Rhizobium inoculants suppress emergence of the weed Striga gesnerioides in cowpea

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Research Article

Keywords: Vigna sp., Striga¸ rhizobium, biocontrol, inoculant, BNF, cowpea

Posted Date: May 26th, 2021

DOI: https://doi.org/10.21203/rs.3.rs-358536/v1

Abstract

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*. Experiments were conducted to assess the potential of rhizobium inoculation in mitigating *Striga* infestation and increasing cowpea productivity. We tested under basal P application and artificial *S. gesnerioides* inoculation the impact of cowpea genotypes (G) (nine *Striga*-resistant and 11 *Striga*–susceptible genotypes) and bradyrhizobium inoculation (N) (two bradyrhizobium strains USDA3384 and IRJ2180A, and uninoculated control) on *Striga* dynamics and cowpea yield. Additional treatments included N supplied as urea (with and without), and no input (i.e., soil inherent N and P) that served as negative check. A first experiment was carried out in potted sterile soils in the screen house excluding addition of N-fertilizers. Significant G x N interactions were observed in counts of nodule ($P = 0.012$), *Striga* attachment ($P < 0.0001$) and emergence ($P = 0.005$), and cowpea shoot growth ($P = 0.016$). Cowpea nodulated poorly across host lines, *Striga* counts were the lowest for resistant varieties with no emerged plants. Rhizobial inoculants depressed *Striga* counts with consistent differences found across cowpea genotypes. Inoculation with IRJ2180A performed the best against *Striga* attachment in resistant genotypes, and its emergence in susceptible genotypes. In the field trial, nodule numbers were lowest in cowpea without inputs ($P < 0.0001$). The G x N interaction was significant in emerged *Striga* plants ($P < 0.0001$). Resistant genotypes were free of emerged *Striga* while for susceptible ones, *Striga* emergence was the highest without any input addition. Significant G x N interaction was observed in cowpea grain yield ($P < 0.0001$). Yield response to inoculation was most obvious for resistant genotypes inoculated with the strain IRJ2180A ($P = 0.0043$). The integrated use of *Striga*-resistant cowpea lines and elite bradyrhizobium inoculant under moderate application of P-based fertilizer could be a promising approach for mitigating *Striga* infestation and increasing productivity.

1. Introduction

Cowpea (*Vigna 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 are 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. For instance, cowpea is often infested by parasitic weeds including *Striga gesnerioides*, which is a major biotic constraint to crop production in the Savannah and Sahel agro-ecologies of West Africa. The degree of infestation is greatest when soil fertility is poor, sometimes causing complete loss of yield and forcing farmers to abandon their cultivated lands (Ejeta, 2007; Kamara et al., 2014).

S. gesnerioides is an autogamous parasite with a life cycle typical of other agriculturally important *Striga* 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, usually strigolactones (SLs), which are derived from root exudates of host and often non-host plant species (usually 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* seed, to the selection of resistant crop varieties. Promising methods to manage *Striga* arising from research include the use mineral fertilizers (Kureh et al., 2003; 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 (Ronald et al., 2017). 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, labor, cash, or organic resources, and reluctance of farmers to experiment with new methods (Oswald, 2005; Giller et al., 2011; Kanampiu et al., 2018).

African farming systems exhibit large variability at agroecological, socioeconomic and individual farm scales, such that there are no single solutions as silver bullets to address the numerous constraints to farm productivity (Giller et al., 2011) including the challenge imposed by *Striga* (Midega et al., 2014; Ronald et al., 2017). An integrated approach is required using direct and indirect measures in a concerted manner to prevent damages of parasitism, and ultimately to eradicate seed bank (Rubiales and Fernandez-Aparicio, 2012). Integrated soil fertility management (ISFM) (Vanlauwe et al., 2010), including incorporation of legumes into cropping systems (Sanginga and Woomer, 2009; Kamara et al., 2014) can contribute to reducing *Striga* infestation. Many leguminous crops including cowpeas can stimulate suicidal germination of seeds of *Striga* spp., and are used as trap crops to reduce *Striga* spp. in cereal-legume rotation and intercropping systems. Control of *Striga* spp. in cereals accounts for ‘non-N or – other rotational effects’ of legume crops as part of their beneficial impacts on soil biological, physical and chemical (except N) properties (Sanginga et al., 2002, 2003; Yusuf et al., 2009; Rusinamhodzi et al., 2012; Franke et al., 2018). However, major impacts of legumes result from their ability to improve N nutrition of subsequent non-legume crop, referred to as ‘N effects’, leading to reduced needs in N fertiliser (Giller, 2001; Franke et al., 2018).

Strains of rhizobia have been identified with potential for controlling the parasitic weed *Orobanche crenata* in inoculated pea (Mabouk et al., 2007a,b). Inoculation of pea with compatible rhizobia was reported to affect *O. orobanche* by reducing seed germination, and decreasing root infection with limited capacity for tubercle development and necrosis of attachments (Mabouk et al., 2007a,b). Like most BNF traits of legumes (Ronner et al., 2016; Van Heerwaarden, 2018), control of S. *gesnerioides* can be anticipated to depend upon multiple component interactions between and among integrated technologies. 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 infestation by *Striga* spp. can be 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. 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 of this study 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* infestation 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* leading to increased cowpea productivity.

2. Materials And Methods

2.1 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° 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 690 mm annual rainfall 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 Figure 1.

Soil samples were taken at random in the field from 0-15 cm depth before land preparation. These were bulked and thoroughly mixed to provide a composite sample, and a sub-sample of this composite was analysed for physical and chemical properties according to standard procedures (IITA, 1989). 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 (9 g kg^{-1}) was relatively low and total nitrogen (0.36 g kg^{-1}) in the very low N fertility class. The concentration of available Cu (1.07 mg kg^{-1}) was low and there was relatively high concentration of Mn (46 mg kg^{-1}) and Fe (178 mg kg^{-1}) due to the slightly acidic pH (5.6) of the soil (Table 1). Available soil P in the field (8.6 mg kg^{-1}) was low, which is common in sandy Sudan savanna soils with low organic matter content (Kwari et al., 2011).

