Research Article

In Vitro and In Vivo Evaluation of Sorghum (*Sorghum bicolor* L. Moench) Genotypes for Pre- and Post-attachment Resistance against Witchweed (*Striga asiatica* L. Kuntze)

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Sorghum (*Sorghum bicolor* L. Moench) production in sub-Saharan Africa is seriously constrained by both biotic and abiotic stresses. Among the biotic stresses is witchweed (*Striga* spp.), a noxious parasitic weed causing major damage in cereal crops, such as sorghum. However, resistance through reduced germination stimulant production or altered germination stimulant composition provides a sustainable and most effective way for managing the parasitic weeds. Laboratory and glasshouse experiments were conducted using seven (7) sorghum genotypes to evaluate their resistance or tolerance the witch weed (*Striga asiatica* L. Kuntze). The first experiment was a laboratory agar gel assay arranged in a completely randomized design with six (6) replications to evaluate the effects of the seven (7) sorghum genotypes on the production of strigolactones by determining the percentage germination and the furthest germination distance of the *Striga* seeds. The second experiment was a seven (7) (sorghum genotypes)∗two (2) (*Striga* treatments) factorial glasshouse experiment conducted to evaluate the effects of *Striga* on sorghum growth, physiological and yield components of sorghum, *Striga* syndrome rating, and number of *Striga* per plant. The genotypes showed a significant ($p < 0.05$) difference in germination percentage and furthest germination of *Striga* seeds in the agar gel assay. Genotypes SV4, Mahube, and ICSV 111 IN showed the least germination percentage and lowest germination distance, implying that these varieties either produced low strigolactones or altered their composition. In contrast, Kuyuma, Wahi, SV2, and Macia caused high *Striga* seed germinations and high furthest germination distances, suggesting that these sorghum genotypes were susceptible to *Striga* infection. The sorghum × *Striga* × time interactions were significant ($p < 0.05$) on sorghum height. It was found that the heights of sorghum genotypes ICSV 111 IN and Mahube were not altered by *Striga* infection, but the heights of Kuyuma, Macia, SV2, SV4, and Wahi were reduced by *Striga* infection. The interaction of sorghum∗*Striga* effects was significant ($p < 0.05$) on chlorophyll fluorescence. *Striga* infection did not alter the chlorophyll content of ICSV 111 IN and SV4. The sorghum∗*Striga* interaction effects were significant ($p < 0.05$) on head index, leaf biomass, leaf index, root biomass, root index, plant biomass, and root : shoot ratio. Assessing *Striga* tolerance based on sorghum heights, chlorophyll content, and root : shoot ratio parameters, it could be concluded that the sorghum genotypes Mahube, ICSV 111 IN, and SV4 tolerated *Striga* infection, whereas Kuyuma and SV2 could be susceptible.

1. Introduction

Sorghum (*Sorghum bicolor* L. Moench) is one of the most important cereal crops in the world after rice (*Oryza sativa* L.), maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), and barley (*Hordeum vulgare* L.) [1]. The crop is a primary food grain for millions of people in the semiarid tropics of Africa, Latin America, and Asia [2]. However, the production of

sorghum in sub-Saharan Africa (SSA) is mainly constrained by *Striga*, commonly known as witch weed, which is a root parasitic weed [3]. Mrema et al. [4] reported that sorghum yield losses due to *Striga* could reach 90%, especially in susceptible genotypes. Sorghum grain yield losses due to *Striga* ranged from 20 to 80% in Africa, reaching 100% under intensive infection, leading to fields being abandoned [1]. *Striga asiatica* L. Kuntze, which is the most problematic parasitic weed affecting cereals in Southern Africa, is responsible for about 26% loss of sorghum and millets in Africa, thereby compounding the food insecurity problem [5]. Furthermore, it was reported that sorghum estimated losses due to *Striga* infection could reach US$ 7 billion per annum [6, 7]. *Striga* species have mainly been found to cause very serious sorghum grain yield losses in the low soil fertility environments, where smallholder farmers hardly apply inorganic fertilizers [8–11].

Striga belongs to the Orobanchaceae family [12] and is an obligate hemiparasite which requires a host during the greater part of its life cycle although it possess chlorophyll [13]. Most of the *Striga* species affect monocotyledonous cereals such as sorghum, rice, maize, and millets except *S. gesneroides* (Wild.) Vatke which affects dicotyledonous plants such as cowpea (*Vigna unguiculata*) and tobacco (*Nicotiana tabacum* L.) [14, 15]. The weed only germinates in response to strigolactones produced by the host and inflicts damage through its haustoria by withdrawing nutrients and other important growth components from the host during its life cycle [8]. The strigolactones have been found to be composed of 5-deoxystrigol, sorgomol, orobanchol, sorgolactone, ent-2′-5-orobanchol, and ent-2′-5-deoxystrigol [16, 17]. The extent to which the *Striga* seed germinates depends on the composition of the strigolactones produced by the sorghum roots [16].

Although there are several *Striga* control methods which are available for smallholder farmers, no single method has been found to be sufficiently effective in reducing this problem. Some of these methods which have been used with little success include hand hoeing, addition of inorganic fertilizers specifically nitrogen, crop rotation, intercropping, use of trap crops, herbicides, germination stimulants, and recent use of resistant or tolerant varieties [18, 19]. It has been shown that biological *Striga* control strategies would be the most feasible approach to control *Striga* in smallholder farming conditions [19–23]. Biological control of *Striga* involves the use of living organisms, e.g., insects, fungi, and other plants. Gworgwor and Weber [20] demonstrated the importance of arbuscular mychorrhizal fungi in reducing *Striga* infection in sorghum. It was also shown that mycoherbicides, specifically, *Fusarium oxysporum* (isolate PSM-197) increased the profitability of growing sorghum in *Striga* infected areas [21]. Khan et al. [22] demonstrated that intercropping sorghum with *Desmodium* or *Crotolaria* reduced *S. hermonthica* infection. Furthermore, it was shown that intercropping soya bean (*Glycine max* L.) with sorghum and seed treatment with *Parkia biglobosa* pulp reduced *Striga* infection in sorghum [23]. The integration of biological control with *Striga* tolerant or resistant sorghum genotypes could be the most effective method of controlling *Striga* in sorghum, rather than using biological control on its own. For example, it was clearly demonstrated that *Striga* resistance/tolerance in sorghum could be combined with *Fusarium oxysporum* sp. *strigae* to reduce the *S. hermonthica* and *S. asiatica* infestation in sorghum [4, 20].

The identification of sorghum genotypes with *Striga* resistance or tolerance could hold the key for developing an integrated control of *Striga* which uses a biological component. *Striga* resistance refers to the ability of plant to reduce or prevent infestation and reproduction of the parasite [24]. Conversely, Rodenburg and Bastinaas [25] defined tolerance as the ability of the plant to support equally severe levels of infection as other varieties of the same host species without associated impairment of growth or loss of grain yield. According to Jamil et al. [26], pre-attachment resistance is dependent on the quantity and quality of strigolactones produced by the host plant, whilst post-attachment resistance implies the ability of crop to produce its potential yield regardless of its level of infestation [27].

Therefore, crop improvement using sorghum varieties which are resistant or tolerant to *S. asiatica* offers a more feasible and sustainable solution [28]. The combination of pre- and post-attachment mechanism to *Striga* species in sorghum can provide a more durable measure of control of the parasite. Hence, the objective of this study was to identify sorghum genotypes which exhibit traits of resistance or tolerance to *S. asiatica*.

2. Methodology

2.1. Site.
The study was carried out between January 2019 and August 2019 at the University of Zimbabwe's Department of Crop Science (17.78°S, 31.05°E and altitude 1523 m).

2.2. Experiment 1

2.2.1. In Vitro Screening of Sorghum Genotypes for Pre-attachment Resistance to S. asiatica.
The experiment was laid out as a completely randomized design (CRD) with six replicates per treatment with two replications. Seven sorghum genotypes obtained from ICRISAT and SEEDCO were used in the in vitro study (Table 1).

2.2.2. Experimental Procedure.
The sorghum genotypes were tested for stimulant production and haustorium initiation by *S. asiatica* in the Weed Science Laboratory at the University of Zimbabwe using the agar gel method as described by IITA [12]. Sterilization of *S. asiatica* seeds was achieved by immersing a total of 0.02 g (10 000 seeds) in 1% sodium hypochlorite solution for 30 minutes. These seeds were thereafter rinsed three times in 10 ml of distilled water before setting up the experiment. The seeds were then placed in 9 cm diameter Petri dishes, sealed with parafilm and incubated for 14 days at 25°C [29]. Ten seeds for each sorghum genotype were soaked in 1% sodium hypochlorite solution for 30 minutes and afterwards rinsed three times with distilled water. The sorghum seeds were then transferred to 9 cm diameter Petri dishes lined with moist

TABLE 1: Sorghum genotypes used in the in vitro experiment.

