

Combined effects of cover crops, mulch, zero-tillage and resistant varieties on *Striga asiatica* (L.) Kuntze in rice-maize rotation systems

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Abstract

In low-input rice-maize rotation systems in the hills of central Madagascar, farmers deal with erratic rainfall, poor soils, high soil erosion risks and infestation by the parasitic weed *Striga asiatica* (L.) Kuntze. Practices combining zero-tillage with permanent soil cover by intercropped legumes and crop residue mulches — known as Conservation Agriculture (CA)— are proposed as remedy against soil and climatic constraints. Implications of these practices for *S. asiatica* are unknown. A 4-season factorial experiment compared the current farmer practice of rice – maize rotation, involving seasonal tillage and crop residue removal (CONV), with three rice – maize rotation systems following CA with different cover crops, i.e. *Vigna unguiculata* (cowpea) and *Mucuna pruriens* (CACM), *Vigna umbellata* (ricebean) (CARB), and *Stylosanthes guianensis* (CAST). Performance of two rice varieties, NERICA-4 and -9, with partial *S. asiatica* resistance, were compared with the locally popular B22. Parasite emergence time, numbers, and seed bank sizes were recorded.

In all CA practices *S. asiatica* infection was significantly reduced. Best results were obtained with *Stylosanthes guianensis* (CAST). This species also suppressed ordinary weeds much better than other cover crops. With CAST, average parasite emergence was delayed by 7.5 days (in rice) and 6.3 days (in maize) and infection levels were reduced by 79% (in rice) and 92% (in maize) compared to the conventional farmer practice (CONV). NERICA varieties delayed *S. asiatica* emergence by 5.7 days (NERICA-9) and 9.7 days (NERICA-4) and reduced infection levels by 57% (NERICA-9) and 91% (NERICA-4) compared to B22. In maize the residual effect of resistance of NERICA-4 resulted in a delay of 7.5 days in *S. asiatica* emergence and a reduction of 60% in parasite numbers. The best combinations delay *S. asiatica* emergence by 17.8 days (CAST + NERICA-9) and 19.1 days (CARB + NERICA-4) and reduce the parasite infection levels by 96% (CAST + NERICA-9 or -4) to 98% (CARB + NERICA-4) in rice, compared to CONV + B22. After two full rice-maize rotation cycles *S. asiatica* seed numbers in the soil (0-10 cm) were 76% (CACM), 78% (CAST) and 86% (CARB) lower

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than under CONV. Even the combination of zero-tillage, crop residue mulching, cover crops and resistant rice varieties does not entirely prevent *S. asiatica* parasitism and seed bank increase. Additional measures, targeted to escaping weeds, would be required for fully effective and long-term control.

Keywords: parasitic weeds, conservation agriculture, NERICA rice varieties, *Mucuna*, *Stylosanthes*, legumes

1. Introduction

Maize (*Zea mays* L.) and rice (*Oryza sativa* L and *O. glaberrima* Steud.) are two of the most important food crops in sub-Saharan Africa (Shiferaw et al., 2011; Seck et al., 2012). Rice varieties adapted to free-draining upland soils can be grown under similar conditions as maize and both crops are therefore often grown by the same farmers, either intercropped or in rotation (Balasubramanian et al., 2007; Shiferaw et al., 2011). These farmers however face a number of —related or mutually reinforcing— production constraints, like drought, suboptimal soil fertility and weed infestation (Balasubramanian et al., 2007; Cairns et al., 2012). *Striga* spp., are important weeds in both crops (e.g. Johnson et al., 1997). The two most important *Striga* species are *S. asiatica* (L.) Kuntze, with weedy forms predominantly found in Eastern and Southern Africa, and *S. hermonthica* (Del.) Benth., mostly found in sub-Saharan Africa north of the equator (Mohamed et al., 2001). Infestation by *Striga* is one of the main biotic production constraints in maize in Africa (Shiferaw et al., 2011; Cairns et al., 2012), with a conservatively estimated incidence of 14% across the continent (De Groote et al., 2008). For rice the importance is less generally acknowledged (Schut et al., 2015) but the average incidence of *Striga* in rice is recently estimated at a conservative 12% (Rodenburg et al., 2016). Reported *Striga*-inflicted yield losses range from 21 to 74% in maize (De Groote et al., 2008) and from 35 to 80% in rice (Rodenburg et al., 2016).

In the mid-west of Madagascar, upland rice-maize rotations are often practiced on poorly textured and poorly fertile soils on sloping land and under conditions of erratic rainfall, with droughts alternated by intense rainfall events (e.g. Bruelle et al., 2015). Soil erosion by run-off therefore occurs frequently in this area (Dusserre et al., 2012). This further impoverishes the soils (Smaling et al., 1996), and facilitates weed seed dispersal (Burton et al., 2005). *Striga asiatica* is one of the most dominant weed species in these rice-maize rotation systems in Madagascar (Geiger et al., 1996). This, in turn, is no surprise as the presence of *Striga* species is often associated with poor soil fertility and erratic rainfall conditions (Kamara et al., 2014).

One of the possible strategies to address the above-described climate and soil-related problems in cereal cropping systems is to replace the practice of seasonal soil tillage and clearance, by an intercropping, zero-tillage system with permanent —living or dead—vegetative soil cover, commonly referred to as Conservation Agriculture (Thierfelder and Wall, 2009, 2012). In mid-west Madagascar, where rice-maize rotation is the predominant system, Conservation Agriculture (CA) practices have been tested with variable outcomes, as socio-cultural and economic benefits and suitability lagged behind agronomic and environmental merits (Sester et al., 2015). Positive effects of CA were reported on rice blast (Sester et al., 2014) and white grub, a soil-dwelling Scarab beetle larvae (Ratnadass et al., 2013). It is not known whether the proposed CA strategies

also reduce *S. asiatica* infestation, but individual components proved successful. Intercropping may reduce *Striga* when the intercropped non-host species can cause seed of the parasite to germinate without supporting parasitism, a principle called ‘suicidal germination’ (e.g. Khan et al., 2010). The intercrop canopy can also reduce *Striga* by increased shading and humidity and decreased temperatures (Oswald et al., 2002). Mulching has also been shown to suppress *Striga* parasitism (Midega et al., 2013) probably partly through similar mechanisms, while zero-tillage may prevent newly produced *Striga* seed to enter the soil deep enough to encounter suitable host roots in subsequent cropping seasons (van Ast et al., 2005).

In the current study, effects of a combination of these measures on *S. asiatica* were tested in an infested farmer’s field in the rice-maize production zone of mid-west Madagascar. The practices were tested with rice varieties differing in resistance level. The use of resistant varieties has often been suggested as an ideal component of an integrated *Striga* management strategy (e.g. Yoder and Scholes, 2010), but broad-based evidence for this is still scarce. The locally predominant farmer practice of rice-maize rotation with seasonal tillage and crop residue removal is treated as the reference. The objectives were to (1) find leads for improvements of this rice-maize rotation system that could benefit smallholder farmers, (2) quantify effects of different rice varieties, management practices and combinations of varieties and practices on *S. asiatica* control and (3) discuss possible factors explaining such effects.

2. Materials and Methods

2.1. Study site

During four cropping seasons — in the period from December 2011 to April 2015— a factorial experiment was conducted at a farmer’s field in Ivory, in mid-west Madagascar. The field was located at 19°33’26’’S and 46°24’55’’E. The elevation at this site is 930 m above sea level.