2.2 Cowpea and Striga *seed sources*

Twenty cowpea genotypes (Table 2) were compared in both screen-house and field station experiments. These lines had contrasting responses to *Striga* (Muranaka et al., 2011) and were obtained from the Genetic Resource Center (GRC) of the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria. 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, cleaned to remove chaff and then were sterilized with a diluted Sodium hypochlorite (NaOHCl, 3.0%) for 3 minutes. Thereafter, the seeds were soaked in detergent for 5 min, thoroughly rinsed with tap water through a fine sieve and left to air-dry in the laboratory.

2.3 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 (Foster et al., 1998; Hashem et al., 1997) and 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 $10^{\wedge 9}$ cell 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 $10^{\wedge 9}$ cell g^{-1} inoculant.

2.4 Treatments, experimental design and crop management

In a first experiment, responses of 20 cowpea genotypes to three inoculation options were assessed 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 × 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 1 h) prior to incorporating *Striga* seed. Growth units consisted of plastic pots (13 cm, height and width) containing ca. 2.5 kg pot^{-1} soil mixture. Four seeds of cowpea were planted and inoculated with 1 ml of bradyrhizobial broth pot^{-1}. 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_2O_5). Seedling leaves were further sprayed with a combined insecticide (35 ml of Lamda cyhalothrine and 75 ml of Cypermethrin plus Dimethoate in 15 liters sprayer) to control insect pests.

In a second experiment conducted in the field, responses of the same cowpea varieties to five N including the above inoculation treatments were monitored. The N treatmemts were urea fertiliser, the two inoculants, a control, and a negative check with no input (inherent soil fertility). Except for the negative check, all N treatments were tested under basal P application as described bellow. A total of 100 individual treatments were defined as factorial combinations of the cowpea genotypes (20) and N-sources (5), and replicated thrice in field-testing using a split design as previously described. Cowpea was planted on land heavily infested with *Striga* (five plants m^{-2} on average). The field was mowed, the soil harrowed and the plant debris removed. The field was then ridged at 0.75 cm apart. Cowpea seeds were pre-treated with fungicide-insecticide Apron Star (20% w/w Thiamethoxam, 20% w/w Metalaxyl-M, 2% w/w Difenoconazole) to prevent soil-borne pests attack on seeds and seedlings. Plots (6 ridges x 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 costed with peat-based inoculants (10 g kg^{-1} seed) using a solution of gum Arabic (ca. 20 g l^{-1}) as sticker. Pre-emergence herbicide Paraquat and Pendimethalin (3 l ha^{-1}) 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^{-1}. Lamda cyhalothrine 25 EC (0.7 l ha^{-1}) and Cypermethrin, plus Dimethoate (1 l ha^{-1}) 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.

2.5 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 hours 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 x strain were considered as fixed effects, and replicate, genotype x 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 (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 (see Table 3 and Table 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).

3. Results

3.1 Striga *infestation, nodulation and plant growth in screen-house bioassay*

At harvest 64 DAP, a majority of inoculated cowpea plants poorly nodulated as it has 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. 3A-B). In addition, nodulation, cowpea growth and *Striga* infection traits showed significant inter-correlation (Fig. 3; Fig. 4A-D).

There was a differential response of cowpea genotypes to inoculation treatments in shoot dry weight (P=0.0155, Table 3). Resistant varieties grew the best, yet were not responsive to inoculation in pots; Opposite to this, susceptible lines showed substantial responses to inoculation gaining on average up to 63% shoot growth improvement (P < 0.0001, Table 3; Fig. 5A). 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 < 0.0001) (Fig. 3; Table 3; Fig. 5B-C). The number of emerged *Striga* plants from pots was the higest (2.5 plant^{-1}) for susceptible genotypes grown without inoculation (control treatment) (P=0.0168; Fig. 5B). Moreover, inoculantion with strain IRJ 2180A was the most effective totally in preventing emergence of *Striga* plants in the potted susceptible genotypes (P=0.0246; Fig. 5C). 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 3; Fig. 5D-E). When compared with the uninoculated (control) treatments, addition of rhizobial inoculants was more effective in reducing *Striga* attachments on resistant (90%) than susceptible (80%) varieties (P=0.0168; Fig. 5D). Resistant genotypes performed best against *Striga* attachment to root with strain IRJ 2180A inoculant (P =0.0246; Fig. 5E).

3.2 Striga *infestation, nodulation and plant growth in the field trial*

At early flowering the field-grown cowpea genotypes had 14.9 nodules plant^{-1} on average with significant differences among varieties (P=0.0315), and between nutrient management options (P < 0.0001; Table 4; Fig. 6A-D). Nodule number was the least (5.3 nodules plant^{-1}) for cowpea managed without any input (P < 0.0001; Fig. 6A). The application of P fertilizer alone improved nodulation (13.1 nodules plant^{-1}), but to a lesser extent than when combined with nitrogen sources (P+N) (P < 0.0001; Fig. 6B). Addition of urea resulted in less nodules (13.3 nodules plant^{-1}) than when rhizobial inoculants were applied (21.5 nodules plant^{-1}) (P < 0.0001; Fig. 6C). Among the inoculant treatments, the largest number of nodules was found in the presence of the strain IRJ 2180A (29.8 nodules plant^{-1}; P < 0.0001, Table 4; Fig. 6D).

Overall, strong positive relationships were found between nodule number and cowpea yield and negative relationships with *Striga* emergence (Fig. 7). Emergence of *Striga* plants decreased with increasing nodule number, which led to improved cowpea yield (Fig. 7A-C). The density of *Striga* plants was highest for the less nodulated cowpea plants managed without any input (≤5 nodules plant^{-1}) and lowest for the abundantly nodulated plants under P+ IRJ 2180A treatment (≥25 nodules plant^{-1}) (Fig. 7A). Cowpea grain yield had a significant (negative) correlation with *Striga* count (Fig. 7B).

