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In vivo and *in vitro* performance studies on groundnut (*Acharis hypogea* L.) genotypes for yellow witchweed (*Alectra vogelii* Benth.) resistance

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ABSTRACT

Witchweed (*Alectra vogelii* Benth.) is a legume parasitic weed that causes severe yield reduction of groundnut (*Acharis hypogea* L.) in Africa. The study was conducted to screen and identify *Alectra vogelii* resistant and/or tolerant groundnut genotypes evaluated under both laboratory and glasshouse at the University of Zimbabwe during 2018/19 cropping season. The findings of the lab agar-gel screening experiment revealed significant differences in germination percentage and germination distance between genotypes. Significant genotype x *A. vogelii* infestation interaction on plant biomass, root to shoot ratio and shelled grain yield were observed. *Alectra vogelii* parasitism significantly reduced plant biomass and shelled grain yield across groundnut genotypes. Conversely, genotypes like Njiva, Ilanda and Guinea fowl did not support any haustorial attachment, and had the highest shelled grain yield under all *A. vogelii* infestation levels. Assessment of *A. vogelii* tolerance based on groundnut growth, physiological and yield related parameters revealed that the groundnut genotypes Njiva, Ilanda and Guinea fowl tolerated *A. vogelii* infection, whereas Dendera, Jessa, Nyanda and Tern could be susceptible. Field studies are expected to validate the initiative of breeding with farmers of tolerance groundnut genotypes to *A. vogelii* infection.

Key words: *Acharis hypogea*; *Alectra vogelii*; Haustorial attachment; Strigolactones; Yield

INTRODUCTION

Climate change is one of the major challenges with a devastating pest and disease evolution in the world. These pests and disease are posing a significant impact food and feed production and in particular, parasitic weeds (Gasura et al., 2019; Mutuku et al., 2021). As a result, most resource-poor farmers are suffering from yellow witchweed (*Alectra vogelii* Benth.) infestation, which is a predominant obligate hemi-parasitic weed species of legumes in African arid and semi-arid regions (Njekete et al., 2017; Dieni et al., 2018; Kabambe and Bokosi, 2020). These regions are prone to drought stress and with more than 50% of arable land inherently infertile (Gwatidzo et al., 2020; Ichihashi et al., 2020; Soropa et al., 2021; Rugare et al., 2013; Itta et al., 2014; Mandumbu et al., 2017; Ojiewo et al., 2020; Mutuku et al., 2021). Approximately 70-100% reduction in the biophysical traits of groundnuts have been reported, which impact global groundnut yield under severe infection (Ugbaa et al., 2020). As a result, smallholder farmers are being forced to abandon their fields unproductive (Motagi et al., 2014; Masumoto et al., 2021).

According to Rugare et al. (2013), *A. vogelii* is defined as a vascular obligate-root parasitic angiosperm plant that invade the host tissues to acquire nutrients, & metabolites (Nyakurwa et al., 2018). The parasite has been reported widely distributed in Sub-Saharan Africa. The known hotspots of *A. vogelii* infestation in legumes include countries like Botswana (Fite et al., 2009), Ethiopia (Hussein et al., 2006), Malawi (Kabambe and Bokosi, 2020), Nigeria (Motagi et al., 2014), Tanzania (Mbega et al., 2010) and Africa-wide (Kureh and Alabi, 2003; Kureh et al., 2005). Its infestation has been reported largely in groundnuts, cowpeas, common beans and bambaranuts (Alonge et al., 2001a; Mandumbu et al., 2016; Mbwando et al., 2017; Phiri et al., 2019).

Nonetheless, the impact of *A. vogelii* is inevitable given the prevalence of *A. vogelii* weed, which is characterized by long lasting seed viability and prolificacy which ranges between 15-20 years and 400-600 thousand seeds respectively (Mukendi et al., 2017; Ugbaa et al., 2020; Aloni, 2021; Mutuku et al., 2020; Ichihashi et al., 2020; Masumoto et al., 2021; Aloni, 2021). This result in total crop damage and yield losses greater than 80% (Phiri et al., 2019; Kabambe and Bokosi, 2020).

Even though, farmers have employed various strategies like hand weeding, crop rotation, trap-catch cropping, and some trying chemical application to manage the impact of *A. vogelii*, all seems economically and technically ineffective since the damage is belowground, and occurs before the parasite emerges from the rhizosphere (Riches et al., 1992; Mandumbu et al., 2019; Masumoto et al., 2021). The rate at which *A. vogelii* is infecting legumes crops is alarming (Mandumbu et al., 2017; Nyakurwa et al., 2018) and groundnuts in Zimbabwe have received little attention to assess the level and responsiveness to *A.vogelii* infestation, yet is one of the principle crop for most Zimbabweans (Rugare et al., 2013; Mbwando et al., 2017; Soropa et al., 2021). Vulnerable poor-resource farmers and some smallholder farmers are highly affected by *A. vogelii* occurrence (Gurney et al., 1999; Gasura et al., 2019).

