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RESEARCH ARTICLE

Essential plant nutrients impair post-germination development of Striga in sorghum

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Societal Impact Statement

Infestation by the parasitic weed Striga is a major cause of cereal crop production losses on smallholder farms in Africa. Essential plant nutrients play an important indirect role in parasite seed germination, the first prerequisite for successful parasitism. Here, we demonstrate that increasing the nutrient availability for the host plant can also impede Striga development beyond its germination, independent of the resistance levels of the sorghum host. This insight provides additional support for crop protection recommendations to Striga-affected farmers. Growing a resistant crop variety combined with adequate levels of fertilisers should be the backbone of defence against this parasitic weed.

Summary

- *Striga hermonthica* is a widespread parasitic weed in sub-Saharan Africa and an important biotic constraint to sorghum production. Resistant varieties and fertilisers are crucial components of integrated Striga management. N and P fertilisers reduce the production of host-plant strigolactones, known as Striga germination stimulants, and thereby reduce infection. Whether essential plant nutrients affect the parasite–host interaction beyond Striga germination is unknown.
- We conducted mini-rhizotron assays to investigate the effects of macronutrient and micronutrient availability on post-germination Striga development. Four sorghum genotypes (Framida, IS10978, N13, IS9830) covering the complete array of known mechanisms of post-attachment resistance were compared with susceptible genotype Ochuti. Plants were infected with pre-germinated Striga seeds and subjected to four nutrient treatment levels: (1) 25% of the optimal concentration of Long Ashton solution for cereals; (2) 25% macronutrient and optimal micronutrient concentration; (3) optimal macronutrient and 25% micronutrient concentration; and (4) optimal macronutrient and micronutrient concentrations.

- Compared with the 25% base nutrient level, treatments supplemented with macronutrients reduced the number of viable vascular connections established by pre-germinated Striga seedlings as well as the total parasite biomass on the sorghum root system. Macronutrient treatment effects were observed across sorghum genotypes, independent of the presence and type of post-attachment resistance, but appeared to specifically improve mechanical resistance, hypersensitive and incompatibility responses before Striga reaches the host-root xylem.
- This study demonstrates, for the first time, that nutrient availability drives Striga parasitism beyond the germination stages. Increased availability of nutrients, in particular macronutrients, enhances host-plant resistance in post-attachment stages, reinforcing the importance of current fertiliser recommendations.

KEYWORDS

fertiliser, host resistance, mini-rhizotron, root parasitic weeds, *Sorghum bicolor*, witchweed

1 | INTRODUCTION

Sorghum is the second most important cereal food crop after maize in sub-Saharan Africa (SSA). Sorghum production in this region is greatly limited by the obligate root hemi-parasitic weed, *Striga hermonthica* Del. Benth. Seedlings of this parasitic weed species attach to the roots of their host plant to syphon water, nutrients and metabolites, resulting in yield losses of 30% to 100% and sometimes host plant death (Dörr, 1997; Ejeta, 2007; Gurney et al., 1995; Hood et al., 1997; Rank et al., 2004).

Various preventive and curative measures have been suggested for Striga control, but none are effective in the long term when applied in isolation (Jamil et al., 2021). It is only through integrated Striga management (ISM), implying a combination of two or more measures, that Striga can be effectively and durably controlled (Hearne, 2009). One potential component of ISM is improving the nutrient availability of the crop by using fertilisers (Jamil et al., 2012; Oswald, 2005; Tippe et al., 2017). The application of fertilisers, primarily nitrogen (N) and phosphorus (P), can lead to reduced Striga infection levels by decreasing the Striga germination rate (Cechin & Press, 1993; Jamil, Charnikhova, et al., 2011; Yoneyama, 2019). A second potential component is the use of Striga-resistant genotypes that lower Striga infection levels (Rodenburg et al., 2005, 2006). Striga resistance genes have been identified in the sorghum germplasm pool (Bellis et al., 2019; Kavuluko et al., 2021; Mbuvi et al., 2017; Mohamed et al., 2010). The use of Striga-resistant cultivars is an efficient and cost-effective approach for smallholders in SSA, making it a potential component of integrated Striga management (Haussmann et al., 2000). The concurrent use of the two Striga control measures, fertilisers and Striga-resistant cultivars, could offer a feasible and sustainable ISM approach (Mwangangi et al., 2021; Tippe et al., 2017). However, each of these components, as well as their combinations, would need to be optimised to achieve the most effective Striga control.

The two known classes of Striga resistance are (1) pre-attachment resistance, which decreases Striga infection by lowering the Striga germination rate (Hess et al., 1992; Jamil, Rodenburg, et al., 2011; Rich et al., 2004), and (2) post-attachment resistance, which impairs Striga after germination to establish a successful vascular connection with the host (Kavuluko et al., 2021; Mbuvi et al., 2017). Pre-attachment resistance is mainly the result of host plant genotypes producing lower quantities or less active forms of strigolactones, compounds known to stimulate Striga seed germination (Gobena et al., 2017; Hess et al., 1992; Jamil, Rodenburg, et al., 2011; Kawa et al., 2021; Mohemed et al., 2018). Post-attachment resistance can be the result of: (1) a hypersensitive response, characterised by necrosis at the point of Striga attachment on the host root (Mohamed et al., 2003), (2) mechanical barriers expressed by enhanced lignin deposition at the epidermis, cortex or endodermis of the host root; and (3) an incompatibility response expressed as an unexplained inability of the parasite to differentiate and form a vascular connection with the host roots (Kavuluko et al., 2021; Mbuvi et al., 2017). Phenotypes and descriptions of all known post-attachment resistance mechanisms are presented in Figure 1.

Nutrients play an important role in the pre-attachment stages of the Striga-host interaction. Deficiencies in nitrogen and phosphorus induce the host plant to increase the production of strigolactones, a class of plant hormones with variants that stimulate Striga seed germination (Babiker & Hamboun, 1983; Bebawi, 1986; Bouwmeester et al., 2003; Yoneyama et al., 2010). In reverse, application of these macronutrients can reduce the production of these compounds, which leads to reductions in Striga seed germination rates and consequently Striga infection levels (Cechin & Press, 1993; Czarnecki et al., 2013; Jamil et al., 2012, 2014; Yoneyama, 2019; Yoneyama et al., 2007). Nitrogen has also been recently observed to play a role in haustorium formation (Kokla et al., 2022) and, indirectly, chemotropism of the Striga radicle towards the host root (Ogawa et al., 2022). The role of nutrients in the post-attachment phases of the host–parasite association is still largely unknown. In other pathogen-host relationships, nutrient availability affects host defence mechanisms (Dordas, 2009). For example, micronutrients and macronutrients are involved in the