Genotype	Days to maturity	Height (cm)	Yield potential (t/ha)	Origin	Colour
Mahube	130	125	3	ICRISAT	Red
ICSV 111 IN	115	129–140	6	DRSS	White
SV2	115–125	140–180	6	ICRISAT	White
Kuyuma	110	100–120	3	ICRISAT	White
Wahi	125	145–170	5	ICRISAT	White
SV4	113–127	113–127	9	ICRISAT	White
SC Macia	120	120–150	5	SEEDCO	White

Whatman number 2 filter paper for pregermination and incubated in the dark at 28°C for 48 hours [30]. Only the healthy looking germinated seeds per genotype were selected for the agar gel assay. The conditioned *S. asiatica* seeds (100 μl) were pipetted into 9 cm diameter Petri dishes using a micropipette. A total of 30 ml (1.05 g of agar) of cooling autoclaved water agar in 150 ml of distilled water were poured onto the *S. asiatica* seeds in each Petri dish shaking it well to ensure even distribution of seeds before it solidified. A germinating sorghum seed was then submerged in the solidifying agar near the edge of the plate, with the root tip pointing across the plate. The Petri dishes were then incubated at 25°C for 72 hours before the first data recording.

2.2.3. Data Collection. Data were collected on germination percentage and furthest germination distance. The Petri dish was divided into four quarters which were clearly marked. Within the demarcated boxes, a total number of *S. asiatica* seeds were counted, and a total number of germinated seeds focused from the bottom of the Petri dish at ×40 magnification. The results were collected from four different spots at which the microscope viewing areas were focused. Germination percentage was calculated using the formula below:

$$\text{germination}\,(\%) = \frac{\text{number of germinated } S.\ asitaica \text{ seeds in the demarcated box}}{\text{total number of } S.\ asiatica \text{ seeds in the demarcated box}} * 100. \tag{1}$$

The furthest distance (cm) of germinating *Striga* seeds from the root of sorghum seedling was used as an index for stimulant production by the host plant, and the distance was recorded, as described by Reda et al. [31] and Berner et al. [12], whereby distance from the furthest germinating *Striga* seed to the sorghum root was recorded using a graduated microscope micrometre.

2.3. Experiment 2

2.3.1. In Vivo Evaluation of the Effect of S. asiatica on the Physiology, Growth, and Biomass of Sorghum Genotypes. The experiment was arranged in a 7 ∗ 2 factorial treatment in a Randomised Complete Block Design (RCBD) with six replications. Factor one was the sorghum genotypes with seven levels (Table 1), and the second factor was *Striga* infestation with two levels (*Striga* infested and noninfested sorghum).

2.3.2. Experimental Procedure. A total of 84 perforated black polythene bags measuring 18 cm diameter and 30 cm height were filled with sandy soil up to three quarters full. The chemical-physical properties of the soil used are shown in Table 2.

The top 8 cm of the soil in the polythene bags was thoroughly mixed with 6 g of compound D (7% N, 14% P_2O_5, and 7% K_2O) basal fertilizer to achieve an application rate of 10.2 kg·N·ha^{-1}, 7.8 kg·P·ha^{-1}, and 8.6 K·ha^{-1}. In 50%

of the pots, the top soil was thoroughly mixed with 0.05 g of *Striga* seeds (approximately 12,580 seeds). Preconditioning of Striga seeds in infested posts was done by watering the soil to field capacity prior to sowing of the sorghum genotypes [1]. Ten sorghum seeds were then planted at a depth of 2 cm in moist soil for all genotypes in both infested and noninfested pots. All work from planting was undertaken by moving from noninfested to infested pots to avoid contamination. Sorghum seedlings were thinned to one plant pot^{-1} at two weeks after crop emergence (WACE). Watering was done at a rate of 400 ml pot^{-1} twice a week to mimic approximate rainfall received in marginal areas. Other weeds were removed from the pots by hand pulling to allow interaction only between sorghum and *S. asiatica*. Ammonium nitrate (34.5% N) was split applied at 1 g pot^{-1} at 4 and 6 WACE to achieve a rate of 30 kg·N·ha^{-1} [32]. These low N-levels were used to mimic typical smallholder farmer conditions [33].

2.3.3. Data Collection. Data were collected on several parameters including plant height, days to flowering, chlorophyll content, chlorophyll fluorescence, and biomass. The plant height of sorghum was measured weekly from week 4 until week 16 using a metre rule from the soil level to the ligule of the last fully expanded leaf following a method that was described by Nyakurwa et al. [5]. The plant internode length was measured as the average length of each plant's internodes at harvest. Sorghum days to flowering were

TABLE 2: Chemical and physical properties of soil used in the study.

pH (CaCl$_2$)	N (mg/kg)	P (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	Na (mg/kg)	Clay (%)	Silt (%)	Sand (%)
3.66	0.005	2.05	11.00	0.02	13.47	3.50	2.00	7.5	90.5

recorded by counting number of days taken by each sorghum plant to flower from day of planting. A SPAD-502 chlorophyll metre (Minolta Corporation, Ltd., Osaka, Japan) was used to record chlorophyll content on the sorghum genotypes nondestructively [34]. The readings were taken on young, fully developed leaves between 1200 and 1300 hours at 8, 10, and 12 WACE. Chlorophyll fluorescence (Fv/Fm) was measured using a portable pulse-modulated OS-30p + chlorophyll fluorimeter (Opti-Sciences, Inc., Hudson, NH, USA), with Fv = variable fluorescence and Fm = the maximal fluorescence value. Measurements were taken on the youngest, fully developed leaves after 30 minutes of dark adaptation using clips provided with the instrument [35]. The readings were taken between 1300 and 1500 hours at 8, 10, and 12 WACE.

After harvesting, the stems were cut off at the base just above the roots, and the leaves were pruned off the stem and then placed in khaki envelopes. Samples were oven-dried for 36 hours at 80°C. The roots were uprooted, cleaned using water before being placed in the khaki papers, and then oven-dried at 80°C. After drying, different plant parts were weighed using a sensitive balance (Compact Scales and Bances–Adams Equipment, USA). Total above ground biomass was obtained by adding the dry weight of the leaves and the stem.

The root dry biomass of each genotype was divided by the total above ground biomass (leaves and stem) to obtain the root to shoot ratio. Indices were calculated as the ratio of a plant tissue to the whole plant weight using the following formula:

$$\text{tissue index} = \frac{\text{tissue weight}}{\text{whole plant weight}}, \qquad (2)$$

where tissues included head, leaf, stem, and root tissue weight.

2.4. Striga Parameters.

Striga asiatica counts were recorded as individual *Striga* emerged plant count pot^{-1} at harvest. *Striga* or haustorial root attachments were recorded as numerical counts of visible attachments of *S. asiatica* to the root of the sorghum plants. Measurements were obtained by gently washing away all the soil surrounding the root area and recording all successful visible attachments. After harvesting of sorghum plants, *Striga* plants were separated from the sorghum plants, washed-off of soil, and placed into the khaki envelopes before being oven-dried for 36 hours in an oven drier at 80°C. The readings were then taken using a sensitive weight scale (Compact Scales and Bances–Adams Equipment, USA).

2.5. Data Analysis.

Data were tested for normality and homogeneity of variance using Ryne–Joiner and Bartlett's test, respectively. Data were then subjected to analysis of variance (ANOVA) using Genstat 14th version. Repeated measures ANOVA were carried out for plant height, chlorophyll content, and chlorophyll fluorescence. Means were separated using Fisher's protected least significant differences (LSD) at the 5% significance level.

3. Results

3.1. Agar Gel Experiment Effect of Root Exudates Produced by Different S. bicolor Genotypes on S. asiatica Germination Percentage and Furthest Germination Distance.

There was a significant ($p < 0.05$) difference among genotypes on germination percentage and furthest germination distance of *S. asiatica* seeds (Table 3). Significantly, a lower germination percentage was found in genotypes Mahube, SV4, and ICSV 111 IN than in Kuyuma, Wahi, and Macia (Table 4). The varieties SV4, ICSV 111 IN, and Mahube had furthest germination distances that were significantly lower than the others. The lowest germination distance was 0.035 cm, and it was observed in SV4, whilst the highest was 2.348 cm for Kuyuma (Table 4).