The study area is characterized by a tropical climate of medium altitude with two well-defined seasons: the hot rainy season from November to April and the cold dry season from May to October. Temperature, radiation and rainfall data were recorded daily by an automatic meteorological station (ENERCO 404 Series, Cimel, France) at 835 m from the experiment. During the experiment (September to May) average monthly radiation ranged from 17 to 28 MJ m⁻², and temperatures ranged from 17.2°C (night) to 30.7°C (day), with monthly averages between 21 and 25 °C, and similar monthly fluctuations across seasons. The cumulative rainfall during the experiment was 976 mm in Season 1, 1,452 mm in Season 2, 1,194 mm in Season 3 and 1,814 mm in Season 4 (Figure 1). The long-term annual mean rainfall is 1,307 mm.

The soil is characterized as clay-loam Oxisol (USDA) with a clay-silt-sand composition of 34-39-27 % in the top layers (0-10 cm). The soil was generally moderately deficient in nutrient and organic matter content, with 17.2 g kg⁻¹ of C, 1.4 g kg⁻¹ of N (total) and 2.5 mg kg⁻¹ of available P (Olsen). Soil pH (H₂O) was 5.3. Nutrient content of applied cattle manure was 0.93% N, 11.9% C, 0.14% P, 0.94% K, 0.50% Ca, and 0.20% Mg. The field was positioned on a moderate slope (0 to 5%). Experimental replicates were laid out along this gradient with Replicate 1 on the top and Replicate 6 at the bottom of the slope.

2.2. Experimental treatments and plant material

The locally predominant farmer practice of rice-maize rotation with seasonal tillage and removal of crop residues (henceforward referred to as conventional practice, or CONV) is compared with three rice-maize rotation systems following conservation agriculture (CA) principles. The three CA practices were (1) CACM: intercropping maize with cowpea (*Vigna unguiculata* [L.] Walp. cv David) and *Mucuna* (*Mucuna pruriens* [L.] DC. cv CTAS MU1); (2) CARB: intercropping maize with ricebean (*Vigna umbellata* [Thunb.] Ohwi & Ohashi cv. CTAS tsiasisa) and (3) CAST: intercropping rice and maize with *Stylosanthes* (*Stylosanthes guianensis* [Aubl.] Sw., cultivar CIAT 184). The choice of cover crop species is based on agronomic and weed control principles. For *Striga* control and soil conservation a suitable intercrop for these rice-maize rotation systems should have good soil coverage during the maize crop, produce enough biomass for mulch during the rice crop and also improve soil fertility. Suitable cover crop species for these systems and soil types, responding to that profile, were identified by Naudin et al. (2015a). From the range of crops they identified, three contrasting species, or species combinations were selected: (1) the short-cycle annual legumes *Vigna unguiculata* (cowpea) *Mucuna pruriens* (velvetbean), (2) the long-cycle annual legume *Vigna umbellata* (ricebean) and (3) the perennial legume *Stylosanthes guianensis* (stylo). Among these species, Velvet bean and cowpea have already shown to reduce *Striga* spp. problems (Oswald et al., 2002; van Mourik et al., 2008; Kiwia et al., 2009). Based on agronomic reasons (e.g. crop-crop competition, ease of management), Naudin et al. (2015a) also recommended rice not to be intercropped with the annual legumes cowpea, mucuna and ricebean. Maize, on the other hand is suitable for intercropping because of the relative large inter-plant spaces.

In all CA practices soils were only tilled at the onset of the first season and no longer thereafter and all crop residues —except grains, panicles and pods— were left on the field as mulch after harvest of crops and intercrops.

Three upland rice varieties were compared simultaneously: (1) the locally popular but *Striga*-susceptible B22, a Brazilian rice variety, and the more recently introduced NERICA (New Rice for Africa) varieties (2) NERICA-4 and (3) NERICA-9. NERICA-4 is *Striga*-resistant, while NERICA-9 is moderately *Striga*-resistant (Rodenburg et al., 2015). The NERICA varieties are offspring from interspecific crosses between the Asian rice species *Oryza sativa* L. and the African rice species *Oryza glaberrima* Steud. (Jones et al., 1997). The maize variety used in this study was IRAT 200, a commercially available but *Striga*-susceptible variety. It was sourced from Ambatolahy, a nearby village (19°34'37"S-46°26'37"E).

2.3 Experimental design

The experiment was laid-out following a split-plot design with cropping practices randomly assigned to the main plots and rice varieties randomly assigned to the sub-plots, in six replicates. Hence, rice variety was used as a sub-treatment factor, even in seasons with maize (to study potential carry-over effects of *S. asiatica* resistance). In order to study the main crops of this rotation each year, the main plots were divided in two, with rice grown in one part and maize in the other part.

The size of the main plot, representing a cropping practice, was 270 m² (15 × 18 m). Each of the three sub-plots, representing a rice variety, measured 90 m² (5 × 18 m).

Each sub-plot, comprised one *S. asiatica* counting area of 37.8 m² (4.2 × 9 m) for rice and 36 m² (4 × 9 m) for maize, four non-overlapping *S. asiatica* seed bank sampling areas of 6 m² (2 × 3 m) and two non-overlapping soil sampling areas of 3 m² (0.6 × 5 m) for chemical analyses.

2.4. Field preparations and crop management

The experimental field was under fallow vegetation during the two years preceding the experiment. The field was ploughed in October 2011, using a tractor-mounted disc plow, and cleaned from all fallow vegetation by hand. After that, harrowing to a finer tilt was done using a tractor-mounted tooth peg harrow. In plots following conventional practice, from the second season onwards, tillage was done manually using a so-called *angady*, a local traditional soil tillage tool, at a depth of 15-20 cm. In plots following CA practices, the soil was not tilled beyond soil preparation for the first season.

Rice was sown from 5 to 8 December in 2011, 19 to 23 November in 2012, 18 to 22 November in 2013 and 24 to 28 November in 2014, at a planting distance of 20 cm in the row and 30 cm between the rows, at 6-7 seeds per planting hole. Maize was sown at the same dates as rice, in paired rows with 50 cm between the two rows of one pair and 150 cm between two pairs, at a rate of two seeds per hole and a within-row plant distance of 50 cm.

For CACM, cowpea was sown at the same time as maize, between two pairs of maize rows, at a rate of two seeds per hole and a plant distance of 25 cm in the row and 50 cm between the rows, resulting in two cowpea rows between each pair of maize. To enhance cover crop biomass production, at 50 days after sowing (DAS) one row of *Mucuna* was sown between two rows of cowpea and another row between the two rows of a pair of maize, at a rate of two seeds per hole. *Mucuna* was sown in relay with cowpea to maintain a vegetative ground cover beyond cowpea harvest and to avoid competition between the two cover crops.

For CARB, ricebean was sown at the same time as maize with two rows of ricebean between two pairs of maize rows, at a rate of 5-7 seeds per hole and a planting density of 50 cm in the row and 50 cm between rows. To increase the biomass of ricebean an additional row was sown in between the paired rows of maize at 50 DAS.

