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Review

Host interactions, pathology, economic impacts and management of the facultative parasitic weed *Rhamphicarpa fistulosa*

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ABSTRACT

Rhamphicarpa fistulosa (Hochst.) Benth., is a facultative parasitic plant causing persistent weed problems in smallholder rice crops across Africa. It was first identified as a rice weed in the 1990's in West Africa. The objective of this review was to comprehensively inform the crop protection research community and extension services on the newly gained insights on *R. fistulosa* since the last review in 2014. Following a systematic literature search in Web of Science on papers published after September 2014, the cut-off date of the last review, the resulting publications are reviewed. Parasitizing *Rhamphicarpa fistulosa* plants gain considerably in biomass and reproductive output, compared to independently growing plants. The host incurs severe reductions in photosynthetic efficiency and biomass production. Host-plant assimilates primarily benefit parasite growth and reproduction. Rice yield losses caused by *R. fistulosa* infestations range from 24 to 73% depending on infestation density and cultivar. Annual crop losses in sub-Saharan Africa were estimated at 204,000 tons of milled rice, with associated annual economic losses of US $82M, affecting >140,000 rural households. Rice cultivars NERICA-L-40 and -31 were identified as resistant and high yielding under *R. fistulosa* infested conditions. Early sowing decreases *R. fistulosa* infection. Contrary to the obligate parasitic weed Striga spp., the facultative *R. fistulosa* is not controlled by fertilisers. The past decade of research generated valuable insights in the genetics, germination biology, environmental and ecological contexts, distribution and impacts on crop yields and economies, and disclosed feasible management options.

1. Introduction

Weeds constitute important production constraints to rice (Waddington et al., 2010), in particular in Africa (Niang et al., 2017; Senthilkumar et al., 2020). One of the unique features of African rice production systems is the prominence of parasitic weeds among weed communities (Rodenburg et al., 2022). This group of weeds comprise plants that parasitise on other plants. Parasitic plants have a specialised organ called haustorium that enables the attachment to the host and penetration into host-plant vascularity which facilitates the flow of water, nutrients and assimilates from the host to the parasite (Joel, 2013).

The prominence of parasitic weeds in African rice can be explained by the distribution of weedy root-parasitic plant species that favour monocotyledonous hosts, many of which are endemic to the African continent (Hansen, 1975; Mohamed et al., 2001). Another important reason is that around 70% of the area under rice production in Africa relies fully on rainfall for water supply (Diagne et al., 2013). These rainfed rice growing environments are habitats of parasitic weed species. Free-draining arable soils in Africa favour species of the *Striga* genus (Cochrane and Press, 1997; Dugje et al., 2006), whereas water-logged soils are typical environments where *Rhamphicarpa fistulosa* thrives (Ouédraogo et al., 1999). Although some ecological plasticity has been observed and reported (Cochrane and Press, 1997; Ouédraogo et al., 1999), *Striga* spp. is mainly restricted to rainfed upland rice and *R. fistulosa* to rainfed lowland rice (Kabiri et al., 2015). Another important difference between these two parasitic weeds is the nature of their parasitism (Rodenburg and Bastiaans, 2024). Striga species are obligate root hemi-parasitic plants whereas *R. fistulosa* is a facultative root parasitic plant. Seeds of obligate parasites only germinate when they perceive the vicinity of a host root (based on biochemical signals) and then require a timely viable connection to the host, by means of terminal and lateral haustoria (Joel, 2013). Facultative parasites start their life-cycle as any autotrophic plant and turn into parasites when

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their roots come into contact with roots of a suitable host and form a connection through lateral haustoria (Neumann et al., 1998).