3.1.1. Effect of S. asiatica on the Height of Different Sorghum Genotypes.

There was a significant *Striga* infestation × genotype × time interaction ($p < 0.05$) on sorghum height (Table 4). *Striga* infection significantly reduced plant height in all genotypes from week 8 to 16 except ICSV 111 IN which showed that height was not significantly different under both infested and noninfested environments (Figure 1).

3.1.2. Effects of S. asiatica on Sorghum Internode Length.

There was a significant ($p < 0.05$) interaction between *Striga* infestation and sorghum genotypes on internode length (Table 4). *Striga* infection significantly reduced sorghum internode length except for Mahube and SV4 whose internode length was not reduced by *Striga* parasitism (Figure 2).

3.1.3. Effect of S. asiatica on Days to Flowering of Sorghum Genotypes.

There was no significant ($p < 0.05$) genotype × *Striga* infestation interaction on days to flowering of different sorghum genotypes (Table 5). Days to flowering significantly differed ($p < 0.05$) among sorghum genotypes (Table 4). The variety varieties Kuyuma and SV2 took significantly a longer period to flower compared to other genotypes (Table 6). *S. asiatica* infestation significantly ($p < 0.05$) delayed flowering in sorghum genotypes (Table 6).

3.1.4. Striga Effects on Chlorophyll Content of Sorghum Genotypes.

There was no significant ($p < 0.05$)

TABLE 3: Mean squares and significant tests on the *S. asiatica* seed germination maximum germination distance from the sorghum root.

Source of variation	df	*S. asiatica* seed germination	*S. asiatica* maximum germination distance
Sorghum genotype	6	12068.0***	10.896***
Residual	77	200.9	0.2084
Total	83		

***Significant at 0.1% probability level.

TABLE 4: Effect of strigolactones produced by different sorghum genotypes on *S. asiatica* germination percentage and furthest germination distance.

Genotype	Germination (%)	Furthest germination distance (cm)	Days to flowering	Chlorophyll fluorescence (mmol m^2·s^{-1})
Mahube	3.43^a	0.25^a	87.67^a	0.66
ICSV 111 IN	2.32^a	0.13^a	87.25^a	0.64
SV2	58.96^{bc}	1.76^c	92.25^b	0.67
Kuyuma	69.86^c	2.35^d	94.67^b	0.64
Wahi	64.86^c	1.02^b	87.67^a	0.63
SV4	0.97^a	0.04^a	86.50^a	0.64
Macia	48.79^b	1.92^d	86.50^a	0.645
p value	<0.001	<0.001	<0.01	0.525
SED	6.960	0.190	6.712	0.019
LSD	13.860	0.378	1.986	ns

Means followed by the different letters in the column are significantly different at $p < 0.05$.

Striga × genotype × time interaction on chlorophyll content (Table 5). However, there was a significant interaction ($p < 0.05$) between genotypes and *Striga* infestation on chlorophyll content (Table 4). Genotypes Kuyuma, Macia, SV2, and Wahi showed a significant reduction in chlorophyll content under *Striga* infestation (Figure 3). Conversely, *S. asiatica* infection did not significantly affect chlorophyll content of genotypes Mahube, ICSV 111 IN, and SV4.

3.1.5. S. asiatica Effects on Chlorophyll Fluorescence. The *Striga* infestation × genotype × time and genotype × *Striga* infestation interaction was not significant ($p < 0.05$) on chlorophyll fluorescence of sorghum genotypes (Table 4). There were no significant ($p < 0.05$) differences among genotypes on chlorophyll fluorescence (Table 5). Similarly, *Striga* infestation did not significantly affect chlorophyll fluorescence of sorghum genotypes ($p < 0.05$) (Table 6).

3.1.6. Effect of Sorghum Genotypes on Striga Counts, Haustorial Attachments, and Biomass. There was a significant difference ($p < 0.05$) on the effect of sorghum genotypes on *S. asiatica* counts, haustorial attachments, and biomass (Table 7). Genotypes Mahube and Wahi did not support *S. asiatica* emergence. Genotype Kuyuma supported a significantly ($p < 0.05$) higher number of *S. asiatica* attachments to sorghum roots compared to the other genotypes (Table 7). In addition, genotypes Kuyuma and Macia had significantly higher *S. asiatica* counts and biomass than the other genotypes (Table 7).

3.1.7. Effect of Striga on the Yield Parameters of Sorghum Genotypes. A summary of the mean square values for the yield parameters of sorghum genotypes used in the study is shown in Table 8.

3.1.8. Effect of S. asiatica on Head Biomass. There was no significant genotype × *Striga* interaction ($p < 0.05$) on sorghum head biomass (Table 8). However, head biomass significantly ($p < 0.05$) differed among sorghum genotypes (Table 8). Genotype Kuyuma had significantly a lower head biomass than the other genotypes, whilst Mahube produced significantly a higher head biomass than the other genotypes (Table 9). *Striga* infection significantly ($p < 0.05$) reduced head biomass of sorghum (Table 10).

3.1.9. Effect of S. asiatica on Sorghum Head Index. There was a significant ($p < 0.05$) interaction between genotypes and *Striga* infestation on head index of sorghum (Table 8). *Striga* infestation reduced head index of only sorghum genotype SV2 (Figure 4). It was noted that the genotype Mahube had the highest head index compared to other genotypes with or without *Striga* infection.

3.1.10. Effect of S. asiatica on Leaf Biomass. There was a significant genotype × *Striga* infestation interaction ($p < 0.05$) on sorghum leaf biomass (Table 8). *Striga* infection significantly ($p < 0.05$) reduced leaf biomass of the sorghum genotypes except for genotypes Mahube and Wahi which were able to maintain their leaf biomass across *Striga* levels (Figure 5). Genotype SV2 had a significantly ($p < 0.05$) higher leaf biomass in infested than in uninfested plants.

3.1.11. Effect of S. asiatica on Sorghum Leaf Index. There was a significant genotype × *Striga* infestation interaction ($p < 0.05$) on sorghum leaf index (Table 8). *Striga* infection significantly reduced leaf index of sorghum genotype ICSV
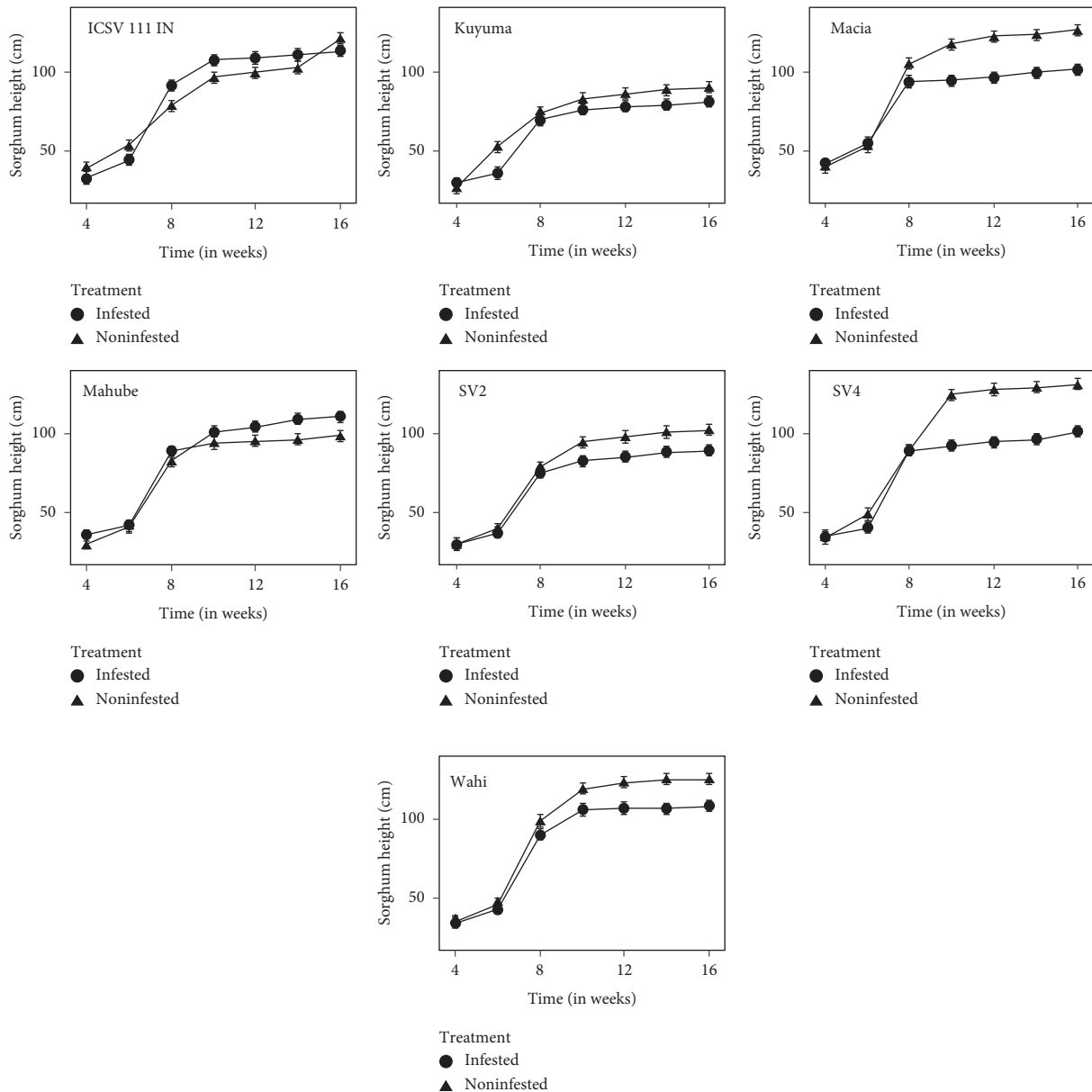
FIGURE 1: Effect of *S. asiatica* infection on sorghum height recorded in the pot experiment. Error bars indicate LSD at $p < 0.05$.