In plots following cropping practice CAST, in the first year, *Stylosanthes* was sown at 14 DAS at 40 cm in the row and 30 cm between rows, between the rice or maize at a seeding rate of about 5 kg ha⁻¹. *Stylosanthes* was sown later to provide the main crop with a head start reducing early-season crop competition. Between two rows of rice, one row of *Stylosanthes* was sown, with 15 cm between the *Stylosanthes* and the rice. Between two pairs of maize rows three rows of *Stylosanthes* were grown, with 45 cm between the maize and the *Stylosanthes* at each side. Between two seasons (i.e. the period May-December), *Stylosanthes* was rolled and slashed back three times: (1) At the end of the rainy season, around mid-June, (2) Half-way the dry season, mid-September and (3) Before sowing of the next crop, at the beginning of November. *Stylosanthes* plants were allowed to re-sprout and seeds produced in the previous year were allowed to germinate and grow.

In each season and for all practices, cattle manure was applied at sowing at a rate equivalent of 11 t ha⁻¹ in the rice plots and 5.5 t ha⁻¹ in the maize plots, following local practices. No inorganic fertilizers were applied. All plots were hand weeded two times

during the season, at 46-50 and 74-85 DAS, whereby all weeds other than *Striga* were removed.

2.5. Measurements and observations

To assess treatment effects on soil fertility, after Season 1 (June 2012) and after Season 4 (June 2015) nine soil samples (0-10 cm depth) were done in each maize and rice plot. Each sample contained 196.3 cm³ of soil. For each plot a composite sample of 500 g air-dried and sieved (at 2 mm) soil was extracted for nitrogen (N Kjeldahl), and available phosphorus (Olsen) assessment at the Radio-Isotope Laboratory of the University of Antananarivo in Madagascar.

To assess treatment effects on the *S. asiatica* seed bank in the soil, sampling of the upper 10 cm of soil was done at the onset of the experiment in rice sub-plots (November 2011), and at the end of the experiment (June 2015), in the same sub-plots, after the maize crop harvest (hence after two complete cycles of the rice-maize rotation). At both dates six soil samples each 1,130.4 cm³ were taken per sub-plot— from fixed locations outside areas used for other sampling— and mixed into one composite sample per replicate from which 100 g (106 cm³) was sub-sampled for *S. asiatica* seed extraction and analysis following Hartman and Tanimonure (1991).

Striga asiatica emergence (i.e. first cotyledon appearance) dates were registered, each season in both crops except for the first season in maize. Aboveground *S. asiatica* numbers were assessed at 70, 90 and 110 days after sowing (DAS) from the central 37.8 m² (rice) and 36 m² (maize) areas. To investigate treatment effects on ordinary weeds, biomass of weeds other than *S. asiatica* was assessed in the fourth season (2014-2015) from four 1.0 × 0.9 m areas within the central area per sub-plot. These weeds were sampled twice, just prior to each manual weeding intervention, and were oven-dried during 48 hours at 60°C for dry matter assessment.

2.6. Analyses

For *S. asiatica* emergence dates (*E-date*) data were expressed as days after sowing (DAS). Cases where *S. asiatica* was not observed were treated as missing data. Based on emerged *S. asiatica* counts at three dates (70, 90 and 110 DAS) the maximum aboveground *S. asiatica* numbers were assessed, and this parameter (*NSmax*) was used for further analysis. All data were checked for homoscedasticity and normality following Sokal and Rohlf (1995). *NSmax* was subjected to logarithmic (Log10) transformations, following (Log [X+C]), where *X* was the original, individual observation and *C* was set to 1.0. Data on aboveground parameters (*E-date*, *NSmax* and Weed Biomass) were subjected to ANOVA, using a mixed model where Season, Cropping Practice and Variety—for *Striga* parameters—and Weeding Time, Cropping Practice and Variety—for ordinary weed biomass— were considered as fixed effects and Cropping Practice × Replicate as random effect (following the split-plot experimental design). Soil fertility parameters (total N and available P) were subjected to ANOVA, using a mixed model, with Time (Season 1, Season 4) and Cropping Practice as fixed effects and Cropping Practice × Replicate as random effect. Adjusted means of all parameters were compared by using Fisher's LSD test. Means and LSD values presented in the paper are back-transformed when necessary. Data on aboveground parameters were analyzed with XLSTAT version 2014.5.03 (MS Excel, 2014).

Striga asiatica seed numbers extracted from the soil after four experimental seasons (two rotation cycles), were analyzed using a generalized linear mixed model with a negative binomial distribution to account for the count data. Seed numbers prior to the experiment (S0) were used as co-variable and we conducted an ANCOVA to test whether they (S0) affected the seed numbers after four seasons. In case this was not significant, an ANOVA was performed, with rice variety (V) and Cropping Practice (CP) as fixed effects and Replicate as random effect, followed by a comparison of means—when effects were significant—using Tukey’s honest significant difference test. *Striga asiatica* seed data were analyzed using SAS/STAT software, Version 9.2 of the SAS System for Windows (SAS Institute, 2011).

3. Results

3.1. Soil nitrogen and phosphorus changes

No significant two-way interaction effects between time and cropping practice were observed on total soil nitrogen or available soil phosphorus. Among main effects, only time had a significant ($F=35.53$; $P=0.002$; $df=1$) effect on total soil nitrogen content. In 2011, mean N content (0-10 cm) was 1.433 g kg^{-1} , and this significantly increased to 1.685 g kg^{-1} in 2015. No time or cropping practice effects on available phosphorus were observed.

3.2 *Striga asiatica* emergence dates in rice and maize

Table 1 shows significant main effects of season ($P<0.0001$ in rice; $P=0.002$ in maize) and rice variety on dates of first *S. asiatica* emergence in rice ($P<0.0001$) and maize following rice ($P<0.01$). Cropping practice only had a near-significant effect on *S. asiatica* emergence dates in rice ($P=0.07$). Season \times rice variety and cropping practice \times rice variety interaction effects on *S. asiatica* emergence dates were significant in rice only ($P<0.05$; Table 1). No other significant interactions were observed.

First *S. asiatica* emergence dates ranges from 69 (Season 1) to 76 (Season 4) DAS in rice and from 60 (Season 2) to 68 DAS (Season 3) in maize (Table 2). Across seasons, *S. asiatica* emergence is earliest in plots with rice variety B22 (67 DAS) and latest with NERICA-4 (77 DAS). The same effect is observed in maize plots preceded by rice, with first emergence at 60 DAS in plots following B22, and 68 DAS in plots following NERICA-4.

In rice, across seasons, *S. asiatica* emerged earliest with variety B22 under CONV (62 DAS), and latest with NERICA-4 following CARB (81 DAS) and with NERICA-9 following CAST (79 DAS).

3.3. Aboveground *S. asiatica* densities in rice

Significant season, cropping practice and rice variety main effects ($P<0.0001$) were observed on aboveground *S. asiatica* plant densities (maximum number m^{-2} ; NS_{max}) in rice (Table 1). Season \times cropping practice ($P=0.006$), season \times rice variety and cropping practice \times rice variety ($P<0.0001$) interaction effects on NS_{max} were also significant.

CAST had the lowest *S. asiatica* densities among cropping practices, followed by CARB (Table 3). Under conventional practice (CONV), the *S. asiatica* density across seasons was significantly higher than under any CA practices, but evaluated per season, only CAST resulted in consistently reduced parasite densities compared to CONV.

