



Can the parasitic weeds *Striga asiatica* and *Rhamphicarpa fistulosa* co-occur in rain-fed rice?

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Summary

Striga asiatica and *Rhamphicarpa fistulosa* are important parasitic weeds of rain-fed rice, partly distributed in similar regions in sub-Saharan Africa (SSA). It is not evident whether their ecologies are mutually exclusive or partially overlapping. In Kyela, a rice-growing area in south Tanzania where both parasites are present, three transects of about 3 km each across the upland–lowland continuum were surveyed in June 2012 and 2013. A total of 36 fields were categorised according to their position on the upland–lowland continuum as High, Middle or Low and soil samples were taken. In each field, parasitic and non-parasitic weed species were identified in three quadrats. Additionally, in two pot experiments with four different moisture levels ranging from wilting point to saturation, influence of soil moisture on emergence and growth of parasites was investi-

gated. *Striga asiatica* was observed in higher lying drier fields, while *R. fistulosa* was observed in the lower lying wetter fields. Furthermore, non-parasitic weed species that were exclusive to *S. asiatica*-infested fields are adapted to open well-drained soils, while species that were exclusive to *R. fistulosa* fields are typical for wet soils. The experiments confirmed that *S. asiatica* is favoured by free-draining soils and *R. fistulosa* by waterlogged soils. These results imply that changes in climate, specifically moisture regimes, will be crucial for future prevalence of these parasitic weeds. The non-overlapping ecological range between their habitats suggests that their distribution and associated problems might remain separate. Thus, management strategies can be focused independently on either species.

Keywords: parasitic weed species, climate change, niche, ecology, agro-ecosystems, soil moisture.

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Introduction

Striga asiatica (L.) Kuntze and *Rhamphicarpa fistulosa* (Hochst.) Benth. are parasitic weeds causing considerable yield losses to rain-fed rice in sub-Saharan Africa (SSA) (Johnson, 1997; Ouédraogo *et al.*, 1999; Mohamed *et al.*, 2001; Rodenburg *et al.*, 2011b). It is

partly due to such production constraints that a large gap remains between regional production and consumption in SSA (Seck *et al.*, 2010). Both *S. asiatica* and *R. fistulosa* are root hemi-parasites of the family Orobanchaceae that extract host assimilates through a developed attachment organ known as haustorium, but also produce assimilates independently through

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photosynthesis (Cochrane & Press, 1997; Ouédraogo *et al.*, 1999). *Striga asiatica* is an obligate parasite and cannot survive without attachment to a host (Cochrane & Press, 1997), while *R. fistulosa* is facultative, as it can complete its life cycle as a free living plant but benefits considerably from attachment to a host (Ouédraogo *et al.*, 1999).

The rain-fed rice (*Oryza sativa* L and *O. glaberrima* Steud.) area in SSA covers 7 million hectares (Diagne *et al.*, 2013). Rice consumption in the last decade has increased by 4.6%, which is twice as much as the continent's 2.6% population growth (USDA, 2012). Despite increased rice production, this demand has not been met, and as a result, SSA has become increasingly dependent on rice imports (Seck *et al.*, 2010). Furthermore, cultivation of rice has been expanded into marginal rain-fed uplands and lowlands (Rodenburg *et al.*, 2014) which are often natural habitats of parasitic weeds (Roques, 1994). *Striga asiatica* is mainly distributed in eastern and southern Africa (Mohamed *et al.*, 2001), whereas *R. fistulosa* is distributed in Sahelian regions (Senegal to Ethiopia), East Africa, South Africa and Madagascar (Hansen, 1975; Ouédraogo *et al.*, 1999).

Despite their distribution in similar regions on the continent and the assumed negative effects they have on the rice sector, quantitative information on habitats of these parasitic weed species is scarce. As the area used for rice production expands, these weeds may spread and establish into new areas. If we are to find out whether areas of these species are likely to expand in future, it is important to determine their habitat range. Knowing this range is particularly relevant in the face of climate change, where rainfall patterns have been predicted to become more erratic (IPCC, 2007). To understand habitat characteristics of both *S. asiatica* and *R. fistulosa* in rain-fed rice, a field study was carried out in Kyela, a major rice growing area in southern Tanzania. Supplementary pot experiments

were conducted to substantiate the role of soil moisture. We tested the hypothesis that the ecological niches of the two parasites are mutually exclusive, resulting in rain-fed rice ecosystems that will form a habitat for either *S. asiatica* or *R. fistulosa*.

Materials and methods

Field survey

In June 2012 and June 2013, field surveys were conducted in Kyela, in southern Tanzania, between 35°41'30"E and 9°25'40"S. Kyela lies around 500 m above sea level where the main rice cultivation months range from January to June. Rainfall is of the unimodal type with an annual average of around 3000 mm, while average temperatures range from 19 to 23°C in cool months (May to October) and 29–31°C in hotter months (November to April) (Kayeke *et al.*, 2010). Rice is grown along the upland–lowland continuum without clear boundaries between upland, hydromorphic and lowland zones.

