



# Integrated management of *Striga gesnerioides* in cowpea using resistant varieties, improved crop nutrition and rhizobium inoculants

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## Abstract

**Background** Cowpea is a grain legume of major importance in sub-Saharan Africa where it is cultivated by smallholder farmers on poor soils and production is often constrained by the parasitic weed *Striga gesnerioides*.

**Method** Experiments were conducted to assess the potential of rhizobium inoculation to mitigate *Striga* infection and increase cowpea productivity. We infested soils with *S. gesnerioides* and assessed the impact of treatments combining cowpea genotypes and bradyrhizobium inoculation on *Striga* dynamics and cowpea yield. In total, 20 cowpea genotypes were included, of which nine were resistant to *Striga* and 11 were susceptible. In the first experiment these

were factorially combined with three inoculation options (two bradyrhizobium strains USDA3384 and IRJ2180A, and uninoculated control) in a screen-house using potted sterile soils. Second, the same trial was repeated in the field with basal phosphorus applied at sowing and a fourth treatment of fertilizer-N (urea) included testing whether N was limiting cowpea growth. The field trial also included a separate treatment with no input that served as a negative check.

**Result** Significant genotype x treatment interactions were observed in nodule counts, *Striga* attachment, emergence, and cowpea shoot growth in the screen-house. There were few nodules across all cowpea lines. *Striga* counts were the lowest for resistant varieties with no emerged plants. Rhizobial inoculants depressed *Striga* counts with consistent differences

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across cowpea genotypes. Inoculation with IRJ2180A performed the best against *Striga* attachment in resistant genotypes, and against *Striga* emergence in susceptible genotypes. In the field trial, cowpea grown without inputs had the least number of nodules. The genotype  $\times$  treatment interaction was significant: resistant cowpea genotypes were free of emerged *Striga* while there was much more *Striga* emergence without input addition with susceptible genotypes. A significant genotype  $\times$  treatment interaction was observed on cowpea grain yield. Yield response to inoculation was clearest with resistant genotypes inoculated with the strain IRJ2180A.

**Conclusion** The integrated use of *Striga*-resistant cowpea lines, basal phosphorus fertilizer and elite bradyrhizobium inoculants is a promising approach to mitigate *Striga* infection and increase cowpea productivity.

**Keywords** *Vigna unguiculata* · *Striga* · Biocontrol · Nodulation · Nitrogen fixation

## Introduction

Cowpea (*V. unguiculata* (L.) Walp.) is a grain legume of high agronomic, nutritional and economic importance in the semi-arid tropics where it is mainly cultivated by resource poor farmers. It constitutes a valuable source of protein in the diets of millions of people (Boukar et al., 2016). About 7.4 million metric tons of cowpea is annually produced worldwide on about 12.6 million hectares (FAOSTAT, 2017). Yet the productivity of cowpea on farmers' fields remains poor due to numerous abiotic and biotic constraints. Cowpea is often infested by parasitic weed *Striga gesnerioides* (Willd.) Vatke, which is a major biotic constraint to crop production in the Savannah and Sahel agroecologies of West Africa. The degree of infestation of *Striga* is greatest when soil fertility is poor, sometimes causing complete loss of yield and forcing farmers to abandon their cultivated lands (Kamara et al., 2014).

*S. gesnerioides* is an autogamous parasite with a life cycle typical of other agriculturally important *Striga* spp., and a wide host range including cowpea and groundnut (*Arachis hypogaea* L.), many other legumes (*Alysicarpus* spp., *Euphorbia* spp., *Indigofera* spp. and *Tephrosia* spp.) as well as tobacco (*Nicotiana*

*tabacum* L.) and *Ipomea* spp. (Berner and Williams, 1998). Adaptations to parasitism of *Striga* species include the ability to produce a large number of tiny seeds with prolonged viability and special germination requirements (Siame et al., 1993). Seeds germinate only after exposure to exogenous germination stimulants, strigolactones, which are derived from root exudates of host and often non-host plant species (referred to as trap crops) (Bouwmeester et al., 2007; Yoneyama et al., 2009; Cardoso et al., 2014). Strigolactones are plant hormones which regulate plant shoot and root architecture in response to the environment (Gomez-Roldan et al. 2008; Cardoso et al., 2014), which also function as host recognition signals for arbuscular mycorrhizal fungi (Akiyama et al., 2005) and rhizobia, and trigger seeds of parasitic weeds such as *Striga* spp. to germinate (Soto et al., 2010; Foo and Davies, 2011; Foo et al., 2013).

Farmer practices to combat *Striga* weeds range from hand-pulling emerged *Striga* plants, crop rotations / intercropping to improve soil fertility, the use of trap crops that stimulate suicidal germination of *Striga* seeds, to the selection of resistant crop varieties. Promising methods to manage *Striga* arising from research include the use of mineral fertilizers (Jamil et al., 2011), chemicals (Kanampiu et al., 2001, 2003; Kountche et al., 2019), intercropping (Rusinamhodzi et al., 2012), improved tolerant/resistant germplasm (Lane et al. 2003) and biological control (Mabrouk et al., 2007a). However, yield loss attributable to *Striga* is increasing because many promising *Striga* control methods suffer from limited adoption and utility (Silberg et al., 2021; Jamil et al., 2021). Low uptake of agricultural technologies is driven by multiple socioeconomic constraints at the farm or higher levels, resulting from lack of/or competing use of land, labour, cash, or organic resources, and reluctance of farmers to experiment with new methods (Oswald, 2005; Giller et al., 2011; Kanampiu et al., 2018).

An integrated approach is required using direct and indirect measures in a concerted manner to prevent damage of parasitism, and ultimately to eradicate the seed bank (Rubiales and Fernandez-Aparicio, 2012). Integrated soil fertility management (ISFM) (Vanlauwe et al., 2010), including incorporation of legumes into cropping systems (Franke et al., 2018; Vanlauwe et al., 2019; Kamara et al., 2020) can contribute to reducing *Striga* infection. Many leguminous

crops such as cowpea can stimulate suicidal germination of seeds of *Striga* spp. that infect cereals as non-host species (Berner and Williams, 1998), and are used as trap crops to reduce *Striga* spp. in cereal-legume rotation and intercropping systems (Midega et al., 2014; Hooper et al., 2015).

Strains of rhizobia have been identified with potential for controlling the parasitic weed *Orobanche crenata* Forsk. in inoculated pea (Mabouk et al., 2007a, b). Inoculation of pea with compatible rhizobia was reported to affect *O. crenata* by reducing seed germination, and decreasing root infection with limited capacity for tubercle development and necrosis of attachments (Mabouk et al., 2007a, b). Considering that the key factors determining productivity/ or performance of legume technologies range from the genotypes of both the legume ( $G_L$ ) and the associated root nodule rhizobia ( $G_R$ ), the test climate and soil environments ( $E$ ), to the agronomic management used ( $M$ ), such relationship can be expressed as  $-(G_L \times G_R) \times E \times M$  (Giller et al., 2013). For a given environment, understanding in the same way the relationship between the effectiveness of various combinations of symbiotic partners ( $G_L \times G_R$ ) and managements options ( $M$ ), and the variability in legume infection by *Striga* spp. is of major interest in view of explaining the potential of matching legume variety and inoculant strain in controlling *S. gesnerioides*.

*Striga*-resistant varieties and promising lines of cowpea have already been identified (Lane et al., 2003; Boukar et al., 2016), which provide a key entry point for testing integrated *Striga* management options. Genotypes of cowpea (Lane et al., 2003) and many cereals such as rice (Rodenburg et al., 2017), sorghum (Rodenburg et al., 2006) and maize (Badu-Apraku et al., 2020) are reported to combine improved degrees of resistance and tolerance to *Striga*. Resistance to *Striga* spp. refers to genotype ability to support fewer infections, whereas tolerance denotes its potential to show less damage for similar infection levels when compared with other varieties of the same species (Rodenburg et al., 2006). Resistant varieties can induce the germination of *Striga* seeds while preventing the parasite from attaching to host roots or killing the attached parasitic plants (Badu-Apraku et al., 2020).

In this paper, we present the results of an integrated evaluation of BNF technologies consisting of

crop varieties, rhizobium inoculants, and the application of phosphorus (P) and nitrogen (N) fertilizers. The objectives are (i) to evaluate under screen-house conditions the potential of rhizobia as biocontrol agents against *S. gesnerioides* in *Striga*-resistant and susceptible cowpea varieties, (ii) to assess the relative performance of rhizobial inoculants to control *Striga* infection of cowpea in the field as compared with standard mineral fertilisation, and (iii) to identify the most effective combination of rhizobia, cowpea genotype and fertilizer for optimal control of *S. gesnerioides*.