Rhamphicarpa fistulosa (Hochst.) Benth., known under the common name rice vampireweed, comprises a relatively new, or at least overlooked, weed problem in Africa. While this species was first reported as a parasitic weed in rice about 90 years ago in Madagascar (Bouriquet, 1933), and relatively soon thereafter in West Africa (Mallamaire, 1949), reports on this species were only followed by others about five decades later (e.g. Cissé et al., 1996; Johnson et al., 1998; Ouédraogo et al., 1999; Gworgwor et al., 2001), all from West Africa. Surveys among rice farmers in inland valleys in Benin conducted in 1998 (Gbèhounou and Assigbé, 2003) and repeated in 2007/2008 (Rodenburg et al., 2011), clearly indicated a progressive spread of *R fistulosa* into new rice growing areas. While farmers lacked knowledge on effective management strategies against this weed, agricultural extension services were generally unaware of the problem. These observations led to intensified research on *R. fistulosa* and a review paper published in 2015, presenting the then contemporary status of knowledge on this weed species (i.e., Rodenburg et al., 2015). In the current article we present how our understanding since that review has evolved. The objective of this article is to summarize the advancements in knowledge regarding *R. fistulosa* and outline future research areas.

2. Literature search

A search in Web of Science was conducted on 14 March 2024, using the following search terms: “Rhamphicarpa fistulosa” OR “Rhamphicarpa” OR ″R. fistulosa” OR “rice vampireweed” or “rice vampire weed” OR “vampireweed” OR “vampire weed”, with a publication date range from September 17, 2014 (acceptance date of: Rodenburg et al., 2015) till the date of search (March 14, 2024). This resulted in 19 publications, published over 4 broad topic areas (1. Parasite biology, ecology and host interactions, 2. Crop yield and economic impact, 3. Agronomic management practices and 4. Institutional and innovation system context) in 11 different journals (Table 1). Three papers were excluded from this selection, as it included the 2015 review itself, as well as a paper by Kabiri et al. (2015) published in the same issue and a paper by Schut et al. (2015b), that were both already referred to in the 2015 review. Hence a total of 16 papers were discussed in the current review (out of a total of 32 in Web of Science).

Table 1
Results of a systematic literature search conducted in Web of Science, using search terms “Rhamphicarpa fistulosa” OR “Rhamphicarpa” OR ″R. fistulosa” OR “rice vampireweed” or “rice vampire weed” OR “vampireweed” OR “vampire weed” and publication date range: 17-09-2014 to 14-03-2024. Papers are categorised in four different subject areas, whereby some papers cover more than one subject area.

Subject area	Journals	References
Parasite biology, ecology and host interactions	*J. Plant Physiol.*; *Weed Res.*; *Acta Oecol.*; *Plant Dis.*; *Ann. Appl. Biol.* (2), *Ann. Bot.*	(Houngbedji and Gibot-Leclerc, 2015; Houngbedji et al., 2016, 2020; Kabiri et al., 2016, 2017, 2021; Zossou et al., 2016; Rodenburg et al., 2023)
Crop yield and economic impact	*Cah. Agric.*; *Field Crop Res.*; *Agr. Econ.*; *Agr. Ecosyst. Environ.*	(Houngbedji et al., 2014; Rodenburg et al., 2016a; Rodenburg et al., 2016b; N'Cho et al., 2019)
Agronomic management practices	*Agr. Econ.*; *Crop Prot.*; *Field Crop Res.* (3)	(Rodenburg et al., 2016a; Tippe et al., 2017a; Tippe et al., 2017b; N'Cho et al., 2019; Tippe et al., 2020)
Institutional and innovation system context	*Crop Prot.* (2)	(Schut et al., 2015a; Tippe et al., 2017a)

3. Parasite biology, ecology and host interactions

We will describe first the new insights in *R. fistulosa* biology and ecology, since 2015. Then new insights in host interactions are outlined, starting with how *R. fistulosa* depends on, or benefits from, presence of a host plant, and then how the host plant is affected by *R. fistulosa* parasitism.