Rainfall data were collected during rice growing seasons of 2012 and 2013 from rain gauges installed in *Striga*-infested areas and in *Rhamphicarpa*-infested areas and averaged over the two measuring points. An additional 7-year period of rainfall data from 2005 to 2011 was provided by the office of the District Agricultural Livestock Development Officer (DALDO) of Kyela.

During the surveys, three transects of about 3 km each in length were aligned across the upland–lowland continuum, from the road to the river (Fig. 1). Each transect covered 12 rice fields ranging from 0.5 to 1 ha in size. A total of 36 rice fields were thus surveyed. The rice fields in each transect were subdivided into high, middle and low categories according to their location on the continuum, that is Fields 1–4 positioned close to the road were denoted as High,

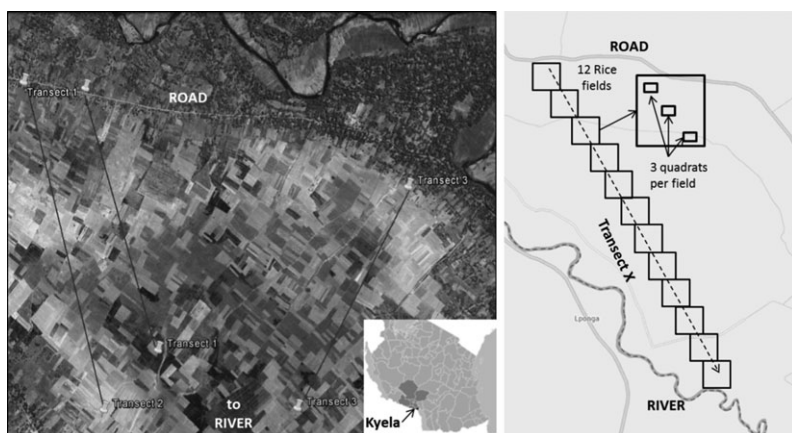


Fig. 1 A Google Earth image showing three transects taken in Kyela district, south of Tanzania in June 2012 and 2013. The transects walks started from the road connecting the three rice cultivating villages, Kilasilo, Mbako and Kaziba and trailed from upland to lowland (road to river). On the side of the figure, a schematic transect is shown covering 12 rice fields in which 36 quadrats were installed.

low-lying fields located closer to the river, 9–12 were denoted as Low, and fields in between High and Low, 5–8 were denoted as Middle. This resulted in a total of 12 rice fields for each category.

In 2012, three quadrats (1 × 1 m) were randomly placed within each field. Location and elevation of each quadrat were recorded using a global positioning system (GPS) device (eTrex Legend; GARMIN International Inc., USA). A 440 cm³ soil sample was taken from the top 10 cm using closable 10 cm length PVC pipes. Wet and dry weights of each soil sample were recorded to determine soil moisture content. One soil sample from each of the 36 rice fields was analysed for texture, organic matter (OM%), nitrogen (N%), pH, electrical conductivity (EC), cationic exchange capacity (CEC), phosphorus (P), potassium (K), magnesium (Mg), calcium (Ca) and sodium (Na). Variation of soil characteristics of rice fields of High, Middle and Low categories was tested via one-way ANOVA using statistical software GenStat for Windows 15th Edition (GenStat, 2000–2013).

Species diversity

Each rice field was visually surveyed for infestation of *S. asiatica* and *R. fistulosa* and, if present, their average cover scored on a 1–5 scale of Braun-Blanquet (1932) (Table 1). Based on infestation, rice fields were classified as *Striga*-infested, *Rhamphicarpa* infested, *Striga* and *Rhamphicarpa* infested or parasite-free.

Presence of both parasitic and non-parasitic weed species was identified and recorded per quadrat ($n = 108$) using the AFROweeds identification tool (CIRAD-AfricaRice, 2012) and the field guide of Johnson (1997). Data on occurrence of plant species obtained from the quadrats were used to calculate the Shannon–Wiener plant species diversity index (H') for *Striga*-infested, *Rhamphicarpa*-infested and parasite-free rice fields following Eqn 1:

$$H' = - \sum_{i=1}^s (P_i)(\ln P_i) \quad (1)$$

where $P_i = n_i / \sum_{i=1}^s n_i$, with n_i = number of quadrats in which species i was observed and s refers to total

number of observed plant species. The H' value indicates diversity of species present in the set of quadrats, and may range from 0, when just one species is present in all quadrats, to about 4.5 for a wide range of species (Molles, 1948). The relationship between species was determined by a distance and similarity measure generated from hierarchical cluster analysis (HCA) with Pearson's correlation as the proximity procedure using statistical software SPSS version 20 (SPSS, 2011).