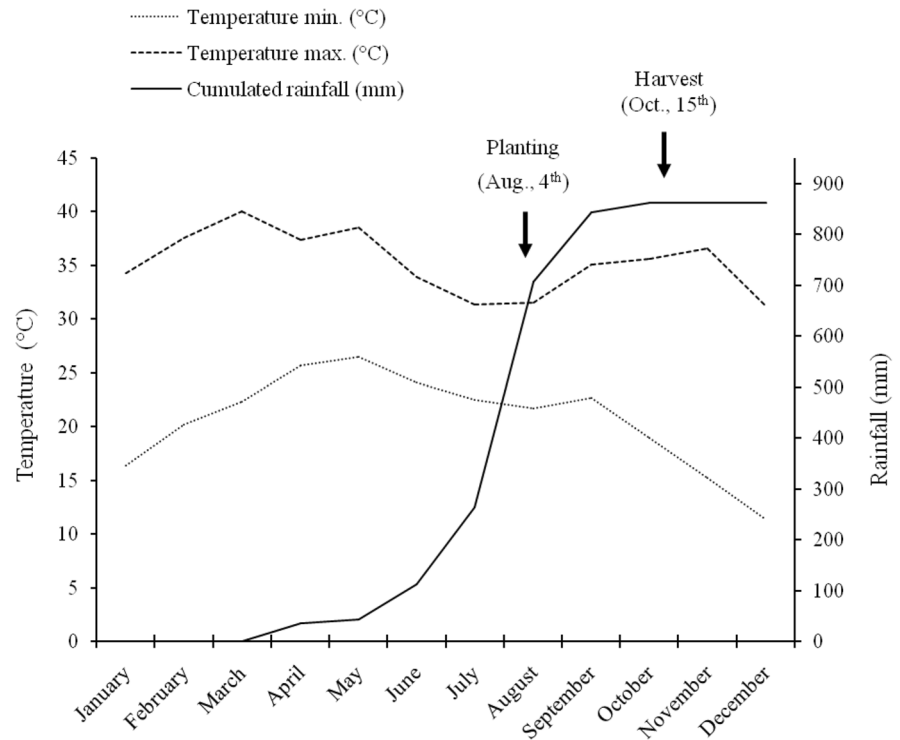
## Materials and methods

### Experimental site and soil description

Two sets of experiments were conducted in 2014 in Kano (Kano state, northern Nigeria) under screen-house and field conditions. A screen-house trial was carried out under artificial irrigation during the dry season at the Kano Station of International Institute of Tropical Agriculture (IITA). A subsequent field trial was conducted under natural rainfall during the following rainy season at the IITA research farm (12°10'42"N, 8°32'39"E at 500 m above sea level), located at Minjibir village 45 km north of Kano. Both locations fall under the Sudan savanna agro-ecological zone, where climate is dry with a unimodal distribution of 700–800 mm annual rainfall (Ronner et al., 2016) over a short growing season (about 120 days) from July to September. The mean monthly rainfall and temperature in 2014 at Minjibir are shown in Fig. 1.

Soil sampling was done before land preparation by taking soil cores from 0 to 15 cm depth at random points describing a “Z” pattern across the whole field. The cores were bulked and mixed thoroughly to provide a composite sample, and a subsample was analysed for physical and chemical properties according to standard procedures (IITA, 1989) in the analytical laboratory of the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria. The abundance of soil bradyrhizobia was determined by the plant infection technique (Vincent, 1970) (Table 1). The soil was coarse textured and texture fell within the loamy sand and sandy loam class (Table 1). Soil organic carbon

**Fig. 1** Weather data for 2014 at the Minjibir experimental site in Kano, Nigeria



(9 g kg<sup>-1</sup>) was relatively low and total nitrogen (0.36 g kg<sup>-1</sup>) in the very low N fertility class. The concentration of available Cu (1.07 mg kg<sup>-1</sup>) was low and there was relatively high concentration of Mn (46 mg kg<sup>-1</sup>) and Fe (178 mg kg<sup>-1</sup>) due to the slightly acidic pH (5.6) of the soil (Table 1). Available soil P in the field (8.6 mg kg<sup>-1</sup>) was as low, as is common in sandy savanna soils with low organic matter content (Kwari et al., 2011).

#### Cowpea and *Striga* seed sources

Twenty cowpea genotypes (Table 2) were compared in both screen-house and field station experiments. These lines have earlier shown variable responses to *Striga* ranging from lack of infection even at high *Striga* infestation rates (resistant genotypes) to presence of parasitism even at low *Striga* infestation (susceptible genotypes) (Muranaka et al., 2011). Seeds of cowpea lines were obtained from the Genetic Resource Center (GRC) of IITA. The *Striga* seeds were harvested in 2010 from a research farm at Malam Madori in Jigawa State, a *Striga* hot-spot where cowpea is widely cultivated. *Striga* seeds

were manually threshed and cleaned to remove chaff. Seeds were then surface-sterilized with a sodium hypochlorite solution (NaOCl, 3.0%) for

**Table 1** Soil chemical characteristics and most-probable number (MPN) of rhizobia at the Minjibir site

Soil property	Value
pH (H <sub>2</sub> O)	5.6
N (g kg <sup>-1</sup> )	0.36
Bray P (mg kg <sup>-1</sup> )	8.61
C (g kg <sup>-1</sup> )	9
Sand (g kg <sup>-1</sup> )	800
Silt (g kg <sup>-1</sup> )	80
Clay (g kg <sup>-1</sup> )	120
Ca (cmol kg <sup>-1</sup> )	1.29
Mg (cmol kg <sup>-1</sup> )	0.57
K (cmol kg <sup>-1</sup> )	0.19
Na (cmol kg <sup>-1</sup> )	0.40
Zn (mg kg <sup>-1</sup> )	<0.01
Cu (mg kg <sup>-1</sup> )	<0.01
Mn (mg kg <sup>-1</sup> )	0.46
Fe (mg kg <sup>-1</sup> )	0.78
ECEC	2.45
Rhizobia (MPN)	1.7 × 10 <sup>3</sup>

**Table 2** Physical characteristics, distinguishing features of cowpea genotypes and their reaction to *Striga*

Genotype	Seed colour	Seed texture	Reaction to <i>Striga</i>	<sup>a</sup> Origin
B301	Cream	Smooth	Resistant	Local land race from Botswana
IT97K-205-8	White	Rough	Resistant	Bred at IITA
IT97K-499-35	White	Smooth	Susceptible	Bred at IITA
IT98K-503-1	Maroon	Rough	Resistant	Bred at IITA
IT98K-573-1-1	White	Smooth	Resistant	Bred at IITA
IT99K-573-2-1	White	Smooth	Resistant	Bred at IITA
Tvu 16,514	Brown	Rough	Resistant	Tropical <i>Vigna unguiculata</i>
UAM09 1046-6-1	Brown	Smooth	Resistant	Bred at UAM
UAM1051-1	White	Smooth	Resistant	Bred at UAM
Aloka local	White	Rough	Susceptible	Local cultivar in Nigeria
Borno brown	Brown	Smooth	Susceptible	Local cultivar in Nigeria
BOSADP	Brown	Smooth	Susceptible	Bred at BOSADP
Danila	White	Rough	Susceptible	Local cultivar in Nigeria
IT81D-994	White	Smooth	Susceptible	Bred at IITA
IT84S-2246-2	Brown	Smooth	Susceptible	Bred at IITA
IT90K-277	White	Smooth	Resistant	Bred at IITA
IT98D-1399	White	Smooth	Susceptible	Bred at IITA
IT98D-288	White	Smooth	Susceptible	Bred at IITA
TVx 3236	Variegated	Smooth	Susceptible	Bred at IITA
UAM102021-1	Brown	Smooth	Susceptible	Bred at UAM

<sup>a</sup>IITA: International Institute of Tropical Agriculture; UAM: University of Agriculture, Makurdi; BOSADP: Borno State Agricultural Development Programme

3 min (Berner and Williams, 1998). Thereafter, the seeds were thoroughly rinsed with tap water through a fine sieve and left to air-dry in the laboratory.

#### Bradyrhizobium strains and inocula preparation

*Bradyrhizobium* sp. strain USDA 3384 (National Rhizobium Culture Collection, Beltsville, Maryland, USA) and *B. Japonicum* strain IRJ 2180A were obtained from the soil microbiology laboratory of IITA. These are reference broad host-range rhizobia strain (Foster et al., 1998; Hashem et al., 1997) and an elite soybean inoculant strain (Sanginga et al., 2002; Okogun and Sanginga, 2003), respectively. Each strain was grown in yeast extract mannitol medium for five days to reach  $10^9$  cell  $\text{ml}^{-1}$ , which was used as liquid inoculant in screen-house studies. Bradyrhizobial broths were used to prepare peat-based inoculants to coat seed for field experiments. Standard peat carrier (APT, USA) was sterilized by gamma irradiation (Ghana Atomic Energy Commission, Accra, Ghana) in bags containing 50 g

of peat each. Upon radiation, each bag was aseptically injected with 50 ml of the appropriate rhizobial broth, injection hole sealed, contain thoroughly mixed and then cured in the same bag at 28 °C for two weeks to obtain at least  $10^9$  cell  $\text{g}^{-1}$  inoculant (Hoben and Somasegaran, 1982).

#### Treatments, experimental design and crop management

In a first experiment, test soil was artificially infested with *Striga* to assess responses of 20 cowpea genotypes to three inoculation options under screen-house conditions. Inoculation treatments comprised of the two bradyrhizobial inoculants used separately, and an uninoculated control. Sixty treatments were studied consisting of  $20 \times 3$  factorial combinations of both factor levels. Treatments were established in three replications using a split plot arrangement where inoculation options were randomly assigned to main plots and cowpea genotypes to sub-plots as to minimize cross contamination. Cowpea plants were grown

on potted-soil infested with *Striga* seeds using a modified protocol of Singh and Emechebe (1990). A mixture of top soil and river sand (2:1; v/v) was prepared and sterilized by autoclaving (120 °C for 1 h) prior to incorporating *Striga* seed. The soil used in screen-house trial was sampled from the field where the field trial was conducted. Growth units consisted of plastic pots (13 cm, height and width) containing ca. 2.5 kg pot<sup>-1</sup> soil mixture. Four seeds of cowpea were planted and inoculated with 1 ml of bradyrhizobial broth pot<sup>-1</sup>. The growth units were subsequently irrigated with tap water as necessary on alternate days to ensure adequate moisture and good germination. Pots were thinned to two seedlings at 2 weeks after planting then fertilized with 180 mg P as single super phosphate (SSP, 18% P). Seedling leaves were further sprayed with a combined insecticide (35 ml of Lamdacyhalothrine and 75 ml of Cypermethrin plus Dimethoate in 15 l sprayer) to control insect pests.