Significant variety x management interactions were observed in the cumulative count of emerged *Striga* plants ($P < 0.0001$, Table 4). Plots with resistant cowpea varieties were remarkably free of emerged *Striga* almost throughout the field experiment (Fig. 8A-D). Susceptible varieties had stronger infestation with *Striga* count dependent upon the management option (Fig. 8A-D). Sprouting of *Striga* was densest without any amendment (no input) compared with nutrient addition ($P < 0.0001$, Table 4; Fig. 8A). 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.8A). Effectiveness in the control ranged from the least with P alone to the highest for P combined with N-sources (Fig. 8B). However, emerged *Striga* count when fertilized with urea was comparable with that for rhizobial inoculants (Fig. 8C-D).

The differential responses of the cowpea genotypes to management options resulted in large grain yield differences at harvest ($P < 0.0001$, Table 4). Grain yield as well as its response to input additions was consistently stronger in resistant than susceptible lines ($P < 0.0001$, Table 4; Fig. 9A-D). Overall, grain yield was more than doubled in response to nutrient supply compared with no input treatments, with increases being greater for resistant (128%) than susceptible (119%) lines (Fig. 9A). On average in addition, grain yield in susceptible varieties was more responsive to P alone (+16%) than P+N treatments ($P < 0.01$, Table 4; Fig. 9B). Under P supply however, yield response of the cowpea varieties to N was significantly higher (*ca* +10%) with inoculant than urea ($P=0.0174$; Fig. 9C). Overall, cowpea yielded substantially more grain (31 – 34 % more) with inoculant strain IRJ 2180A than USDA 3384 ($P < 0.0001$; Fig. 9D). 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. 9D).

4. Discussion

Our results demonstrate that integration of resistant varieties, fertilizer application and inoculation with *Bradyrhzobium* could effectively control *Striga* in cowpea. A potted-soil system was used first to investigate genotypic variability in cowpea responses to co-inoculation with rhizobia and *Striga* in the screen-house. In the presence of viable *Striga* seeds, rhizobial inoculants were unable to trigger an adequate nodule formation in cowpea plants (< 1 nodule plant^{-1} on average), but strongly reduced plant infestation by *Striga* as compared to the control without inoculation. On average, the resistant cowpea varieties had the least number of attachments to root and emerged *Striga* shoots and dry weight. 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 parasites. For the susceptible cowpea lines on the other hand, *Striga* infestation was best controlled by inoculation contributing to a better shoot growth.

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 switched 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). In this regard, our findings compare well with effective control methods described for *S. hermonthica* management in maize, which consist of the application of herbicide chemicals (imazapir) to herbicide-resistant maize hybrid (Kanampiu et al., 2001, 2002). This maize technology is reported to induce death of *Striga* organs including attachments and germinating seeds around maize roots over several weeks after planting, therefore leading to host plants clean of *Striga*, depleting *Striga* seed bank and improving crop productivity (Kanampiu et al. 2002, 2003).

Cowpea lines grown in fields infested with *S. gesnerioides* readily formed root nodules without inoculation, demonstrating the presence of adequate native populations of compatible rhizobia. 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 with addition of P is indicative of inadequate soil P supply, as also reported on various legumes in sub-Saharan Africa (Ronner et al, 2016; van Heerwaarden et al., 2018; Belete et al., 2019; Rurangwa et al., 2018). It appears that cowpea generally needs fertilization with P, except in some favourable sites such as in Ghana where field-grown cowpea genotypes nodulated well without any nutrient addition (Adjei-Nsiah et al., 2008).

Cowpea nodulation was enhanced by the combined application of P and rhizobial inoculants, which gave better nodulation then when urea was, applied (Fig. 5). Combined nitrogen is often recommended for legumes as starter N at moderate rates not inhibitory for nodule formation (Streeter, 1988; Sylvester-Bradley and Cross, 1991; Thies *et* al., 1991; Waswa et al., 2014; Giller et al., 2016). The slight improvement in nodule number observed with N addition suggests the rate of 20 kg N ha^{-1} to be suitable to serve as an effective starter N. In a field study conducted in Brazil by Freitas and Silva (2012), however, the same rate of urea was reported to have negative effects on the symbiotic performance of indigenous rhizobia in cowpea. There is little justification to use starter N on legumes in sub-Saharan Africa.

This study reports the first investigation of the potential benefits that can be derived from the management of rhizobial inoculants under pressure of S. *gesnerioides* pest on field-grown cowpea. As expected from previous genotypic characterization studies (Lane et al., 2003; Muranaka et al., 2011) the results revealed a consistent varietal effect on *Striga* infestation with a clear discrimination between resistance and susceptible lines. *Striga* plants were not observed in the plots planted to resistant lines and significant interactions between the variety and the management option were evident. Nodule abundance increased in the field with the strain IRJ 2180A demonstrating its high competitive ability, as also reported by earlier studies conducted in the semi-arid zone of Brazil with various inoculant strains (Martins et al., 2003). Competitive Brazilian strains were observed to improve nodulation of field-grown cowpea in Ghana (Boddey et al., 2016) and in Mozambique (Boddey et al., 2016; Kyei-Boahen et al., 2017), leading to improved productivity.

Nutrient addition options, either P alone or in combination with N also supressed *Striga* emergence. The positive effects of both fertilizers can partly be explained by the alleviation of nutrient deficiency (N and/or P), as poor soil fertility is known to favor the spread of S. *gesnerioides* (Sanginga and Woomer, 2009). Jamil et al. (2011) showed that N and P deficiencies induce increased secretion of *Striga* spp. seed germination stimulants (SLs) by maize resulting in increased infection of the host plants, which was reduced with the application of fertilizers. In our study, emergence of *Striga* was best controlled with rhizobial inoculants (as bio-fertilizers), and this was clearly due to the striking performance of the strain IRJ 2180A. By contrast strain USDA 3384 performed poorly in suppressing *Striga* infestation, possibly because of it being a poor competitor compared with native soil rhizobia. Besides being a good competitor, the inoculant strain IRJ 2180A appears also to be highly effective in N_2-fixation, which together P fertilizer, led to a better nutrition of the host. Taken together, our findings suggest that the improved nutritional status of cowpea, indicated by better vigour, as the most likely major mechanism through which *Striga* infestation was mitigated. In addition, colonization of the roots by rhizobia and nodule formation may compete with *Striga* for potential colonization sites as a barrier contributing to reducing the infestation by the parasite.