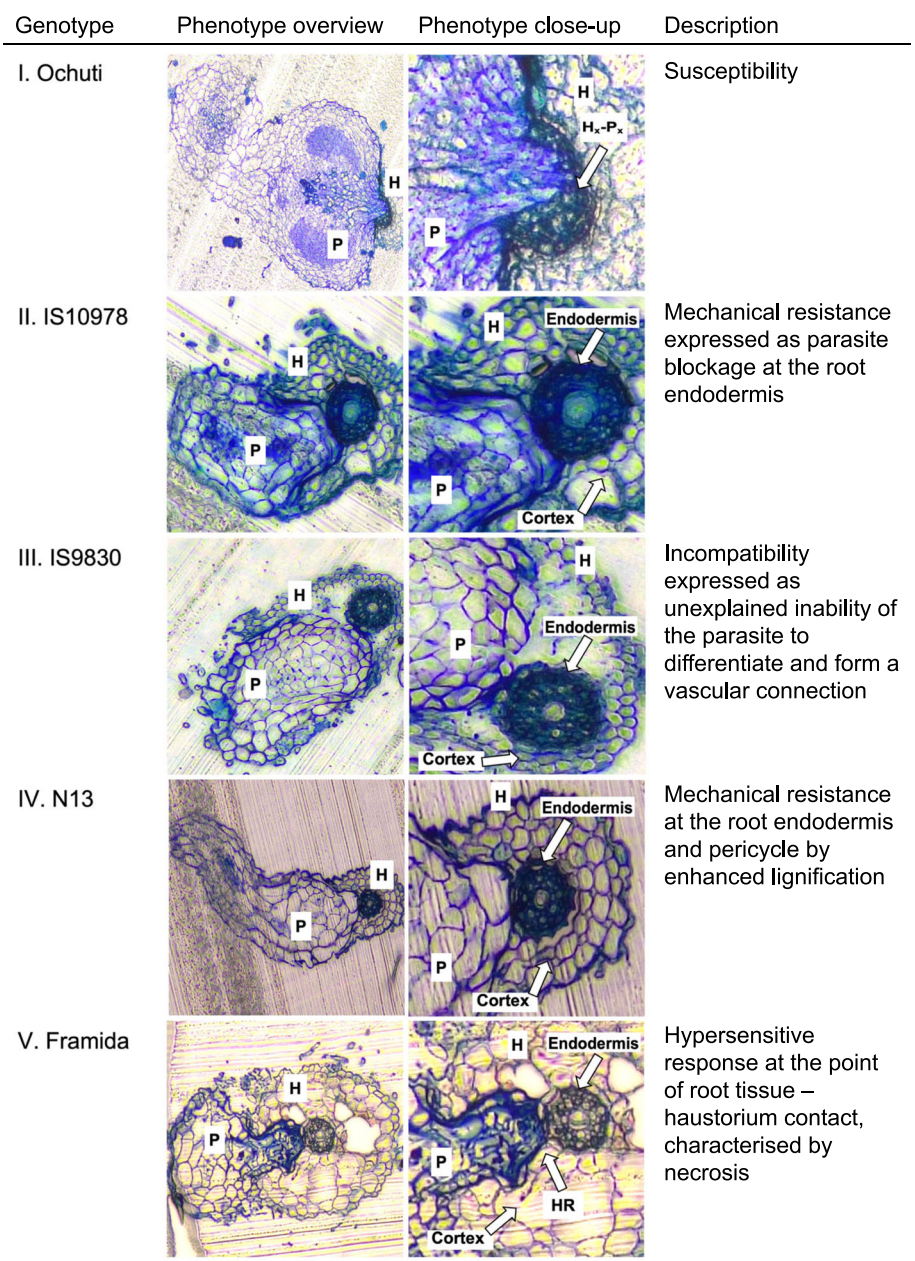

FIGURE 1 Overview and close-up photos of transverse sections of host roots (H) with parasite attachments (P) of the sorghum–Striga association at 9 days post-infection across different genotypes (I–V). (I) Susceptible genotype Ochuti: successful host xylem–parasite xylem (H_x–P_x) connection and a well-developed parasite tissue; (II) Resistant genotype IS10978: parasite penetrating the host cortex is impaired at the endodermal layer; (III) Resistant genotype IS9830: parasite penetration is arrested at the cortex level and the haustorium seems unable to differentiate to form a vascular connection; (IV) Resistant genotype N13: parasite is impaired at the endodermis level due to enhanced lignification; (V) Resistant genotype Framida: parasite is arrested at the endodermis following a hypersensitive response (HR) at the host–parasite interface. Right column: reported descriptions of host–parasite interactions for each sorghum genotype: (I) Striga susceptibility in Ochuti (Mbuvi et al., 2017); (II) mechanical resistance in IS10978 (Kavuluko et al., 2021); (III) Striga incompatibility in IS9830 (Kavuluko et al., 2021); (IV) mechanical resistance in N13 (Maiti et al., 1984); and (V) hypersensitive response in Framida (Mohamed et al., 2003). All photos were made by I.M. Mwangangi (NRI, 2022).

induction of hypersensitive responses and mechanical barriers against root and foliar pathogenic infections (González-Hernández et al., 2019; Imada et al., 2016; Mittelstraß et al., 2006; Reuveni & Reuveni, 1998; Sugimoto et al., 2010; Yamazaki et al., 2000; Yang et al., 2018).

The questions we address are: (1) whether nutrient availability plays a role in the parasite–host interaction beyond Striga germination, and if so, (2) is the effect of nutrient availability on post-germination Striga success mediated by micronutrients or macronutrients, and (3) can increased levels of micronutrients or macronutrients enhance any post-attachment resistance mechanisms? This was tested in sorghum growing in root observation chambers called mini-rhizotrons (Gurney et al., 2003) in a controlled greenhouse setting. Four nutrient treatments comprising micronutrients and macronutrients at different concentrations, four sorghum genotypes with different mechanisms of post-attachment Striga resistance, and one Striga susceptible genotype were used.

2 | MATERIALS AND METHODS

2.1 | Plant material

Five *Sorghum bicolor* (L.) Moench genotypes (i.e., Framida and IS9830 of the Caudatum race, Ochuti, IS10978 and N13 of the Durra race) were used (Figure 1). Sorghum seeds were obtained from Kenyatta University in Kenya. *S. hermonthica* seeds were obtained from infested sorghum farms in Alupe, Western Kenya in 2019.

2.2 | Growth, infection and fertigation of sorghum

To investigate the effect of different nutrient treatments on post-attachment *Striga* resistance in sorghum, a mini-rhizotron experiment was set up, as previously used by Gurney et al. (2006) and Cissoko et al. (2011), whereby individual sorghum plants were grown out of 24.5 × 24.5 cm large and 2.5 cm deep Perspex bioassay dishes (ThermoFisher Scientific, UK). Sorghum seeds were first germinated between sterile rockwool layered with mesh in plant propagators. Seven-day-old sorghum seedlings were transferred from the propagators to a mini-rhizotron dish packed with moist autoclaved rockwool. Roots were allowed to grow on a fine mesh (50 µm, polyester) placed onto the rockwool and 3-cm openings at the top allowed for shoot growth and drip irrigation. The mini-rhizotron dishes were closed with insulating tape and covered with aluminium foil to provide a dark environment for the roots. Each individual dish was connected to a dripper connected by tubes to a reservoir with a base-level nutrient solution (see below) and a water pump connected to a timer to ensure a scheduled and controlled water and nutrient supply to each plant. Each sorghum plant received a daily total of 50 mL of this solution through five irrigation events of 10 mL at 4-h intervals. Each dish received a complement of nutrients according to their respective treatment allocation (see below). These nutrient treatments were applied every third day by manual application of 25 mL of each solution, while the dishes allocated to the base-level low nutrient treatment received the equivalent of 25 mL of plain water.