In the second experiment conducted in the field, responses of *Striga* infection and crop performance of the same cowpea varieties to five treatments were tested on land heavily infested with *Striga* (five plants m<sup>-2</sup> on average). The treatments were a negative check with no input (inherent soil fertility), a control treatment which received only P fertilizer, the two inoculants applied together with P fertilizer, and a treatment which received urea-N and P fertilizer (Table 3). We refer to the inoculant treatments and the N fertilizer treatment jointly as “N sources”. P fertilizer was applied at the rate of 30 kg P ha<sup>-1</sup> as single-super phosphate and N applied as urea at a rate of 20 kg N ha<sup>-1</sup>. All fertilizer was applied at sowing in furrows and covered with soil to minimise losses. The experiment was set up as a split plot with 20 cowpea genotypes and 5 soil fertility treatments, replicated three times. The field was mown, harrowed

and plant debris removed. The field was then ridged at 0.75 m inter-ridge spacing. Cowpea seeds were pre-treated with fungicide-insecticide Apron Star (20% w/w Thiamethoxam, 20% w/w Metalaxyl-M, 2% w/w Difenconazole) to prevent soil-borne pests attack on seeds and seedlings. Plots (6 ridges × 4 m) were planted manually at the rate of three seeds per hill with 0.2 m intra-row spacing. Immediately before planting, cowpea seed was coated with peat-based inoculants (10 g kg<sup>-1</sup> seed) using a solution of gum arabic (ca. 20 g l<sup>-1</sup>) as sticker. Pre-emergence herbicide Paraquat and Pendimethalin (3 l ha<sup>-1</sup>) was sprayed immediately after sowing to control weeds. Two weeks after planting, plots were thinned to two plants per hill and SSP fertilizer was applied at the rate of 30 kg P ha<sup>-1</sup>. Lamdacyhalothrine 25 EC (0.7 l ha<sup>-1</sup>) and Cypermethrin, plus Dimethoate (1 l ha<sup>-1</sup>) was applied at flowering stage to control insect pests. The field was maintained free of weeds except *Striga* plants by regular manual weeding at three, six and eight weeks after planting.

#### Data collection and statistical analyses

In the screen-house study, plants were harvested at 64 days after planting (DAP). Potted plants were cut at the soil level and pots were gently flushed with tap water to discard soil from the root systems for count assessment of nodules, *Striga* attached to roots and emerged *Striga*. All plant parts were oven-dried separately at 65 °C for 48 h for biomass. In the field trial data were collected from the flowering stage onward. Twenty plants were randomly uprooted from border rows of each plot, nodules recovered, counted and oven-dried as above for dry mass assessment. Number of emerged *Striga* plants was monitored three times from the two central rows of plots until 70 DAP and cumulative number calculated. At maturity, the same inner rows were harvested, shoots, pods and grains air-dried and weight recorded.

Biomass data (cowpea and *Striga* dry weights) from the screen-house trial, and grain yield from the field study were analysed using a linear mixed model where genotype, strain, and genotype × strain were considered as fixed effects, and replicate, genotype × replicate as random effects. Count data across screen-house and field experiments (number of nodules, *Striga* attachments and emerged plants) were analysed using a generalized mixed model

**Table 3** Details of treatments applied to cowpea genotypes in the field experiment

Treatment	Fertilizer	
	Phosphorus (P)	Nitrogen N
Negative check	–	–
+P(control)	+	–
+P + N (urea)	+	+
+P + inoculant (strain IRJ 2180A)	+	–
+P + inoculant (strain USDA 3384)	+	–



(McCullagh and Nelder, 1989) assuming a Poisson distribution. Least-squares means and the associated standard errors derived from the mixed model were computed. Custom hypothesis tests were used to perform contrast comparisons between specific groups among cowpea genotypes and N-sources (Tables 4 and 5). All data were analysed using MIXED (linear mixed model) and GLIMMIX (generalized linear mixed model) procedures in SAS/STAT software, Version 9.4 of the SAS System for Windows (SAS Institute, 2019).

## Results

*Striga* infection, nodulation and plant growth in the screen-house

At harvest 64 DAP, the majority of inoculated cowpea plants were poorly nodulated as they had reached physiological maturity (Fig. 2). The occurrence of nodulation appeared to be inversely-related to infection of cowpea roots by *Striga*, with most plants exhibiting either nodules or *Striga* attachments (Fig. 3B, C). In addition, the smallest values for cowpea dry weight were found on plants with the least number of nodules (Fig. 3A).

There was a differential response of cowpea genotypes to inoculation treatments in shoot dry weight

( $P=0.0155$ , Table 4). Resistant varieties grew the best, yet were not responsive to inoculation in pots. By contrast, susceptible lines showed substantial responses to inoculation with an average of 63% increase in shoot dry weight ( $P\leq 0.0001$ , Table 4; Fig. 4A). Similarly, there were large differences between susceptible cowpea varieties which had significantly larger counts of emerged *Striga* plants ( $P=0.0047$ ) and number of *Striga* attachments to cowpea than resistant varieties ( $P\leq 0.0001$ ) (Fig. 3; Table 4; Fig. 4B-C). The number of emerged *Striga* plants from pots was the greatest ( $2.5 \text{ plant}^{-1}$ ) for susceptible genotypes grown without inoculation (control treatment) ( $P=0.0168$ ; Fig. 4B): Moreover, inoculation with strain IRJ 2180A was the most effective totally in preventing emergence of *Striga* plants in the potted susceptible genotypes ( $P=0.0246$ ; Fig. 4C). On average, the smallest numbers of *Striga* attachments to cowpea roots were observed in resistant varieties ( $P=0.0046$ ), and in inoculated plants ( $P=0.0065$ , Table 4; Fig. 4D-E). When compared with the uninoculated (control) treatments, addition of rhizobial inoculants was slightly more effective in reducing *Striga* attachments on resistant (90%) than susceptible (80%) varieties ( $P=0.0168$ ; Fig. 4D). Resistant genotypes performed best against *Striga* attachment to root with strain IRJ 2180A inoculant ( $P=0.0246$ ; Fig. 4E).

**Table 4** Summary of analysis of variance (ANOVA) of nodule number, cowpea shoot and *Striga* dry weights, and counts of plants and attachment of *Striga* for cowpea grown in potted-soils under screen-house conditions

Effect	df	<sup>a</sup> F or t values				
		Nodule number(number plant <sup>-1</sup> )	Cowpea shoot dry weight (g plant <sup>-1</sup> )	<i>Striga</i> dry weight (g pot <sup>-1</sup> )	<i>Striga</i> count (number pot <sup>-1</sup> )	<i>Striga</i> attachment (number plant <sup>-1</sup> )
Variety	19	0.33 NS	8.75 ****	1.32 NS	0.87 NS	1.87 NS
(R vs. S)	1	-0.74 NS	-8.29 ****	3.65 **	3.01 **	4.53 **
Inoculation	2	1.86 NS	6.10 **	11.64 ****	5.99 **	54.23 ****
(Inoculantsvs. Control)	1	1.87 NS	3.48 ***	-1.45 ****	-2.80 **	-10.29 **
(IRJ vs. US)	1	0.42 NS	0.30 NS	1.5 *	-2.23 *	-2.39 *
Inoculation*variety	38	1.84 *	1.78 NS	-1.84 *	2.00 **	4.38 ****
(Inoculantsvs. Control @ R)	1	1.76 NS	-1.10 NS	-1.84 *	-0.02 NS	-2.8 NS
(Inoculantsvs. Control @ S)	1	0.95 NS	5.69 ****	-4.54 ****	-4.30 ****	-14.22 ****
(IRJ vs. US @ R)	1	-0.51 NS	0.98 NS	0.29 *	0.21 NS	-0.64 NS
(IRJ vs. US @ S)	1	0.98 NS	-0.48 NS	-2.21 *	-3.35**	-2.82 **

\*, \*\*, \*\*\* and \*\*\*\*:  $P<0.05$ ,  $P<0.01$ ,  $P<0.001$ , and  $P<0.0001$ , respectively; NS: Not significant

<sup>a</sup>: Main and interaction effects tested with an F test; others (contrasts) tested with a t test

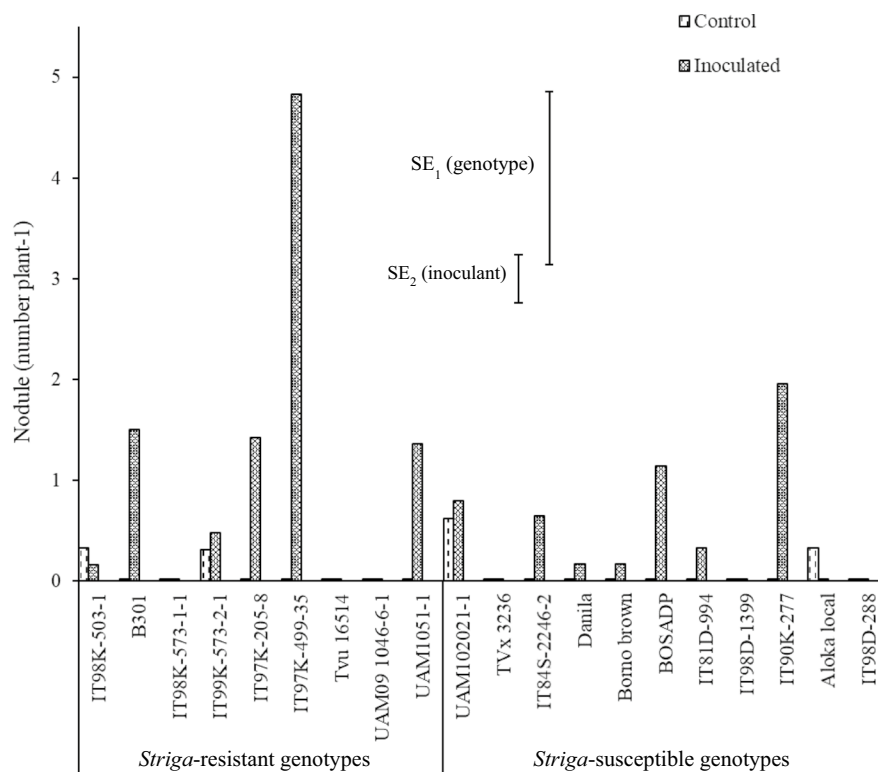
**Table 5** Summary of analysis of variance (ANOVA) of nodule number, count of emerged *Striga* and cowpea grain yield of cowpea grown under field conditions