Pot experiments

Two pot experiments were conducted, the first (Experiment 1) in a screen house at Mikochehi Agricultural Research Station (MARI), located in Dar es Salaam in Tanzania, from January to June 2012. Experiment 2 was established in a screen house at Sokoine University of Agriculture (SUA), located in Morogoro in Tanzania from September 2012 to January 2013. The design was a split-plot with five replicates containing four moisture levels at main plot level and parasitic weed species (*S. asiatica* and *R. fistulosa*) at subplot level. A total number of 40 pots, sealed at the bottom, were used in each experiment. The pots had a capacity of 15 L with a diameter of 26 cm and were filled with a dry mixture of sand and loam soil (5:1 v/v) (≈ 17 kg soil mixture). To determine field capacity, ten pots with the same dry mixture of sand and loam soil, but with holes at the bottom, were weighed and then gradually filled with water, until addition of any extra water created a tiny flood layer. The pots were then left to drain freely for 48 h and weighed again. This way it was established that pots at field capacity [FC] contained around 2 L of water. Accordingly, moisture levels were installed in the pots without holes by adding 1 L of water per pot [FC-1 L] (resulting in drier soil conditions), 2 L of water per pot [FC] (resulting in field capacity conditions), 3 L of water per pot [FC+1 L] (resulting in a moderately saturated soil) and 4 L of water per pot [FC+2 L] (resulting in a totally saturated soil). The weight of each pot was then recorded, and pots were regularly weighed and watered to retain the intended moisture level.

The parasitic weed seeds used were collected in Kyela in 2009 from farmers' fields. Germination percentages were 40% (for *S. asiatica*) and 60% (for *R. fistulosa*). In the first experiment, about 2400 viable seeds of *S. asiatica* (0.022 g) were mixed through the upper 10 cm of the pot. For *R. fistulosa*, with seeds requiring daylight to germinate, about 150 viable seeds (0.00315 g) were thoroughly mixed with 100 cm³ of soil and spread evenly on the soil surface in each pot. In Experiment 2, the added amount of seed was doubled for both parasites because in Experiment 1 the

Table 1 Species cover classes of Braun-Blanquet's five point scale (Braun-Blanquet, 1932)

Cover class	% of species coverage
0	No parasite species observed
1	<5
2	5–25
3	25–50
4	50–75
5	75–100

achieved emergence was suboptimal. Two rice seeds were then sown in the centre of each pot. Around 2 weeks after emergence, rice seedlings were thinned to one rice plant per pot. Above-ground *S. asiatica* and *R. fistulosa* numbers were counted every 3 days, starting from 7 days after sowing (DAS). At 60 DAS, all above-ground plant parts of *S. asiatica* and *R. fistulosa* were cut and dried at 70°C for 48 h. Root systems of rice with *S. asiatica* and rice with *R. fistulosa* were washed and placed in plastic bags and cooled at 4°C for 2 days. This was to enable both *S. asiatica* and *R. fistulosa* roots to turn into a dark blue shade, which permitted separation from rice roots that retained a lighter hue. *Striga asiatica* and *R. fistulosa* roots were then separated from rice roots and dried at 70°C for 48 h to determine dry weights.

Data on emergence and dry weight of both parasites were subjected to analysis of variance (ANOVA) using statistical software package GenStat for Windows 15th Edition (GenStat, 2000–2013). Count data (i.e. number of emerged parasite seedlings) were transformed prior to analyses to meet assumptions of ANOVA, using $\log(x + 1)$, where x is the original observation (Sokal & Rohlf, 1995). The analysis was then followed by comparison of means by least significant difference (LSD).

Results

Rainfall

Average total rainfall in the growing season of the last 7 years (2005–2011) was 2326 mm. The rainfall distribution showed that the rainy season in Kyela begins in January, peaks in April, declines in May and finally drops in June (Fig. 2). The rainfall pattern in 2012

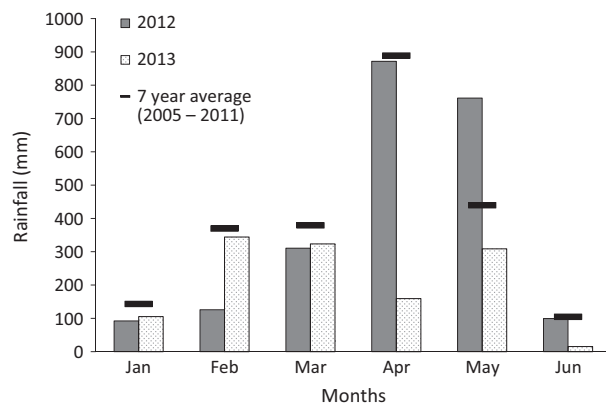


Fig. 2 Rainfall distribution of Kyela during the main rice crop calendar of the years 2012 and 2013. The black bar (—) represents 7-year monthly average rainfall received in the first 6 months of the years 2005–2011.

showed a similar trend with the exception of May that was above the 7-year average. In 2013, rainfall was clearly below the 7-year average for the month of April. Total rainfall received during the rice-growing season was 2260 mm in 2012 and 1255 mm in 2013 creating a 1005 mm difference in precipitation between the years.