Therefore, scientists devised an understanding of the joint smart-climate and environmental technologies that can be urgently employed to improve groundnut crop production, food security and utilization of marginal infected lands under harsh and adverse conditions and get purged of the parasite (Mbwando et al., 2017; Mandumbu et al., 2019; Gasura et al., 2019; Dieni et al., 2019). Others consider the suggestion, a green sustainable and economic way devised in which researchers believe that the strategy will contribute to food security and nutrition and can increase income generation especially for resource-poor farmers (Alonge et al., 2001b; Phiri et al., 2019; Gwatidzo et al., 2020).

Breeding with farmers and promoting the utilization of resistant or tolerant high yielding groundnut genotypes, is one of the sustainable long-term and economically benign method of *A. vogelii* control which may benefit Zimbabwean smallholder and poor-resource farmers. Based on these conditions and scenarios, this study was developed aiming at screening and identifying genotypes that resist or tolerate *A.vogelii* infection.

MATERIALS AND METHODS

A total of seven groundnut genotypes from Zimbabwe super seed (ZimSuperSeed), Department of Research and Specialist Services (DRSS) and ICRISAT Zimbabwe were evaluated (Table 1). The attributes of the genotypes used are shown in Table 1.

Table 1. Sources of genotypes and its attributes

Genotype	Source	Attributes
Tern	Zim-Super Seed	A medium size pale coloured seed of medium season variety exhibits high yield potential, high kernel/seed potential, tolerance to dry spells/drought conditions, fair tolerance to early and late leaf spot diseases.
Ilanda	DRSS	A medium size pale coloured seed of medium season variety exhibits high yield potential, high kernel/seed potential, tolerance to dry spells/drought conditions, fair tolerance to early and late leaf spot diseases.
Jessa	DRSS	Medium size pale coloured seed, short season variety, high pod yield potential (4 t ha^{-1}), high kernel yield potential (2.8 t ha^{-1}), escapes Cercospora leaf spots and late season drought.
Njiva	ICRISAT Zimbabwe	An early maturing variety to reach physiological maturity, high pod yield potential (4.3 t ha^{-1}) and seed yield (2.85 t ha^{-1}), drought tolerant genotype with moderately to highly tolerant to leaf spot diseases and rust, good tolerance to aphids and *Hilda patruelis.*
Guinea fowl	ICRISAT Zimbabwe	A medium maturing variety, very high pod yield potential (4.5 t ha^{-1}) and potential seed yield (3.3 t ha^{-1}), tolerant to drought, highly tolerant to leaf spot diseases and rust and good tolerance to aphids and *Hilda patruelis.*
Dendera	ICRISAT Zimbabwe	A pale-coloured seed variety exhibiting medium maturing variety, potential pod and yield potential, has high tolerant to Groundnut Rosette Disease (GRD) and leaf spot diseases and rust, with good tolerance to aphids and *Hilda patruelis.*
Nyanda	ICRISAT Zimbabwe	Pale coloured seed variety exhibiting medium maturing variety, potential pod and yield potential, can tolerate early and late leaf spot diseases and rust.

Agar gel experiment procedure

Alectra vogelii seeds were collected in 2012 from the Rushinga community area in Mashonaland Central Province. With six replications, the experiment was set up as a RCBD. The seeds of *A. vogelii*, as used in the pot experiment A. planned the experiment before starting it. *A. vogelii* seeds were sterilised for 25 minutes in a solution of 1 per cent sodium hypochlorite (NaOCl). The seeds were then sterilised before being rinsed 3 times.

The healthy germinated seedlings were chosen for the agar gel experiment. 50 ul of conditioned pipette *A. vogelli* seeds onto Petri dishes with a diameter of 9 cm. Thirty millilitres of 0.67 percent v/w autoclaved water agar were poured over the A before it solidified. In each Petri plate, place *A. vogelii* seeds.

Germination percentages were calculated in four separate areas where the microscope's scope was

focused. As indicated by Reda et al. (1994), the quantity of germinated *A. vogelii* seeds and furthermost germination distance (mm) of *A. vogelelli* germinating seeds from groundnut root were employed as indices for stimulant production.