Effect	df	<sup>a</sup> F or t values	<i>Striga</i> count (number 72.86 ha <sup>-1</sup> )	Cowpea grain Yield (kg ha <sup>-1</sup> )
Variety (V)	19	1.75 *	72.86 ****	19.89 ****
(R vs. S)	1	-1.90NS	33.15 ****	-15.48 ****
Management (M)	4	280.00****	5.13***	27.36****
(No input vs. Others)	1	19.06 ****	-4.12 ****	16.77 ****
(Urea vs. Inoculants)	1	9.74 ****	-0.91 NS	2.40 *
(IRJ2180A vs. USDA3384)	1	18.76 ****	0.06 NS	9.46 ****
(P vs. P+N)	1	6.99 ****	-1.73 NS	-1.64 NS
M x V	76	0.79NS	2.51****	3.92****
(No Input vs. Others @ R)	1	12.12 ****	0.00 NS	14.36 ****
(No Input vs. Others @ S)	1	14.70 ****	-18.75 ****	9.63 ****
(Urea vs. Inoculants@ R)	1	7.08 ****	0.00 NS	2.24*
(Urea vs. Inoculants@ S)	1	6.73 ****	-3.03 **	1.21 NS
(IRJ vs. UDSA @ R)	1	-13.23 ****	0.00 NS	-8.49****
(IRJ vs. UDSA @ S)	1	-13.35 ****	-0.17 NS	-5.08****
(P vs. P+N @ R)	1	4.89 ****	0.00 NS	1.05 NS
(P vs. P+N @ S)	1	5.00 ****	-6.55 ****	-3.12**

<sup>a</sup>: Main and interactions' effects tested with an F test; others (contrasts) tested with a t test;

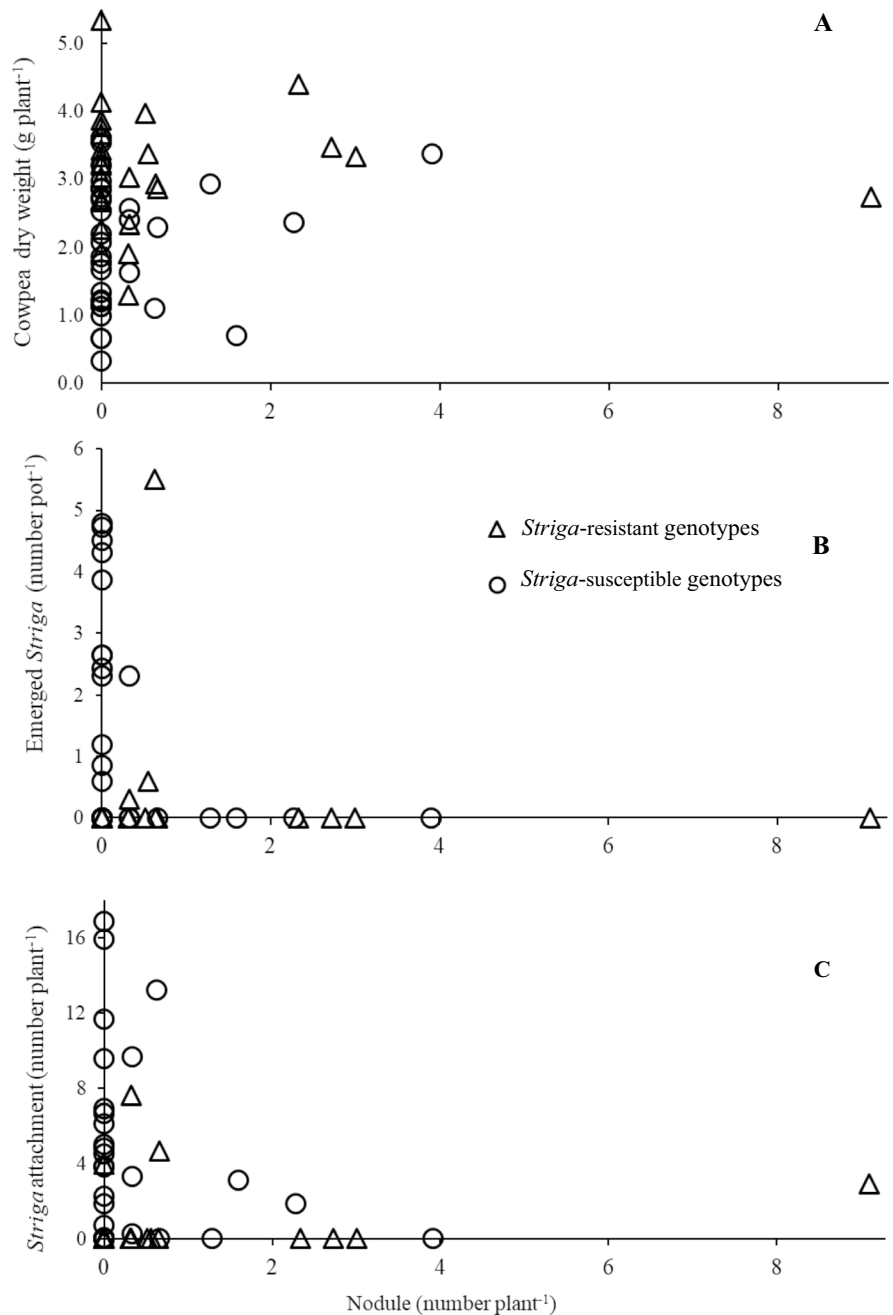
\*, \*\*, \*\*\* and \*\*\*\*:  $P < 0.05$ ,  $P < 0.01$ ,  $P < 0.001$ , and  $P < 0.0001$ , respectively; NS: Not significant

**Fig. 2** Average nodule number of 20 cowpea genotypes inoculated with bradyrhizobia under screen-house conditions. Error bars represent the standard errors of difference between means





**Fig. 3** Relationships between (A) cowpea shoot dry weight, (B) emerged *Striga* count and (C) number of *Striga* attachment, and nodule number of *Striga*-resistant and -susceptible cowpea genotypes inoculated under screen-house conditions

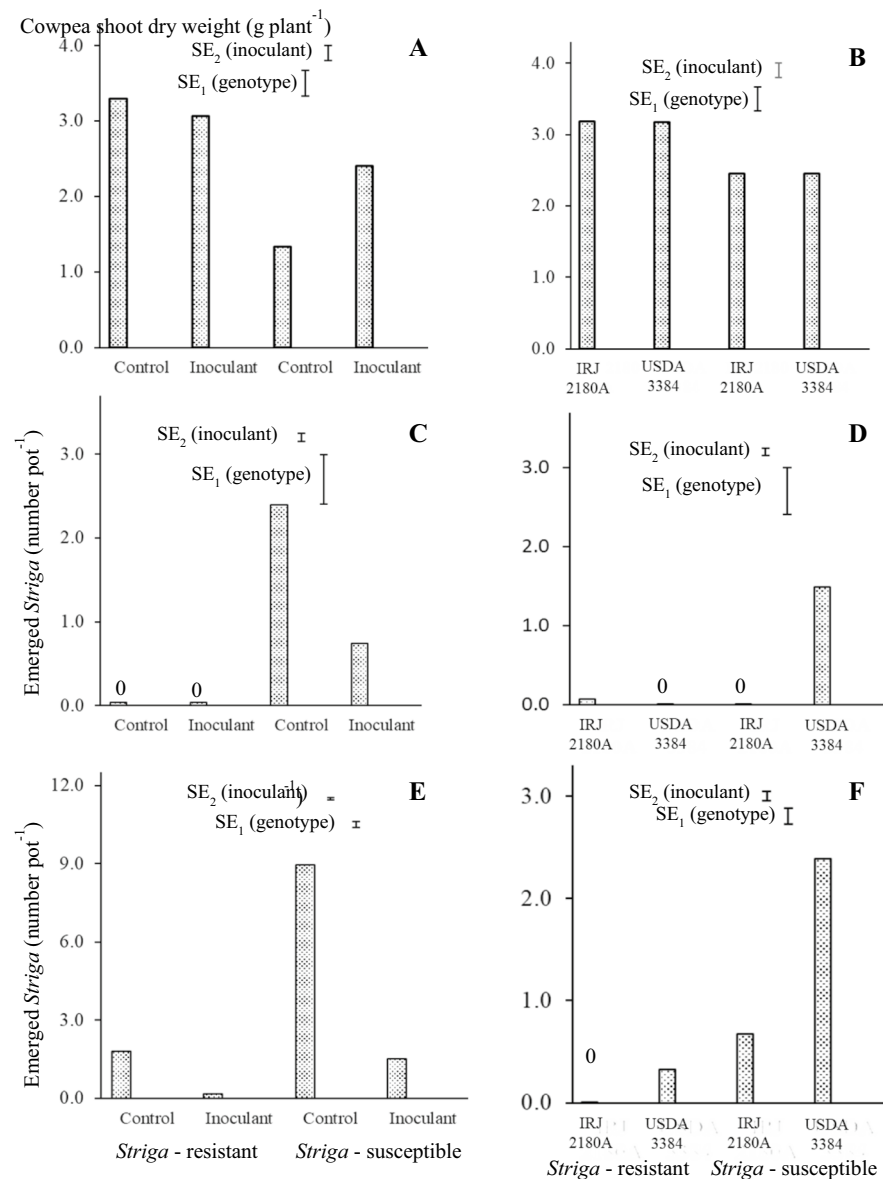


*Striga* infection, nodulation and plant growth in the field trial

At early cowpea flowering stage, the number of nodules was 14.9 nodules plant<sup>-1</sup> on average with significant differences among varieties ( $P=0.0315$ ), and between nutrient management options ( $P\leq 0.0001$ ; Table 5; Fig. 5A-D). The least nodule number (5.3

nodules plant<sup>-1</sup>) was found for cowpea managed without any input ( $P\leq 0.0001$ ; Fig. 5A). The application of P fertilizer alone improved nodulation (13.1 nodules plant<sup>-1</sup>), but to a lesser extent than when P and N sources were combined ( $P\leq 0.0001$ ; Fig. 5B). Addition of urea resulted in less nodules (13.3 nodules plant<sup>-1</sup>) than when rhizobial inoculants were applied (21.5 nodules plant<sup>-1</sup>) ( $P\leq 0.0001$ ; Fig. 5C).