Relative to CONV, *S. asiatica* densities were on average reduced by 24% following CACM, by 53% following CARB and by 79% following CAST.

Striga asiatica densities under NERICA-9 and NERICA-4 were significantly lower than under B22 (Table 3). The difference between B22 and moderately resistant NERICA-9 was only significant in the two last seasons, when *S. asiatica* infection levels were generally higher. The more resistant variety NERICA-4 had significant lower infection levels than B22 throughout the four seasons. Relative to B22, the reduction in *S. asiatica* densities was 57% under NERICA-9 and 91% under NERICA-4. The *S. asiatica* densities under NERICA-4, in turn, were significantly lower than under NERICA-9.

Across seasons, highest *S. asiatica* densities were observed under CONV with B22. With any of the NERICA varieties under CONV these numbers were already significantly lower. Even lower infection levels were obtained when NERICA varieties were combined with CA cropping practices, although for the most resistant variety — NERICA-4— differences in *S. asiatica* densities across cropping practices were not significant. The best combinations were NERICA-4 under CARB, followed by CAST and CACM and NERICA-9 under CAST (Table 3). Relative to CONV with B22, infection levels were reduced by more than 95% following these combinations.

3.4. Aboveground *S. asiatica* densities in maize

Significant season, cropping practice, and rice variety main effects and season \times cropping practice, cropping practice \times rice variety and season \times cropping practice \times rice variety interaction effects (all $P < 0.01$) were found on aboveground *S. asiatica* densities in maize (Table 3). Statistical analysis was done from Season 2 onwards, as in Season 1 the maize was not preceded by rice.

Across seasons, the conventional practice (CONV) showed significant higher *S. asiatica* infection levels than any CA practice (Table 3). Among CA practices, CAST resulted in significant lower infection levels compared to CACM and CARB. The latter practices reduced *S. asiatica* infection overall by 35%, compared to CONV, whereas CAST reduced infection even by 92%. CAST resulted in significant reductions in parasite infection in Season 2 and 3, but not in Season 4. The other two CA practices were only effective in Season 2.

In maize following rice variety NERICA-4, the *S. asiatica* density averaged over all three seasons, was significantly lower than in maize following rice varieties NERICA-9 and B22 (Table 3). Compared to B22, densities were reduced by 20% following NERICA-9 and by 60% following NERICA-4. The most significant reduction in *S. asiatica* densities in maize was obtained with CAST in plots preceded by NERICA-9 and NERICA-4. Changing the preceding rice variety from B22 to NERICA-4 under CONV already reduced *S. asiatica* infection in maize by 79%. Changing the cropping practice of maize, with B22 as preceding rice variety, from CONV to CAST, reduced *S. asiatica* infection by 95%. Combining the two options —maize under CAST following NERICA-4— reduced the parasite density by 97% compared to the conventional practice following B22.

3.5. *Striga asiatica* seed bank changes

Only the cropping practice had a significant effect on *S. asiatica* seed densities after four seasons (Table 4). *Striga asiatica* seed densities in the soil are significantly higher after

conventional rice-maize rotation (CONV), compared to any of the CA practices (CACM, CARB and CAST) while differences between CA practices were not significant (Table 4). Compared to CONV, *S. asiatica* seed densities in the soil can be reduced by a factor 4 (CACM) to 7 (CARB) after four seasons. None of the treatments however resulted in a decrease of the *S. asiatica* seed bank size compared to the initial situation (not shown).

3.6. Effects of cropping practice and rice variety on ordinary weed biomass

No significant three-way or two-way interaction effects between weeding intervention time, rice variety and cropping practice were observed on ordinary weed biomass in rice in Season 4. Among the main effects, only weeding intervention time ($F=15.7$; $P=0.0001$; $df=1$) and cropping practice ($F=83.5$; $P<0.0001$; $df=3$) had significant effects on weed biomass. Both CONV and CAST, had significant less weed biomass than the other two practices (Figure 2). The practice with cowpea-*Mucuna* (CACM) had a significant higher weed biomass than the practice with rice bean (CARB).

4. Discussion

This study showed that through a combination of zero-tillage, crop residue mulching and cover crops—collectively indicated as Conservation Agriculture (CA)—*S. asiatica* infection in a rice-maize rotation could be delayed and reduced. The best results were obtained with *S. guianensis* as cover crop and NERICA-4 as variety, whereby control effects of this resistant rice variety were noticeable in the following maize crop. *Stylosanthes guianensis* also proved effective in terms of ordinary weed control.

This section is broken down in a discussion on the benefits of conservation agriculture (CA) practices regarding weed and *Striga* control (4.1), the role that resistant varieties can play to enhance *Striga* control efficacy under CA (4.2) and the notion that such innovations are only relevant in areas where smallholder cereal farmers deal with similar (parasitic) weed and soil constraints as encountered in the study area (4.3).

4.1. Can conservation agriculture contribute to (parasitic) weed control?

Conservation agriculture (CA) is a broad term to describe the more or less simultaneous application of (1) reduced soil tillage, (2) permanent soil protection through mulching and (3) increased biodiversity through crop diversification (Scopel et al., 2013). In the current study, three CA practices, with different crop diversification options—rice rotated with a maize-cowpea-*Mucuna* or maize-ricebean intercrop, and rice intercropped by *Stylosanthes* and rotated with a maize-*Stylosanthes* intercrop—were compared with the conventional farmer practice of rice-maize rotation without intercropping. This study presents the first evidence that applying a CA practice significantly delays parasitism of a *Striga* species and reduces parasite infection levels in both rice and maize. A wide range of direct and indirect causes may underlie the observed effect of CA practices (Fig. 3). These causes can be physical, biochemical or biological, they can emerge at different levels and they can either strengthen or weaken one another. All of the CA practices, by not tilling the soil, may reduce parasite infection because less *Striga* seeds reach the root zone (e.g. van Ast et al., 2005). In addition, the seeds remaining at the soil surface may be prone to increased seed predation by ground beetles as shown with ordinary weed seeds (Kulkarni et al., 2015). The increased living and dead biomass of cover crops, in addition, may further increase abundance and activity of the micro-fauna and therefore

seed predation (Pullaro et al., 2006) and decay. Because of the entanglement of the different components of CA, and the numerous potential direct and indirect effects they may unleash (as shown in Fig. 3), the contribution of individual principles cannot be assessed by this study. This is the typical weakness of many CA studies, as previously postulated by Giller et al. (2009). It is indeed essential to further investigate the effectiveness or ineffectiveness of each of the components as it would help optimizing or simplifying the approaches for smallholder farmers.

The set-up of the current study does however allow assessment of the role of different cover crop species within the CA practices, because the other treatments (zero-tillage and non-removal of crop residues) are the same across practices. Cover crops may differ in their effectiveness to (1) cause suicidal germination, (2) improve soil fertility (3) and produce biomass, providing (weed-suppressive, temperature decreasing and humidity increasing) canopy and mulch.

The *S. asiatica* suppressive effect of CA practices could be due to the suicidal germination of *S. asiatica* seeds caused by the cover crops (Fig. 3). Several leguminous crops have shown to be effective trap crops for *Striga* species that parasitize on cereal crops (Ransom, 2000). There are studies that confirm effectiveness of cowpea (Carsky et al., 1994; Gbehounou and Adango, 2003) and *Mucuna* (Kiwia et al., 2009) in that respect, although the mechanisms of suppression by *Mucuna* are not yet revealed. Whether *Stylosanthes* can cause suicidal germination of *S. asiatica* is subject to further studies. For a perennial species like *Stylosanthes*, it would be a very effective *S. asiatica* control mechanism, as it would work during both seasons of the rotation cycle.