Pot experiment procedure

The pot experiment was conducted out in a well-ventilated glasshouse over the 2018/19 summer season. In a RCBD, was set up as a 7 x 2 factorial trial with six replications. The seven levels of groundnut genotypes are listed and described in Table 1, whereas the other component was *A. vogelii* infection, which had two levels (infested and non-infested). Eighty-four pots with a top diameter of 30 cm, a bottom diameter of 15 cm, and a height of 40 cm were filled three-quarters full with sandy soil, followed by thorough mixing of 2g pot-1 of compound D in the first 5 cm of soil (7 per cent N, 14 per cent P2O5, and 7 percent K2O). All of the pots were watered to their capacity and left that way for a week to precondition the seed. Following that, three kernels of each groundnut genotype were planted at a depth of 5 cm in both infected and uninoculated pots, with seeds spaced 3 cm apart. At four weeks after crop emergence (WACE), two grammes of ammonium nitrate (34.5 percent N) was applied as a top-dressing fertilizer to all of the pots. Watering was done on a regular basis. Hand-pulling was used to control other weeds besides *A. vogelii*.

Data Collection

From 2 to 15 WACE, groundnut plant height and number of primary branches were measured weekly. Groundnut phenology (days to 50% anthesis and physiological maturity), physiological parameters (chlorophyll content and fluorescence), biomass, and yield components were also collected (number of seeds crop^{-1}, 100 kernel weight and shelled grain yield. The content of chlorophyll was determined using a SPAD-502 and measurements were collected at 8 WACE on young, completely formed leaves between 12:00 and 13:00 hours. A portable, chlorophyll fluorometer was used to assess chlorophyll florescence (Fv/Fm), After 30 minutes of dark adaption, measurements were obtained on the freshest, matured leaves using clips provided with the equipment (Nyakurwa et al., 2018). Between 13:00 and 15:00 hours, readings were taken at 8, 10, 12, 14, 15, and 16 WACE. The number of haustorial attachments at 14 WACE and biomass weight after oven-drying at the end of the experiment were recorded as *Alectra vogelii* characteristics.

Data analyses

An ANOVA was achieved by Genstat 18th version, and means were separated at the 5% significant level using Fisher's protected LSD. The R statistical programme version 3.5.2 was used to exhibit the data in a graphical format.

RESULTS

Agar-gel experiment

The mean square values for *A. vogelii* germination and the furthest germination distance are summarized in Table 2.

There were significant differences between genotypes on A. vogelii germination percentage and furthest germination distance (Table 2). Genotype Njiva did not support any *A. vogelii* germination consequently no furthest germination distance was recorded compared to other genotypes. Dendera and Nyanda had significantly higher germination percentage and furthest germination distances than the other genotypes (Table 2).

Glasshouse experiment

Effect of groundnut genotype on number of A. vogelii attachments and biomass

Summary of mean square values for *A. vogelii* parameters is shown in Table 2. Substantial variations were recorded among groundnut genotypes on *A. vogelii* attachments (Table 2). Genotypes Dendera, Guinea fowl and Ilanda did not significantly differ on haustorial attachment (Table 2). Njiva did not support *Alectra* attachment.

Table 2. Effects of strigolactones in diverse groundnut genotypes on *A. vogelii* germination per centage (G %), furthest germination distance (FDA), haustorial attachment and *Alectra* biomass

Genotype	*Alectra* G%	*Alectra* FDA (mm)	Haustorial attachment	*Alectra* root biomass (g)
Dendera	12.4^{c}	2^{b}	1.17^{bc}	0.58^{ab}
Guinea fowl	3.2^{ab}	0.7^{a}	0.83^{bc}	0.67^{ab}
Ilanda	7.7^{b}	0.8^{a}	1.00^{bc}	1.33^{bc}
Jessa	6.7^{b}	0.7^{a}	1.33^{cd}	1.75^{c}
Njiva	0.00^{a}	0.00^{a}	0.00^{a}	0.00^{a}
Nyanda	22.2^{d}	3.34^{c}	2.00^{d}	1.67^{c}
Tern	5.2^{b}	0.8^{a}	0.50^{ab}	0.52^{ab}
p-value	<0.001	<0.001	0.001	0.004
SED	2.386	0.393	0.404	0.459
LSD	4.712	0.777	0.824	0.937

Table 3. Mean square values for plant height and number of branches recorded under glasshouse conditions

Source	Plant height (cm)	Number of branches
Block	98	9.04
Genotype	751.6***	59.53*
Alectra	254.7^{ns}	703.1***
Genotype × *Alectra*	68.1^{ns}	9.64^{ns}
Residual	135.3	24.84
Time	5764.5***	1449.05***
Time × Genotype	9.02***	3.19**
Time × *Alectra*	8.6*	27.72***
Time × Genotype × *Alectra*	2.6^{ns}	1.62^{ns}

Effect of A. vogelii infection on groundnut growth

Table 3 summarises the mean square values for A. vogelii impacts on groundnut plant height and primary branch number recorded in the glasshouse.