Edaphic and weed ecological associations are studied by Houngbedji et al. (2016, 2020) in northern Togo. During two cropping seasons weed communities of a total of 66 lowland rice fields were surveyed across a range of *R. fistulosa* infestation levels, including absence of this species. A total of 122 different weed species were observed in these lowland sites. Correcting for geographic position of survey sites, this study observed a significant influence of *R. fistulosa* presence and abundance on weed community composition, but not species richness (Houngbedji et al., 2016). Certain weed species were specifically associated with presence or absence of *R. fistulosa*. Previously, Kabiri et al. (2015) observed weed species that were exclusively found in (lowland) *R. fistulosa* habitats as well as species that were present on site (observed higher up the catena) but absent in *R. fistulosa* infested fields. This was however thought to reflect the ecological niches of species rather than a species selection effect caused by the parasite. The weeds observed in *R. fistulosa* infested fields were species that prefer water-logged conditions, whereas the other weeds are known to thrive on free-draining soils where *R. fistulosa* is absent.

The same sites in northern Togo surveyed by Houngbedji et al. (2016) for weed communities were also characterised based on soil texture and soil chemical traits (Houngbedji et al., 2020). Soils with medium to high *R. fistulosa* infestation levels appeared to be composed of a higher percentage of course sand, which corroborated earlier reports from Benin by N'cho et al. (2014). These infested soils also had higher potassium (K) contents and pH levels than soils where *R. fistulosa* was not observed. In a study in Tanzania by Tippe et al. (2020), positive correlations were observed between exchangeable potassium content of the soil and *R. fistulosa* plant numbers, which seems to confirm this relation. Houngbedji et al. (2020) observed no correlation between *R. fistulosa* infestation and soil organic carbon (or organic nitrogen) contents, whereas Tippe et al. (2020) also found a positive correlation between *R. fistulosa* numbers and soil organic matter content.

Zossou et al. (2016) observed *R. fistulosa* in a mountainous area in Senegal, which was environmentally distinct from the typical wetland that was identified (by Kabiri et al., 2015) or described (by Hansen, 1975) as the species' preferred and dominant habitat. Earlier reports by Gbèhounou and Assigbé (2003), who observed it at hill tops in Benin, and Rodenburg et al. (2015), who observed it in free-draining uplands in Uganda, also demonstrate that *R. fistulosa* can occur outside their dominant habitat. In that case, it could also become a weed of other crops types than lowland rice, including maize (Rodenburg et al., 2015) and sorghum (Ouédraogo et al., 1999), but potentially also non-cereal crops such as cowpea (*Vigna unguiculata* [L.] Walp.) (according to an unconfirmed report in Kuijt, 1969) and groundnut (*Arachis hypogaea* L.) and soybean (*Glycine max* [L.] Merr.) which have been observed to be infected by the parasite (Houngbedji and Gibot-Leclerc, 2015).

Genetic diversity in populations of *R. fistulosa*, from Benin and Senegal, was explored by Zossou et al. (2016). They collected 180 specimen of *R. fistulosa* from 60 sites in two West African countries (30 from Benin, 30 from Senegal) and screened these on polymorphic loci enabling the identification of genetically coherent groups. High genetic diversity has been observed among the specimen. Four distinct genetic groups were identified, but although genetic diversity was observed between populations of both countries, these groups were not exclusively associated with a specific agroecological zone or location and therefore not classified as distinct ecotypes. Within a specific location or zone, representatives of more than one genetic group were found (Zossou et al., 2016).