Leguminous cover crops may also increase soil fertility and thereby contribute to *S. asiatica* suppression. Legumes that are able to fix atmospheric nitrogen can improve soil N content after several cropping cycles (e.g. Giller, 2001) but this process requires additional phosphorus (Rotaru and Sinclair, 2009). Both N and P play important roles in the production of host-root derived strigolactones (Yoneyama et al., 2013) whereby increasing levels of these elements can reduce the production of these plant hormones and decreasing levels will do the opposite. Changes in N and P consequently affect the *S. asiatica* infection chances (Jamil et al., 2012). In the current study the changes in either soil N or P, observed by comparing the situation before and after the 4-season experiment, were not significantly affected by cropping practices. Hence the observed differences in *S. asiatica* infection across cropping practices cannot be assigned to differences in soil fertility enhancing effects of these treatments.

Increased shading by the cover crops could be another explanation for *S. asiatica* suppression following CA practices (Fig. 3). *Stylosanthes* spp. are known for their prolific biomass production and therefore often proposed as weed control agents in tropical cereal cropping systems (Chikoye et al., 2008; Saito et al., 2010). It is likely that the *S. asiatica* control obtained by *Stylosanthes*, is at least partly due to this very weed suppressive ability, as the current study also shows superior control of ordinary weeds, compared to the other CA practices. Weed competition constitutes a major weakness of CA unless the ground cover would be effective enough to suppress weeds (Giller et al., 2009). The current study seems to confirm this. Averaged over four seasons, CACM and CARB produced respectively 1.3 to 1.8 times the biomass produced under CONV, while CAST produced 6.7 times as much biomass (Randrianjafizanaka, unpublished). One obvious reason for this differentiation is, again, the cycle length of cover crop species.

While cowpea, *Mucuna* and ricebean are annual species that are only intercropped with maize, *Stylosanthes* is a perennial producing biomass in both the maize and the rice season.

4.2. What is the combined effect of conservation agriculture and resistant varieties on *S. asiatica*?

Clear *S. asiatica*-reducing effects of zero-tillage cropping practices with cover crops, crop residue mulching and the use of resistant rice varieties have been observed in both cycles of a rice-maize rotation system, compared to the farmer practice with the locally popular variety B22. Both a change in cropping practice and a change in rice variety contributed to this observed effect, and the different solutions have shown to be synergetic. Hence inclusion of a resistant rice variety in an integrated *Striga* management strategy, as previously proposed by many authors and for different crops (e.g. Kamara et al., 2008; Yoder and Scholes, 2010), proved indeed important here.

Striga asiatica resistance of the two NERICA varieties showed to be an important cause of *Striga* suppression under all practices. While existence of differences in *Striga* resistance among rice germplasm have been shown before (Johnson et al., 1997; Rodenburg et al., 2015, 2017) their compatibility with alternative cropping practices and synergy with other *Striga* control options are shown here for the first time. Moreover, this is the first study to show a positive carry-over effect of resistance in rice on the infection levels in the following maize crop. Therefore, the use of resistant varieties seems a very useful component technology in crop rotation systems, where two suitable hosts of the same parasite are alternated.

An integrated *Striga* management strategy should ideally reduce the seed bank (Westerman et al., 2007). In the current study no variety by cropping practice interaction effects on the *S. asiatica* seed bank were observed. CA practices alone, irrespective of cover crop species, showed reduced seed bank size increments compared to the conventional practice, but no seed bank size reduction compared to the situation before the experiment. Previously, van Mourik et al. (2008) showed a limited effect of legume intercropping on the *S. hermonthica* seed bank. Seed output from the seed bank is caused by decay, predation and germination. Under CA the latter category is reduced, causing a reduced seed output. With respect to seed input, only few reproductive *Striga* plants per area are required to replenishment or even increase the seed bank (Rodenburg et al., 2006).

Despite differences in resistance among rice varieties, and contradicting the observed carry-over effect of resistance, the factor variety also had no significant effect on the *S. asiatica* seed bank size over time. The use of *Striga*-resistant host plant varieties has shown before to decrease the production of parasite seed numbers compared to susceptible varieties, without concomitant reductions in the seed bank size (Rodenburg et al., 2006). This is mainly due to the prolific seed production of *Striga*, with an estimated production of close to 1,200 seeds per capsule for related *S. hermonthica* (van Delft et al., 1997). A modeling study showed that a decrease in the *Striga* seed bank could only be attained with varieties with either very successful pre-attachment resistance mechanisms—i.e. low production of germination stimulants— or with a combination of resistance mechanisms that affect the parasite at later stages (Westerman et al., 2007). In the current study, despite the combination of pre- (Jamil et al., 2011) and post-attachment (Cissoko

et al., 2011) resistance in NERICA-4, a decrease in the seed bank could not be achieved. It should be stressed however that the rice in this experiment, irrespective of the resistance level of the variety, was followed each next season by a susceptible maize crop.

Compared to the conventional combination of B22 under conventional tillage and crop removal, the combination of NERICA-4 grown in zero-tillage plots with ricebean intercropping in the previous season and mulching of crop residues —among the best combination in terms of control—, resulted in an average delay in *S. asiatica* emergence of 19 days. Also with other combinations of CA practices and improved varieties, important delays in *S. asiatica* emergence were obtained. Delaying *Striga* parasitism has proven to be an important strategy to reduce overall parasite biomass —and consequently parasite reproduction— and to minimize *Striga*-induced crop losses (van Ast and Bastiaans, 2006), hence this finding potentially has great significance for farmers dealing with *Striga* infestation.

The observations on differences in *S. asiatica* emergence dates and infection rates also reiterate the importance of integrating management options. With the use of a resistant variety (NERICA-4) alone, parasitism can be delayed by nearly 10 days compared to the susceptible rice variety (B22). When it is combined with the other strategies —i.e. cover crops, mulching of crop residues, zero-tillage— this delay can be almost doubled. Likewise, a change from conventional to a CA practice using ricebean or *Stylosanthes*, reduced infection levels by 53 and 79%. The use of resistant NERICA varieties compared to the susceptible variety B22 reduced infection levels with 57% (with NERICA-9) and 91% (NERICA-4). Combinations of these practices and varieties resulted in reductions of 96 (NERICA-9 and -4 with CAST) to 98% (NERICA-4 with CARB).

4.3. Implications for smallholder cereal farmers in *Striga*-prone areas

This study confirms the broadly accepted assumption, supported by a relatively scant body of evidence (e.g. Schulz et al., 2003; Aliyu et al., 2004; Ellis-Jones et al., 2004; Kamara et al., 2008; Tesso and Ejeta, 2011), that an integrated *Striga* management approach indeed works. It seems however impossible to reach 100% control, even with combinations of highly efficient technologies. For long-term beneficial effects, farmers following this approach are therefore recommended to continue uprooting escaping parasites by hand before they flower, to avoid replenishment or even a buildup of the seed bank.