**Fig. 4** A-B Shoot dry weight, (C-D) emerged *Striga* count, and (E-F) *Striga* attachment responses to inoculation with bradyrhizobia of *Striga*-resistant and -susceptible cowpea genotypes in potted soils under screen-house conditions; the cowpea plants were inoculated with strains IRJ 2180A or USDA 3384 (inoculant) or not (control). (B): Variety x strain not significant. Errors bar represents the standard error of means



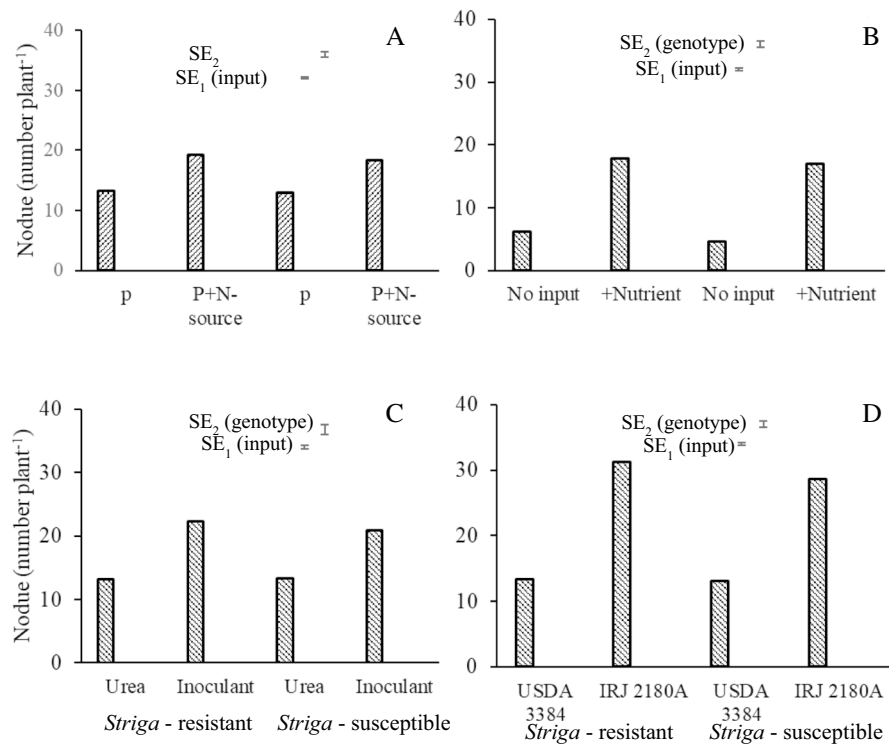
Among the inoculant treatments, the largest number of nodules was found in the presence of the strain IRJ 2180A (29.8 nodules plant<sup>-1</sup>;  $P \leq 0.0001$ , Table 5; Fig. 5D).

Overall, strong positive relationships were found between nodule number and cowpea yield and negative relationships with *Striga* emergence (data not shown). Emergence of *Striga* plants decreased with increasing nodule number, which led to improved cowpea yield. The density of *Striga* plants was highest for the less well nodulated cowpea plants managed without any input

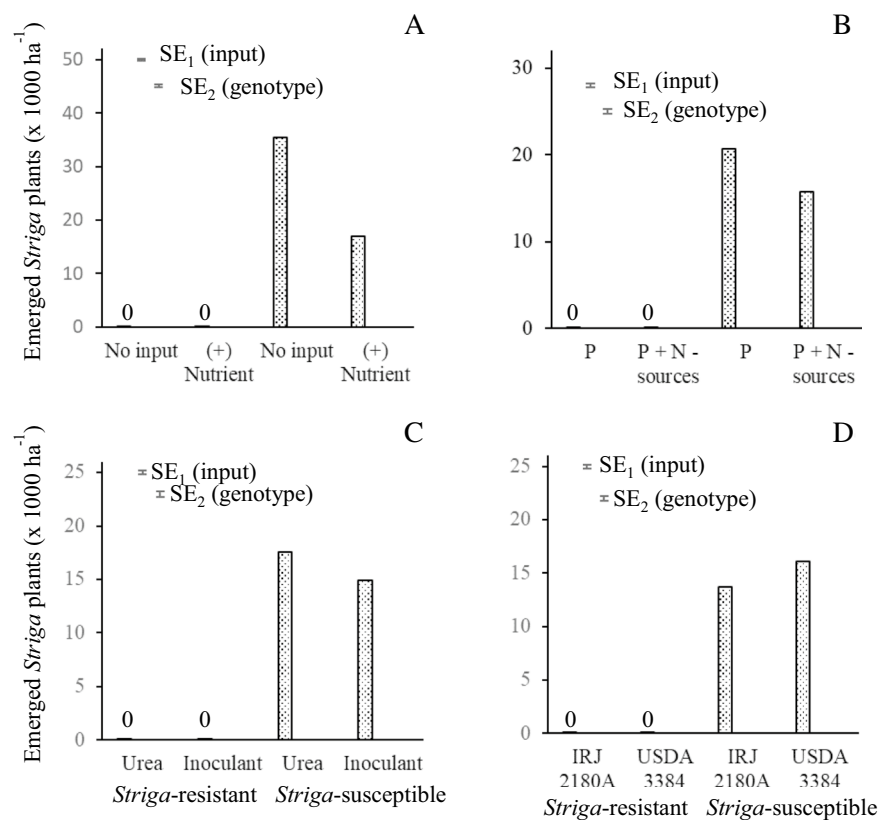
( $\leq 5$  nodules plant<sup>-1</sup>) and lowest for the abundantly-nodulated plants in the P+ IRJ 2180A treatment ( $\geq 25$  nodules plant<sup>-1</sup>). For most cowpea genotypes, grain yield had a significant negative correlation with *Striga* count.

Significant variety x management interactions was observed in the cumulative count of emerged *Striga* plants ( $P \leq 0.0001$ , Table 5). Plots with resistant cowpea varieties were remarkably free of emerged *Striga* almost throughout the field experiment (Fig. 6A-D). Susceptible varieties had stronger infection with *Striga* count dependent upon the management option

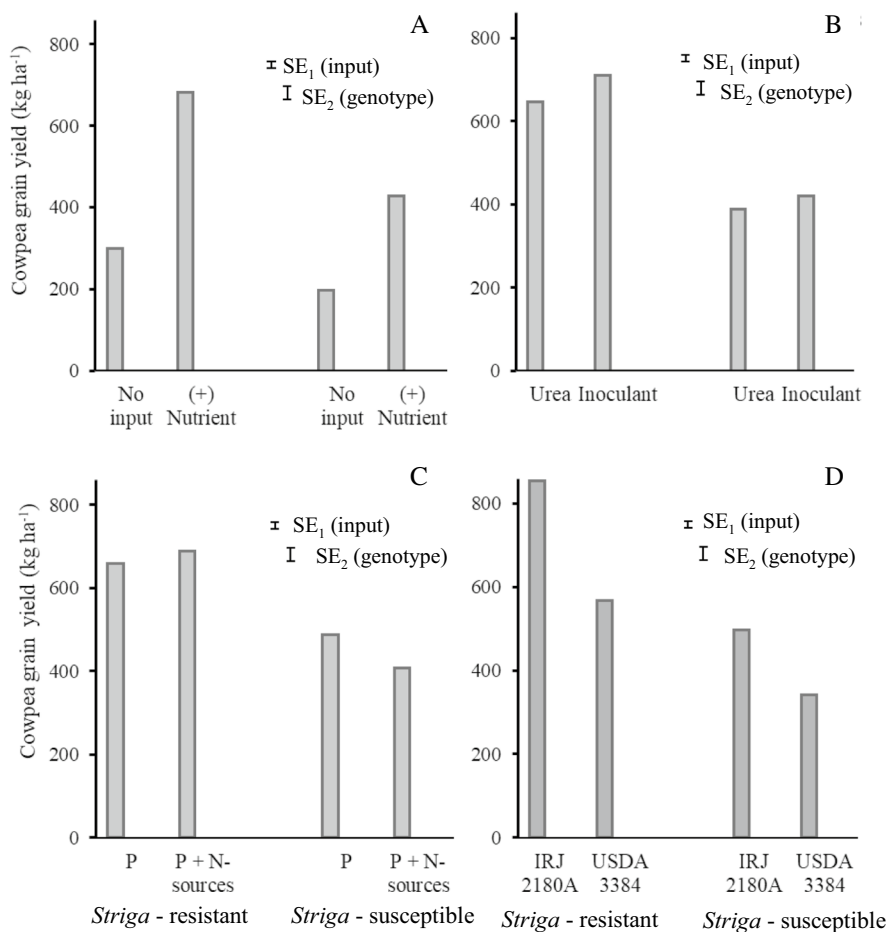
**Fig. 5 A-D** Average nodule number of cowpea plants grown under five management options under field conditions; No input: No fertilization; + P: phosphorus; urea: urea-N; IRJ 2180A and USDA 3384: bradyrhizobial inoculants; Error bars represent the standard error of means



**Fig. 6 A-D** Average number of emerged *Striga* plants for cowpea grown under five management options in the field; No input: No fertilization; + P: phosphorus; urea: urea-N; IRJ 2180A and USDA 3384: bradyrhizobial inoculants; Error bars represent the standard error of means



**Fig. 7** A-D Average grain yield response of cowpea grown under five management options in the field; No input: No fertilization; + P: phosphorus; Urea: urea-N; IRJ 2180A and USDA 3384: bradyrhizobial inoculants; Error bars represent the standard error of means



(Fig. 6A-D). Sprouting of *Striga* was densest without any amendment (no input) compared with nutrient addition ( $P \leq 0.0001$ , Table 5; Fig. 6A). On average, managing susceptible cowpea varieties with various combinations of P and N-sources led to more than 2.6-fold reduction in the number of *Striga* plants relative to plots without any input (Fig. 6A). Effectiveness in the control ranged from the least with P alone to the highest for P combined with N-sources (Fig. 6B). However, emerged *Striga* count when fertilized with urea was comparable with that for rhizobial inoculants (Fig. 6C-D).