Fourteen days after transfer in the mini-rhizotron dishes, the roots of the sorghum seedlings were infected with pre-germinated *S. hermonthica* seeds (25 mg) on the secondary roots using a paintbrush (Gurney et al., 2003), previously prepared as follows: Striga seeds were surface sterilised using 10% sodium hypochlorite (v/v) for 10 min, followed by rinsing with distilled water (500 mL). The sterilised seeds were spread on moist 90-mm Petri dishes layered with filter paper (Whatman, GFA), sealed with parafilm, wrapped with aluminium foil and incubated at 31°C for 7 days. On the 8th day, the Petri dishes were unwrapped, and 3 mL of 0.1 ppm synthetic germination stimulant, GR24, was added to the Striga seeds. The seeds were further incubated at 31°C for 12 h to induce germination. After infection, the mini-rhizotron chambers were sealed with insulation tape, wrapped with aluminium foil and connected to the drip-feed irrigation system. The sorghum plants were maintained in greenhouse conditions for another 21 days. Plants in the mini-rhizotron were grown in a greenhouse with supplemented HPS lights (High-Pressure Sodium lamps, Philips, SON-T Agro 400 W) providing a light intensity at canopy level of 136 µmol m^{-2} s^{-1} (wavelength peak at 600 nm) on top of the daylight. Minimum temperatures in the greenhouse were maintained at 28°C/21°C day and night, with a relative humidity in the range of 60%–70%. The mini-rhizotron system allows a non-destructive study of the sorghum roots and Striga attachments.

2.3 | Experimental design and treatments

The experiment was laid out in a split-plot design with six replications. The experiment consisted of four levels of nutrient treatments, randomly assigned at the main plot level, and five sorghum genotypes randomly assigned at the split-plot level. Nutrient compositions were based on the Long Ashton solution (Hudson, 1967), and concentrations were based on standard recommendations for mini-rhizotron assays with cereal species (Table 1; Hudson, 1967: Gurney et al., 2006). The nutrient treatments consisted of micronutrients (B, Zn, Mn, Fe, Na, Cl and Mo) and macronutrients (N, P, K, Ca and Mg) categorised into four levels: (1) 'Base': a base-level low nutrient treatment (25% of the optimal concentration of Long Ashton solution for cereals); (2) '+Micro': a micronutrient treatment (100% of the optimal concentration of micronutrients and 25% of the optimal concentration of macronutrients); (3) '+Macro': a macronutrient treatment (25% of the optimal concentration of micronutrients and 100% of the optimal concentration of macronutrients); and (4) '+Micro-Macro': a complete nutrient treatment (100% of the optimal concentration of Long Ashton solution for cereals in terms of micronutrients and macronutrients). The selection of sorghum genotypes was both comprehensive and balanced, as it included one representative of all known post-attachment resistance mechanisms (i.e., Framida, IS10978, IS9830 and N13, see Figure 1), including one genotype that lacked any (post-attachment) resistance (Ochuti). This latter genotype served as a control.

Three complete experimental runs were done in a greenhouse at the University of Greenwich in Medway, United Kingdom in the period February to March (run 1), May to June (run 2) and August to September (run 3) in 2021.

2.4 | Observations

On the 9th day post-infection, from four replicates of each genotype and nutrient treatment, the sorghum root tissue at the point of a Striga attachment (one per mini-rhizotron dish) was carefully cut out under a stereomicroscope. The cut root sections were fixed in Carnoy's fluid (4:1100% analytical ethanol: glacial acetic acid) and stained with 1% safranin in 30% ethanol for 5 min, following the methods explained by Kavuluko et al. (2021). The tissues were de-stained with chloral hydrate (2.5 g/mL) for 12 h. Pre-infiltration was done by transferring the tissues into Technovit 1 (Haraeus Kulzer GmbH, Germany): absolute ethanol solution (1:1 v/v) for 1 to 2 h. The tissues were then infiltrated in a 100% Technovit 1 solution for 15 min and later transferred to a fresh 100% Technovit 1 solution for 72 h. The tissues were embedded by erecting them in a vertical position in Hardener 2 and Technovit 1 solutions in a 1:15 ratio in 1.5-mL Eppendorf tube lids. The moulds were air-dried for 24 h, wrapped in aluminium foil and incubated at 37°C for further drying. Embedded tissues were then mounted on wooden histoblocks using the Technovit® 3,040 kit (Haraeus Kulzer GmbH, Germany).

Tissue sections (5-µm-thick) were cut using the Leica HistoCore Multicut R semi-motorised microtome. The tissues were dried on glass slides at 65°C for 30 min and stained for 2 min using 0.1% toluidine blue O dye in 100 mM phosphate buffer. The tissues were de-stained

TABLE 1 The complete list of elemental macronutrients and micronutrients included in the nutrient treatments to investigate the effect of nutrient availability on post-germination Striga development using mini-rhizotron assays. The column 'Salt' shows the chemical constitution in which each element is applied. The values in the last four columns represent the concentrations (in g/l) of salts in the Long Ashton solution applied (50 mL per plant per day for 35 days) for each nutrient treatment, that is, Base, +Micro, +Macro and +MicroMacro. Base: 25% of the optimal concentration for cereals; +Micro: 100% of the optimal concentration of micronutrients and 25% of the optimal concentration of macronutrients; +Macro: 25% of the optimal concentration of micronutrients and 100% of the optimal concentration of macronutrients; +MicroMacro: 100% of the optimal concentration of micronutrients and macronutrients.

			Nutrient treatments			
	Element	Salt	Base	+Micro	+Macro	+MicroMacro
Macronutrients	K	K_2SO_4	.034848	.034848	.139392	.139392
	Ca	$CaCl_2.H_2O$	.058808	.058808	.235232	.235232
	Mg	$MgSO_47H_2O$	.036976	.036976	.147904	.147904
	P	Na_2HPO_4	.019872	.019872	.079488	.079488
	N	$NH4NO_3$	.040024	.040024	.160096	.160096
Micronutrients	Fe	Fe (EDTA)	.003672	.014688	.003672	.014688
	Zn	$ZnSO_4.7H_2O$	.000029	.000116	.000029	.000116
	Mn	$MnSO_4.4H_2O$	.000223	.000892	.000223	.000892
	Cu	$CuSO_4.5H_2O$	.000025	.000100	.000025	.000100
	B	H_3BO_3	.000309	.001236	.000309	.001236
	Mo	$NaMoO_4.2H_2O$	.000012	.000048	.000012	.000048
	Na	NaCl	.000584	.002336	.000584	.002336

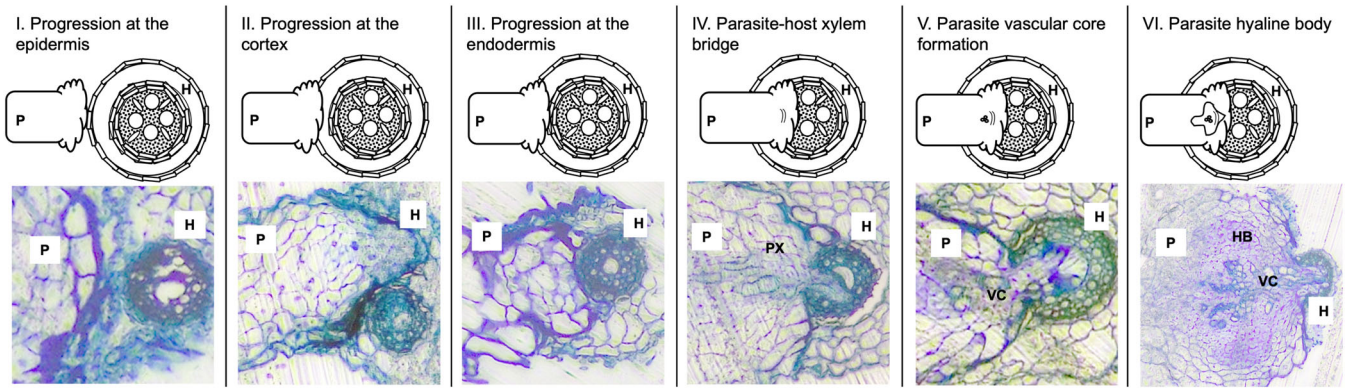

FIGURE 2 Progression of Striga into the sorghum (*Sorghum bicolor* [L] Moench.) host root tissue at different nutrient treatments. The upper panel shows a schematic diagram of the progression of the parasite (P) within the host (H), while the lower panel shows corresponding microscopic images obtained in the current study. Px: parasite xylem (IV), VC: parasite vascular core (V) and HB: parasite hyaline body (VI).