Transects

During the transect walks, it was observed that soils in the lowlands (Low) were completely flooded, while those in the uplands (High) were dry. In addition, soils in the transition between lowlands and uplands Middle were moderately wet. For all three transects, there were clear differences in elevation, that is 514–529 m (Transect 1), 516–533 m (Transect 2) and 513–525 m (Transect 3). The elevation differed significantly, with Low fields on average 1.7 and 3.0 m lower than Middle fields and High fields respectively.

All fields had saline acidic soils, with low levels of nitrogen, phosphorus and organic matter, while they had high levels of sodium, potassium, calcium and magnesium. Soil moisture was significantly higher in Low fields and lowest in High fields (Table 2). In addition to this obvious difference in soil moisture content, some other differences were observed. Soil calcium (Ca) and sodium (Na) contents and cationic exchange capacity (CEC) were significantly higher in Low fields than in High fields. Soil potassium (K) content was highest in High fields, while it did not differ between Low and Middle fields. Soil pH, organic matter (OM %), nitrogen (% total N) and phosphorus (P) contents did not differ between the three positions on the slope.

In 2012, in all three transects, *S. asiatica* was observed in 92% of rice fields located in the High parts of the slope and 42% of fields in the Middle part of the slope. *Striga asiatica* was not observed in the Low parts of the slope. *Rhamphicarpa fistulosa* on the other hand was observed in 100% of the low-lying fields (Low), 8% in the Middle part of the slope, but was not observed in the High part of the slope (Fig. 3). There were 16 *Striga*-infested fields, 13 *R. fistulosa*-infested fields and seven parasite-free fields. Coverage of parasitic weeds was generally higher in *Rhamphicarpa*-infested fields than in fields infested with *S. asiatica*. Just over 85% of *Rhamphicarpa*-infested fields had a parasite cover between 50–100%, whereas 69% of *Striga*-infested fields had a parasite cover of <5%. In between parasite-infested fields, there were parasite-free fields, showing a clear demarcation between the two species. In 2013, *S. asiatica* was observed in 100% of the fields located in the High parts of the slope and in 67% of the fields in the Middle parts while the species

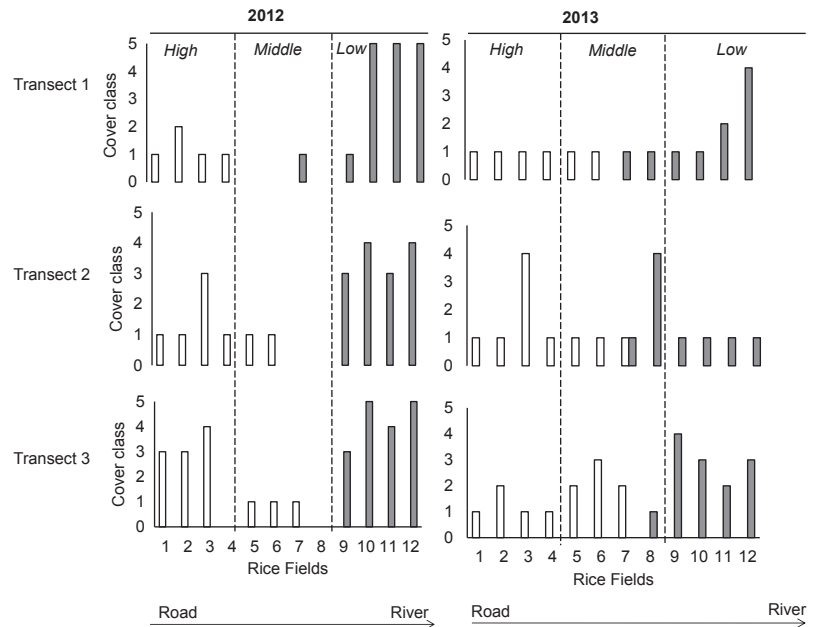
Table 2 Mean values of soil characteristics from rice fields located at High ($n = 12$), Middle ($n = 12$) and Low ($n = 12$) elevations

Position on the slope	Rep	Moisture (g dm ⁻³)	OM %	N %	mg kg ⁻¹					pH	C.E.C (meq/100)	E.C. (S)/us/cm
					P	K	Ca	Mg	Na			
High	12	598 ^{b*}	2.18	0.14	6.05	267 ^a	433 ^b	101 ^b	59 ^b	5.33	6.7 ^b	51.2
Middle	12	617 ^b	2.11	0.11	6.45	199 ^b	544 ^b	111 ^{ab}	75 ^b	5.45	7.2 ^b	50.8
Low	12	774 ^a	2.19	0.13	4.71	199 ^b	706 ^a	143 ^a	99 ^a	5.45	9.1 ^a	65.2
	<i>P</i>	0.023	n.s†	n.s	n.s	0.043	0.006	0.042	0.004	n.s	0.007	n.s

*Means followed by a different letter are significantly different between elevations.