The differential responses of the cowpea genotypes to management options resulted in large grain yield differences at harvest ( $P \leq 0.0001$ , Table 5). Grain yield as well as its response to input additions was consistently stronger in resistant lines than susceptible ones ( $P \leq 0.0001$ ,

Table 5; Fig. 7A-D). Overall, grain yield was more than doubled in response to nutrient supply compared with no input treatments, with increase being marginally larger for resistant (128%) than susceptible (119%) lines (Fig. 7A). On average in addition, grain yield in susceptible varieties was more responsive to P alone (+16%) than P+N treatments ( $P \leq 0.01$ , Table 5; Fig. 7B). When P was applied the yield response of the cowpea varieties to inoculant was significantly greater ( $ca + 10\%$ ) than with urea ( $P = 0.0174$ ; Fig. 7B). Overall, cowpea yielded substantially more grain (31–34% more) with inoculant strain IRJ 2180A than USDA 3384 ( $P \leq 0.0001$ ; Fig. 7D). Also, resistant varieties outperformed susceptible lines in yield responses to inoculation, which was most obvious in the presence of inoculant strain IRJ 2180A ( $P = 0.0043$ ; Fig. 7D).

## Discussion

Our results demonstrate that integration of resistant varieties, fertilizer application and inoculation with *Bradyrhizobium* could effectively control *Striga* in cowpea. A pot experiment was used first to investigate genotypic variability in cowpea responses to co-inoculation with rhizobia and *Striga* in the screen-house. Although the cowpea plants were poorly-nodulated by time of harvest ( $< 1$  nodule plant<sup>-1</sup> on average; Fig. 2), plant infection by *Striga* was strongly reduced as compared to the control without inoculation. Poor nodulation in the screen-house could be partly due to the harvest of mature plants, as well as the soil sterilization which would have killed off arbuscular mycorrhizal (AM) fungi as well as native rhizobia. In addition to the well-established role of AM in plant uptake of phosphorus in P-deficient soils which supports good nodulation and nitrogen fixation in legumes (Hayman, 1986, de Novais et al., 2020), there is evidence that AM fungi can suppress *Striga* infection in cereals. While the precise mechanisms need to be elucidated, AM both suppress germination of *Striga* seeds and attachment to host roots, leading to reduced root colonisation and emergence of *Striga* plants (Gworgwor and Weber 2003; Lendzemo et al., 2005, 2006), by altering the release of *Striga* seeds germination stimulants in host root exudates (Akiyama et al., 2005; Lendzemo et al., 2007). This suggests that further studies on the role of the tripartite interaction of the host legume, AM and rhizobia on *Striga* suppression are warranted. On average, the resistant cowpea varieties had the least number of *Striga* attachments to the roots as well as the number and weight of emerged *Striga* shoots (Fig. 3). Surprisingly, resistant varieties were also found to be the most responsive to rhizobial inoculants for the control of *Striga*: compared with the uninoculated control plants of these varieties, there was as high as a tenfold reduction in the number of *Striga* attachments which resulted in cowpea plants almost clean of the parasites (Fig. 4).

In comparison with some practices recommended against *Striga* such as hand or hoe-weeding and conventional biocontrol, which operate only when the parasite has already infected the crop and subsequently developed emerged shoots, eradicating the seed bank and preventing root colonization by *Striga* may be the ideal solution to its control (López-Ráez

et al., 2008; Kountche et al., 2019). The use of crop varieties that combine resistance with high tolerance levels is presently suggested among the most promising and easy to adopt control options against the weed *Striga*, particularly when combined also with other management practices (Rodenburg et al., 2006, 2017; Badu-Apraku et al., 2020). Although much literature has emphasised the importance of integrated technologies involving improved crop germplasm, companion legumes, fertilizer and crop management option for control of *Striga* spp. (Tesfaye and Ejeta, 2011; Midega et al. 2014; Randrianjafizanaka et al., 2018; Kamara et al., 2020), little attention has so far been paid to the potential contribution of rhizobial inoculants against the weed. Our study shows the potential of using rhizobial inoculants as part of integrated management to aid *Striga* control. We provide insights into how resistant varieties, fertilizer and rhizobial inoculants can be combined to manage *Striga* in cowpea, although our results need to be further confirmed across more locations and seasons.

Cowpea lines grown in fields infested with *S. esne-rioides* readily formed root nodules without inoculation, demonstrating the presence of adequate native populations of compatible rhizobia (Fig. 5). Unlike other legume crops such as soyabean which have a symbiotic requirement for specific rhizobial strains, cowpea is a promiscuous host, able to form root nodules with a broad range of highly diverse rhizobia (Giller, 2001). On the other hand, poor soil fertility is a major constraint to the proper establishment and function of legume symbiosis in sub-Saharan Africa (Vanlauwe et al., 2019). The improved nodulation of cowpea in response to addition of P is consistent with widespread reports of soil P limitations for growth and production of grain legumes in sub-Saharan Africa (Ronner et al., 2016; vanHeerwaarden et al., 2018; Belete et al., 2019; Rurangwa et al., 2018). It appears that cowpea generally needs to be fertilized with P, except in a few locations such as in Ghana where field-grown cowpea genotypes nodulated well without any nutrient addition (Adjei-Nsiah et al., 2008).

As expected from previous studies, our results confirmed a consistent varietal effect on *Striga* infection with a clear discrimination between resistance and susceptible cowpea lines in the field (Lane et al., 2003; Muranaka et al., 2011). *Striga* plants were not observed in the plots planted with

resistant cowpea genotypes and significant interactions between the variety and management were evident. This confirms the importance of resistant varieties to control *Striga* (Rodenburg et al., 2006; Badu-Apraku et al., 2020). Alleviation of nutrient deficiency through addition of P fertilizer and either rhizobial inoculant or N fertilizer also suppressed *Striga* (Fig. 6.), as poor soil fertility is known to favour the spread of *S. gesnerioides*. In a similar vein, Jamil et al. (2011) showed N and P fertilizers reduced secretion of *Striga* seed germination stimulants in maize resulting in less *Striga* infection.

We further found a large difference in performance of the two rhizobial strains. Strain IRJ 2180A was much more effective in promoting cowpea nodulation and in suppressing *Striga* than strain USDA 3384. Our findings suggest that the improved nutritional status of cowpea is the most likely mechanism through rhizobial inoculants contributed to mitigate *Striga* infection. This could be mediated through reduced strigolactone production from inoculated cowpea plants leading to less *Striga* germination, and/or the ability of more vigorous plants to tolerate and escape the deleterious effects of *Striga*. It could also involve mechanisms of induced systemic resistance in the host roots by rhizobia, which leads to mechanical and chemical barriers against parasitic weeds (Mabrouk et al., 2007a, b, 2008, 2010). *Rhizobium leguminosarum* strain P.SOM reduces pea root infection by the parasitic weed *O. crenata* through inhibition of seed germination (more than 3-fold less parasite seeds germinated, with a large proportion of necrotic sprouted seeds), and attachment (up to 7-times less tubercles per plant, Mabrouk et al., 2014). Histological studies have shown that lignification of host endodermal and pericycle cells may be an additional resistance mechanism that prevents parasite penetration at the initial stage of infection, and leads to necrosis and death of developed tubercles (Perezde Luque et al., 2005). Further research is needed to elucidate the mechanisms. The effective reduction in the number of *Striga* plants in the field consistently resulted in better cowpea grain yields, and differences were consistent with trends in the repression of the parasite (Figs. 6 and 7). The increase of cowpea yield obtained here with the combined use of improved germplasm, fertilizers and rhizobial inoculants is a clear application of the concept of integrated soil fertility management

(ISFM) needed for the sustainable intensification of African agriculture (Vanlauwe et al., 2015).

The productivity of cowpea grown without any inputs was very poor (211–280 kg ha<sup>-1</sup>), the choice of cowpea genotype was clearly the most relevant starting point to increase yields. The use of improved cowpea seed alone led to the highest impacts both in the control of the weed (46 times less infection) and grain yield (+33%). As a second step, P fertilization was effective for controlling *Striga* in susceptible varieties (38% less emerged plants), though responses in grain yield remained strongest for resistant lines (2.6-compared with 2.1-fold increase for susceptible lines). Effective rhizobial inoculants formed a third level of intervention. For the susceptible lines, the most effective strain (IRJ 2180A) led to additional decrease (52%) in *Striga* emergence and enhancement in grain yield (18%) over and above the effects of P fertilization alone (442 kg ha<sup>-1</sup>). For the resistant varieties also, responses were almost similar with around 56% less *Striga* emergence and 15% increase in grain yield in comparison with P fertilization alone (715 kg ha<sup>-1</sup>). This suggests overall a sequence of improved germplasm, P fertilizer and rhizobial inoculant as steps towards implementation of ISFM.

## Conclusion

We have demonstrated the potential of using bradyrhizobial inoculants as effective biocontrol agents as part of an integrated strategy against *S. gesnerioides* weed infection of cowpea. Field-grown cowpea was confirmed to perform well in terms of grain yield and in control of infection by *Striga* when improved germplasm was used together with P fertilization. The use of appropriate cowpea genotypes is therefore suggested to be a suitable entry point for ISFM application, followed by P fertilizer and rhizobium inoculants. P fertilization was found to be crucial to both cowpea productivity and its responsiveness to rhizobial inoculants. Further evidence of a strong genotypic host plant x rhizobia strain interaction highlights the possibility for further selection of combinations to counter *Striga* damage. Whilst these are promising results, further investigations are needed to confirm the robustness these control options across more agroecological environments and seasons.