The effective reduction in the number of *Striga* plants in the field always resulted in better grain yields and differences were consistent with trends in the repression of the parasite (Figs. 6 and 7). Unless supplemented with rhizobial inoculants and P fertilizer, productivity of cowpea was generally very poor. This demonstrates that the comparative advantage of varieties bred specifically for resistance to *Striga* was insufficient to ensure good yields. The increase of cowpea yield obtained here with the combined use of fertilizers, rhizobial inoculants and improved germplasm 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).

5. Conclusion

We have demonstrated the potential of using bradyrhizobial inoculants as effective biocontrol agents as part of an integrated strategy against S. *gesnerioides* weed infestation of cowpea. Infestation of field-grown cowpea by *Striga* was strongly reduced by rhizobial inoculants together with moderate P fertilization. Further, evidence of a strong genotypic host plant x rhizobia strain interaction highlights the possibility for further selection of combinations to counter *Striga* damage.

Declarations

Acknowledgements

The authors thank the Bill & Melinda Gates Foundation for funding this research through the N2Africa project grant to Wageningen University. We are grateful to IITA staff at Kano Station and Mijibir farm technical assistance.

Conflict of interest

The authors declare no conflict of interest.

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Tables

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

Soil property	Value
pH (H_2O)	5.6
N (g kg^{-1})	0.36
Bray P (mg kg^{-1})	8.61
C (g kg^{-1})	9
Sand (g kg^{-1})	800
Silt (g kg^{-1})	80
Clay (g kg^{-1})	120
Ca (cmol kg^{-1})	1.29
Mg (cmol kg-1)	0.57
K (cmol kg^{-1})	0.19
Na (cmol kg^{-1})	0.40
Zn (mg kg^{-1})	$<$0.01
Cu (mg kg^{-1})	$<$0.01
Mn (mg kg^{-1})	0.46
Fe (mg kg^{-1})	0.78
ECEC	2.45
Rhizobia (MPN)	$1.7x10^3$

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

S/N	Genotype	Seed colour	Seed texture	Reaction to *Striga*	[a]Origin
1	B301	Cream	Smooth	Resistant	Local land race from Botswana
2	IT97K-205-8	White	Rough	Resistant	Bred at IITA
3	IT97K-499-35	White	Smooth	Susceptible	Bred at IITA
4	IT98K-503-1	Maroon	Rough	Resistant	Bred at IITA
5	IT98K-573-1-1	White	Smooth	Resistant	Bred at IITA
6	IT99K-573-2-1	White	Smooth	Resistant	Bred at IITA
7	Tvu 16514	Brown	Rough	Resistant	Tropical *Vigna unguiculata*
8	UAM09 1046-6-1	Brown	Smooth	Resistant	Bred at UAM
9	UAM1051-1	White	Smooth	Resistant	Bred at UAM
10	Aloka local	White	Rough	Susceptible	Local cultivar in Nigeria
11	Borno brown	Brown	Smooth	Susceptible	Local cultivar in Nigeria
12	BOSADP	Brown	Smooth	Susceptible	Bred at BOSADP
13	Danila	White	Rough	Susceptible	Local cultivar in Nigeria
14	IT81D-994	White	Smooth	Susceptible	Bred at IITA
15	IT84S-2246-2	Brown	Smooth	Susceptible	Bred at IITA
16	IT90K-277	White	Smooth	Resistant	Bred at IITA
17	IT98D-1399	White	Smooth	Susceptible	Bred at IITA
18	IT98D-288	White	Smooth	Susceptible	Bred at IITA
19	TVx 3236	Variegated	Smooth	Susceptible	Bred at IITA
20	UAM102021-1	Brown	Smooth	Susceptible	Bred at UAM

[a] IITA: International Institute of Tropical Agriculture; UAM: University of Agriculture, Makurdi; BOSADP: Borno State Agricultural Development Programme

Table 3: Summary of analysis of variance (ANOVA) of nodule number, cowpea shoot and Striga dry weights, and counts of plants and attachement of *Striga* for cowpea grown in potted-soils under screen-house conditions.

Effect	df	P-value				
		Nodule number (number plant^{-1})	Cowpea shoot dry weight (g plant^{-1})	*Striga* dry weight (g pot^{-1})	*Striga* count (number pot^{-1})	*Striga* attachment (number plant^{-1})
Variety	**19**	NS	****	NS	NS	NS
(R vs. S)	1	NS	****	**	**	**
Inoculation	**2**	NS	**	****	**	****
(Inoculants vs. Control)	1	NS	***	****	**	**
(IRJ vs. US)	1	NS	NS	*	*	*
Inoculation*variety	**38**	*	NS	*	**	****
(Inoculants vs. Control @ R)	1	NS	NS	*	NS	NS
(Inoculants vs. Control @ S)	1	NS	****	****	****	****
(IRJ vs. US @ R)	1	NS	NS	*	NS	NS
(IRJ vs. US @ S)	1	NS	NS	*	**	**

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

Table 4: Summary of analysis of variance (ANOVAs) of nodule number, count of emerged *Striga* and cowpea grain yield of cowpea grown under field conditions.