Parasitism appears to be of pivotal importance for the fitness of a

R. fistulosa plant and consequently for maintenance or expansion of a population. Compared to independently growing *R. fistulosa* plants, parasitizing a host results in a doubling of the parasite biomass (Kabiri et al., 2017) and a near 4-fold increase of parasite seed production (weight), with mean seed size increases of 15% (Kabiri et al., 2016). Part of the advantage the parasite derives from a host plant is thought to be through the extraction of host plant assimilates, similar to the obligate parasitic plant *Striga* (Press et al., 1991). For *R. fistulosa* plants, another advantage of parasitism seems to be the increased uptake capacity of plant nutrients from the soil, as shown by Rodenburg et al. (2023). Independently growing *R. fistulosa* plants hardly respond to changes in plant available nutrients but when attached to a host plant the parasite biomass increases proportionally with an incrementing nutrient supply (Rodenburg et al., 2023). *Rhamphicarpa fistulosa* has a rather small and undeveloped root system and by parasitizing a host plant it exploits the root system of the host and thereby increases the uptake potential. Being a facultative parasite, seed germination was assumed to be possible without the presence of a host. This was indeed confirmed in lab studies (Kabiri et al., 2016). Interestingly, however, despite the aforementioned clear fitness benefits from host parasitism, the presence of a host showed also no stimulatory effect on *R. fistulosa* germination. Contrary to *Striga hermonthica* seeds, that only germinated upon contact with specific types of host-derived or synthetic germination stimuli (see for instance also: Yoneyama et al., 2010; Jamil et al., 2012), *R. fistulosa* seeds germinated equally successfully when exposed to root exudates of rice varieties that did not contain these compounds and even to plain water (Kabiri et al., 2016). Further tests confirmed that *R. fistulosa* seed germination requirements were abiotic, rather than biotic of nature. Preconditions to successful germination are water-saturated soils and exposure to light (Kabiri et al., 2016). This last prerequisite ensures that only seeds near the soil surface will germinate, which is considered a sound ecological adaptation following the small seed size of the parasite (11 μg/seed).

The first sign of *R. fistulosa* effects on the host, soon after the start of parasitism, appears to be an increase of the root to shoot biomass ratio. Next, the leaf area of parasitised host plants is reduced and the concurring reduction in light interception occurs before a reduction in light use efficiency (Kabiri et al., 2017). Host photosynthesis is severely reduced by parasitism, and interestingly, this occurs well before the reduction in light use efficiency too (Kabiri et al., 2021). A range of associated leaf-level physiology parameters was seriously negatively affected by parasitism too. Among the leaf level parameters measured, only dark respiration was unaffected (Kabiri et al., 2021). The aforementioned increase of the root:shoot ratio stems from a steeply reduced shoot biomass (up to 71%) associated to reductions in plant height, leaf area and tiller numbers. The host root biomass also reduces upon infection, but this reduction is much lower than that in shoot biomass (Rodenburg et al., 2023). At the individual host-plant level, relative grain production losses caused by parasitism ranged from 92% to 98% depending on infestation level, i.e. from 11.3 g without the parasite to 0.88 g with 6 parasites and 0.22 g with 13 parasites (Kabiri et al., 2017).

The timing of host-derived benefits to the parasite and parasite-induced effects on the host appeared not to be synchronised (Fig. 1). Around 5–6 weeks after rice sowing (WAS) *R. fistulosa* plants start to visibly grow more vigorously than plants growing without a host, indicating the start of parasitism. It takes another two to three weeks however, for this difference in parasite biomass between parasitizing and independently growing plants to become consistently significant. Some early effects on the host plant, on the other hand, are already significant within the first week after the start of parasitism, as the root: shoot ratio of host plant biomass is significantly higher in infected compared to parasite-free rice plants around six weeks after sowing. Exhibition of consistent negative effects on host plant photosynthesis start around 8 WAS (Kabiri et al., 2021). Around a week later (9 WAS), biomass accumulation of host plant comes to a complete standstill, while biomass accumulation of the parasite continues.