using distilled water and dried for 30 min at 65°C. The dried slides were covered with coverslips and glued using DePex (BDH, Poole, UK) for permanent preservation. The tissues were observed and photographed using a Leica DM750 microscope fitted with a Leica ICC50E camera (Leica, Germany). The microscopic images were scored (blindly) based on the parasite's progression and development, distinguishing six stages (as shown in Figure 2): (1) Striga impediment at the epidermal layer of the host tissue; (2) Striga impediment at the cortex layer of the host tissue; (3) Striga impediment at the endodermal layer of the host tissue; (4) parasite xylem-host xylem connection and the development of the parasite vegetative tissue observed; (5) presence of the parasite vascular core; (6) presence of parasite storage tissue, hyaline body.

At 21 days post-infection, Striga attachments were detached from the sorghum roots using forceps. The Striga attachments were counted, then dried at 80°C for 48 h and weighed using an analytical weighing scale. Three metrics were determined: the number and total biomass dry weight (mg) of Striga attachments on the sorghum roots, and the mean biomass dry weight (mg) per Striga attachment.

2.5 | Data analysis

All data analyses were done using R 4.0.2 (R Core Team, 2021). Linear mixed models were applied to test the effect of nutrient treatments and sorghum genotypes on the three response variables, number of

Striga attachments, total Striga biomass and mean biomass per Striga attachment, using the R package 'nlme' (Pinheiro et al., 2012). Nutrient and sorghum genotype treatments were categorised as fixed effects and the experimental runs and replicates as random effects, and the hierarchical structure of the split plot design was considered. Pairwise differences, based on the estimated marginal means from the mixed models, were tested with a Tukey HSD test using the 'emmeans' package (Russel, 2021).

3 | RESULTS

3.1 | The effects of nutrient treatments and sorghum genotype on Striga infection

Two variables, the number of successful Striga attachments and the total biomass of the Striga plantlets, were used to assess the resistance of sorghum genotypes to Striga.

A significant effect of both nutrient treatments and sorghum genotypes was observed on the number of Striga attachments ($p < .001$, Table 2). Across all genotypes, the treatments supplemented with macronutrients (+Macro and +MicroMacro) resulted in significantly fewer attachments than the low nutrient (Base) and the micronutrient (+Micro) treatments (Figure 3a). Across all nutrient treatments, the number of attachments on Framida and N13 was significantly lower than on Ochuti and IS10978, while IS9830 showed intermediate values (Figure 3b). No significant interaction between the two factors occurred ($p = .147$, Table 2, Figure 3c).

A similar pattern was observed for the main effect of nutrient treatments and genotypes on total Striga biomass (Table 2, Figure 4a,b), with the exception of Framida supporting significantly lower Striga biomass than IS9830 (Figure 4b). However, on Striga biomass, a significant interaction between the two factors was observed ($p = .005$, Table 2, Figure 4c). When assessed independently for each genotype, Ochuti showed a significant reduction in total Striga biomass compared with the Base for all the nutrient treatments, including +Micro (Figure 4c).

3.2 | The effects of nutrient treatments and sorghum genotypes on Striga development

Regarding the mean biomass per Striga attachment, an indicator of Striga plantlets growth, there was no significant effect of the nutrient treatments ($p = .122$, Table 2, Figure 5a). However, there were significant differences in mean Striga biomass between the sorghum genotypes across nutrient treatments ($p = .001$, Table 2). Striga plantlets on Framida showed significantly lower biomass than those on the susceptible Ochuti and two of the other resistant genotypes, IS10978 and IS9830 (Figure 5b), while the mean biomass per Striga attachment on genotype N13 had an intermediate value. No significant nutrient by genotype interaction was observed for biomass per attachment ($p = .451$, Table 2, Figure 4c).

The development of Striga attachments on the sorghum root tissue at 9 days after infection was assessed under a microscope, providing some descriptive insights into the potential mechanisms behind the observed results. For the susceptible genotype Ochuti, an increased frequency of impairment was observed at or before stage III following the +Micro treatment (Figure 6). At IS10978, Striga progression was frequently impaired at or before stage V (i.e., formation of the vascular core), without clear differentiation between nutrient treatments. At IS9830, Striga progression impairment was increasingly observed at stage I (i.e., the host root epidermis) or II (i.e., the host root cortex) following the +Macro treatment. At N13, no cases of Striga progression beyond stage V were observed following +Macro. At Framida, impairment of Striga progression was more frequent following the augmented nutrient treatments (+Micro, + Macro or +MicroMacro). Most notably was the relative frequent impairment at stage I (i.e., the host root epidermis) following the +MicroMacro treatment (Figure 6).

4 | DISCUSSION

The aim of this study was to investigate the effect of the availability of nutrients on post-attachment stages of Striga infection to understand whether such an effect is mediated by micronutrients or macronutrients and whether such an effect specifically enhances any post-attachment Striga resistance mechanisms in sorghum.

4.1 | Effects of nutrient availability on Striga beyond germination

We compared the effect of the type and level of nutrient availability on (1) the parasite infection level, expressed by the numbers and total biomass of Striga attachments, and (2) the parasite performance, expressed by the mean biomass per Striga attachment and its

TABLE 2 Output of the mixed effects model of the effect of nutrient treatments and sorghum genotypes on the number of Striga attachments, total Striga biomass and mean biomass per Striga attachment.

			Number of Striga attachments		Total Striga biomass		Mean biomass per Striga attachment	
	df	denDF	F-value	*p*-value	F-value	*p*-value	F-value	*p*-value
Nutrient (N)	3	51	16.2	<.001	9.0	.001	2.0	.122
Genotype (G)	4	207	7.8	<.001	11.0	<.001	4.9	.001
N * G	12	207	1.4	.147	2.5	.005	1.00	.451