Effect	Df	P-value		
		Nodule number (number plant^{-1})	*Striga* count (number ha^{-1})	Cowpea grain Yield (kg ha^{-1})
Variety (V)	**19**	*	****	****
(R vs. S)	1	NS	****	****
Management (M)	**4**	****	***	****
(No input vs. Others)	1	****	****	****
(Urea vs. Inoculants)	1	****	NS	*
(IRJ2180A vs. USDA3384)	1	****	NS	****
(P vs. P+N)	1	****	NS	**NS**
M x V	**76**	NS	****	****
(No Input vs. Others @ R)	1	****	NS	****
(No Input vs. Others @ S)	1	****	****	****
(Urea vs. Inoculants @ R)	1	****	**NS**	*
(Urea vs. Inoculants @ S)	1	****	**	NS
(IRJ vs. UDSA @ R)	1	****	NS	****
(IRJ vs. UDSA @ S)	1	****	NS	****
(P vs. P+N @ R)	1	****	****	NS
(P vs. P+N @ S)	1	****	****	**

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

Figures

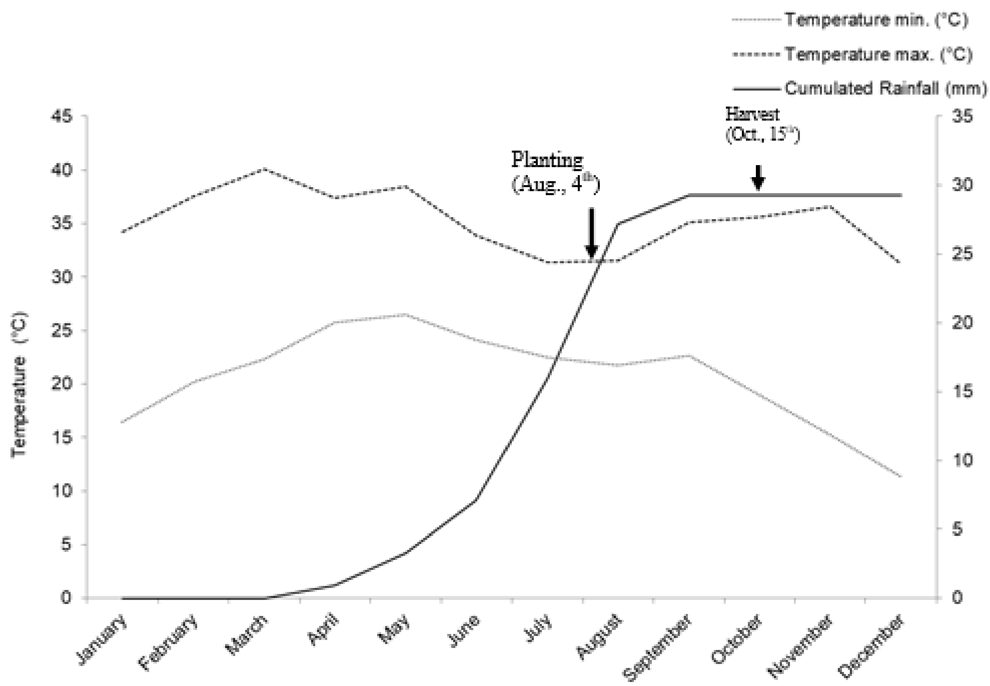

Figure 1

Weather data for the Minjibir experimental site in Kano, Nigeria

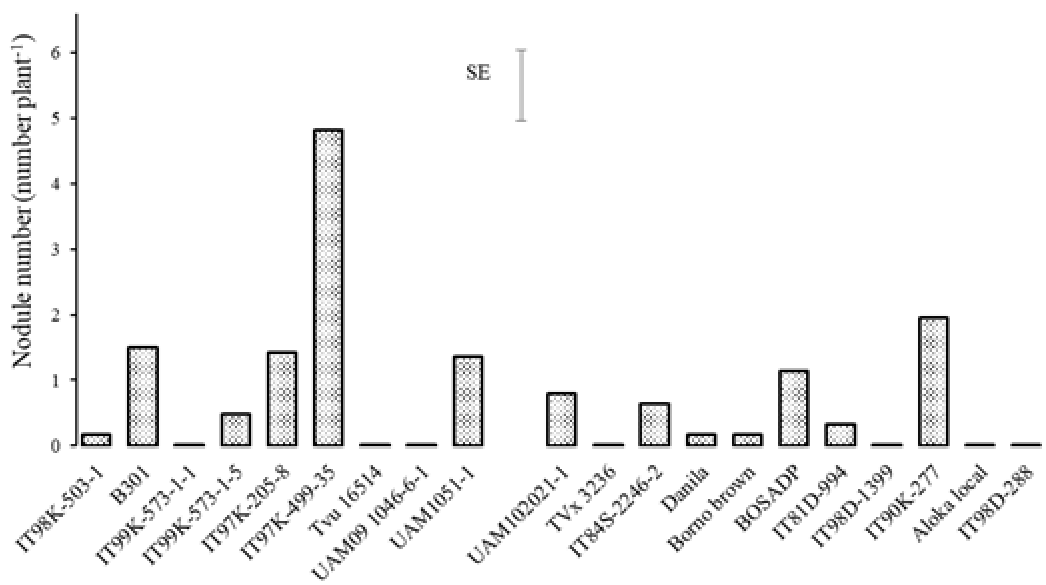

Figure 2

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

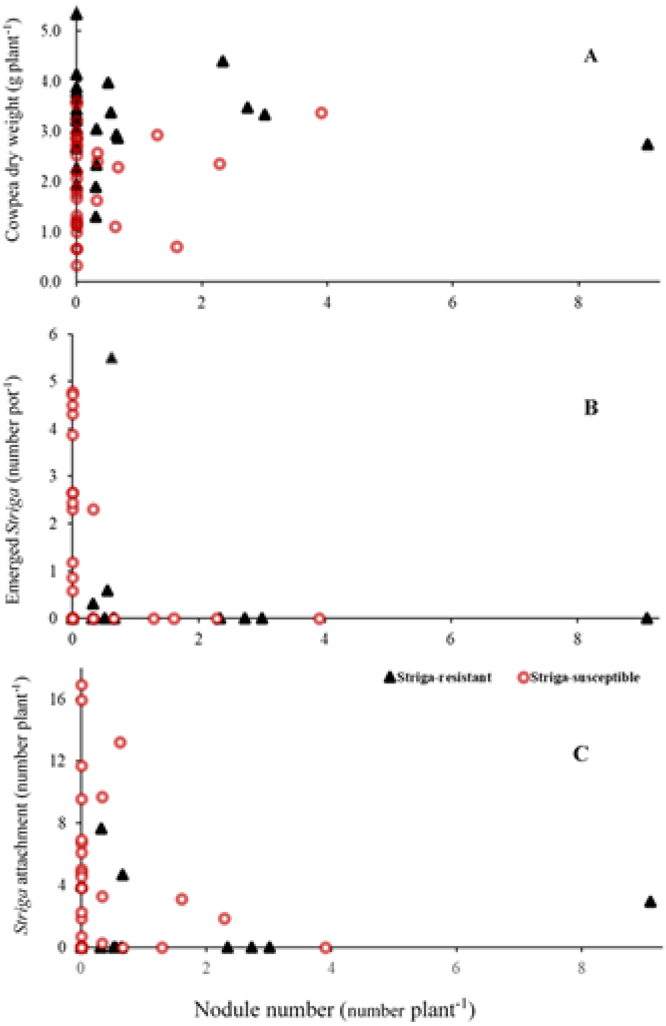

Figure 3

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

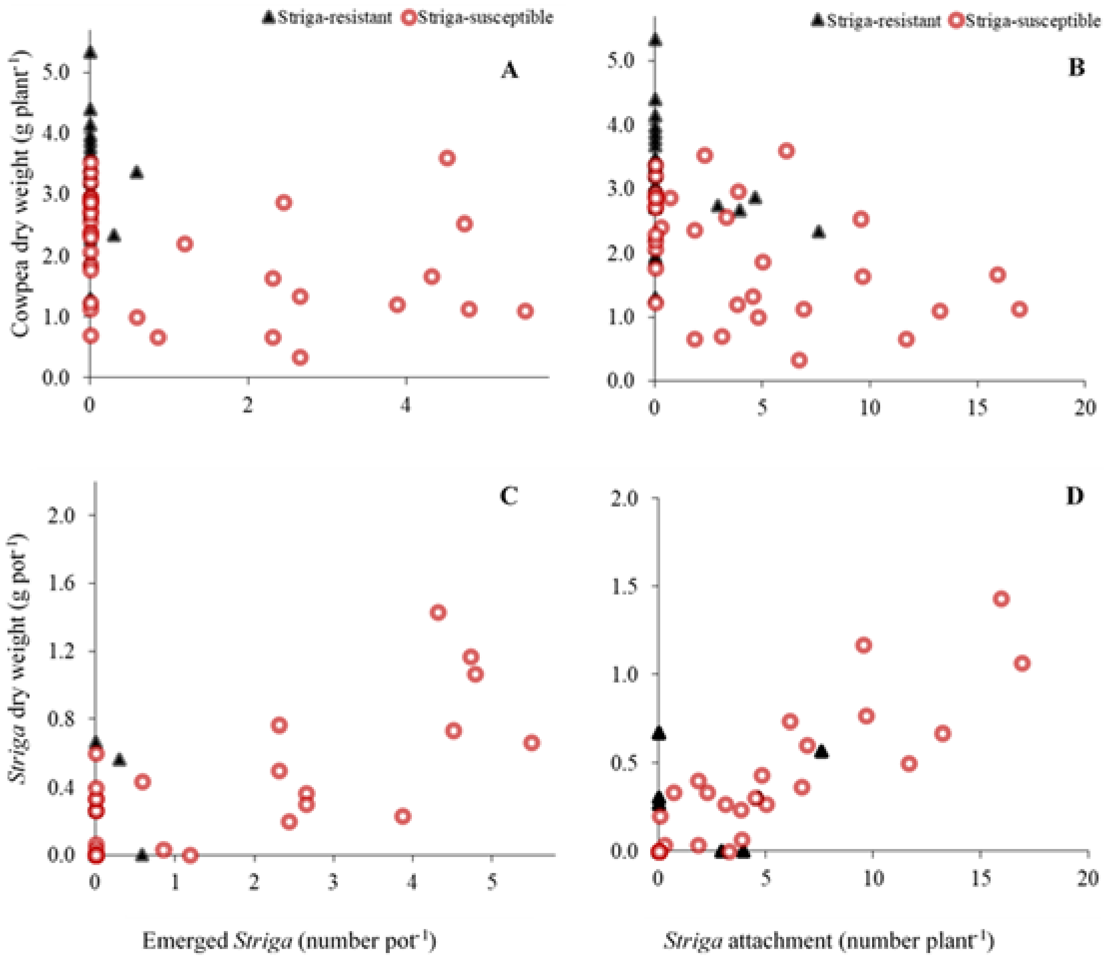

Figure 4

Relationships between emerged Striga count and (A) dry weight of Striga and (B) cowpea shoot dry weight, and between number of Striga attachment and (C) dry weight of Striga and (D) cowpea shoot dry weight under screen-house conditions.