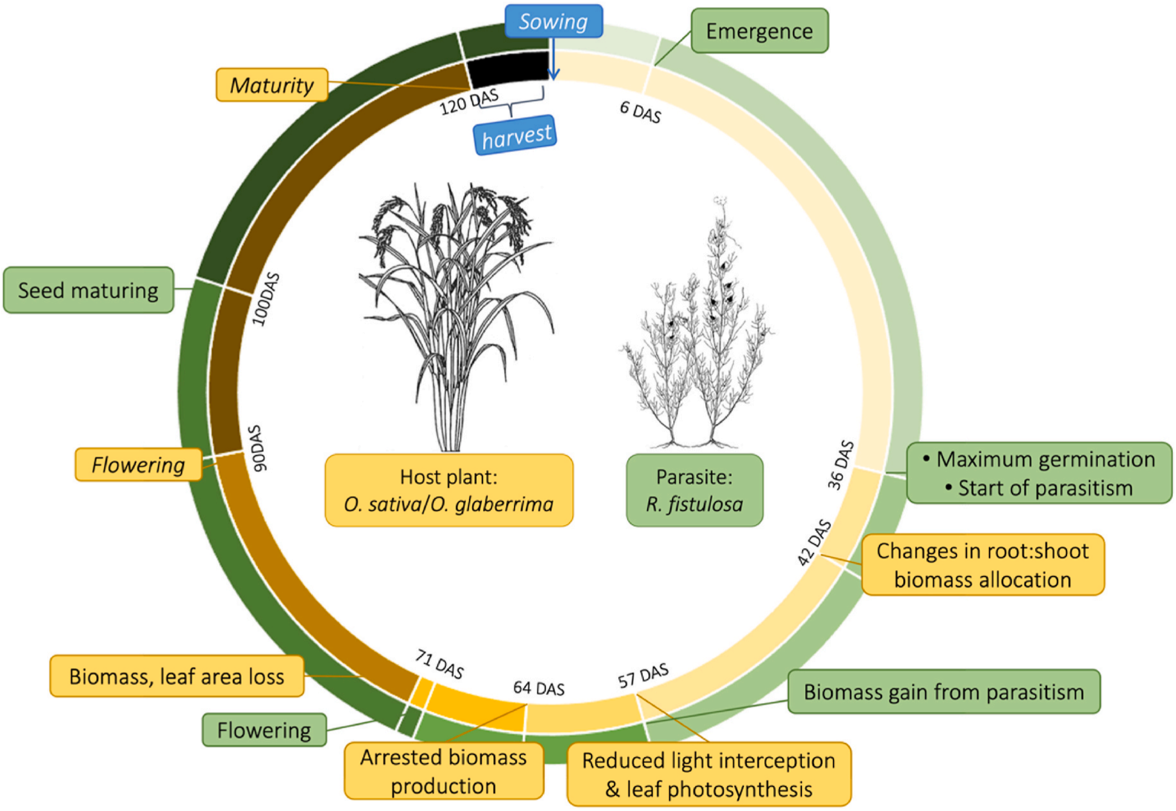
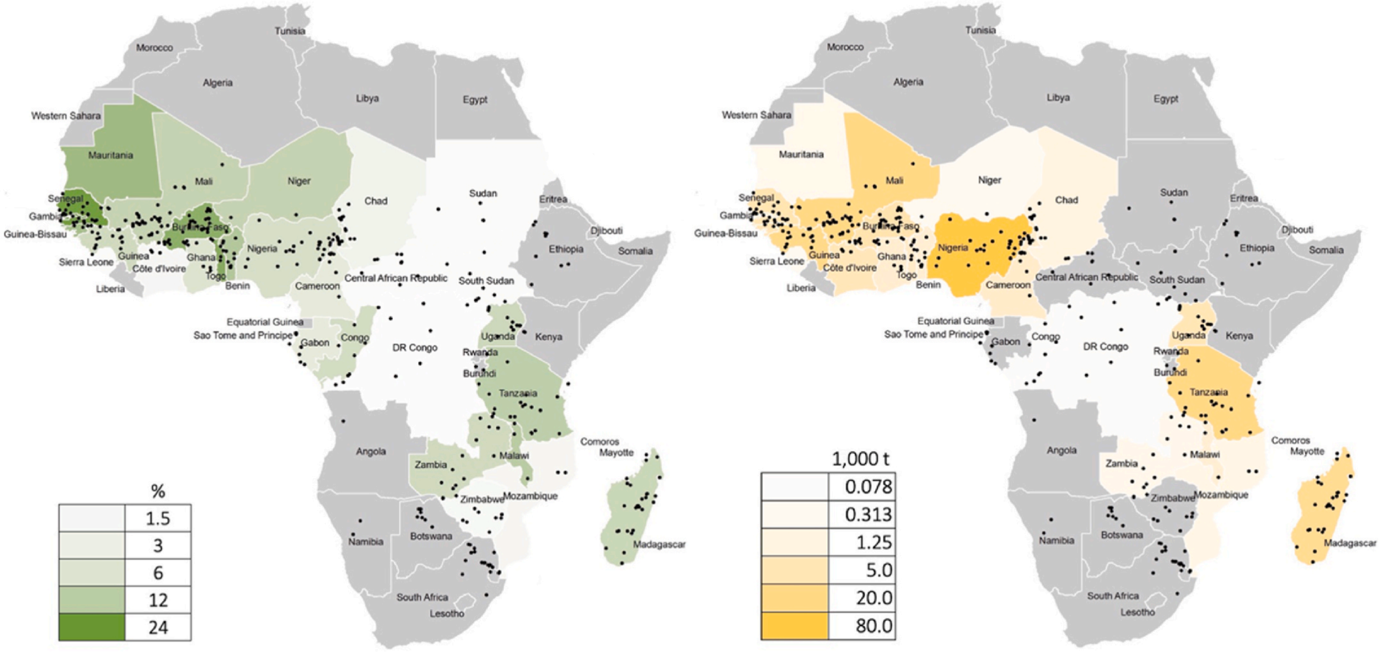