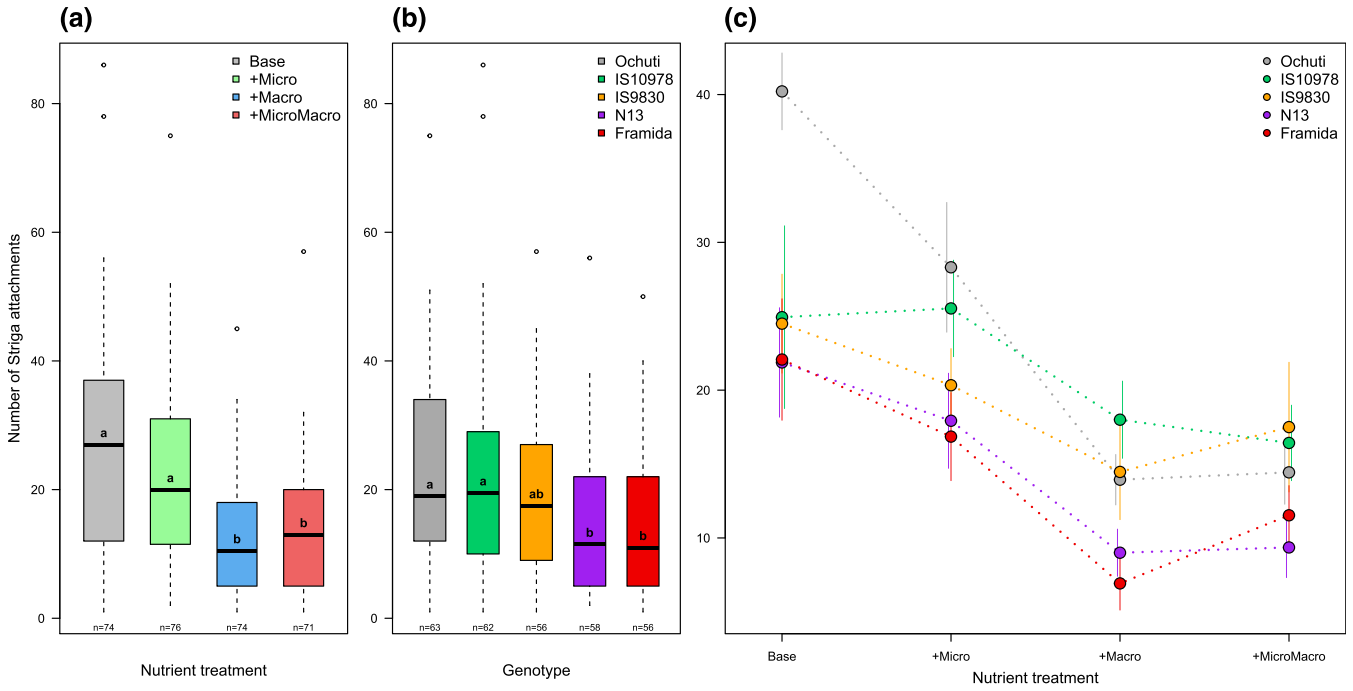

FIGURE 3 The effect of nutrient treatments (a), sorghum genotypes (b) and their interactions (c) on the number of Striga attachments at 21 days after infection. For panels a and b, the boxes show the distribution of the data across all levels of the other factor (genotypes for panel a and nutrient treatments for panel b). Boxes with different letters indicate significant differences at $p < .05$ based on a Tukey post-hoc comparison of estimated marginal means. Numbers under each box show the sample size. Panels a and b: the bold horizontal lines in the boxes indicate the median value; the boxes represent the upper and lower quartiles. The whiskers extend to the most extreme data points within +/−1.5 x interquartile range from the box. For panel c, the points show the mean of the data for the 20 combinations of nutrient treatment levels and genotypes. The error bars in panel c represent ±1 × the standard error of the original data. Sample size for each point was between 12 and 17. Nutrient treatments: 'Base': low concentration l of micronutrients and macronutrients; '+Micro': optimal concentration of micronutrients and low concentration of macro; '+Macro': low concentration of micronutrients and optimal concentration of macronutrients; '+MicroMacro': optimal concentration of micronutrients and macronutrients.

progression into the plant tissue level and towards a viable vascular connection and parasitism.

The application of supplemented macronutrient levels (+Macro, +MicroMacro) significantly reduced the number of Striga attachments and total biomass dry weight across the sorghum genotypes, including the susceptible genotype Ochuti, compared with low nutrient (Base) and supplemented micronutrient (+Micro) treatments. A relative stronger Striga biomass reduction effect was observed on the Striga susceptible genotype Ochuti compared with the Striga resistant genotypes Framida, N13, IS9830 and IS10978.

Various studies have shown that the application of macronutrients and micronutrients induces plant defence responses to pathogenic attack (Dordas, 2009), some of which (e.g., hypersensitivity, lignification) may mechanistically be similar to resistance responses against parasitic plants. The observed high Striga infection level following the low nutrient treatment (Base) is in line with findings of the negative effects of low nutrient availability on plant immunity against pathogens (Val-Torregrosa et al., 2021). The high Striga infection levels at low nutrient availability reflect the relation between poor soil fertility and Striga prevalence in field crops (Kamara et al., 2014; Parker, 2009). Previously, this relation was purely explained based on N- and P-deficiency effects on Striga-germination stimulant production by the host roots. Roots of host plants growing with sub-optimal availability of N and P are observed to increase the production of strigolactones, presumably to attract symbiotic mycorrhizal fungi (Yoneyama et al., 2007). Some of these overproduced strigolactones are potent Striga-germination stimulants, and, therefore, the indirect effect of N- and P-deficiency is an increase in Striga germination and consequently infection (Yoneyama et al., 2013). The reverse has also been demonstrated before: increased availability of N and P, achieved by fertiliser application, aids in the reduction of Striga infection levels (Jamil et al., 2014). Nitrogen and phosphorous availability also indirectly affect the success rate of Striga radicles in finding a host root, as strigolactones are drivers of chemotropism (Ogawa et al., 2022). Singly applied nitrogen further suppresses the formation of haustoria in Striga seedlings (Kokla et al., 2022). The current study shows, for the first time, that macronutrients also play a role in the post-attachment stages of Striga. Which specific macronutrient or combination of macronutrients is particularly mediating this effect remains to be elucidated.

Despite the beneficial effect of micronutrients (e.g., boron and manganese) on plant-pathogen defence responses (Dordas, 2009) that are relevant to parasitic plant resistance (e.g., lignification), in the current study, supplemented micronutrient levels (+Micro) did not