†n.s indicates not significant.

Fig. 3 Parasitic weed cover class (0 = no parasite species observed, 1 = < 5%; 2 = 5–25%; 3 = 25–50%; 4 = 50–75%; 5 = 75–100%) for *Striga asiatica* and *Rhamphicarpa fistulosa* in three transects in Kyela in 2012 and 2013. The light bars indicate the cover class of *S. asiatica* - infested fields, while the dark bars indicate the cover class of *R. fistulosa* - infested fields. Numbers refer to the position of the rice field along the transect. 1, 2, 3 and 4 are rice fields in the uplands (High), 5, 6, 7 and 8 are fields at middle elevation (Middle) while 9, 10, 11 and 12 are fields in the lowland (Low).



was not observed in the Low parts. *Rhamphicarpa fistulosa* on the other hand was observed in 100% of the fields classified as Low, in 17% of the fields classified as Middle and in none of the fields classified as High (Fig. 3). In 2013, a parasite-free zone was not observed. There were 19 *Striga*-infested rice fields and 16 *R. fistulosa* -infested fields. In just one occasion, both parasites were observed in the same field, although at opposite ends. Apart from this field, a clear separation between *Striga*-infested and *Rhamphicarpa*-infested fields was maintained. Coverage of *S. asiatica* was comparable with that in the previous year, whereas *R. fistulosa* clearly had a lower coverage, with only 18% of *Rhamphicarpa*-infested fields with a cover score above 50%.

Species diversity and abundance

A total of 43 non-parasitic weed species were encountered in 108 quadrats installed in 36 rice fields. Non-parasitic species most frequently encountered were *Oldenlandia herbacea* (Linn.) Roxb, *Fimbristylis ferruginea* (L.) Vahl, *Pycreus lanceolatus* (Poir.) C.B. Clarke,

Eragrostis tremula Hochst., *Melochia corchorifolia* (Linn.) and *Hyptis spicigera* (Lam.) Marubio. These species were observed in 30% to 45% of the quadrats. The Shannon–Wiener (H') index was relatively high and did not differ significantly between *S. asiatica* (3.08), *R. fistulosa* (3.06) and parasite-free (3.14) fields.

The cluster analysis showed a division of non-parasitic weed species that were more frequently associated with either one of the two parasitic weed species (Fig. 4). *Ammannia auriculata* Willd., *Oryza longistaminata* A. Chev. & Roehr., *Scleria vogelii* C.B. Clarke, *Fimbristylis littoralis* Gaud. and *Cyperus distans* L. were exclusively encountered in *Rhamphicarpa*-infested fields, while *Spermacoce octodon* (Hepper) Hakki., *Pennisetum polystachion* (L.) Schult., *Mitracarpus hirtus* (L.) DC. and *Rottboellia cochinchinensis* (Lour.) Clayton, were only encountered in *Striga*-infested fields. None of the species were exclusive to parasitic weed-free fields.

Pot experiments

In Experiment 1, emerged plants of both *S. asiatica* and *R. fistulosa* were observed at all moisture