111 IN only (Figure 6). In contrast, noninfested plants had a higher leaf index than noninfested plants.

3.1.12. Effect of S. asiatica on Sorghum Stem Biomass. There was no significant interaction ($p < 0.05$) between sorghum genotypes and *S. asiatica* infestation on stem biomass (Table 8). However, there was a significant difference ($p < 0.05$) between genotypes on stem biomass (Table 8). Genotypes differed significantly on stem biomass, with genotypes SV4 and Macia showing highest stem biomass (Table 9). *Striga* infection significantly ($p < 0.05$) reduced stem biomass of sorghum genotypes (Table 10).

3.1.13. Effect of S. asiatica on Sorghum Stem Index. There was no significant interaction ($p < 0.05$) between sorghum genotypes and *S. asiatica* infestation on stem index (Table 8). The sorghum genotype Mahube had the lowest stem index. *S. asiatica* infection significantly reduced stem index (Table 9). However, there were significant differences ($p < 0.05$) among genotypes and between *S. asiatica* infestation levels on stem index (Table 10).

3.1.14. Effect of S. asiatica on Root Biomass of Sorghum Genotypes. There was a significant interaction ($p < 0.05$) between genotypes and *S. asiatica* infestation on root biomass (Table 8). Root biomass was high in *S. asiatica* infested than uninfested sorghum plants (Figure 7). However,
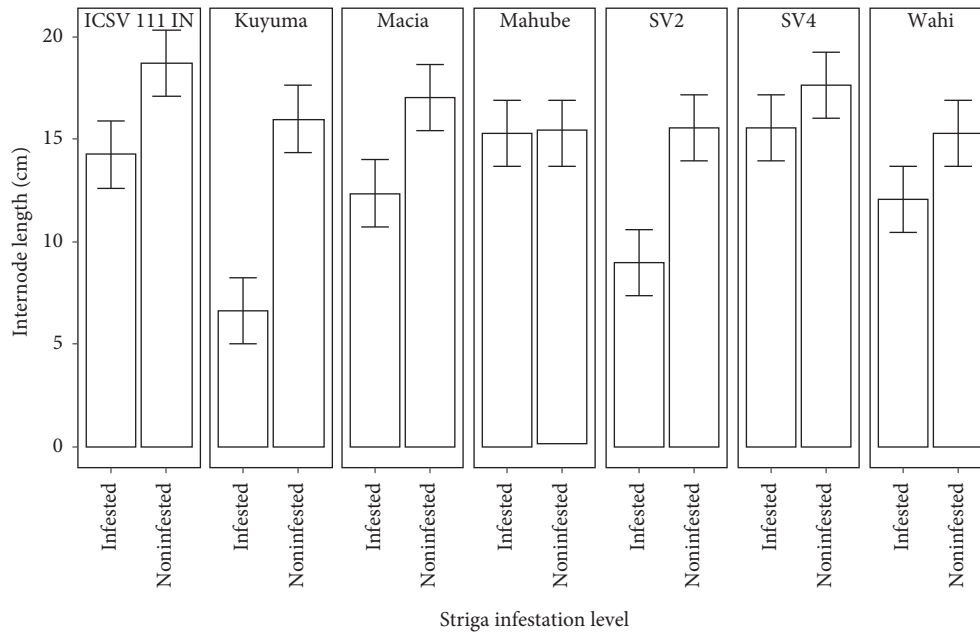
FIGURE 2: Effect of *S. asiatica* infestation on sorghum genotypes internode length recorded under pot experiment. Error bars indicate LSD at $p < 0.05$.

TABLE 5: Response of sorghum genotypes to *S. asiatica* infestation under pot environments.

Source	Height (cm)	Internode length (cm)	Days to flowering	Chlorophyll content (mmol m^2)	Chlorophyll fluorescence (mmol $m^2 \cdot s^{-1}$)
Block	876.36	12.41	125.19	15.22	0.09
Genotype	6538.50***	49.05***	125.18**	330.39***	0.008ns
Striga	10133.47***	359.12***	756.00***	2165.39***	0.003ns
Genotype * *Striga*	9351.23***	27.70*	60.42ns	278.48***	0.007ns
Genotype × *Striga* × time	8009.01***	N/A	N/A	8.34ns	0.009ns
Residual	19877.62	7.91	29.32	18.24	0.009

*, **, and *** represent significance at the 5%, 1%, and 0.1% probability levels, respectively. ns, not significant at 5% probability level; N/A, not applicable.

TABLE 6: Effect of *S. asiatica* on the days to flowering of sorghum.

Treatment	Days to flowering	Chlorophyll fluorescence (mmol $m^2 \cdot s^{-1}$)
Striga	91.90[b]	0.6461
No *Striga*	85.90[a]	0.6523
p value	**<0.001**	**0.544**
SED	**7.241**	**0.010**
LSD	**3.545**	**Ns**

Means followed by the different letters in the column are significantly different at $p < 0.05$.

genotypes Mahube and Wahi maintained their biomass under both *Striga* levels. Interestingly, genotype SV4 had high biomass on the noninfested plants.

3.1.15. Effect of S. asiatica on Sorghum Root Index. There was a significant interaction ($p < 0.05$) between the sorghum genotypes and *Striga* infestation on root index (Table 8). *Striga* infestation significantly increased root index of sorghum genotypes except for genotypes Mahube, SV4, and Wahi (Figure 8).

3.1.16. Effect of S. asiatica on Sorghum Whole Plant Biomass. There was a significant ($p < 0.05$) interaction between genotypes and *Striga* infestation on sorghum whole plant biomass (Table 8). All genotypes maintained whole plant biomass across *Striga* infestation levels except for genotype SV4 whose whole plant biomass was significantly reduced by *Striga* infection (Figure 9).

3.1.17. Effect of S. asiatica on Sorghum Root to Shoot Ratio. There was a significant ($p < 0.05$) interaction between genotypes and *Striga* infestation on sorghum root to shoot ratio (Table 8). *Striga asiatica* infection significantly reduced root to shoot ratio of sorghum genotypes except Mahube and SV4 which maintained their root to shoot ratio in divergent *Striga* infestation environments (Figure 10).