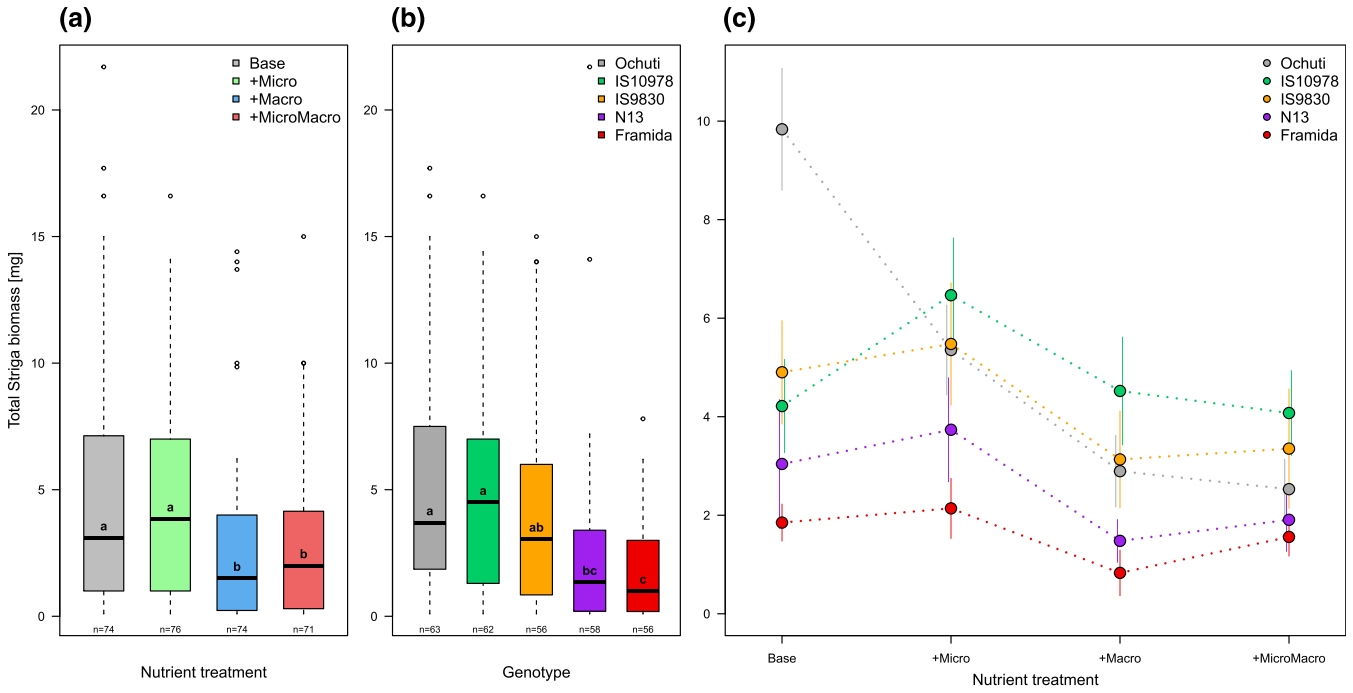

FIGURE 4 The effect of nutrient treatments (a), sorghum genotypes (b) and their interactions (c) on the total Striga biomass at 21 days after infection. For panels a and b, the boxes show the distribution of the data across all levels of the other factor (genotypes for panel A and nutrient treatments for panel b). Boxes with different letters indicate significant differences at $p < .05$ based on a Tukey post-hoc comparison of estimated marginal means. Numbers under each box show the sample size. Panels a and b: the bold horizontal lines in the boxes indicate the median value; the boxes represent the upper and lower quartiles. The whiskers extend to the most extreme data points within +/−1.5 x interquartile range from the box. For panel c, the points show the mean of the data for the 20 combinations of nutrient treatment levels and genotypes. The error bars in panel C represent ±1 × the standard error of the original data. Sample size for each point was between 12 and 17. Nutrient treatments: 'Base': low level of micronutrients and macronutrients; '+Micro': optimal concentration of micronutrients and low level of macro; '+Macro': low level of micronutrients and optimal concentration of macronutrients; '+MicroMacro': optimal concentration of micronutrients and macronutrients.

systematically decrease Striga infections compared with the low nutrient treatment (Base). Only on Striga-susceptible genotype Ochuti, micronutrient application appeared to reduce the biomass of the parasite load. We conclude that micronutrients do not consistently reduce Striga infection in the post-attachment stages. Previous findings have shown that the combination of copper, iron, manganese and zinc might result in an antagonistic interaction, whereby the positive effects of one element are cancelled out by another (Rietra et al., 2017). This might explain the absence of a consistent, notable effect of the micronutrients on post-attachment Striga resistance in the current study.

4.2 | Effects of nutrient availability on post-attachment Striga resistance mechanisms

To answer the second research question, we will zoom in on the nutrient effects on Striga infections across sorghum genotypes with different post-attachment Striga resistance mechanisms.

For Framida, which exhibits resistance through a hypersensitive response (HR), the treatment with supplemented macronutrients (i.e., +Macro, +MicroMacro) significantly reduced the total biomass dry weight of the Striga attachments, and this was most obviously associated with increased impaired Striga progression at the root epidermis following the +MicroMacro treatment. Previous work has shown the role of magnesium, phosphorous and potassium in enhancing the salicylic acid pathway, which plays an important role in inducing HR against fungi and bacteria (Fauteux et al., 2006; Imada et al., 2016; Reuveni et al., 2000; Reuveni & Reuveni, 1998; Wang et al., 2017). Such nutrient effects could explain the observed enhanced HR in sorghum plants, conferring increased resistance against Striga. As mentioned before, the set-up of the current study does not allow identification of the active nutrient involved in enhanced HR in Framida, and this would require further investigation.

Whereas studies on other plant pathogens have shown that micronutrients such as boron, manganese and copper induce systemic resistance, for instance against the pathogenic fungi *Drechslera tritici-repentis* in wheat (*Triticum aestivum*), causing tan spot disease (Simoglou & Dordas, 2006), in the current study, supplementing micronutrients (+Micro) did not result in significant differences in Striga infection levels and clear differences in successful Striga-host xylem connections in Framida compared with the low nutrient treatment (Base).

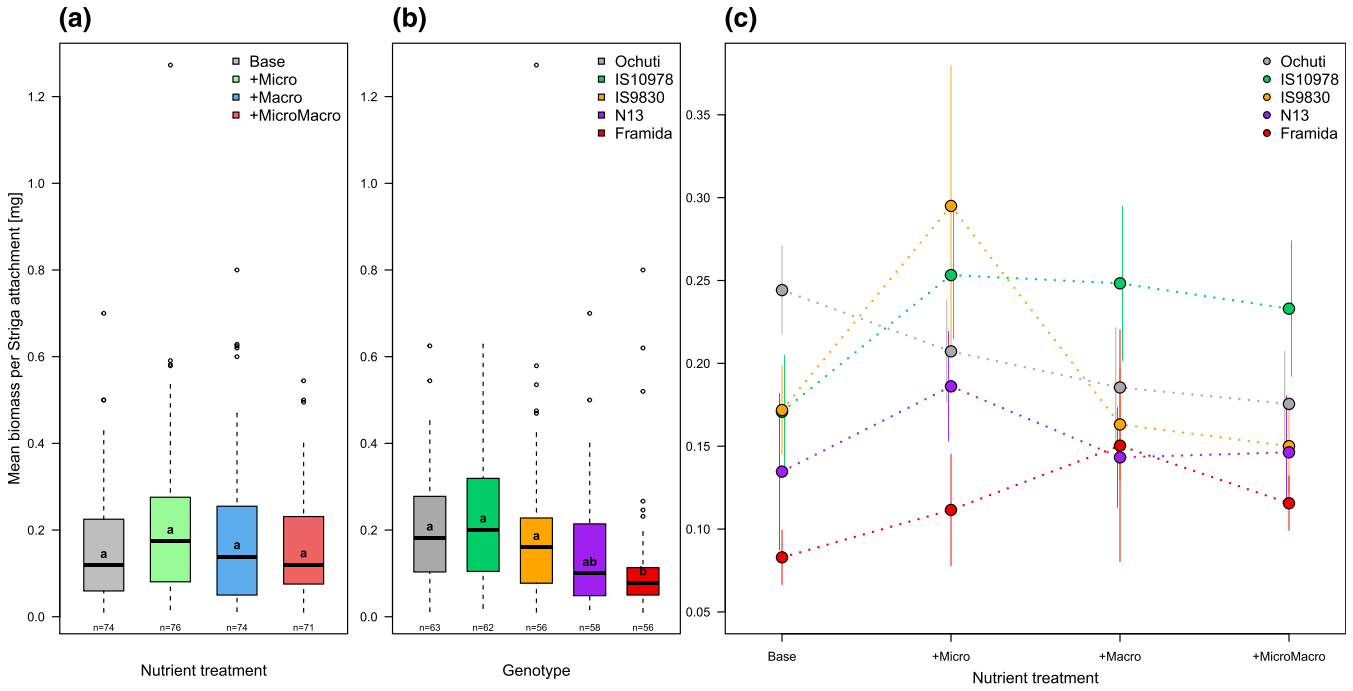

FIGURE 5 The effect of nutrient treatments (a), sorghum genotypes (b) and their interactions (c) on the mean biomass per Striga attachment. For panels a and b, the boxes show the distribution of the data across all levels of the other factor (genotypes for panel a and nutrient treatments for panel b). Boxes with different letters indicate significant differences at $p < .05$ based on a Tukey post-hoc comparison of estimated marginal means. Numbers under each box show the sample size. Panels a and b: the bold horizontal lines in the boxes indicate the median value; the boxes represent the upper and lower quartiles. The whiskers extend to the most extreme data points within +/−1.5 x interquartile range from the box. For panel c, the points show the mean of the data for the 20 combinations of nutrient treatment levels and genotypes. The error bars in panel c represent ±1 × the standard error of the original data. Sample size for each point was between 12 and 17. Nutrient treatments: 'Base': low level of micronutrients and macronutrients; '+Micro': optimal concentration of micronutrients and low level of macro; '+Macro': low level of micronutrients and optimal concentration of macronutrients; '+MicroMacro': optimal concentration of micronutrients and macronutrients.