Fig. 1. Circular timeline (clockwise) of the parasite, rice vampire weed (*Rhamphicarpa fistulosa*; in pale to dark green) and the host, rice (*Oryza sativa or O. glaberrima*; in yellow to brown) from rice sowing to rice harvest. Time is expressed in days after sowing (DAS). Based on data reported in Kabiri et al. (2016, 2017, 2021).



A. *Rhamphicarpa fistulosa* incidence (% of rainfed rice area infested)

B. *Rice grain production losses caused by R. fistulosa per country*

Fig. 2. Country-level estimates of incidence (%) of *Rhamphicarpa fistulosa* in rainfed rice (A) and concomitant (milled) rice grain production losses (in tonnes) incurred by *R. fistulosa* infestation (B). Source: (Rodenburg et al., 2016b).

4. Crop yield and economic impact

The above-described parasite effects on host plant physiology and morphology have severe negative effects on crop yields. While, based on the above, a complete crop failure would be a possible outcome, this would only occur under blanket (homogeneous and high) infestation levels. In an actual crop situation that would not often be the case, as infestations are commonly rather heterogeneous within a crop field. Yield losses could nevertheless be high and persistent enough for farmers to decide to abandon their field, as reports from Benin and Togo demonstrate (Rodenburg et al., 2011; Houngbedji et al., 2014).

Based on three years of assessments in Tanzania, with a large number (64) of rice cultivars and against seasonally varying infestation levels, parasite-induced yield losses range from 24 to 73%, with a mean of 50% (Fig. 3; Rodenburg et al., 2016b). Model estimates of rice yield losses, based on a large sample of farm surveys, range from 21%, in Côte