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## Declarations

**Conflict of interest** The authors declare no conflict of interest.

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## References

- Adjei-Nsiah S, Kuyper TW, Leeuwis C, Abekoe MK, Cobbinah J, Sakyi-Dawson O, Giller KE (2008) Farmers' agronomic and social evaluation of productivity, yield and N<sub>2</sub>-fixation in different cowpea varieties and their subsequent residual N effects on a succeeding maize crop. *Nutr Cycl Agroecosyst* 80:199–209. <https://doi.org/10.1007/s10705-007-9133-3>
- Akiyama K, Matsuzaki K, Hayashi H (2005) Plant sesquiterpenes induce hyphal branching in arbuscular mycorrhizal fungi. *Nature* 435(7043):824–827. <https://doi.org/10.1038/nature03608>
- Badu-Apraku B, Adewale S, Paterne A, Gedil M, Asiedu R (2020) Identification of QTLs controlling resistance/tolerance to *Striga hermonthica* in an extra-early maturing yellow maize population. *Agronomy* 2020(10):1168. <https://doi.org/10.3390/agronomy10081168>
- Belete S, Bezabih M, Abdulkadir B, Tolera A, Mekonnen K, Wolde-meskel E (2019) Inoculation and phosphorus fertilizer improve food-feed traits of grain legumes in mixed crop livestock systems of Ethiopia. *Agric. Ecosyst Environ* 279:58–64. <https://doi.org/10.1016/j.agee.2019.04.014>
- Berner DK, Williams OA (1998) Germination stimulation of *Striga gesnerioides* seeds by hosts and nonhosts. *Plant Dis* 82:1242–1247. <https://doi.org/10.1094/pdis.1998.82.11.1242>
- Boukar O, Fatokun CA, Huynh B-L, Roberts PA, Close TJ (2016) Genomic tools in cowpea breeding programs: status and perspectives. *Front Plant Sci* 7:757. <https://doi.org/10.3389/fpls.2016.00757>
- Bouwmeester HJ, Roux C, Lopez-Raez JA, Becard G (2007) Rhizosphere communication of plants, parasitic plants and AM fungi. *Trends Plant Sci* 12:224–230. <https://doi.org/10.1016/j.tplants.2007.03.009>
- Cardoso C, Zhang Y, Jamil M, Hepworth J, Charnikhova T, Dimkpa SON, Meharg C, Wright MH, Liu J, Meng X, Wang Y, Li J, McCouch SR, Leyser O, Price AH, Bouwmeester HJ, Ruyter-Spira C (2014) Natural variation of rice strigolactone biosynthesis is associated with the deletion of two MAX1 orthologs. *Proc Natl Acad Sci U S A* 111:2379–2384. <https://doi.org/10.1073/pnas.1317360111>
- de Novais CB, Sbrana C, da Conceição Jesus E, Rouws LFM, Giovannetti M, Avio L, Siqueira JO, Saggin Júnior OJ, da Silva EMR, de Faria SM (2020) Mycorrhizal networks facilitate the colonization of legume roots by a symbiotic nitrogen-fixing bacterium. *Mycorrhiza* 30:389–396. <https://doi.org/10.1007/s00572-020-00948-w>
- FAOSTat (2017). FAOSTAT, Statistical data base. Food and Agricultural Organizations of the United Nations, Rome. <http://www.fao.org/faostat/> 2017
- Foo E, Davies NW (2011) Strigolactones promote nodulation in pea. *Planta* 234:1073–1081. <https://doi.org/10.1007/s00425-011-1516-7>
- Foo E, Yoneyama K, Hugill CJ, Quittenden LJ, Reid JB (2013) Strigolactones and the regulation of pea symbioses in response to nitrate and phosphate deficiency. *Mol Plant* 6:76–87. <https://doi.org/10.1093/mp/sss115>
- Foster CM, Horner HT, Graves WR (1998) Nodulation response of woody Papilionoid species after inoculation with rhizobia and soil from Hawaii, Asia and North America. *Plant Soil* 205:103–111. <https://doi.org/10.1023/A:1004309414388>
- Franke AC, van den Brand GJ, Vanlauwe B, Giller KE (2018) Sustainable intensification through rotations with grain legumes in sub-Saharan Africa: A review. *Agric Ecosyst Environ* 261:172–185. <https://doi.org/10.1016/j.agee.2017.09.029>
- Giller KE (2001) Nitrogen fixation in tropical cropping systems, 2nd edn. CAB International, Wallingford
- Giller, K.E., Franke, A.C., Abaidoo, R., Baijuka, F., Bala, A., Boahen, S., Dashiell, K., Kantengwa, S., Sanginga, J.-M., Sanginga, N., Simmons, A.J., Turner, A., de Wolf, J., Woomer, P., and Vanlauwe, B. (2013). "N2Africa: putting nitrogen fixation to work for smallholder farmers in Africa," In *Agro-ecological Intensification of Agricultural Systems in the African Highlands*, eds. B. Vanlauwe, P.J.A. van Asten, and G. Blomme (Routledge, London), 156–174
- Giller KE, Titttonell P, Rufino MC, van Wijk MT, Zingore S, Mapfumo P, Adjei-Nsiah S, Herrero M, Chikowo R, Corbeels M, Rowe EC, Baijuka F, Mwijage A, Smith J, Yeboah E, van der Burg WJ, Sanogo OM, Misiko M, de Ridder N et al (2011) Communicating complexity: integrated assessment of trade-offs within African farming systems to support development policy. *Agric Syst* 104:191–203. <https://doi.org/10.1016/j.agry.2010.07.002>
- Gomez-Roldan V, Feras S, Brewer PB, Puech-Pagès V, Dun EA, Pillot J-P, Letisse F, Matusova R, Danoun S, Portais J-C, Bouwmeester H, Bécard G, Beveridge CA, Rameau

- C, Rochange SF (2008) Strigolactone inhibition of shoot branching. *Nature* 455:189–194. <https://doi.org/10.1038/nature07271>
- Gworgwor NA, Weber HC (2003) Arbuscular mycorrhizal fungi-parasite-host interaction for the control of *Striga hermonthica* (Del.) Benth. In sorghum [*sorghum bicolor* (L.) Moench]. *Mycorrhiza* 13:277–281. <https://doi.org/10.1007/s00572-003-0238-5>
- Hashem FM, Saleh SA, van Berkum P, Voll M (1997) Survival of *Bradyrhizobium* sp. (Arachis) on fungicide-treated peanut seed in relationship to plant growth and yield. *World J Microbiol Biotechnol* 13:335–340. <https://doi.org/10.1023/a:1018595310239>
- Hayman DS (1986) Mycorrhizae of nitrogen-fixing legumes. *MIRCEN J Appl Microbiol Biotechnol* 2:121–145. <https://doi.org/10.1007/BF00937189>
- Hoben HJ, Somasegaran P (1982) Comparison of the pour, spread, and drop plate methods for enumeration of *Rhizobium* spp. in inoculants made from presterilized peat. *Appl Environ Microbiol* 44:1246–1247. <https://doi.org/10.1128/aem.44.5.1246-1247.1982>
- Hooper AM, Caulfield JC, Hao B, Pickett JA, Midega CAO, Khan ZR (2015) Isolation and identification of *Desmodium* root exudates from drought tolerant species used as intercrops against *Striga hermonthica*. *Phytochem* 117:380–387. <https://doi.org/10.1016/j.phytochem.2015.06.026>
- IITA (1989). Automated and Semi-automated Methods for Soil and Plant Analysis. Manual Series No. 7. IITA, Ibadan, Nigeria
- Jamil M, Charnikhova T, Cardoso C, Jamil T, Ueno K, Verstappen F, Asami T, Bouwmeester HJ (2011) Quantification of the relationship between strigolactones and *Striga hermonthica* infection in rice under varying levels of nitrogen and phosphorus. *Weed Res* 51:373–385. <https://doi.org/10.1111/j.1365-3180.2011.00847.x>
- Jamil M, Kountche BA, Al-Babili S (2021) Current progress in *Striga* management. *Plant Physiol* 185:1339–1352. <https://doi.org/10.1093/plphys/kiab040>
- Kamara AY, Ekeleme F, Jibrin JM, Tarawali G, Tofa I (2014) Assessment of level, extent and factors influencing *Striga* infestation of cereals and cowpea in a Sudan savanna ecology of northern Nigeria. *Agric Ecosyst and Environ* 188:111–121. <https://doi.org/10.1016/j.agee.2014.02.027>
- Kamara AY, Menkir A, Chikoye D, Tofa AI, Fagge AA, Dahiru R, al. (2020) Mitigating *Striga hermonthica* parasitism and damage in maize using soybean rotation, nitrogen application, and *Striga*-resistant varieties in the Nigerian savannas. *Exp Agric* 56:620–632. <https://doi.org/10.1017/S0014479720000198>
- Kanampiu FK, Ransom JK, Gressel J (2001) Imazapyr seed dressings for *Striga* control on acetolactate synthase target-site resistant maize. *Crop Prot* 20:885–895. [https://doi.org/10.1016/S0261-2194\(01\)00038-2](https://doi.org/10.1016/S0261-2194(01)00038-2)
- Kanampiu FK, Kabambe V, Massawe C, Jasi L, Friesen D, Ransom JK, Gressel J (2003) Multi-site, multi-season field tests demonstrate that herbicide seedcoating herbicide-resistance maize controls *Striga* spp. and increases yields in several African countries. *Crop Prot* 22:697–706. [https://doi.org/10.1016/S0261-2194\(03\)00007-3](https://doi.org/10.1016/S0261-2194(03)00007-3)
- Kanampiu FK, Makumbi D, Mageto E, Omany G, Waruingi S, Musyoka P, Ransom J (2018) Assessment of management options on *Striga* infestation and maize grain yield in Kenya. *Weed Sci* 66:516–524. <https://doi.org/10.1017/wsc.2018.4>
- Kountche BA, Jamil M, Yonli D, Nikiema MP, Blanco-Ania D, Asami T, Zwanenburg B, Al-Babili S (2019) Suicidal germination as a control strategy for *Striga hermonthica* (Benth.) in smallholder farms of sub-Saharan Africa. *Plants, People, Planet* 1:107–118. <https://doi.org/10.1002/ppp3.32>
- Kwari, J.D., Kamara, A.Y., Ekeleme, F., and Omoigui, L. (2011). Soil fertility variability in relation to the yields of maize and soybean under intensifying cropping systems in the tropical savannas of northeastern Nigeria. *Innovations as Key to the Green Revolution in Africa*. Springer, Netherlands, pp. 457–464
- Lane JA, Bailey JA, Butler RC, Terry PJ (2003) Resistance of cowpea [*Vigna unguiculata* (L.) Walp.] to *Strigasterioides* (Willd.) Vathe, a parasitic angiosperm. *New Phytol* 125:405–412. <https://doi.org/10.1111/j.1469-8137.1993.tb03893.x>
- Lendzemo VW, Kuyper TW, Kropff MJ, van Ast A (2005) Field inoculation with arbuscular mycorrhizal fungi reduces *Striga hermonthica* performance on cereal crops and has the potential to contribute to integrated *Striga* management. *Field Crop Res* 91:51–61. <https://doi.org/10.1016/j.fcr.2004.05.003>
- Lendzemo VW, van Ast A, Kuyper TW (2006) Can arbuscular mycorrhizal fungi contribute to *Striga* management on cereals in Africa? *Outlook Agric* 35:307–311. <https://doi.org/10.5367/000000006779398236>
- Lendzemo VW, Kuyper TW, Matusova R, Bouwmeester HJ, and van Ast, A. (2007) Colonization by arbuscular mycorrhizal fungi of sorghum leads to reduced germination and subsequent attachment and emergence of *Striga hermonthica*. *Plant Signaling Behav* 2:58–62. <https://doi.org/10.4161/psb.2.1.3884>
- López-Ráez JA, Matusova R, Cardoso C, Jamil M, Charnikhova T, Kohlen W, Ruyter-Spira C, Verstappen F, Bouwmeester H (2008) Strigolactones: ecological significance and use as a target for parasitic plant control. *Pest Manag Sci* 65:471–477. <https://doi.org/10.1002/ps.1692>
- Mabrouk Y, Zourgui L, Sifi B, Delavault P, Simier P, Belhadj O (2007a) Some compatible *Rhizobium leguminosarum* strains in peas decrease infections when parasitized by *Orobanche crenata*. *Weed Res* 47:44–53. <https://doi.org/10.1111/j.1365-3180.2007.00548.x>
- Mabrouk Y, Zourgui L, Sifi B, Belhadj O (2007b) The potential of *Rhizobium* strains for biological control of *Orobanche crenata*. *Biologia* 62:139–143
- Mabrouk Y, Zourgui L, Sifi B, Belhadj O (2008) Mechanism of induced resistance in pea by *Rhizobium* against *Orobanche crenata*. *Rev Arid Areas* 3:1234–1240
- Mabrouk Y, Mejri S, Hemissi I, Simier P, Delavault P, Saidi M, Belhadj O (2010) Bioprotection mechanisms of pea plant by *Rhizobium leguminosarum* against *Orobanche crenata*. *Afr J Microbiol Res* 4:2570–2575
- Mabrouk Y, Mejri S, Delavault P, Simier P, Delavault P, Saidi M, Belhadj O (2014) Lipopolysaccharide isolated from *Rhizobium leguminosarum* strain P.SOM induces resistance in pea roots against *Orobanche crenata*. *Afr*