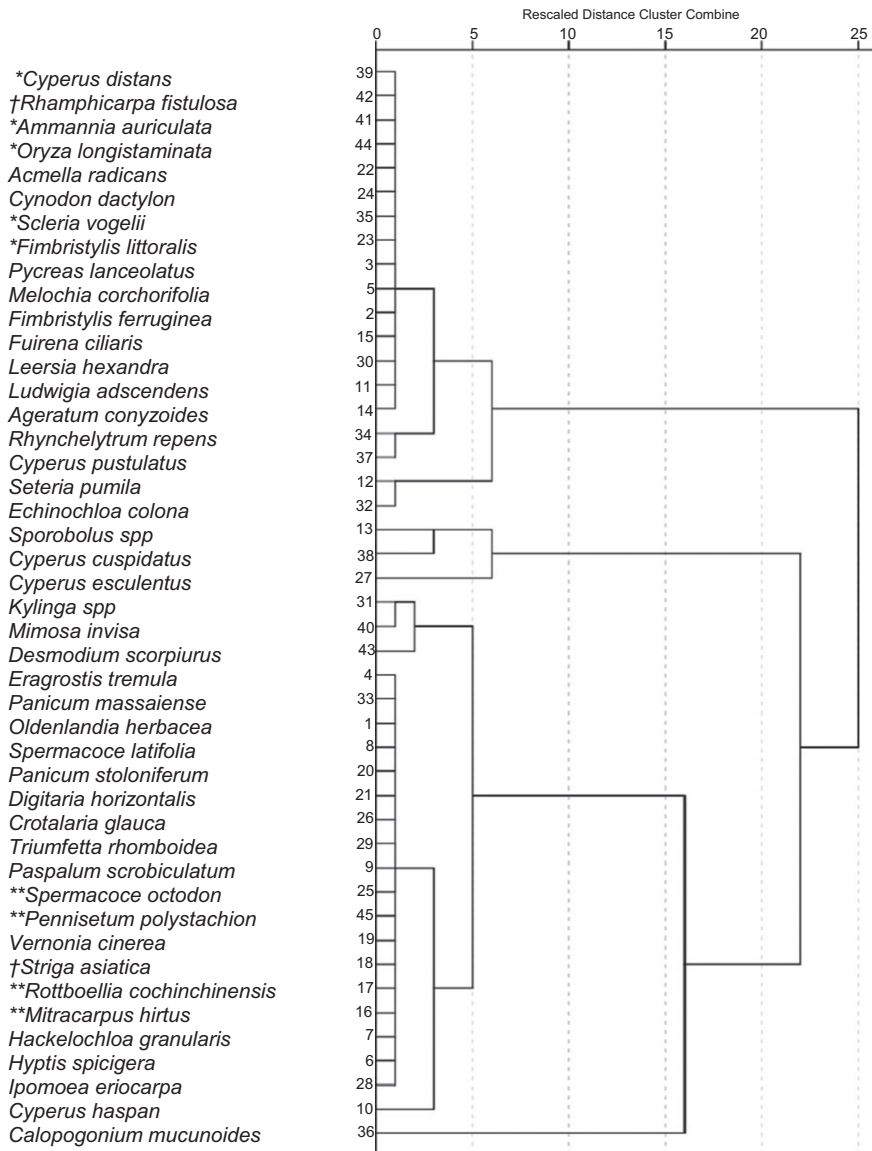


Fig. 4 Dendrogram showing the relation between frequency of occurrence of non-parasitic ($n = 43$) and parasitic weed species ($n = 2$) in the study area in 2012. Distance and similarity measures were generated from hierarchical cluster analysis, using Pearson's correlation as the proximity procedure. The symbol † shows position of parasitic weed species, ** represents non-parasitic weed species that were exclusive to the *Striga asiatica* habitat while * represents non-parasitic weed species that were exclusive to the *Rhamphicarpa fistulosa* habitat.

treatments. However, *S. asiatica* emergence gradually decreased ($P = 0.009$) at the higher moisture levels (Fig. 5A), while *R. fistulosa* emergence steadily increased ($P < 0.001$) with increasing moisture levels (Fig. 5B). The highest emergence for *S. asiatica* was at the 2 L moisture level (FC). In Experiment 2, the response of emergence to moisture was largely similar to that observed in Experiment 1, except that *S. asiatica* did not emerge at the highest moisture level (4 L). The highest emergence was observed at both 1 and 2 L ($P < 0.001$) (Fig. 5A). *Rhamphicarpa fistulosa* had the highest emergence at both 3 and 4 L, while the lowest

emergence was observed at 1 and 2 L ($P < 0.001$) (Fig. 5B).

In both experiments, total biomass dry weight of *S. asiatica* decreased with increasing moisture levels (Fig. 5C), while biomass of *R. fistulosa* peaked at the higher moisture level (Fig. 5D). The highest biomass dry weight for *S. asiatica* was observed at both 1 and 2 L moisture levels, while no biomass was produced at the 4 L moisture level (Experiment 1; $P = 0.004$ and Experiment 2; $P < 0.001$). For *R. fistulosa*, the highest biomass dry weight was produced at the 4 L moisture level, while there was no difference between the