Plant height

The genotype x *A. vogelii* infestation interaction was not significant. However, genotype significantly affected plant height among the different genotypes (Figure 1a) but *A. vogelii* infestation level did not (p>0.05) (Table 3). Figure 1a shows that *A. vogelii* infection reduced the height of all groundnut genotypes except Guinea fowl and Ilanda. Njiva recorded the highest plant height under all levels of *A. vogelii* infestation (Figure 1a).

The effects of time x genotype x *A. vogelii* infection and genotype x *A. vogelii* infestation on groundnut branch number were not significant. Except for genotype Njiva, *A. vogelii* infestation considerably reduced the number of branches of all groundnut genotypes under infestation (Table 3, Figure 1b). Non-infested groundnut genotypes produced significantly more primary branches than infested groundnut genotypes over a period of time.

Groundnut physiological, agronomic and yield related components response to A. vogelii infection

Table 3 shows the mean square values for physiological, phenological, plant biomass, and yield parameters recorded in the pot study for groundnut genotypes.

Number of primary branches

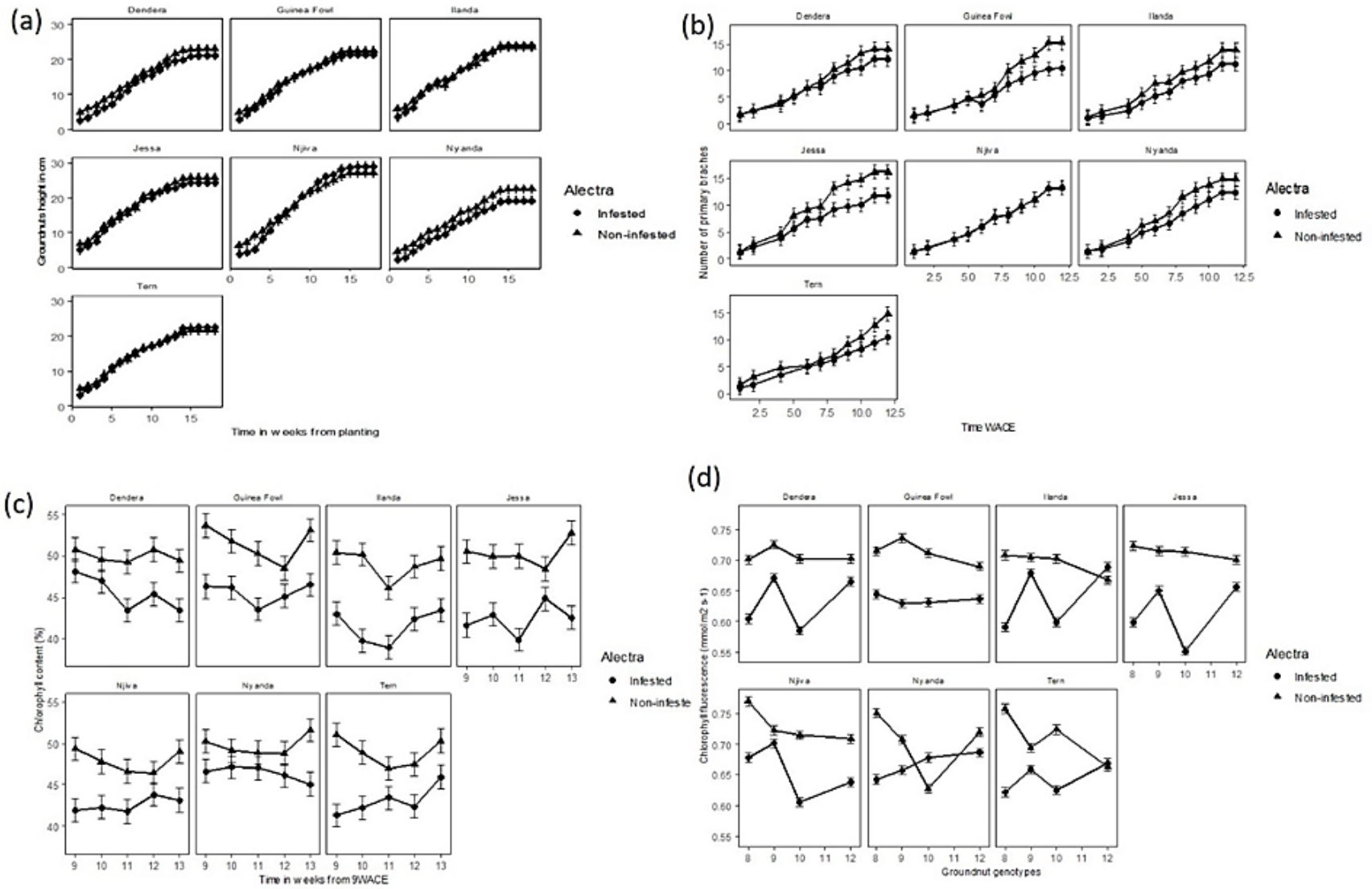

Figure 1. The effects of time x *A. vogelii* infection x genotype on (a) plant height (b)number of primary branches (c) Chlorophyll content (d) Chlorophyll florescence on groundnut genotypes evaluated under glasshouse conditions.