- J Microbiol Res 8:2624–2630. <https://doi.org/10.5897/AJMR2013.5762>
- McCullagh, P., and Nelder, J.A. (1989). Generalized linear models. London, UK, Chapman & Hall
- Midega CAO, Salifu D, Bruce TJ, Pittchar J, Pickett JA, Khan ZR (2014) Cumulative effects and economic benefits of intercropping maize with food legumes on *Striga hermonthica* infestation. Field Crop Res 155:144–152
- Muranaka S, Fatokun C, Boukar O (2011) Stability of *Striga gesnerioides* resistance mechanism in cowpea under high-infestation level, low soil fertility and drought stresses. J Food Agric Environ 9:313–318
- Okogun JA, Sanginga N (2003) Can introduced and indigenous rhizobial strains compete for nodule formation by promiscuous soybean in the moist savanna agroecological zone of Nigeria? Biol Fertil Soils 38:26–31. <https://doi.org/10.1007/s00374-003-0611-8>
- Oswald, A. (2005). *Striga* control: technologies and their dissemination. Crop Prot 24, 333–342. <https://doi.org/10.1016/j.cropro.2004.09.003>
- Perezde Luque A, Rubiales D, Cubero JJ, Press MC, Scholes J, Yoneyama K, Takeuchi Y, Plakhine D, Joel M (2005) Interaction between *Orobanche crenata* and its host legumes: Unsuccessfulhaustorialpenetration and necrosis of the developing parasite. Ann Bot 95:935–942. <https://doi.org/10.1093/aob/mci105>
- Randrianjafizana MT, Autfray P, Andrianavo AP, Ramonta IR, Rodenburg J (2018) Combined effects of cover crops, mulch, zero-tillage and resistant varieties on *Striga asiatica* (L.) Kuntze in rice-maize rotation systems. Agric. Ecosyst and Environ 256:23–33. <https://doi.org/10.1016/j.agee.2017.12.005>
- Rodenburg J, Bastiaans L, Kropff MJ (2006) Characterization of host tolerance to *Striga hermonthica*. Euphytica 147:353–365. <https://doi.org/10.1007/s10681-005-9030-2>
- Rodenburg J, Cissoko M, Kayongo N, Dieng I, Bisikwa J, Irakiza R, Masoka I, Midega CAO, Scholes JD (2017) Genetic variation and host–parasite specificity of *striga* resistance and tolerance in rice: the need for predictive breeding. New Phytol 214:1267–1280. <https://doi.org/10.1111/nph.14451>
- Ronner E, Franke AC, Vanlauwe B, Dianda M, Edeh E, Ukem B, Bala A, van Heerwaarden J, Giller KE (2016) Understanding variability in soybean yield and response to P-fertilizer and rhizobium inoculants on farmers' fields in northern Nigeria. Field Crop Res 186:133–145. <https://doi.org/10.1016/j.fcr.2015.10.023>
- Rubiales D, Fernandez-Aparicio M (2012) Innovations in parasitic weeds management in legume crops. A review Agron Sust Dev 32:433–449. <https://doi.org/10.1007/s13593-011-0045-x>.hal-00930517
- Rurangwa E, Vanlauwe B, Giller KE (2018) Benefits of inoculation, P fertilizer and manure on yields of common bean and soybean also increase yield of subsequent maize. Agric Ecosyst Environ 261:219–229. <https://doi.org/10.1016/j.agee.2017.08.015>
- Rusinamhodzi L, Corbeels M, Nyamangara J, Giller KE (2012) Maize–grain legume intercropping is an attractive option for ecological intensification that reduces climatic risk for smallholder farmers in Central Mozambique. Field Crop Res 136:12–22. <https://doi.org/10.1016/j.fcr.2012.07.014>
- Sanginga N, Okogun J, Vanlauwe B, Dashiell K (2002) The contribution of nitrogen by promiscuous soybeans to maize based cropping the moist savanna of Nigeria. Plant Soil 241:223–231. <https://doi.org/10.1023/A:1016192514568>
- SAS Institute (2019). The SAS System for Windows, version 9.4. Cary, NC, USA, SAS Institute Inc.
- Siame BA, Weerasuriya Y, Wood K, Ejeta G, Butler LG (1993) Isolation of Strigol, a germination stimulant for *Striga asiatica*, from host plants. J Agric Food Chem 41:1486–1491. <https://doi.org/10.1021/jf00033a025>
- Silberg TR, Renner K, Schmitt Olabisi L, Richardson RB, Chimonyo VGP, Uriona-Maldonado M, al (2021) Modeling smallholder agricultural systems to manage Striga in the semi-arid tropics. Agric Syst 187:103008
- Singh BB, Emechebe AM (1990) Inheritance of *Striga* resistance in cowpea genotype B301. Crop Sci 30:879–881. <https://doi.org/10.2135/cropsci1990.0011183X003000040023x>
- Soto MJ, Fernandez-Aparicio MN, Castellanos-Morales V, Garcia-Garrido JM, Ocampo JA, Delgado MJ, Vierheilig H (2010) First indications for the involvement of strigolactones on nodule formation in alfalfa (*Medicago sativa*). Soil Biol Biochem 42:383–385. <https://doi.org/10.1016/j.soilbio.2009.11.007>
- Tesfaye TT, Ejeta G (2011) Integrating multiple control options enhances *Striga* management and sorghum yield on heavily infested soils. Agron J 103:1464. <https://doi.org/10.2134/agronj2011.0059>
- vanHeerwaarden J, Bajukya F, Kyei-Boahen S, Adjei-Nsiah S, Ebanyat P, Kamai N, Wolde-Meskel E, Kanampiu F, Vanlauwe B, Giller KE (2018) Soyabean response to rhizobium inoculation across sub-Saharan Africa: patterns of variation and the role of promiscuity. Agric. Ecosyst. Environ. 261:211–218. <https://doi.org/10.1016/j.agee.2017.08.016>
- Vanlauwe B, Bationo A, Chianu J, Giller KE, Merckx R, Mkwunye U, Ohiokpehai O, Pypers P, Tabo R, Shepherd K, Smaling EMA, Woomer PL (2010) Integrated soil fertility management operational definition and consequences for implementation and dissemination. Outlook Agric. 39:17–24. <https://doi.org/10.5367/000000010791169998>
- Vanlauwe B, Descheemaeker K, Giller KE, Huising J, Merckx R, Nziguheba G, Wendt J, Zingore S (2015) Integrated soil fertility management in sub-Saharan Africa: unravelling local adaptation. Soil 1:491–508. <https://doi.org/10.5194/soild-1-1239-2014>
- Vanlauwe B, Hungria M, Kanampiu F, Giller KE (2019) The role of legumes in the sustainable intensification of African smallholder agriculture: lessons learnt and challenges for the future. Agric Ecosyst Environ 284:106583. <https://doi.org/10.1016/j.agee.2019.106583>
- Vincent, J.M. (1970). A manual for the practical study of root-nodule bacteria, (IBP handbook no 15) Blackwell, Oxford
- Yoneyama K, Xie X, Yoneyama K, Takeuchi Y (2009) Strigolactones: structures and biological activities. Pest Manag Sci 65:467–470. <https://doi.org/10.1002/ps.1726>

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