3.1.18. Effect of S. asiatica on Grain Yield of Sorghum Genotypes. The genotype × *S. asiatica* infestation interaction was not significant ($p < 0.05$) on sorghum grain yield (Table 8). Genotypes differed significantly ($p < 0.05$) in grain yield with genotype Mahube having the highest grain yield which was significantly different from the other genotypes
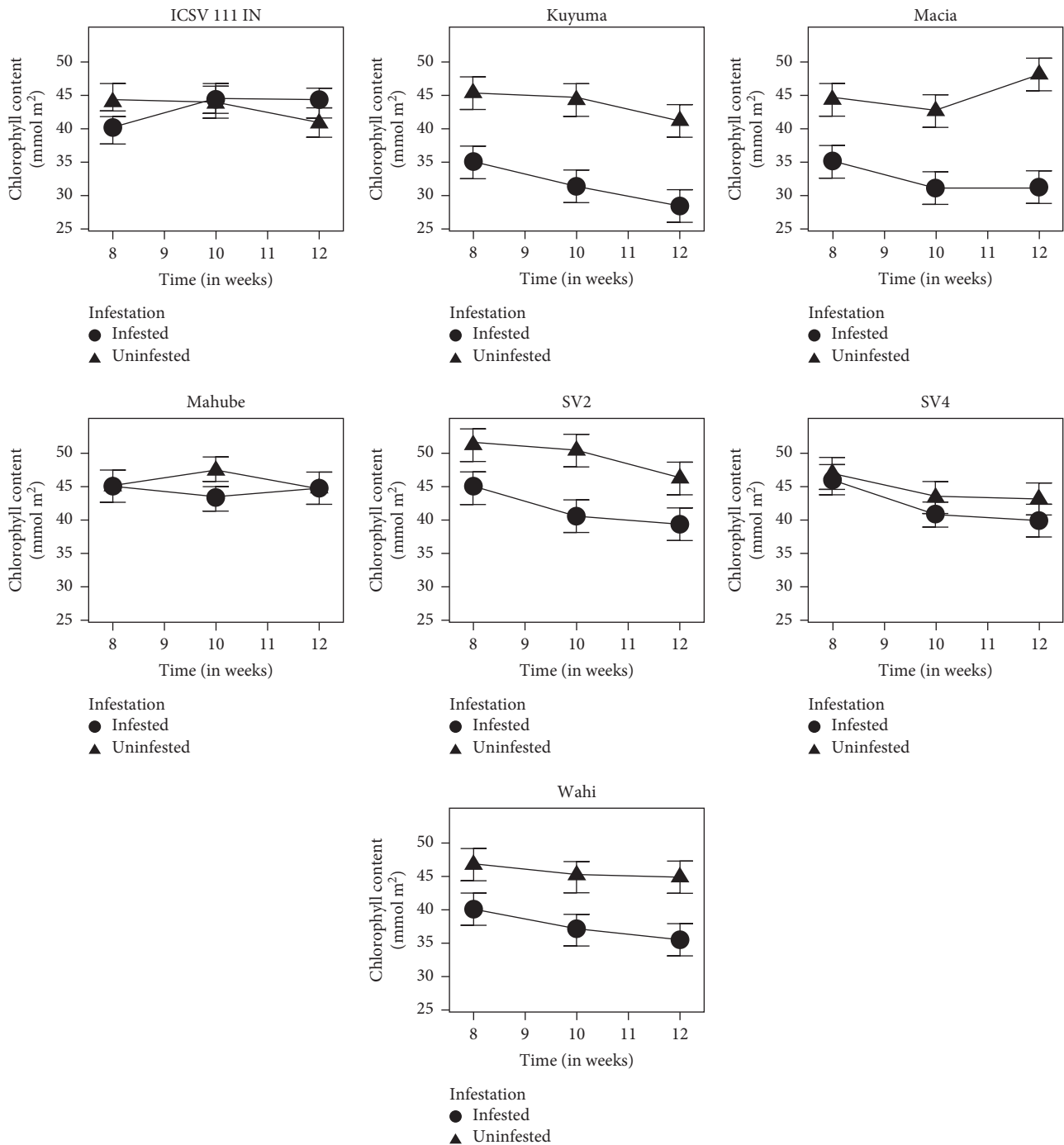
FIGURE 3: Effect of *S. asiatica* infestation on chlorophyll content of sorghum genotypes recorded in pot experiment. Error bars indicate LSD at $p < 0.05$.

(Table 9). *Striga* infestation significantly ($p < 0.05$) reduced grain yield of sorghum genotypes (Table 10).

4. Discussion

4.1. Effect of Root Exudates Produced by Different S. bicolor Genotypes on S. asiatica Germination Percentage and Furthest Germination Distance. The results from this study demonstrated that sorghum genotypes produce different amounts of germination stimulants. Highest germination percentages were recorded in genotypes SV2, Wahi, and Kuyuma, whilst Mahube and ICSV 111 IN had the least. These results suggest that the genotypes with low *Striga* seed germinations (Mahube, SV4, and ICSV 111 IN) could be *Striga* resistant, whereas those which produced high *Striga* seed germinations (Kuyuma, Wahi, and Macia) could be susceptible to *Striga* infection. This result was supported by the findings of Mandumbu et al. [1], who reported high

TABLE 7: Effects of sorghum genotype on *Striga* counts, haustorial attachments, and biomass.

Genotype	*Striga* counts (pot^{-1})	*Striga* attachments (pot^{-1})	*Striga* biomass (kg pot^{-1})
Mahube	0.00[a]	0.00[a]	0.00[a]
ICSV 111 IN	3.00[a]	2.67[ab]	0.54[a]
SV2	0.00[a]	2.33[ab]	0.53[a]
Kuyuma	10.83[b]	13.50[c]	2.78[b]
Wahi	0.00[a]	0.00[a]	0.00[a]
SV4	0.33[a]	2.33[ab]	0.38[a]
Macia	8.33[b]	7.00[b]	0.71[b]
p value	<0.001	<0.001	0.003
SED	1.920	<0.001	0.660
LSD	3.897	5.157	1.34

Means followed by the different letters in the column are significantly different at *p* < 0.05.

TABLE 8: Mean square values for sorghum genotypes yield parameters recorded under glasshouse conditions at the University of Zimbabwe.

Source	Head biomass	Head index	Leaf biomass	Leaf index	Stem biomass	Stem index	Root biomass	Root index	Plant biomass	Root-shoot ratio	Grain yield
Block	0.577	0.389	0.19	0.005	0.128	0.019	0.193	0.067	3.23	0.143	0.118
Genotype	0.815***	0.066***	0.127***	0.002 ns	22.160**	0.022**	3.075***	0.038***	9.531***	0.627***	1.385*
Striga	0.758***	0.014**	0.149**	0.001 ns	86.417***	0.086***	3.288***	0.194***	3.093 ns	4.714***	5.401***
Genotype ∗ *Striga*	0.066 ns	0.007**	0.148***	0.004**	0.972 ns	0.010 ns	1.561***	0.020**	2.840*	0.420**	0.608 ns
Residual	0.372	0.219	0.193	0.009	0.427	0.064	0.337	0.054	1.13	0.1029	0.401

*, **, and *** represent significance at the 5%, 1%, and 0.1% probability levels, respectively. ns, not significant at 5% probability level.

TABLE 9: Response of sorghum genotype on yield parameters evaluated under glasshouse conditions.

Genotype	Head biomass (kg pot^{-1})	Stem biomass (kg pot^{-1})	Stem index	Grain yield (kg plot^{-1})
Mahube	0.036[e]	0.032[a]	0.225[a]	0.096[c]
ICSV 111 IN	0.027[c]	0.062[bc]	0.317[b]	0.079[b]
SV2	0.018[b]	0.051[b]	0.285[ab]	0.071[ab]
Kuyuma	0.011[a]	0.054[b]	0.310[b]	0.077[b]
Wahi	0.019[bc]	0.048[ab]	0.284[ab]	0.061[a]
SV4	0.028[d]	0.074[c]	0.349[b]	0.087[b]
Macia	0.019[bc]	0.075[c]	0.348[b]	0.087[b]
p value	<0.001	<0.001	0.005	<0.01
SED	0.004	0.012	0.046	0.003
LSD	0.007	0.024	0.092	0.087

Means followed by the different letters in the column are significantly different at *p* < 0.05.

TABLE 10: Effect of *Striga* on yield parameters evaluated under glasshouse conditions.

Striga	Head biomass (kg pot^{-1})	Stem biomass (kg pot^{-1})	Stem index	Grain yield (kg pot^{-1})
Infested	0.019[a]	0.3398[a]	1.893[a]	0.473[a]
Noninfested	0.025[b]	0.4180[b]	2.342[b]	0.586[b]
p value	<0.001	<0.001	<0.001	0.003
SED	0.001	0.009	0.017	0.013
LSD	0.003	0.021	0.035	0.012

Means followed by the different letters in the column are significantly different at *p* < 0.05.

germination percentage of *Striga* and attributed the result to more strigolactones production and high degree of susceptibility. The sorghum *Striga* resistance which is influenced by the production of strigolactones is sometimes referred to as pre-attachment resistance [27].