Smallholder cereal farmers working in *Striga*-prone areas could be reluctant to adopt the practices studied here. Growing an intercrop usually requires more labor, for crop establishment and harvesting. A perennial like *Stylosanthes* also requires additional work, as the cover crop needs to be rolled or slashed before planting the next crop (see section 2.4) and sometimes also during the season, to avoid undesired competition with the main crop.

Mulching crop residues implies a clear trade-off with other uses of crop biomass, such as feeding cattle (Naudin et al., 2015b). Finally, an important driver for adoption of alternative crop management strategies is the level of crop yields. On this point, CA often underperforms, at least in first ten years after introduction (Giller et al., 2009). One of the reasons is that cereal crop residues have a high C:N ratio resulting in immobilization of

nitrogen, and additional (and costly) mineral fertilizer inputs seem therefore necessary to compensate this (Vanlauwe et al., 2014).

Conservation agriculture practices need to be adjusted to the locally prevailing conditions, to render them useful for smallholder farmers (Knowler and Bradshaw, 2007). The successful control of *S. asiatica* by practices investigated in the current study, suggests that in areas where *Striga* is a dominant production constraint, this strategy—or components of it— will be a good fit for smallholder farmers.

5. Conclusion

Conservation agriculture (CA) practices, combining leguminous cover crops with zero-tillage and crop residue mulching, delay and reduce *Striga asiatica* infection in rice-maize rotation systems. These practices also slow down seed bank increments compared to conventional rice – maize rotations. Most effective cover crop in terms of *S. asiatica* control is *Stylosanthes guianensis*. This species also proved to be the only cover crop capable of keeping ordinary weed biomass at similar, manageable levels as under the conventional practice with seasonal tillage. The weed suppressive nature of *Stylosanthes* is probably due to its perennial nature and high biomass production. This is also thought to be one of the reasons for the effective *S. asiatica* suppression. However, as good *S. asiatica* control was also obtained by the CA practice with the less prolific species *Vigna umbellata* (ricebean), other mechanisms should be involved as well.

Striga control obtained by the agronomic practices of CA can be enhanced by integration of a *Striga*- resistant rice variety such as NERICA-4. Inclusion of a resistant rice variety even has a strong residual control effect, as evidenced by the reduced *Striga*-infection levels in the following maize crop. The combination of CA practices and a resistant variety proved however not enough to entirely prevent *S. asiatica* parasitism and seed bank increase. Additional measures, such as hand-pulling of escaping *S. asiatica* plants before flowering, would therefore be required for effective and long term control.

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Table 1. Analysis of variance of first emergence date (*E-date*) and maximum aboveground numbers (*NSmax*) of *S. asiatica* in rice and maize, with season (S), cropping practice (CP), rice variety (V) and interactions as sources of variation.

Source	<i>S. asiatica in rice</i>					<i>S. asiatica in maize</i>				
	<i>E-date</i>			<i>NSmax</i>		<i>E-date</i>			<i>NSmax</i>	
	df	F	P	F	P	df	F	P	F	P
Season (S)	3	12.6	< 0.0001	67.5	< 0.0001	2	6.6	0.002	6.7	0.0016
Cropping practice (CP)	3	2.9	0.07	16.9	< 0.0001	3	2.4	0.10	14.5	0.0003
Variety (V)	2	13.9	< 0.0001	83.4	< 0.0001	2	6.8	0.001	14.3	<0.0001
S × CP	9	0.6	0.79	2.7	0.006	6	1.6	0.14	9.1	<0.0001
S × V	6	2.6	0.02	7.7	< 0.0001	4	0.68	0.61	1.0	0.4159
CP × V	6	2.4	0.03	5.1	< 0.0001	6	0.89	0.50	4.1	0.0008
S × CP × V	18	0.6	0.92	1.3	0.17	12	1.1	0.35	2.7	0.0028

Table 2. Means and standard errors of differences (SED) of first *S. asiatica* emergence date (*E-date*; in days after sowing, DAS) in rice and maize, following four cropping practices (CP; CONV, CACM, CARB and CAST) and three rice varieties (V; B22, NERICA-9 and NERICA-4) during four cropping season (S1-S4).

		Days to <i>S. asiatica</i> emergence in rice (<i>E-date</i> ; DAS)								Days to <i>S. asiatica</i> emergence in maize (<i>E-date</i> ; DAS)							
		S1	S2	S3	S4	Mean			S1	S2	S3	S4	Mean				
S × CP	CONV	76.9	72.9	59.9	64.7	68.6			-	55.3	64.4	63.0	60.9				
	CACM	78.9	72.3	65.0	73.3	72.4			-	62.9	71.6	63.2	65.9				
	CARB	77.7	72.9	66.9	68.7	71.6			-	59.1	69.0	58.4	62.2				
	CAST	79.1	78.6	70.3	76.2	76.1			-	64.0	66.2	71.3	67.2				
	Mean (S)	68.6	B ¹	72.4	AB	71.6	B	76.1	A	-	60.3	B	67.8	A	64.0	AB	
	LSD (S)	4.20								4.04							
S × V	B22	76.1	abc	69.4	cd	56.7	e	65.8	d	67.0	Z	-	54.8	65.1	60.9	60.3	Y
	NERICA-9	77.8	ab	78.8	a	63.8	de	70.6	bcd	72.7	Y	-	62.4	65.4	64.1	64.0	XY
	NERICA-4	80.5	a	74.3	abc	76.1	abc	75.8	abc	76.7	X	-	63.7	72.9	66.9	67.8	X
	LSD (V)	3.64								4.04							
	LSD (S × V)	7.28															
CP × V		CONV	CACM	CARB	CAST					CONV	CACM	CARB	CAST				
	B22	61.5	f	67.3	def	65.0	ef	74.2	abcd	59.0	59.2	58.2	64.7				
	NERICA-9	68.6	cdef	73.9	abcd	69.1	bcde	79.3	a	62.4	67.2	59.9	66.5				
	NERICA-4	75.7	abc	75.9	ab	80.6	a	74.6	abc	61.2	71.4	68.5	70.3				
	LSD (CS × V)	7.28															

¹Means followed by different letters are significantly different ($P < 0.05$).

Table 3. Means of maximum aboveground *S. asiatica* numbers (*NSmax*; m⁻²) in rice and maize, following four cropping practices (CP; CONV, CACM, CARB and CAST) and three rice varieties (V; B22, NERICA-9 and NERICA-4) during four cropping season (S1-S4).