Striga infection levels (i.e., infection numbers and total biomass dry weight of Striga) on sorghum genotypes N13 and IS10978, previously characterised to harbour mechanical resistance following enhanced root cell wall lignification (Kavuluko et al., 2021; Maiti et al., 1984), were reduced following supplemented macronutrient treatments (+Macro). Further observations on the host root tissue showed a (slightly) higher frequency of impaired Striga penetration at the root tissue cortex or endodermis (IS10978) and root epidermis or endodermis (N13) under supplemented macronutrient treatments (+Macro). However, other nutrient treatments also showed impaired Striga progression in IS10978 and N13, and consequently, the evidence of a specific macronutrient effect remains to be confirmed. Previously, magnesium was shown to play an important role in root lignification (Huang et al., 2019), whereas nitrogen (N), phosphorous (P) and potassium (K) were shown to impair lignin deposition (Entry et al., 1998; Eppendorfer & Eggum, 1994; Fritz et al., 2006; Teixeira et al., 2006; Wang et al., 2015; Zhang et al., 2017; Ziegler et al., 2016).

A potential antagonistic effect of macronutrients on cell walls could perhaps explain the inconsistent results in the current study. Comparable to observations on HR in Framida, the micronutrient treatment (+Micro) did not reduce Striga infection levels in the genotypes with mechanical resistance. Again, this points out potential differences with other plant-pathogen systems. For instance, the effect of micronutrients on mechanical barriers following enhanced lignin biosynthesis has been observed in cucumber (*Cucumis sativus*) against the fungal pathogen *Podosphaera fuliginea* (Eskandari & Sharifnabi, 2020).

Treatments with supplemented macronutrients (i.e., +Macro, +MicroMacro) significantly reduced the total biomass dry weight of Striga attachments in genotype IS9830, harbouring a Striga incompatibility response, compared with nutrient treatments without these supplemented levels of macronutrients (i.e., Base, +Micro). The observations at the host root tissue support this quantitative information on Striga infections only for the +Macro treatment, which showed increased frequencies of impairment at the epidermis and root cortex. Comparable Striga impairment was not observed following +MicroMacro nutrient treatment.

To date, the incompatibility response (IR) mechanism is not well understood in Striga (Mbuvi et al., 2017). The resistance response in IS9830 is described by Kavuluko et al. (2021) as the inability of the parasite haustorium to differentiate and breach the endodermis, but the exact reason for this inability is not yet elucidated. This gap in our knowledge poses a challenge in postulating the physiological pathway

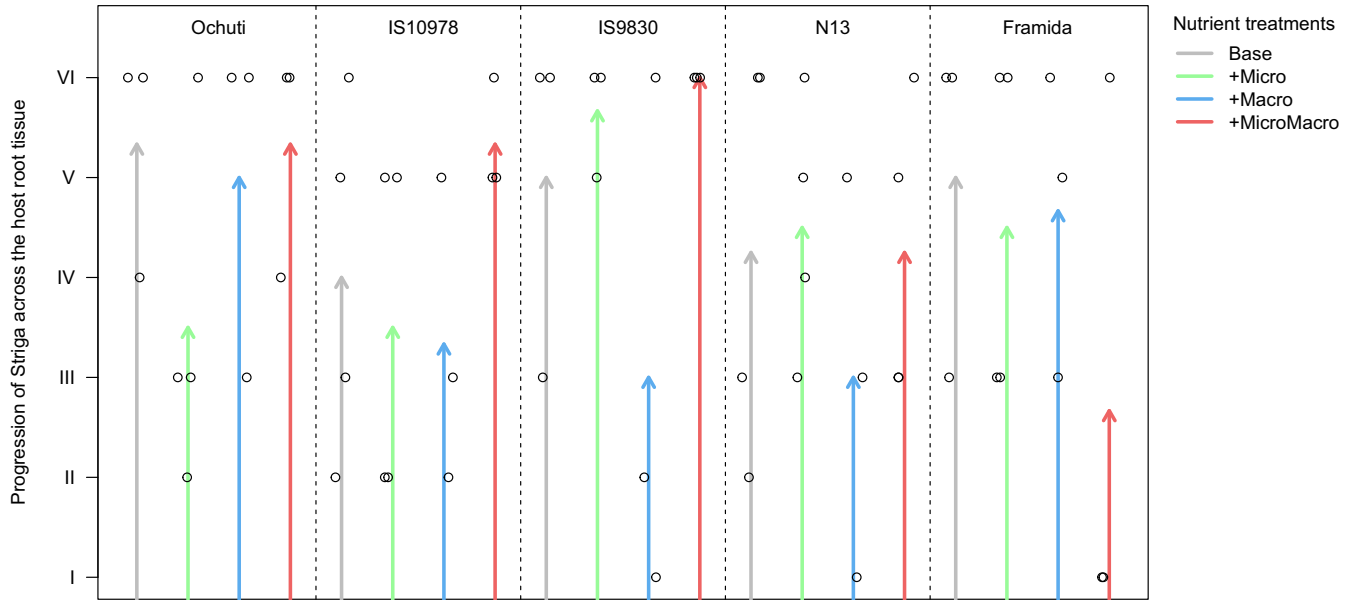

FIGURE 6 Graphical representation of the progression of Striga into the sorghum (*Sorghum bicolor* [L] Moench.) host root tissue for different genotypes and nutrient treatments. Progression reached by Striga attachments is indicated by the different stages (I–VI). The mean progression stages are represented by the tips of the arrows (based on $n = 3$ or $n = 4$ observations), and the empty circles show the individual data points. The arrow colours represent the different nutrient treatments: 'Base' (grey): low level of micronutrients and macronutrients; '+Micro' (green): optimal concentration of micronutrients and low level of macro; '+Macro' (blue): low level of micronutrients and optimal concentration of macronutrients; '+MicroMacro' (red): optimal concentration of micronutrients and macronutrients. On the y-axis, stages I–VI represent the extent of Striga progression (see also Figure 2). I: the host root epidermis; II: the host root cortex; III: the host root endodermis; IV: connection of parasite xylem and host xylem; V: formation of the Striga vascular core; VI: formation of the Striga hyaline body.

that macronutrients seem to play in reducing Striga infection numbers. However, the application of nitrogen has been shown before to impair the growth and development of Striga (Igbinnosa et al., 1996), and increased nutrient availability was observed previously to cause broomrape necrosis after the establishment of a vascular connection (Labrousse et al., 2010). In both previous studies, the mechanisms were not clarified but could be based on increased IR or an attainment of a nutrient-toxicity level in the parasites.