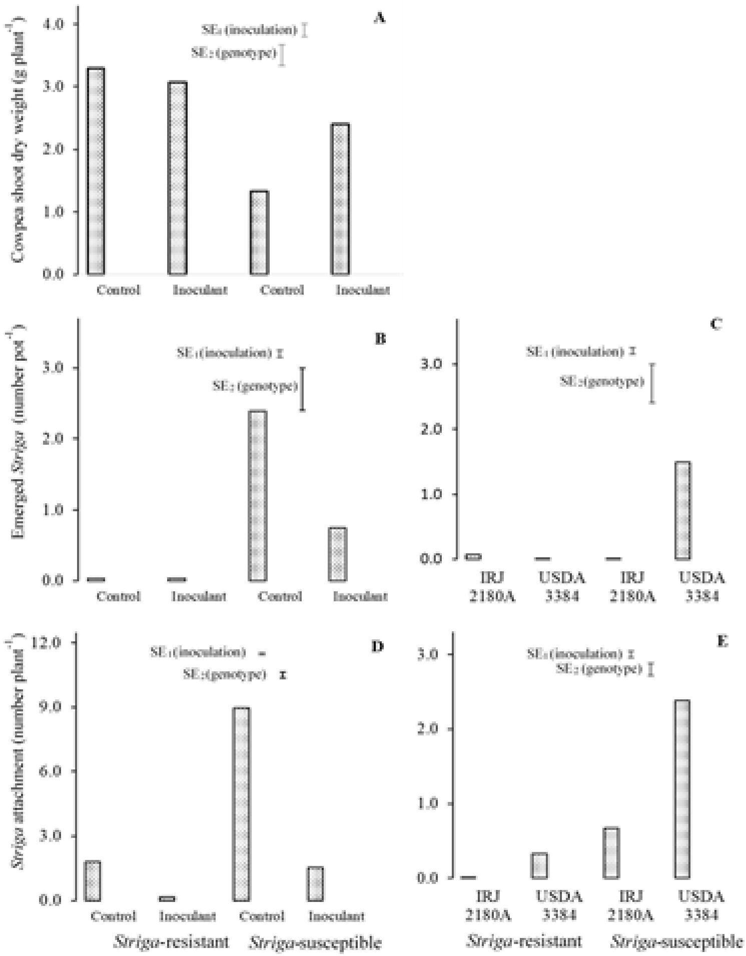

Figure 5

(A) Shoot dry weight, (B-C) emerged Striga count, and (D-E) 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). Errors bar represents the standard error of means.

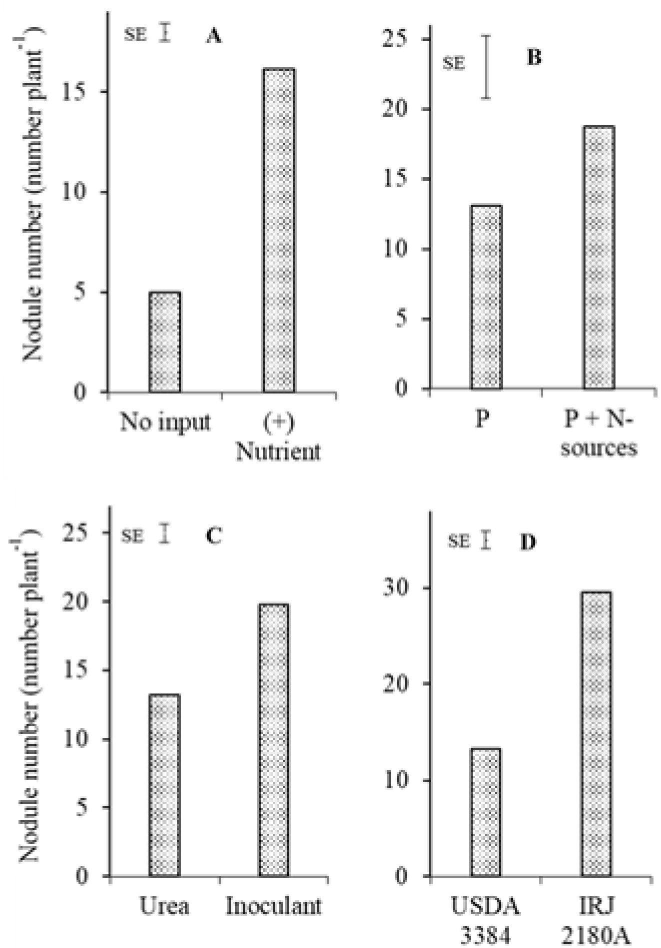

Figure 6

(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.

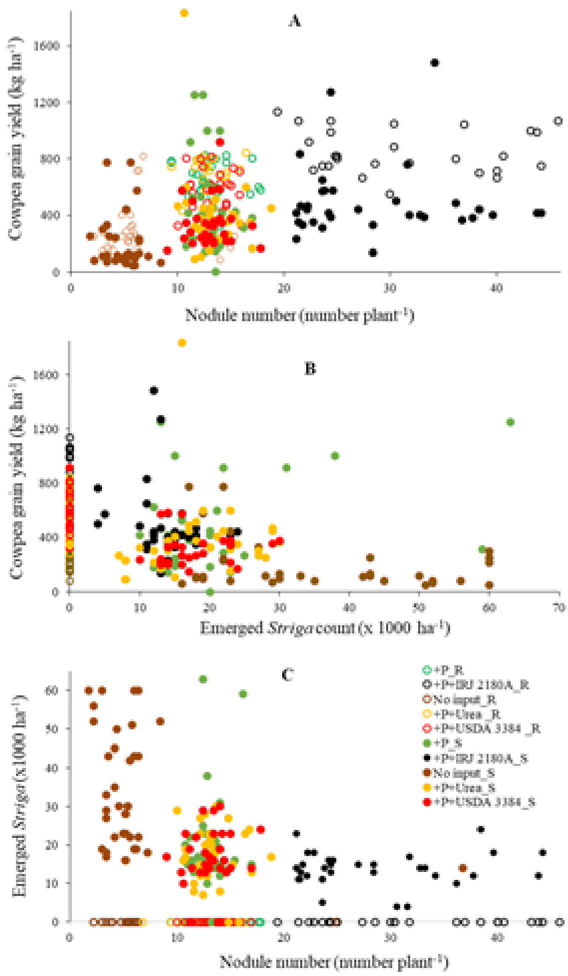

Figure 7

(A-C) Relationships between cowpea grain yield, nodule number and emerged Striga count for Striga-resistant (_R) and -susceptible (_S) cowpea genotypes; The cowpea plants were grown under five management options under field conditions; No input: No fertilization; + P: phosphorus; urea: urea-N; IRJ 2180A and USDA 3384: bradyrhizobial inoculants;