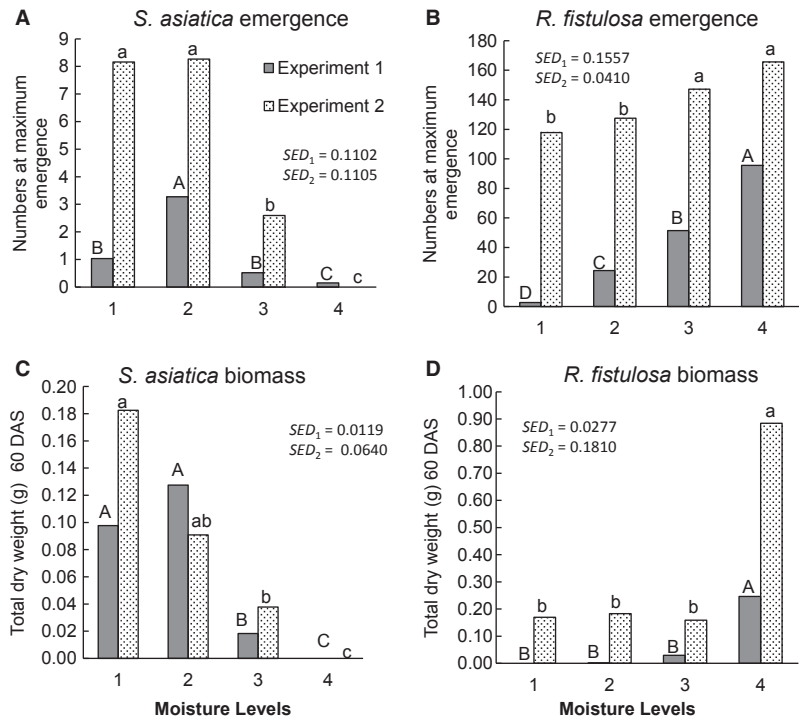


Fig. 5 Maximum emergence of *Striga asiatica* (A) and *Rhamphicarpa fistulosa* (B) and total dry weight of *S. asiatica* biomass (C) and total dry weight of *R. fistulosa* biomass (D) at four moisture levels in Experiment 1 and 2. Soil moisture levels within each experiment with a different letter on top of the bar differed significantly ($P < 0.05$) (Experiment 1: capital; Experiment 2: small). SED values for both experiments are presented in the graphs. Note that SED values are provided on log-scale.

biomass produced at the other moisture levels (Experiment 1; $P = 0.034$) and Experiment 2; $P < 0.001$).

Discussion

There were significant differences in soil moisture between *Striga*-infested and *Rhamphicarpa*-infested fields. *Striga asiatica* was exclusively observed in high lying fields with free-draining upland soils, while *R. fistulosa* was observed in low-lying wetter fields, ranging from hydromorphic to temporarily flooded soils. This confirms what has previously been described as favourable growing environments of these species (Ouedraogo *et al.*, 1999). In the drier second year of observation, even though both parasitic weeds had extended into fields that had been free of parasites the year before, there was still a clear demarcation between *S. asiatica* and *R. fistulosa* fields. Soil analyses further revealed differences between habitats of each parasitic weed species. CEC and extractable cations such as Ca and Na were markedly higher in *Rhamphicarpa*-infested fields than in *Striga*-infested habitats. This implies that *R. fistulosa* can thrive in more saline conditions, confirming observations of the parasite in briny waters near the sea (Hansen, 1975). Soil OM, N, P, pH and EC were not significantly different between habitats, yet K was markedly higher in *Striga*-infested habitats. The N, P and K values could give an indication of the land use and how farmers respond to these parasitic weeds. Farmers in uplands tend to apply

inorganic fertilisers, while those in lower parts of the catena found this practice unfeasible due to regular floods (M. Saidia, pers. comm.). Prevalence of both parasitic weeds in the area implies that soil N, P, K levels in the study area were generally too low to affect their incidence. There is evidence that N, P, K fertilisation can dramatically affect incidence of *S. asiatica* and *R. fistulosa* (Rodenburg *et al.*, 2011b; Jamil *et al.*, 2013). The lack of exclusivity of the fields in the middle zone in terms of soil characteristics enables it to act as an ecological transition zone that can be prone to either of the two parasitic species, depending on prevailing environmental conditions. Seeds of both species are likely to be present here, but it is the annual specifics of the environmental conditions that determine whether one of the two species will occur or whether the fields remain parasite-free, like in 2012.

The Shannon–Wiener diversity index (H') of the community of weed species observed was high. This indicates that there was a large diversity of species encountered in the study area (Molles, 1948). Crop type, crop sequence and tillage systems have been shown to strongly influence weed community composition (Bastiaans *et al.*, 2008; Bohan *et al.*, 2011). From field observations and informal surveys, it was established that farmers used hand weeding as a weed control measure and had only one cropping season per year.

Although species diversity was similar across habitats (based on H'), weed community composition was

more related to particular parasite habitats. Following cluster analysis, non-parasitic weeds clustered into two major groups that were more closely, but not necessarily exclusively, related to either *S. asiatica* or *R. fistulosa* habitats. Non-parasitic weed species that were exclusive to *S. asiatica* habitats typically are indicator species of less fertile areas and frequently observed as weeds in rain-fed rice systems. For instance *Pennisetum polystachion* (e.g. Akobundu *et al.*, 1999; Kent *et al.*, 2001), *Rottboellia cochinchinensis* (e.g. Ampongnyarko & Dedatta, 1993) and *Mitracarpus hirtus*, syn. *M. villosus* (e.g. Chikoye & Ekeleme, 2001) are well adapted weeds of poor upland soils and marginal habitats. Similarly, non-parasitic weed species that were exclusive to *R. fistulosa* are indicator species of vegetation commonly found in moist areas. *Ammannia auriculata* (e.g. Caton *et al.*, 1997), *Cyperus distans* (e.g. Kent *et al.*, 2001; Rodenburg *et al.*, 2009), *Fimbristylis littoralis* and *Oryza longistaminata* (Rodenburg & Johnson, 2009) are all common weeds of lowland rice.