Furthermore, furthest germination distance (fgd) differed across sorghum genotypes, with genotypes Kuyuma and Macia having highest germination distance. Based on stipulations by Hess et al. [36], genotypes with furthest germination distance less than 1 cm are resistant to *S. asiatica* whilst those with more than 1 cm are susceptible. Therefore, the results suggest that genotypes Mahube, ICSV 111 IN, and SV4 (fgd < 1 cm) were resistant, whereas SV2, Wahi, Macia, and Kuyuma with furthest germination
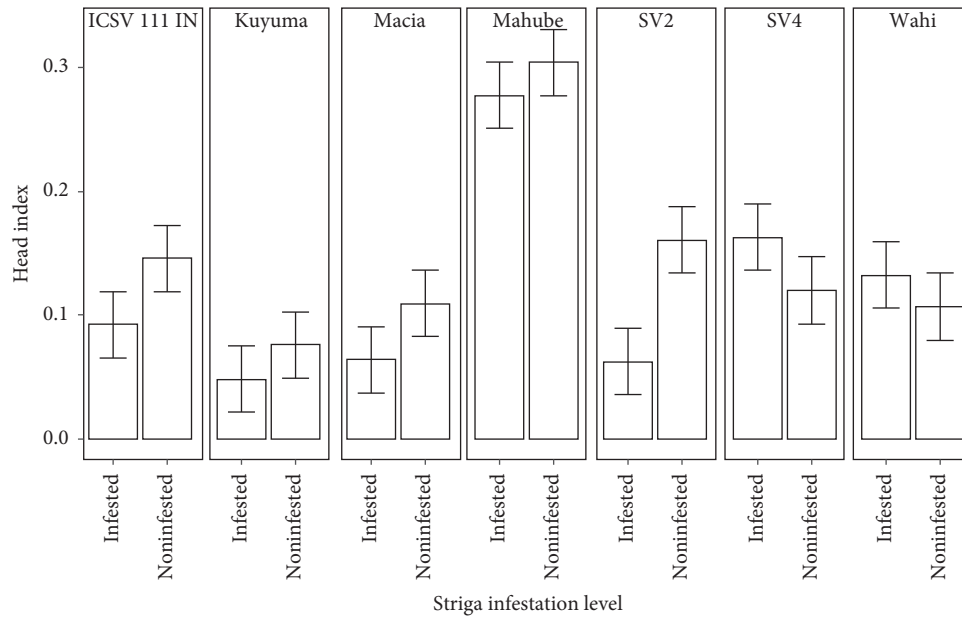
FIGURE 4: Effect of *Striga* infestation on sorghum head index. Error bars represent LSD at $p < 0.05$.
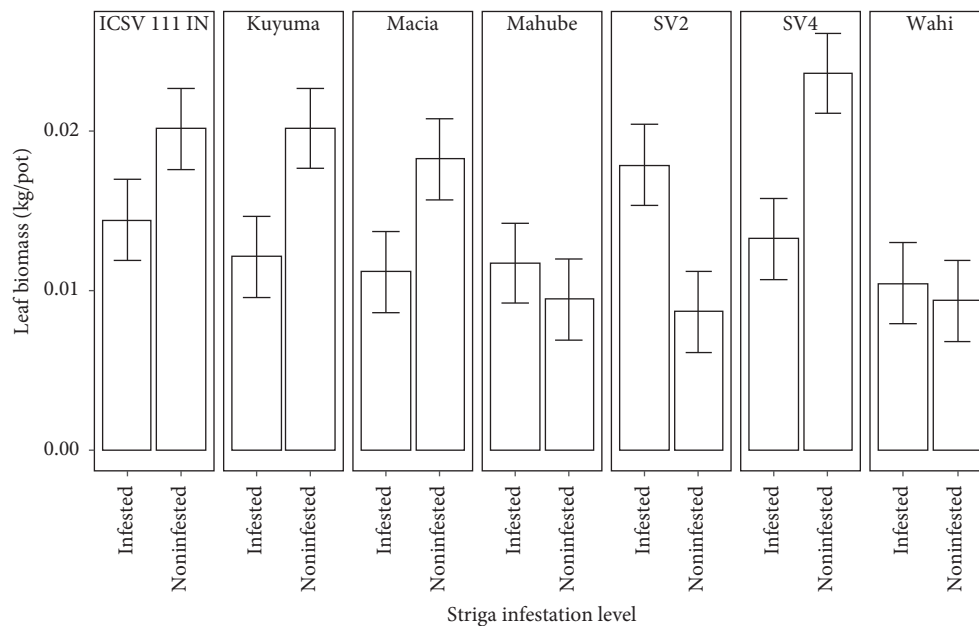

FIGURE 5: Interaction effects of sorghum genotype and *Striga* infestation on sorghum leaf biomass (kg pot^{-1}). Error bars represent LSD at $p < 0.05$.

distance of more than 1 cm were susceptible to the *S. asiatica* ecotype that was used in this study. These results were consistent with observations in rice [26] and sorghum [6, 37]. This could be attributed to the fact that genotypes produce different levels of germination stimulants. It has been reported that strigolactones are composed of different proportions of chemicals produced by the sorghum root; for example, sorghum could produce different proportions of orobanchole and 5-deoxystrigol, and this has an impact on the germination of *Striga* seeds [16, 17]. For instance, high amounts of 5-deoxystrigol in sorghum root exudates could

have resulted in high *Striga* seed germination, whereas high orobanchol caused low *Striga* seed germination [16, 17]. It is likely that the sorghum genotypes used in this study could have variable 5-deoxystrigol: orobanchol ratios in their root exudates. Furthermore, up to about 500-fold difference exists in amount of strigolactones exuded by cereals [26].

4.2. Effect of Sorghum Genotypes on S. asiatica Emergence, Attachment, and Biomass. In this study, genotypes Mahube and Wahi did not support *S. asiatica* emergence, and this
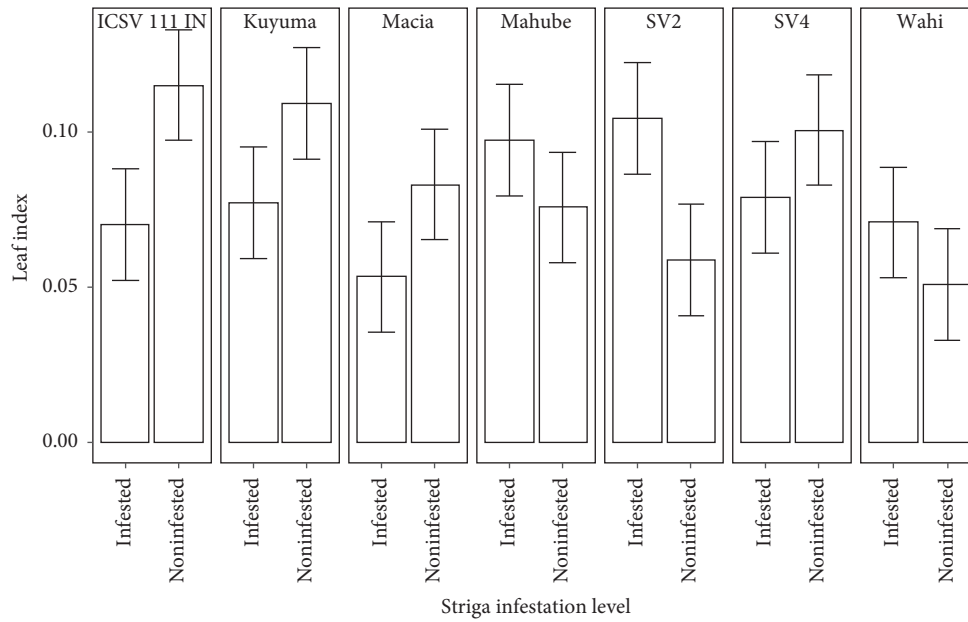
FIGURE 6: Effect of genotype and *Striga* interaction on sorghum leaf index. Error bars represent LSD at $p < 0.05$.
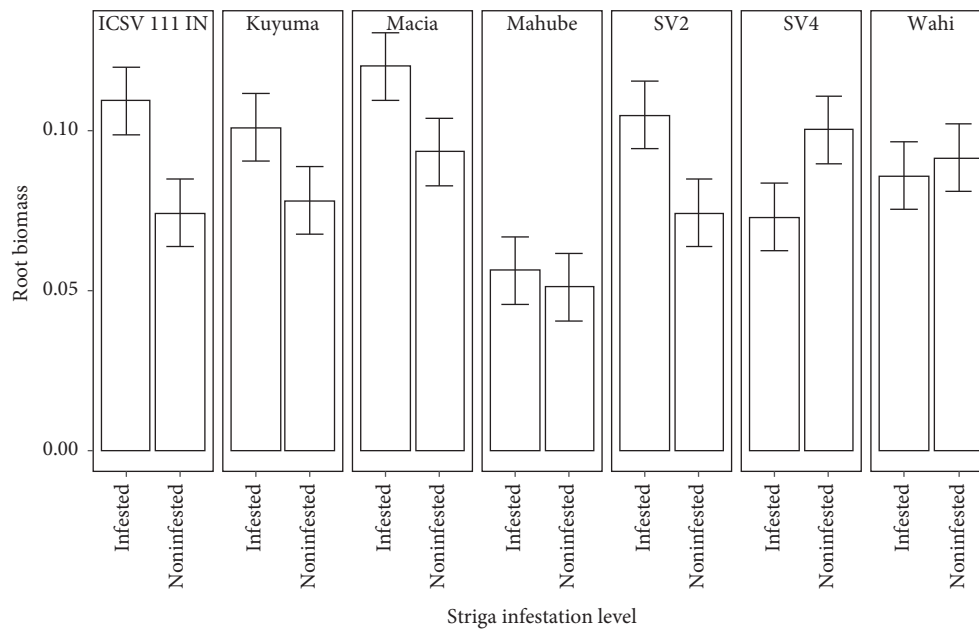