Interestingly, on the susceptible genotype Ochuti, nutrient treatments with supplemented nutrient concentrations (i.e., +Micro, +Macro, +MicroMacro) also showed a strong Striga-reducing effect, and this was associated with increased frequencies of impaired Striga progression at the host root cortex (+Micro) and endodermis (+Micro and +Macro). Hence, the effects of nutrient availability on Striga parasitism seem not to be restricted to those genotypes that already inherently have improved levels of resistance.

Based on the current study, the best combination of Striga control components comprises the genotype Framida, which expresses a hypersensitive response against Striga, and a supplemented level of macronutrients (+Macro). Compared with a Striga susceptible genotype grown under conditions of suboptimal nutrient availability, each of the components (i.e., increased nutrient availability through application of fertiliser or reduced infection success through the use of a resistant host-plant variety) in their own right can significantly reduce Striga infection levels, independent of the Striga germination rate. However, the combination of these two components further reduces the Striga infection levels compared with individual component effects, and this provides valuable leads for integrated Striga management strategies (Figure 7).

We hypothesise that high macronutrient treatments enhance both the innate immunity present in susceptible phenotype and the acquired immunity present in genotypes with post-attachment resistant mechanisms against Striga. Additional studies, such as lignin staining showing mechanical barriers and gene expression analysis on hypersensitive and incompatibility response mechanisms, might potentially give more insight into the mechanisms behind the observed findings.

In conclusion, macronutrients and micronutrients differentially affect the success rate of germinated Striga seedlings developing into viable parasites on sorghum roots. The application of macronutrients improves resistance throughout host plant genotypes, harbouring different levels and mechanisms of post-attachment resistance. The macronutrients alone seem to enhance mechanical resistance and incompatibility responses before or at the host root endodermis; the combination of macronutrients and micronutrients seems to enhance the hypersensitive response at the epidermis level. The application of high micronutrients alone does not seem to have the same effect, although such treatments may reduce parasite biomass loads on genotypes that have no inherent resistance mechanism. A genotype with a hypersensitive response, combined with the application of fertilisers, including macronutrients, seems to provide the most effective reduction in Striga success beyond germination. This highlights the

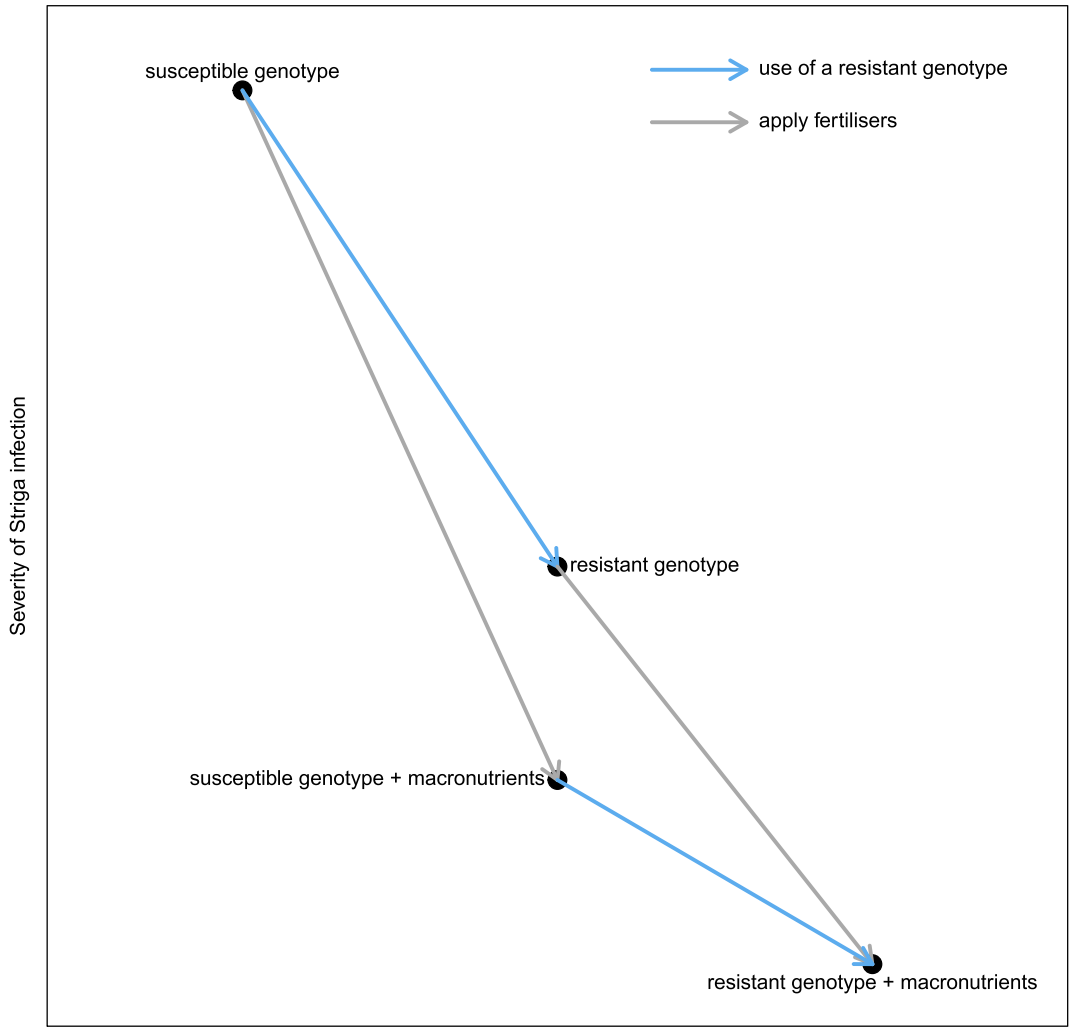

FIGURE 7 Schematic representation of Striga-reducing effects from individual management components (i.e., use of a Striga-resistant genotype or application of fertiliser for increased macronutrient availability) and from a combination of these components (i.e., resistant genotype and fertiliser), demonstrating the potential of integrated Striga management strategies. Relative positions of the black dots and lengths of the arrows are based on actual data presented in this paper.

importance of macronutrients not only in the germination stage of Striga but also in the post-germination and attachment stages. This is a novel finding that, to our knowledge, has not been reported before in the literature. Also, macronutrients seem to not only enhance resistance in resistant genotypes but also reduce Striga infection in susceptible genotypes. The findings reported here provide strong additional support to current fertiliser recommendations for Striga-affected sorghum and other cereal crops in sub-Saharan Africa. By combining a resistant cultivar with adequate levels of (macronutrient-based) fertilisers, farmers not only reduce Striga seed germination rates but also the likelihood of successfully germinated Striga seeds establishing viable connections to a host plant, leading to parasitism and host damage.

AUTHOR CONTRIBUTIONS

Immaculate M. Mwangangi, Lucie Büchi and Jonne Rodenburg designed the research. Immaculate M. Mwangangi, Lucie Büchi, Jonne Rodenburg and Steven Runo wrote the manuscript. Immaculate M. Mwangangi collected the data. Immaculate M. Mwangangi and Lucie Büchi analysed the data and created the figures. Immaculate M. Mwangangi and Steven Runo prepared the microscopic images.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support these findings are available on request from the corresponding author.

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