Table 4. Mean square values for groundnut genotypes physiological, phonological and yield parameters recorded under glasshouse conditions

	Chlorophyll content (mmol m^2)	Chlorophyll fluorescent (mmol m2 s^{-1})	Days to 50% anthesis	Days to physiological maturity	Total plant biomass (kg)	Shoot biomass (kg)	Root biomass (kg)	Shoot/Root ratio	Number of seeds per plant	100 kernel weight (kg)	Shelled grain weight (kg)
Block	351.7^{ns}	0.02188	33.2	26.7	0.0012	0.0008	0.0004	0.1	27.1	0.005	0.0002
Genotype	331.3^{ns}	0.004875^{ns}	621.6***	302.7***	0.0009*	0.0006*	0.0004*	1.7***	60.3***	0.002^{ns}	0.0002*
Alectra	3197.2***	0.246219***	186.0*	3.1^{ns}	0.004***	0.001*	0.00007^{ns}	0.6^{ns}	980.6***	0.04***	0.002***
Genotype x *Alectra*	251.2^{ns}	0.001486^{ns}	22.8^{ns}	10.6^{ns}	0.0007*	0.0001^{ns}	0.0002^{ns}	1.1*	12.1^{ns}	0.002^{ns}	0.00007*

Number of primary branches

The effects of time x genotype x *A. vogelii* infection and genotype x *A. vogelii* infestation on groundnut branch number were not significant. However, except for genotype Njiva, *A. vogelii* infestation significantly reduced the number of branches of all groundnut genotypes under infestation (Table 3, Figure 1b). Over a period of time, non-infected groundnut genotypes developed considerably more primary branches than infested groundnut genotypes.

Groundnut physiological, agronomic and yield related components response to *A. vogelii* infection

Table 3 shows the mean square values for physiological, phenological, plant biomass, and yield parameters recorded in the pot study for groundnut genotypes.

Chlorophyll content (mmol m^2)

The genotype x *A. vogelii* infestation on chlorophyll content was had non-significant interaction. *Alectra vogelii* infection significantly (p<0.001) reduced chlorophyll content of groundnut genotypes (Table 6). All groundnut genotypes did not vary significantly (p>0.05) in terms of chlorophyll content under contrasting levels of A. *vogelii* infestation (Table 4 and Figure 1c).

Chlorophyll fluorescence

The amount of chlorophyll in the groundnut genotypes did not differ significantly (p>0.05) (Table 4). Infestation with *A. vogelii*, on the other hand, reduced chlorophyll fluorescence considerably (p0.05) (Figure 1d, Table 4).

Days to 50 per cent anthesis

The days to 50 per cent anthesis was not significantly interaction between genotype and *A. vogelii* infestation. It was differed significantly amongst groundnut genotypes across all seven genotypes (Table 4). Guinea fowl had a considerably higher than the other genotypes. *A. vogelii* infection, on the other hand, significantly (Table 4 and 6)

Days to physiological maturity

Infestation with *A. vogelii* had no effect on the days to physiological maturity (Table 6). The groundnut genotypes, on the other hand, showed significant (p>0.001) differences. Guinea chicken takes longer than the other genotypes to reach physiological maturity (Table 6).

Table 5. Response of groundnut physiological and biomass traits to *Alectra* infestation

Genotype	Days to 50% anthesis	Days to physiological maturity	Shoot biomass (kg)	Root biomass (kg)	Number of seeds per plant	100 kernel weight (kg)
Dendera	43.3^{ab}	70.8^{a}	0.03^{b}	0.036^{c}	8.4^{ab}	0.05
Guinea fowl	57.8^{d}	84.3^{ab}	0.02^{ab}	0.022^{ab}	9.9^{b}	0.02
Ilanda	38.2^{a}	71.5^{a}	0.03^{ab}	0.02^{ab}	10.6^{b}	0.02
Jessa	36^{a}	70.7^{a}	0.025^{b}	0.03^{abc}	6.7^{a}	0.05
Njiva	41^{abc}	70.4^{a}	0.04^{c}	0.022^{ab}	13.3^{c}	0.03
Nyanda	44.5^{c}	71^{a}	0.02^{ab}	0.022^{ab}	8.3^{ab}	0.02
Tern	39.2^{ab}	71.7^{a}	0.02^{a}	0.02^{a}	7.5^{a}	0.02
p-value	<0.001	<0.001	0.003	0.004	<0.001	0.502
SED	2.541	1.250	0.005	0.004	1.2	0.02
LSD	5.075	2.496	0.01	0.0084	2.4	Ns