Differences in sensitivity of the two parasites to moisture were further revealed by results from pot experiments. *Striga asiatica* clearly performed better under drier conditions, while *R. fistulosa* thrived under wetter conditions. In the first experiment, both parasites emerged at all moisture levels but could not always reach maturity when moisture levels were sub-optimal. In the second experiment, *S. asiatica* did not emerge at saturated moisture conditions at all. Of the two species, *R. fistulosa* seemed to have the broadest ecological range, as it was able to produce biomass under each of the four moisture conditions, even the less favourable ones, while *S. asiatica* was unable to produce any biomass under saturated conditions. Weed species with such a broad ecological range are potentially invasive and may spread and adapt to ecosystems beyond the original or most favourable ones (Booth *et al.*, 2010).

The clear demarcation in occurrence and success of each parasite in a specific ecological setting suggests that their niches are strictly separated. In between those two niches is a transition zone, in which seeds of the two species are likely to be present and the prevailing environmental conditions determine the occurrence of either of the two species. The occupation of this transition zone may differ from year to year and might even be largely parasite-free, as was the case in 2012. The occurrence of these parasite-free fields in 2012 could be attributed to the rainfall pattern, with an unusual wet month of May. The high rainfall months might well have resulted in conditions that prolonged preconditioning period critical for *S. asiatica* germination in that year. Some *Striga* species are known to stay dormant when in wet and poorly aerated soil,

only to germinate when conditions get drier (Mohamed *et al.*, 2006). Germination of *Striga* spp. is regulated by specific chemical signals exuded by roots of host plants (Matusova *et al.*, 2004). To be responsive to these chemical signals (germination stimulants), the seeds require a moist environment for a certain preconditioning period at a suitable temperature. Matusova *et al.* (2004) observed that the length of this preconditioning time had a substantial effect on the sensitivity of *Striga* seeds to germination stimulants. The optimum preconditioning period was found to be between 21 and 28 days for *Striga* seeds. Being a drier year, 2013 might well have favoured germination of *S. asiatica* seeds that lay dormant in 2012 or the previous years. A farmer, who owned one of the fields that were parasite free in 2012, claimed that he had never encountered either parasite before 2013, when his field was infested by *S. asiatica*. In 2013, *R. fistulosa* extended into previously parasite-free fields. Extension of this species into previously parasite-free fields could not be clearly explained, but the fact that its coverage was remarkably reduced in the drier year, implies that soil moisture variation, was a likely cause.

The influence of soil moisture on growth and success of the two parasitic species implies that changes in climate and specifically moisture regimes will be crucial for their future prevalence. As impacts of climate change on agriculture now become evident, it is anticipated that weed species' distribution and prevalence within weed and crop communities will be affected (Rodenburg *et al.*, 2011a). Changes in climate are likely to favour parasitic weed species of the Orobanchaceae family (Mohamed *et al.*, 2006), depending on prevailing rainfall patterns or incidences of drought and floods predicted to occur in Africa (IPCC, 2007).

Besides moisture and nutrients, the distribution of *S. asiatica* and *R. fistulosa* is influenced by their hosts. The continuous rice cultivation in the study area sustains the continuity of these parasites, but it is also possible that some of the non-parasitic weed species can be potential hosts. The host range of *Striga* spp. includes cereal crops and grasses of the *Poaceae* family (Johnson, 1997). Of the 17 non-parasitic weed species that segregate along with *S. asiatica* (Fig. 4), eight are of the family *Poaceae*. In the case of *R. fistulosa*, the entire host range has not been confirmed, but wild rice (*Oryza longistaminata*) that was exclusive to *R. fistulosa* habitat is a known host species (Hansen, 1975).

Our results show a clear, non-overlapping, ecological range between *S. asiatica* and *R. fistulosa* niches. This clear separation implies that management strategies can typically be focused independently on one of the two species. For instance, in *Striga* areas, the use of phosphorus and nitrogen fertiliser (Jamil *et al.*,

2011), resistant and tolerant cultivars (Rodenburg & Bastiaans, 2011) or intercropping with legumes (e.g. Van Mourik *et al.*, 2008) can be promoted. In the case of *R. fistulosa*, a lesser-known parasite, more studies are required to find effective control strategies.

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