		Maximum <i>S. asiatica</i> densities in rice (<i>NSmax</i> ; plants m ⁻²)								Maximum <i>S. asiatica</i> densities in maize (<i>NSmax</i> ; plants m ⁻²)											
		S1 ¹		S2		S3		S4		Mean		S1 ²		S2		S3		S4		Mean	
S × CP	CONV	0.5	efgh ¹	1.6	cd	8.7	a	1.6	cd	2.1	A	0.05	9.4	a	1.7	bc	1.9	bc	3.4	A ¹	
	CACM	0.3	gh	0.9	defg	5.3	b	1.9	c	1.6	B	0.05	1.9	bc	2.1	b	2.8	b	2.2	B	
	CARB	0.2	h	0.5	fgh	3.3	b	1.0	cdef	1.0	C	0.03	2.7	b	1.9	bc	2.0	bc	2.2	B	
	CAST	0.2	h	0.1	h	1.3	cde	0.4	fgh	0.4	D	0.04	0.00	d	0.00	d	1.0	c	0.3	C	
	Mean	0.28	l	0.69	J	3.92	L	1.14	K	2.14			2.3	A	1.2	B	1.8	A			
	LSD (S)	0.22										0.23									
	LSD (CS)	0.22										0.27									
	LSD (S×CS)	0.48										0.52									
S × V	B22	0.66	def	1.5	c	12.2	a	2.9	b	2.8	A		3.7		1.59		2.4		2.5	A	
	NERICA-9	0.20	fg	0.9	cd	4.1	b	1.0	cd	1.2	B		2.6		1.57		1.9		2	A	
	NERICA-4	0.1	g	0.1	g	0.8	de	0.3	efg	0.3	C		1.1		0.65		1.3		1	B	
	LSD (V)	0.19										0.23									
	LSD (S×V)	0.41																			
CS × V		CONV		CACM		CARB		CAST				CONV		CACM		CARB		CAST			
	B22	6.1	a	4.1	a	2.1	b	0.9	cd			7.0	a	2.7	bcd	2.5	bcd	0.4	fg		
	NERICA-9	2.2	b	1.6	bc	1.2	c	0.3	e			3.1	bc	2.2	bcd	3.9	b	0.2	g		
	NERICA-4	0.4	de	0.3	e	0.1	e	0.2	e			1.5	cd	1.8	cde	0.9	ef	0.2	g		
	LSD (CS×V)	0.41										0.52									

¹ Means and LSD values are back-transformed after analysis; means followed by different letters are significantly different ($P < 0.05$). ² No rice variety factor in S1

Table 4. Results of the three-stage analysis of *S. asiatica* seed numbers in the soil, following a negative binomial distribution with 1. Analysis of Co-variance (ANCOVA), 2. Analysis of variance (ANOVA), and 3. Comparison of means (Tukey's). Rice variety (V), cropping practice (CP), seed numbers at the start of the experiment (S0), and interactions are sources of variation in the ANCOVA, and rice variety (V), cropping practice (CP) and interactions are sources of variation in the ANOVA. Means of *S. asiatica* seed numbers in the soil at 0-10 cm depth (seeds m⁻²), are compared across four cropping practices (CP; CONV, CACM, CARB and CAST).

Analysis	Effect	df	F	P
1. ANCOVA	Variety (V)	2	3.61	0.04
	Cropping Practice (CP)	3	11.04	0.00
	V × CP	6	0.74	0.62
	Seed # at start (S0)	1	0.34	0.56
	S0 × V	2	0.53	0.60
	S0 × CP	3	0.95	0.43
	S0 × V × CP	6	1.25	0.31
2. ANOVA	Variety (V)	2	1.77	0.18
	Cropping Practice (CP)	3	9.77	<0.0001
	V × CP	6	0.89	0.51
3. Comparison of means	Cropping Practice	<i>S. asiatica</i> seed number m ⁻² (0-10 cm)		
	CONV		8022	a ¹
	CACM		1943	b
	CAST		1725	b
	CARB		1098	b

¹ Means followed by different letters are significantly different ($P < 0.0001$)

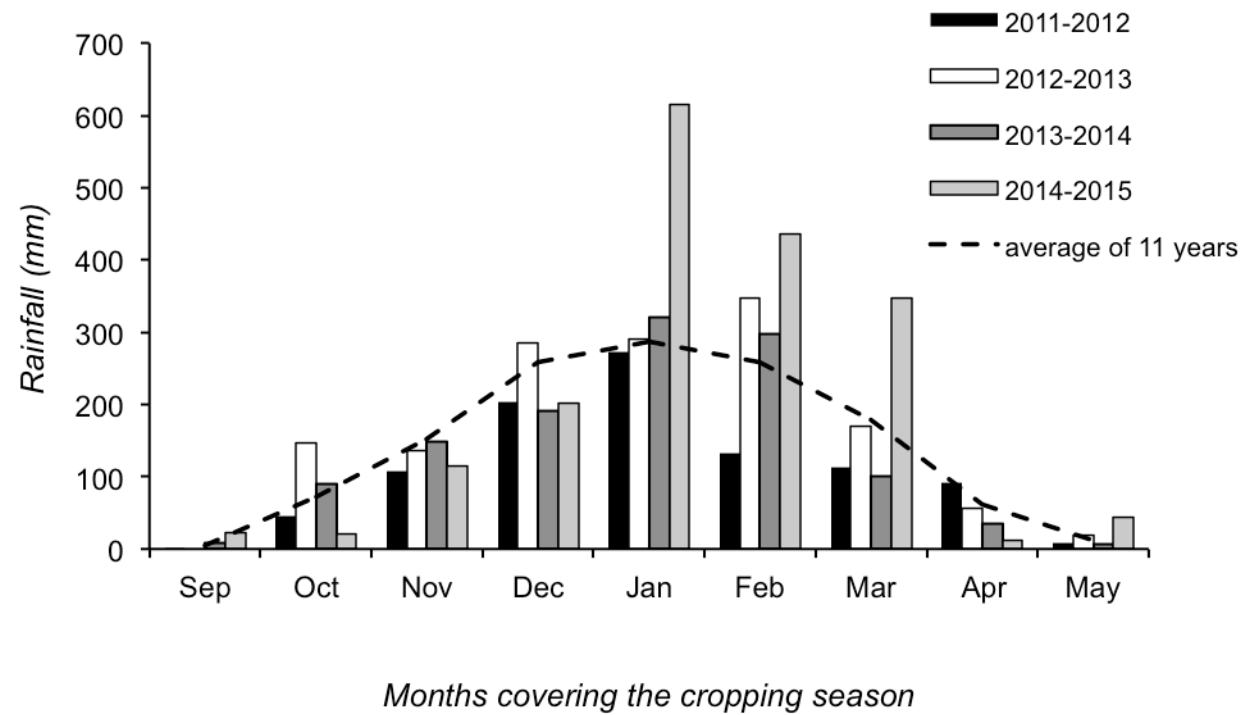


Figure 1. Monthly rainfall (mm) per season, during the four cropping seasons from 2011-2012 (S1) to 2014-2015 (S4), and the 11-year average.