Table 6. Means of *A. vogelii* infestation levels recorded for different groundnut phenological and biomass traits evaluated under glasshouse conditions

A. vogelii infestation	Days to 50% anthesis	Days to physiological maturity	Shoot biomass (kg)	Root biomass (kg)	Number of seeds per plant	100 kernel weight (kg)
Infested	44.3^{b}	73.1	0.02^{a}	0.024	5.8^{a}	0.008^{a}
Non-infested	41.4^{a}	72.7	0.03^{b}	0.024	12.7^{b}	0.053^{b}
p-value	0.032	0.570	0.014	0.8	<0.001	<0.001
SED	1.358	0.668	0.003	0.002	0.6	0.01
LSD	2.713	Ns	0.005	Ns	1.3	0.02

Total plant biomass

Genotype x *A. vogelii* infestation interaction was significant on plant biomass (Table 4). Plant biomass was significantly lower in infested pots in the genotypes Dendera, Nyanda and Tern (Figure 2a).

Shoot biomass

Groundnut shoot biomass was observed that there was no substantial interaction amid genotype and *A. vogelii* infection (Table 4). Groundnut genotypes with *Alectra vogelii* infection have considerably lower shoot biomass. Njiva had considerably larger shoot biomass than the other genotypes. Among the groundnut genotypes, there were considerable variances in shoot biomass (Table 5).

Shoot/root ratio

Njiva had significantly higher shoot/root ratio than all groundnut genotypes whilst Jessa recorded the least shoot/root ratio. *A. vogelii* infestation reduced shoot to root biomass across all groundnut genotypes (Figure 2b).

Number of seeds per plant

The number of seeds per plant did, however, differ significantly amongst groundnut genotypes (Table 4). Njiva produced much more seeds per plant than the other groundnut genotypes (Dendera, Guinea fowl, Ilanda, and Nyanda), whereas Jessa and Tern produced the fewest (Table 5). Alectra infestation reduced the number of seeds per plant on all groundnut genotypes significantly (Table 5 and Table 6).

100 kernel weight

One hundred groundnut kernel weight, also not significant for genotype x Alectra interaction. However, the performance of groundnut genotypes on 100 kernel weights did not differ substantially (Table 4 and Table 5).

Groundnut genotypes that were not affected had significantly greater 100 kernel weight ($p>0.001$) than infested genotypes (Table 4 & Table 5).