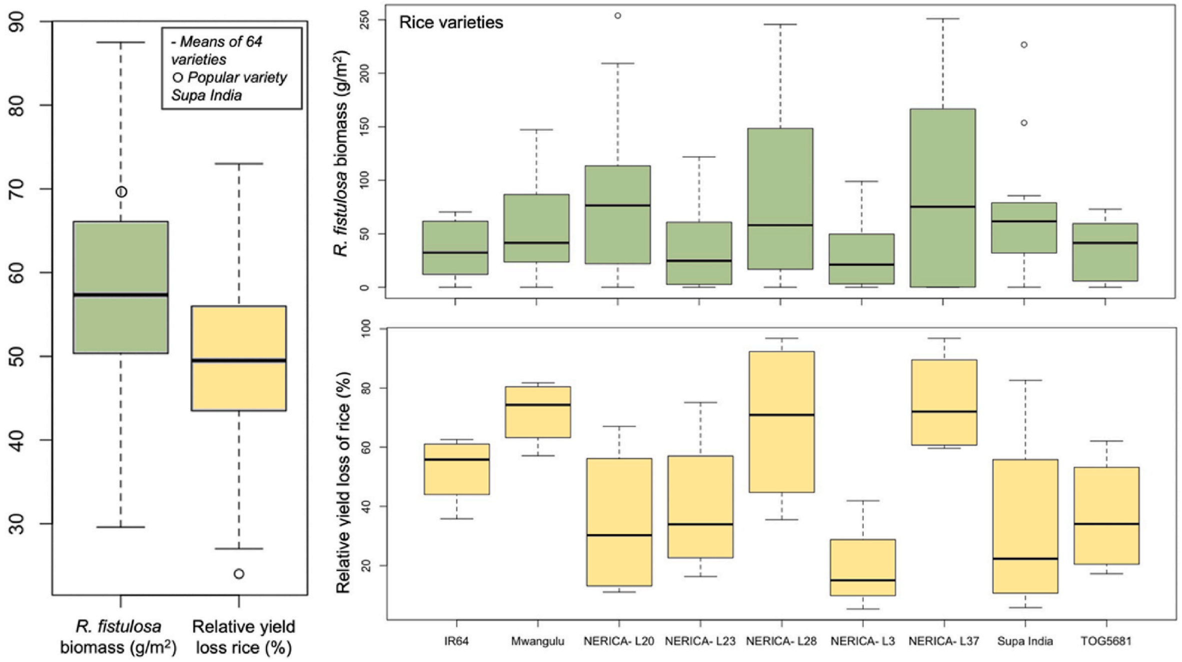


Fig. 3. Range of *R. fistulosa* biomass (g/m^2) and relative yield losses (%) of rice (left pane) across all 64 rice cultivars screened, and across a selection of these cultivars (top right and bottom right panes, respectively). Source: (Rodenburg et al., 2016b).

d'Ivoire to 50% in Benin (N'Cho et al., 2014), whereas farmers themselves overwhelmingly perceive yield losses to exceed 60% (Rodenburg et al., 2011).

The above yield loss estimates, whilst variable, demonstrate that the impact from *R. fistulosa* infestation at the crop level is substantial. These estimates are however available from a rather limited number of locations, which sharply contrasts with the wide distribution of the species across the continent. Based on public, mostly online, geo-referenced herbaria specimen and observations in published reports, *R. fistulosa* is found in at least 35 countries in Africa (Rodenburg et al., 2015) with 28 of them harbouring rainfed lowland rice areas, the production environment where this species can develop into a serious agronomic weed problem. These geographical references were superimposed on a composite and high-resolution rainfed rice map of the region to assess the extent of overlap and calculate infestation likelihoods (Fig. 2A and B). Based on this the area infested by *R. fistulosa* was estimated at 6% of the rainfed lowland area under rice, equating to around 225,000 ha (Rodenburg et al., 2016b) and affecting an estimated 140,000 farm households (based on number of households depending on rainfed lowland rice environments estimated by Diagne et al., 2013). Countries with the highest estimated infestation rates were The Gambia, Senegal, Burkina Faso, Togo and, to a lesser extent, Mauritania, Guinea-Bissau, Benin, Malawi and Tanzania (Fig. 2A). This information combined with yield loss estimates and rice production statistics formed the input of a stochastic impact assessment model. Following this exercise, Africa-wide impact of this parasitic weed was estimated to be 204,000 tons of (milled) rice grain losses, worth US $82 million (Rodenburg et al., 2016b). By far the hardest hit country, in terms of production losses, is Nigeria (80,000 tons). Other countries with important grain production losses are Mali (21,000 tons), Guinea and Tanzania (nearly 20, 000 tons) and Madagascar (15, 000 tons; Fig. 2B). It is important to note that these impact figures are only available for rice. *Rhamphicarpa fistulosa* however also parasitises on sorghum (Ouedraogo et al., 1999) and maize (Rodenburg et al., 2015), and potentially other cereal crops. Although infestation in other crops does not seem to be as common as in rice, the total economic losses inflicted by this weed are likely higher. In addition, alongside a projected increase in infestation area (by an estimated annual increase of 2%), the economic impact is expected to increase by an estimated US $12 million per year (Rodenburg et al., 2016b).