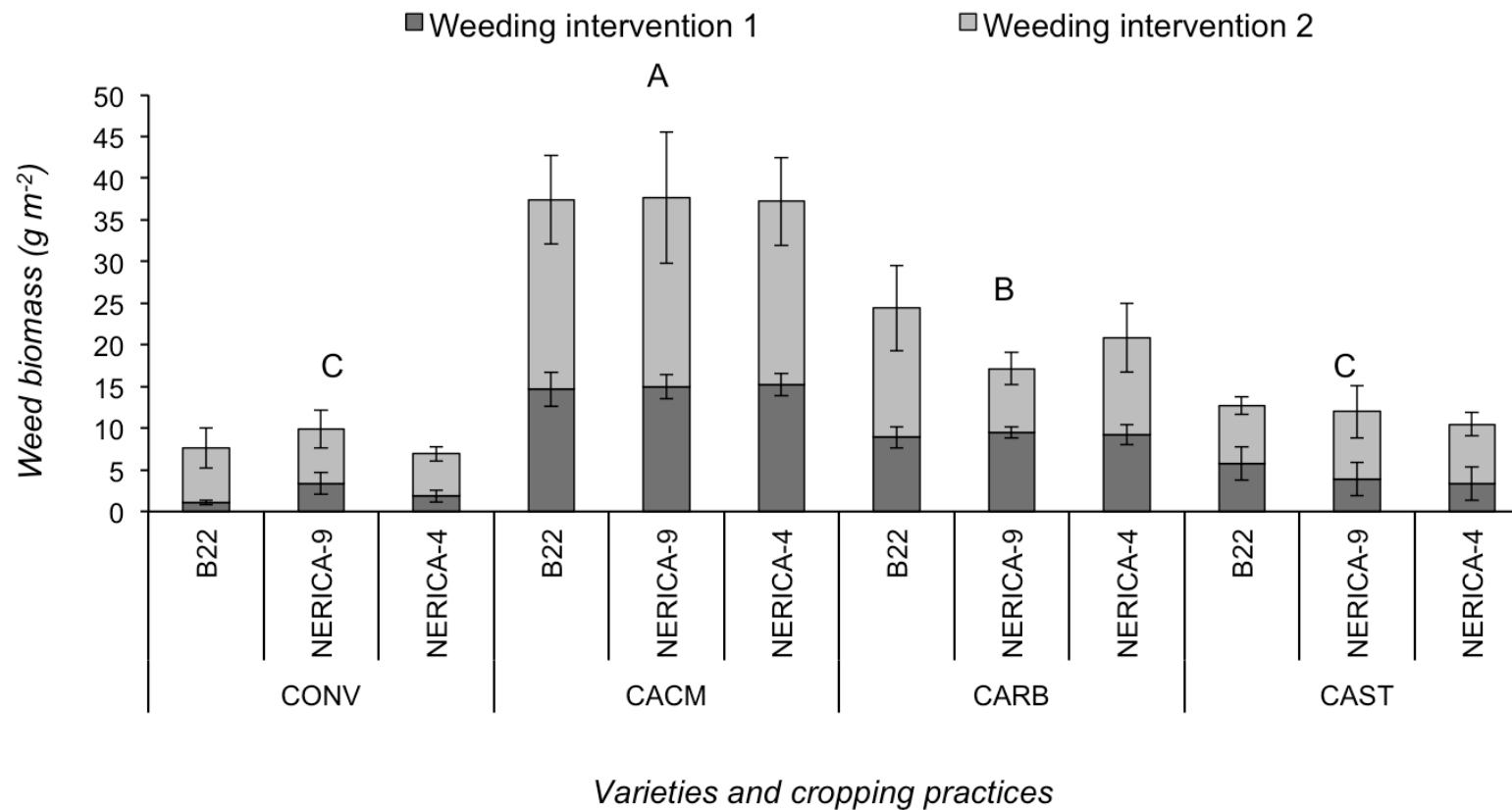


Figure 2. Weed biomass dry weight in season 4 with weeding time (Dark grey: W1; Light grey: W2), cropping practice (CONV, CACM, CARB, CAST), rice variety (B22, NERICA-9, NERICA-4) as factors. Comparison of means conducted on total (W1 and W2 samplings) weed biomass dry weights per cropping practice (WB_{tot} ; g m⁻²). Different letters (A, B, C) indicate significant differences ($P < 0.0001$).

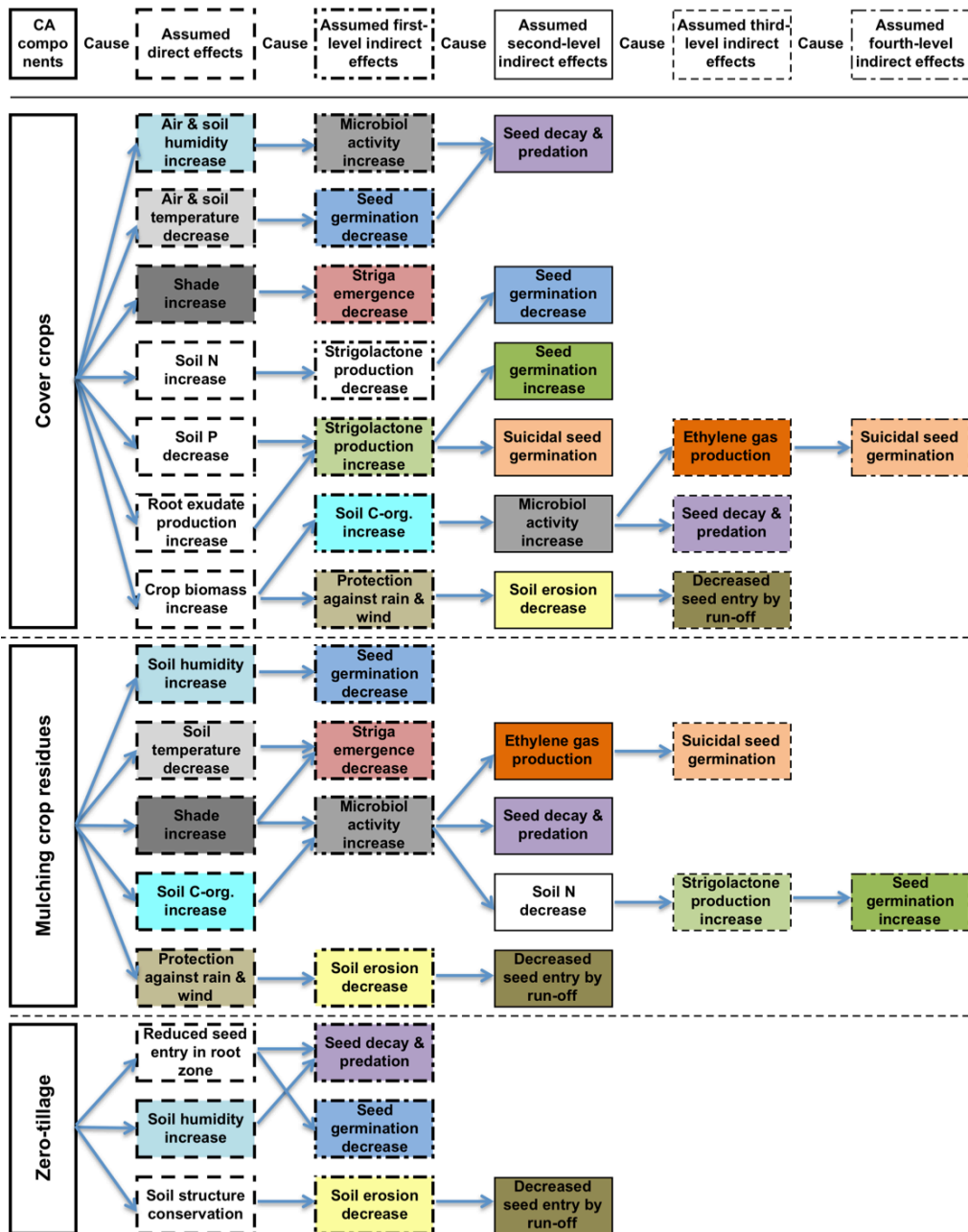


Figure 3. Assumed direct and indirect causal relations between Conservation Agriculture (CA) components — cover crops, crop residue mulching and zero-tillage — and *S. asiatica*. Boxes with the same border style indicate the same level in process. Boxes of the same color indicate the same assumed effect.