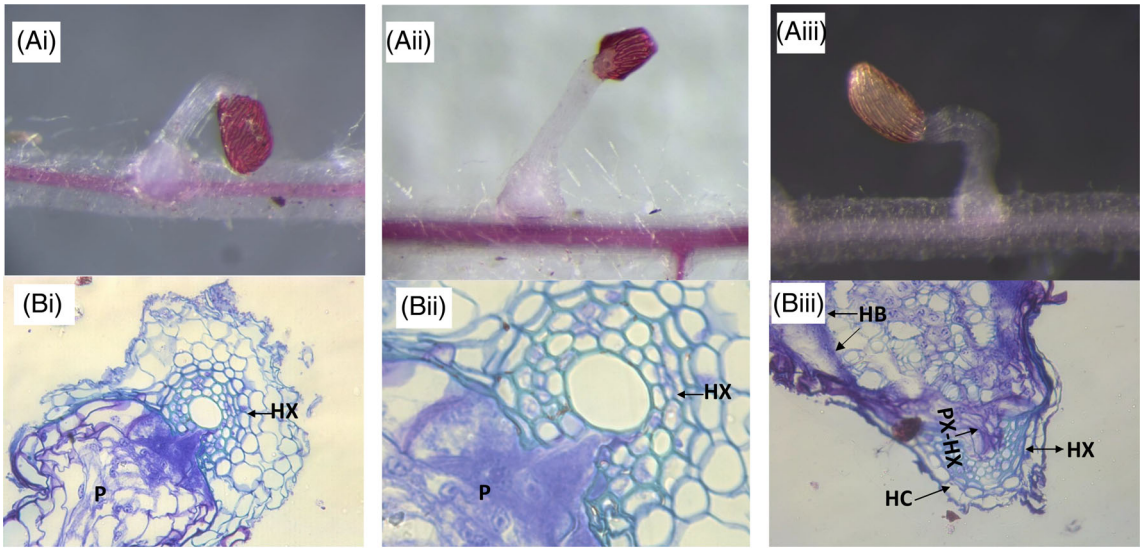

FIGURE 3 *Striga* parasite establishment on the various host roots. (A) Successful attachment of the parasite to plant roots at 3 DAI. (Ai) OKHALE1. (Aii) LESK10. (Aiii) GBK029646A. (B) Transverse sections taken at 3 DAI. (Bi) An incompatible reaction is observed with OKHALE1 at 3 DAI. The parasite advanced beyond the cortex without xylem–xylem interaction. (Bii) An incompatible reaction observed in LESK10 with visible failure of the parasite to penetrate the cortex. (Biii) Successful penetration of the cortex and endodermis of the host plant is observed with GBK029646A. HB, hyaline body; HX, host xylem; P, parasite cells; PX, parasite xylem.

cost-effective and quick way of classifying the reaction of genotypes of interest before taking them out in the field.

Future studies attempting to correlate lab and field experiments will need to consider the complexity of conditions and the high outcrossing nature of *S. hermonthica* that results in larger effective population sizes and broader host–parasite interaction ranges (Huang et al., 2012). Rhizotron studies are often done with specific *Striga* isolates, while several mixtures of isolates exist in the field, making it harder to obtain consistent results between the lab and field. *Striga* virulence is also known to be further influenced by several factors including soil fertility temperature, and soil moisture (Jamil et al., 2013; Mwangangi et al., 2021).

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We focused on post-attachment resistance rather than pre-attachment, which is regulated by the type of SLs produced by the host (Fishman & Shirasu, 2021). There are currently no known studies reporting the characterisation of SLs from finger millet. Studies in sorghum have reported the production of different SLs in root exudates, including orobanchol, sorgolactone, strigol, 5-deoxystrigol and sorgomol (Awad et al., 2006; Mohemed et al., 2018; Motonami et al., 2013). Each of these SLs potentially have differing abilities to induce *Striga* germination. For example, orobanchol is a less potent germination stimulant than 5-deoxystrigol (Gobena et al., 2017). Characterising different SLs and their stimulant activities in finger millet will pave the way for more structured pre-attachment studies.

We included wild relatives (*E. coracana* ssp. *africana*) of finger millet to increase the chances of identifying novel sources of resistance. In sorghum, wild relatives have been reported as good sources of resistance (Mbuvi et al., 2017; Muchira et al., 2021). The incompatible reactions observed in both LESK10 (wild) and OKHALE1 (cultivated) were similar to the reaction reported by Mbuvi et al. (2017) in wild sorghum, which was likely mechanical and/or biochemical. Similar incompatible reactions with *S. hermonthica* have been described in rice (Mutuku et al., 2015; Yoshida & Shirasu, 2009) but will need more investigations in finger millet. The genetic basis of each of the resistances observed in LESK10 and OKHALE1 will need to be better characterized through the development of relevant mapping populations, as has been done in sorghum (Gobena et al., 2017). Post-attachment resistance is believed to be primarily quantitative in nature (Fishman & Shirasu, 2021), although qualitative forms have also been reported (Duriez et al., 2019).

Our study included only a few genotypes, as a proof of concept. Future studies should incorporate larger numbers of genotypes for screening against target isolates in order to capture the high genetic variability of *Striga* in the fields.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data generated or analysed during this study are included in this published article.

ORCID

Josephine S. Kunguni https://orcid.org/0009-0009-5322-225X
Steve Runo https://orcid.org/0000-0002-9043-2338

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