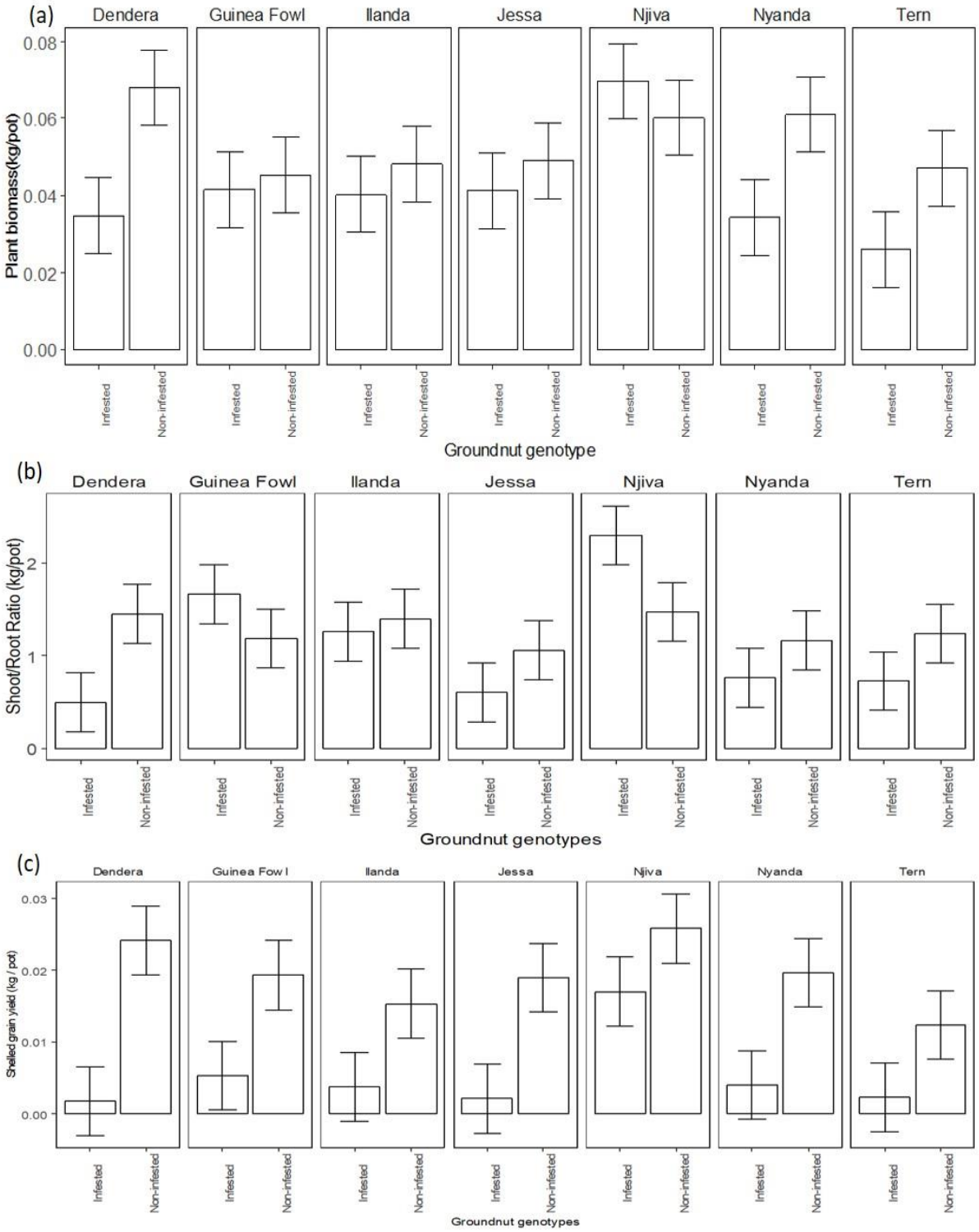

Figure 2. The interaction between groundnut genotypes and *A.vogelii* infection on (a) total plant biomass (b) shoot/root ratio (c) shelled grain yield evaluated under glasshouse conditions.

Shelled grain yield

A significant Genotype x Alectra interaction was observed shelled grain yield (Table 4). Shelled grain yield of all genotypes was significantly lower in infested pots than in non-infested pots except in the genotype Njiva where there were no significant differences (Figure 2c).

DISCUSSION

The present study aim was to identify groundnut genotypes that were resistant or tolerable to A. vogelii. Because strigolactones generated by the host plant trigger germination of *A. vogelii,* the results demonstrated that genotype Njiva did not support germination and attachment of *A. vogelii,* indicating that it is a resistant genotype. Conversely, the genotypes Dendera and Nyanda had high germination percentages and longest germination distances which suggests that they produce large quantities of strigolactones and are therefore susceptible to *A. vogelii* infection (Hussein et al., 2006; Masumoto et al., 2021). These results concur with findings of Hess et al. (1992) and Gwatidzo et al. (2020) who reported that any genotype with maximum germination distance (MGD) that is greater than 10 mm is susceptible whilst those with less than 10 mm could either be tolerant or resistant. Results from the agar gel assay therefore suggest that genotype Njiva has pre-attachment resistance to *A. vogelii*. Researchers revealed that genetic variations within genotypes potentially confer pre-attachment resistance to parasitic weeds (Kamara et al., 2008; Dieni et al., 2018; Ichihashi et al., 2020). Similar findings were reported in Nigeria where groundnut genotypes with low germination stimulant production were classified as resistant (Kwaga et al., 2010; Motagi et al., 2014).

From this study, *A. vogelii* infection did not reduce plant height of the genotypes evaluated except Nyanda. In some instances, groundnut plants grown in *A. vogelii* infested pots were taller than those grown in witchweed free soil but number of branches were different. Stunted growth, one of the main indications of *A. vogelii* infection, is responsible for the reduction in groundnut plant height (Ejeta, 2007; Kabambe et al., 2013; Njekete et al., 2017). Low susceptibility to A. vogelii infection in these genotypes could be attributed to the parasite's late attachment to the host as well as genetic heterogeneity among groundnut genotypes (Mukendi et al., 2017; Phiri et al., 2019; Mandumbu et al., 2019). One of the most sensitive indicators that reflects the effect of A. vogelii on groundnuts is plant height (Kamara et al., 2008; Karanja et al., 2011). These findings further conform the resistance and susceptibility of Njiva and Nyanda, respectively. The other genotypes exhibited tolerance to *A. vogelii* despite their ability to support the germination of the parasite from an average distance of 7 mm.