FIGURE 7: Effect of genotype and *Striga* on sorghum root biomass (kg pot^{-1}). Error bars represent LSD at $p < 0.05$.

suggested that these genotypes had post-attachment *Striga* resistance. It was also noted that the genotypes Mahube, ICSV 111 IN, SV4, and SV2 had low emerged *Striga* counts, low *Striga* attachments, and low *Striga* biomass. Therefore, these sorghum genotypes are likely to have some post-attachment *Striga* resistance. The latter suggests that the *Striga* could have failed to attach to the sorghum roots [27]. Mbuvi et al. [3] used microscopic studies to demonstrate that *Striga* failed to penetrate into the sorghum root endodermis. In rice, it was found that lignin accumulated at the point of *S. hermonthica* attachment in the rice genotype Nipponbare, therefore accounting for the post-attachment resistance [38].

This could possibly explain the low emerged *Striga* and low *Striga* attachments in the sorghum genotypes Mahube, ICSV 111 IN, SV4, and SV2. It is interesting to note that the genotypes Mahube, ICSV 111 IN, and SV4 had the lowest germination and lowest germination distances to the sorghum root under the laboratory agar gel assay conditions. This means that Mahube, ICSV 111 IN, and SV4 possess both pre- and post-emergence resistance. In contrast, Wahi and SV2 are likely to have post-emergence resistance. Pierce et al. [39] reported that Macia and Wahi had low susceptibility to *S. asiatica* and *S. hermonthica*. According to Botanga and Timko [40], low germination suggested that the
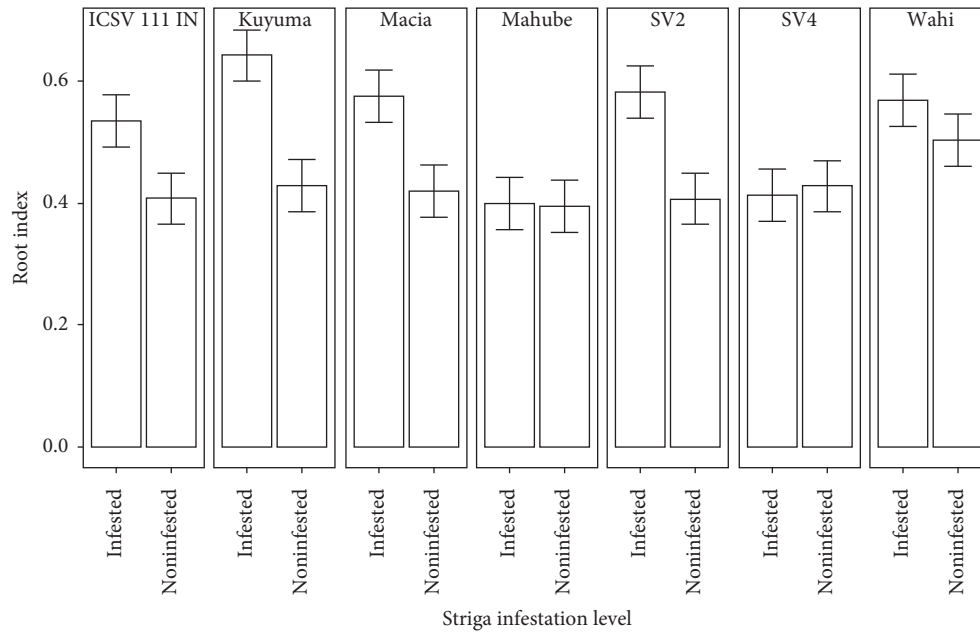
FIGURE 8: Effect of genotype and *Striga* infestation on sorghum root index. Error bars represent LSD at $p < 0.05$.
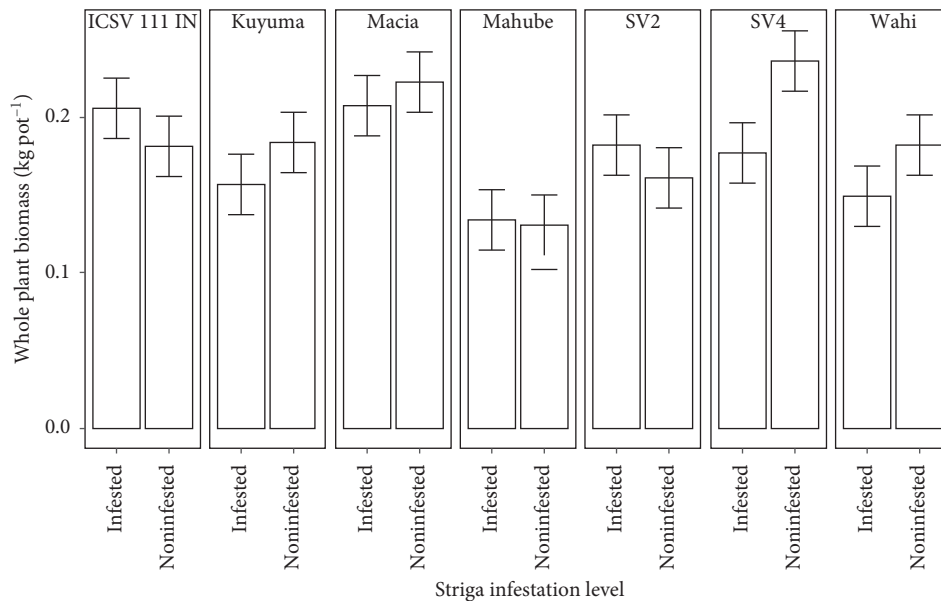

FIGURE 9: Effect of genotype and *Striga* infestation on sorghum whole plant biomass (kg pot^{-1}). Error bars represent LSD at $p < 0.05$.

host produced low strigolactones to germinate *Striga* seeds. The genotype Kuyuma had the highest number of *Striga* counts, number of attachments, and biomass showing that this genotype is susceptible to *Striga* infection. This can be attributed to production of sufficient strigolactones and haustorial initiation factors facilitating growth of the parasite.

4.3. Effect of Striga Infection on the Height and Internode Length of Different Sorghum Genotypes. Plant height is considered as one of the most sensitive parameters which indicate the effects of witch weeds on plants [41, 42]. In this

study, height and internode lengths of Mahube and ICSV 111 IN genotypes were not significantly lowered by *S. asiatica*. This suggested that the genotypes did not succumb to the dwarfing effects of the parasitic weed. This was supported by work done by Mandumbu et al. [29] and Nyakurwa et al. [5] who found that sorghum and maize (*Zea mays* L.) varieties differed significantly in plant height when affected by *Striga*. Differences in height and internode length observed between infested and noninfested plants also reflected that the parasite acted as a sink for carbon, inorganic solutes, and water. Many of the genotypes (Macia, SV2, and Kuyuma) had decreased heights and internode length reflecting their susceptibility to parasitic effects of *S. asiatica*. This reduction
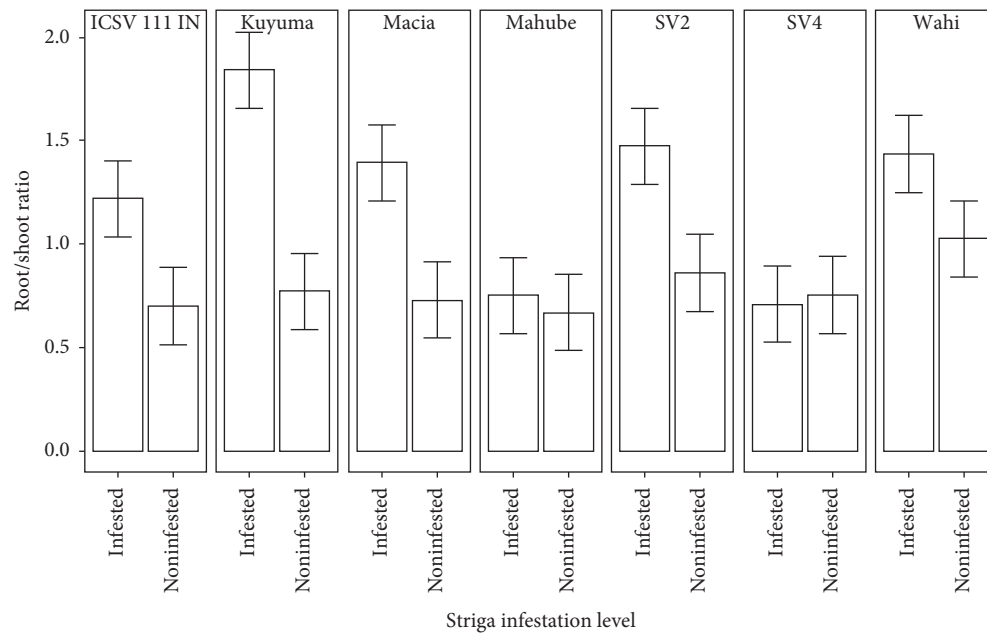
FIGURE 10: Effect of genotype and *S. asiatica* infestation on sorghum root to shoot ratio. Error bars represent LSD at $p < 0.05$.