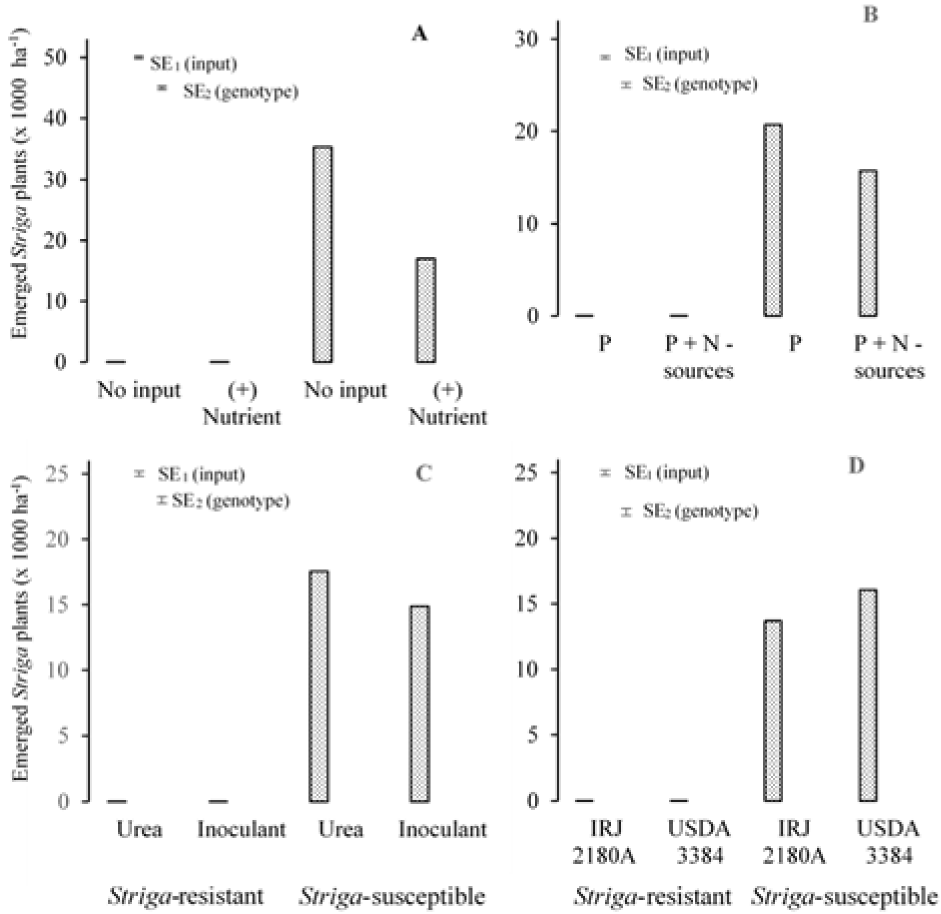

Figure 8

(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.

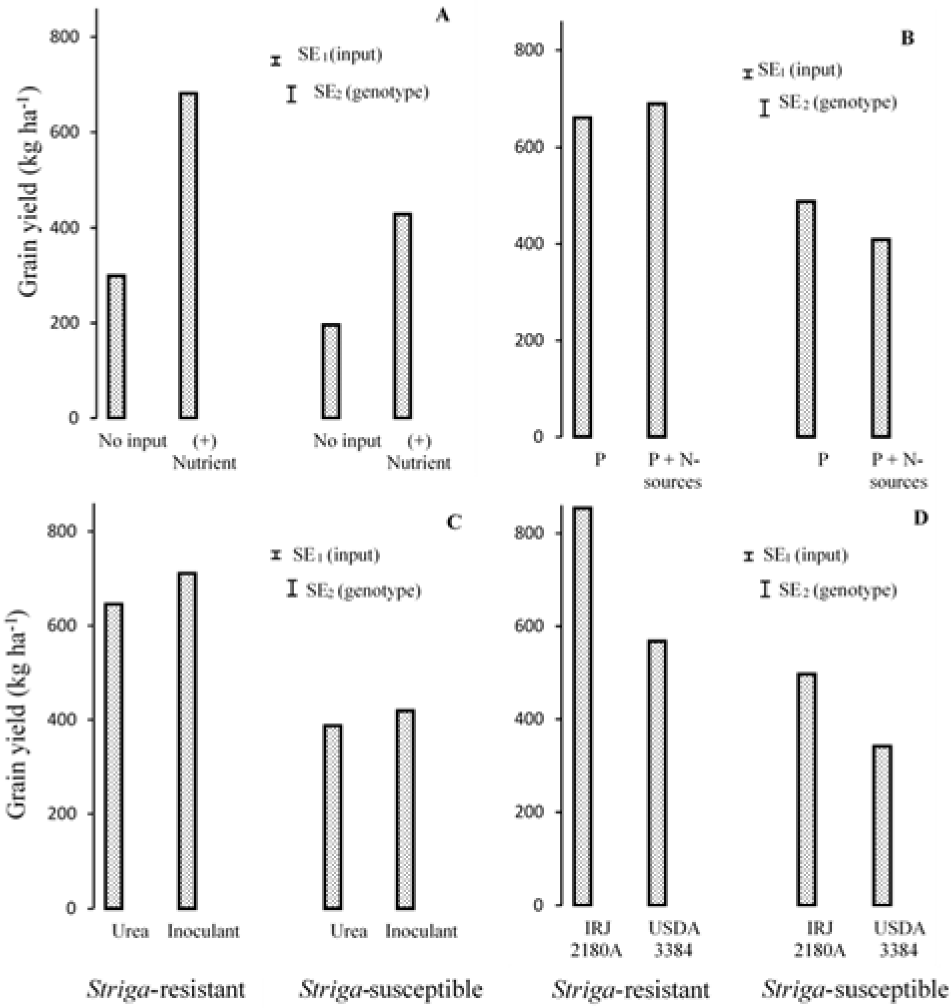

Figure 9

(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.