Generally, *A. vogelii* infestation decreased number of primary branches on Guinea fowl, Jessa and Tern. Groundnut branches are now key most sensitive indicator of groundnut performance under *A. vogelii* (Kwaga, 2014) because susceptible genotypes have consequently reduced primary branches, correlated to the number of spikes produced (Magani and Lagoke, 2009) which contribute to pod formation (Mbwando et al., 2016; Mutuku et al., 2020). The reason might be the effect of reduced canopies/ aboveground biomass to support photosynthesis leading to reduced dry matter accumulation on host plants as well as shelled grain yield (Parker, 2012; Kabambe et al., 2013; Ugbaa et al., 2020). The devastating effects of *A. vogelii* were not apparent on number of branches in the genotype Njiva which further confirms its resistance to this parasitic weed.

Nonetheless, chlorophyll content and fluorescence were significantly lower in *A. vogelii* pots than uninfected pots. Similar findings were obtained by Kwaga (2014) who reported that chlorophyll was altered under *Alectra* infection and the rate of photosynthesis decreased (Rodenburg et al., 2016; Nyakurwa et al., 2018; Gasura et al., 2019). This could have resulted in a reduction in carbon dioxide assimilation (Ejeta, 2007; Masumoto et al., 2021). It is postulated that all susceptible groundnut genotypes to *A. vogelii* allowed haustorial attachment, penetration and development on phloem and/ or xylem connection (Hussien et al., 2006; Phiri et al., 2019; Ichihashi et al., 2020; Mutuku et al., 2020; Masumoto et al., 2021). Thus, lowering chlorophyll content, shoot biomass, shoot to root ratio and grain yield (Kabambe et al., 2008; Fite et al., 2009). Tolerant genotypes proved to adjust itself on chlorophyll content and become independent to keep photosynthesis at optimal rates, simultaneously supplying the parasite in rhizosphere (Parker, 2012; Mandumbu et al., 2016; Gasura et al., 2019). High shoot/root ratio recorded on tolerant and resistant genotypes indicated low strigolactones production (Gwatidzo et al., 2020).

This may explain less carbohydrates translocation to the root under *Alectra* infection, thus minimising growth and development of the parasite; therefore, high capacity to produce adequate carbohydrates to sustain both parasite and host (Gasura et al., 2019; Gwatidzo et al., 2020). This was the same when

genotype x *Alectra* interactions were significant on plant biomass, shoot/root ratio and shelled grain yield. The shoot/root ratio indicates the direction of movement of carbohydrates (Lagoke and Magani, 2009). Njiva, Guinea Fowl and Ilanda exhibited this tolerant trait. In contrast, Dendera, Jessa, Nyanda and Tern were susceptible, as they lost much of biomass to *Alectra* which was acting as a sink (Hussien et al., 2006; Masumoto et al., 2021). This could have contributed to the reduced shelled kernel yield of susceptible infected groundnut genotypes. The fact that Njiva resisted the dwarfing effects of *A. vogelii* demonstrates that it is resistant.

On groundnut phenology, number of days to 50% anthesis and days to physiological maturity significantly varied across all genotypes. This is a result of genetic variation across all genotypes where some genotypes exhibited early maturity (Jessa and Njiva), medium maturity (Nyanda, Tern, Dendera and Ilanda) and late maturity (Guinea fowl). Minimum and maximum days to 50% anthesis were recorded on Jessa and Guinea fowl which took mean days of 36 and 58, respectively. These results contradict the findings of Alonge et al. (2001a) who reported that *A. vogelii* infection expedited anthesis in cowpea. In this study, infected plants exhibited late flowering compared to non-infested and they varied with about 3-4 days across genotypes. *Alectra* induced pod filling before actual physiological time such that the size of the grain became very small and had a negative effect on the grain yield.

CONCLUSIONS

Based on the results recorded from agar-gel assay and the pot experiment, groundnut genotypes revealed different levels of resistance, tolerance and susceptibility. Njiva was identified as a resistant genotype because it did not support *A. vogelii* germination and attachment. The study revealed that the genotypes Ilanda and Guinea fowl are tolerant because they resisted the debilitating effects of *A. vogelii* infection. Njiva, Ilanda and Guinea fowl may provide a better option to farmers in *A. vogelii* endemic areas of SSA as they produce better yields under infestation.

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AUTHORS CONTRIBUTION

WM: methodology, data collection and analysis, writing. JTR, ED, SM and RM: Project leaders, conceptualization, student supervision, funding acquisition, writing and correction, final approval for submission; OVG: Writing and revising of the manuscript.

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