in plant growth rate could also have been attributed to changes in host growth regulators. It was reported that an increase in abscisic acid (ABA) released in the xylem sap of infested plants resulted in stomatal closure [2, 5, 29]. This led to reduction in photosynthesis and cell enlargement thus explaining reduction in heights and internode lengths observed in this study.

4.4. Effect of S. asiatica and Sorghum Genotype on Days to Flowering of Sorghum.
Genotypes differed significantly in days to flowering. Kuyuma and SV2 genotypes took longer to flower under *Striga* infestation. The increase in days to flowering could be attributed to high levels of *Striga* infestation with great effects on the physiology of plants during the susceptible vegetative phase to flower initiation. However, early maturity is one attribute to avoid *Striga* infestation effects which may have been displayed by genotypes ICSV 111 IN, Macia, Mahube, SV4, and Wahi whose flowering was not affected by *Striga*. According to Nyakurwa et al. [5], *Striga* affected host nutrient uptake which could be a contributing factor to late flowering because of lack of essential nutrients needed for the stage.

4.5. Effect of S. asiatica on Chlorophyll Content and Fluorescence.
Chlorophyll content and fluorescence are related to nitrogen availability, and these indicate the photosynthetic function and carbon dioxide assimilation rates of a plant [43]. Chlorophyll content is an indirect indication of tolerance to *Striga* infestation [44]. Genotypes used in this study differed significantly in chlorophyll content under *Striga* infestation especially Kuyuma, Wahi, Macia, and SV2, where low chlorophyll content was observed indicating the susceptibility of these genotypes to *Striga* infestation. These results were in agreement with the findings of Mandumbu et al. [1], who reported that sorghum genotypes differed significantly in chlorophyll content under *Striga* infestation. *Striga* is likely to decrease carbon production by the host thereby limiting nitrogen assimilation which concomitantly reduces chlorophyll synthesis [45]. However, Mahube, Wahi, and SV4 genotypes maintained their chlorophyll content under *Striga* infestation, which suggested that these genotypes are tolerant to *Striga* infestation. In addition, these results could be due to a positive correlation between chlorophyll content and photosynthetic rates [2]. Therefore, these genotypes were able to produce photoassimilates in abundance which sustained the host thereby withstanding the effects of *Striga* infestation. The fact that *Striga* infestation did not affect chlorophyll fluorescence (Fv/Fm) of the genotypes suggested that this parameter was not sensitive to *Striga* parasitism and was therefore not a good indicator of resistance or susceptibility of sorghum genotypes to parasitism. However, these findings contradicted those of Mandumbu et al. [1], who reported that *Striga* affects chlorophyll fluorescence through inducing photo inhibition. Gurney et al. [2] defined photo inhibition as the inactivation of photosystem II reaction centre causing reduced photosynthetic rates.

4.6. Effect of S. asiatica on Sorghum Biomass and Grain Yield.
It was observed in this study that *Striga* reduced head biomass of some sorghum genotypes, implying that the parasite had the ability to affect allocation of photoassimilates. These results concurred with Mabasa [46] who found that, under *Striga* infestation, the parasite channelled all photoassimilates to itself rather than the host plant. Genotypes differed significantly in head biomass, with genotype Mahube and SV4 having more biomass under both levels of *Strig*a infestation. These results implied that the

genotypes were tolerant to the witchweed. These results concurred with the findings of Taiz and Zieger [43], who observed that tolerant varieties produce high yields even under *Striga* infestation. Moreover, these yield differences can be attributed to the inherent genotype yield potential.

From the study, it was observed that *S. asiatica* significantly affected leaf biomass and index. *Striga* reduced leaf biomass and index of some sorghum genotypes except Mahube, SV2, and Wahi. This means that these genotypes maintained a high photosynthetic rate, leading to more photoassimilates being allocated to the host. However, other genotypes had their leaf biomass significantly reduced by the weed and hence were more susceptible. This reduction in leaf yield could be due to positive feedback that exists between assimilates production, leaf area, and light interception during host growth [40]. In addition, *Striga* infestation affects leaf arrangement and growth, subsequently causing leaf shading thereby reducing photosynthesis and dry matter allocation [47].

According to Mabasa [46], host stem is one of the most sensitive plant parts under *Striga* infestation. In this study, *Striga* infestation reduced stem biomass and index of sorghum. This result was similar to the findings of Li et al. [48] who found that *S. gesneroides* resulted in reduced stem biomass of cowpeas (*Vigna unguiculata* L. Walp). Rodenburg et al. [44] reported that, under *Striga* infestation, there was a change in carbon transfer, from the shoots to the roots due to changes in sink demand accounting for reduction in shoot biomass. *Striga* infestation resulted in reallocation of dry matter to below ground parts rather than development of above ground. The results showed that *S. asiatica* managed to increase root biomass and index of some sorghum genotypes. However, the root biomass and index of genotypes SV4, Mahube, and Wahi were not affected, implying tolerance. This agreed with Parker and Riches [49], who found out that *Striga* infestation causes an imbalance of hormones resulting in stimulation of root growth. This reduction in plant biomass can be attributed to two main damage mechanisms of the parasitic weeds, namely, phytotoxic or pathological effect of the parasite on the host and directly through the role of parasite as additional sink for carbon, inorganic solutes, and water [9].

Consequently, the response of root to shoot ratio differed significantly among genotypes. There was a marked increase in root to shoot ratio of some sorghum genotypes except for Mahube and SV4 in the presence of *Striga* suggesting that the two genotypes were tolerant. Similar results were also reported by Chitagu et al. [47], who observed that maize genotypes differed in root to shoot ratio when infested by *Striga*. This increase in root biomass at the expense of shoot biomass can be attributed to the competition for photoassimilates, amino acids, and water with the parasite causing more to be channelled to the roots.

5. Conclusion

In the agar gel study, the sorghum genotypes Mahube, SV4, and ICSV 111 IN had low values for *Striga* seed germination and furthest germination distances, whereas Kuyuma, Wahi, SV2, and Macia had high values for *Striga* seed germination and furthest germination distances. It was concluded that the sorghum genotypes Mahube, SV4, and ICSV 111 IN, which could have produced low germination stimulants (sorgolactones) or altered sorgolactone composition, were likely to have pre-attachment *Striga* resistance. In contrast, the genotypes Kuyuma, Wahi, SV2, and Macia which could have produced high germination stimulants were susceptible to *Striga* infection. In the pot study, Mahube and Wahi, which did not support *Striga* attachments at all, were likely to have post-emergence resistance. The genotypes ICSV 111 IN, SV4, and SV2, which supported low *Striga* attachments, low emerged *Striga* attachments, and low *Striga* biomass could have partial post-emergence *Striga* resistance. The genotypes Macia and Kuyuma, which supported high numbers of *Striga* attachments and emergence, could be highly susceptible to *Striga* infection. After assessing *Striga* tolerance based on sorghum heights, chlorophyll content, and root shoot/ratio parameters, it could be concluded that the sorghum genotypes Mahube, ICSV 111 IN, and SV4 tolerated *Striga* infection, whereas Kuyuma, SV2, Macia, and Wahi could be susceptible.

Data Availability

Data are available from the corresponding author upon request.

Conflicts of Interest

The authors declare that they have no conflicts of interest.

Acknowledgments

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