5. Agronomic management practices

An important knowledge gap concerned ways in which farmers can manage *R. fistulosa* infestations. At the time of the first review (i.e., Rodenburg et al., 2015), herbicides and hand weeding were identified as the only two options that farmers could employ. Both options, would be feasible and effective as Kabiri et al. (2017) has shown that parasitism usually does not start before five weeks after sowing, giving the farmer a fair control window. However, current farmer practices do not seem to be efficient. Surveys conducted on a large number of farms (406) in Benin and Côte d'Ivoire, show that farmers invest more time in (hand) weeding than justified by the gain in crop productivity (N'Cho et al., 2019). A survey from Togo shows that farmers are using sub-optimal rates of herbicides (Houngbedji et al., 2014) which very likely results in sub-optimal control. In addition, a continent-wide study among rice farmers have shown a low diversity (in terms of product range) and quality (in terms of certification) of herbicides at rural agrochemical supply markets, and ill-informed farmers leading to incorrect product choices and application timings (Rodenburg et al., 2019). Therefore, other management practices were explored that would better suit smallholder farmers, implying less labour, capital or knowledge intensive input levels.

As indicated above, the extent of yield losses caused by *R. fistulosa* depends on the rice cultivar. Among rice cultivars there appears to be a great deal of variation in yield losses and this observation could inform the best choice of cultivar to be grown on *R. fistulosa* infested soils (Fig. 3; Rodenburg et al., 2016b). Sixty-four rice cultivars, including all 60 lowland NERICAs, their parents (IR64 and TOG5681) and two locally popular checks, were screened during three cropping seasons in a *R. fistulosa* infested field in southern Tanzania (Rodenburg et al., 2016b). Fig. 3 shows a selection of 9 contrasting cultivars as illustration of the range of resistance and tolerance levels across these 64 cultivars. The screening identified cultivars that were more resistant to *R. fistulosa* infection, expressed as significant lower parasite biomass (e.g., NERICA-L-3 and -23), as well as more tolerant to *R. fistulosa* parasitism, expressed as low relative yield loss despite high infection levels (e.g., NERICA-L-20 and local check Supa India). The low relative yield losses observed with NERICA-L-3 and -23, and to a latter extent TOG5681 could partly be explained by their relative lower infection levels resulting from their higher resistance against the parasite. These cultivars would make good material for breeding programmes (aiming to introgress these individual traits into lines with high-yield potential). Cultivars that were generally high yielding, presumably resulting from high inherent yield potential combined with effective resistance and/or good levels of tolerance, were also identified (e.g., NERICA-L-39 and -20).This group of cultivars would be most interesting for direct use by farmers (in particular the ones exhibiting good resistance). Choosing high yielding rice cultivars with effective resistance and tolerance against *R. fistulosa* could be considered the first line of defence.

Apart from the choice of cultivar, farmers could adjust their sowing times. To investigate this option, a field experiment was conducted in an *R. fistulosa* infested farmer's field in Tanzania whereby rice was sown at five different dates, each with a 2-week interval. The timing of crop establishment was shown to have a significant effect on *R. fistulosa* biomass as well as rice yields (Fig. 4; Tippe et al., 2017b). Fig. 4 shows the results of this experiment in one of the years, with increasing parasite biomass and decreasing rice yields over time. *Rhamphicarpa fistulosa* parasitism starts around 7 weeks after its germination (Fig. 1). Establishing the crop at or before conditions for *R. fistulosa* germination are optimal would make best use of this lag time. Maximizing this time advantage will also increase the shading effect of the crop, which is expected to hinder the parasite growth. The earlier the rice is sown the longer the parasite-free period and the lower the parasite effects will be. This is also reflected by the higher rice grain yields at the earlier sowing times (Fig. 4).

Whether fertilisers could be employed as management option against *R. fistulosa*, as often suggested against *Striga* spp., was the leading research question of another study (Tippe et al., 2020). In two nearby experiments, one in an upland field with *Striga asiatica*, and one in a lowland field with *R. fistulosa* infestation, comprising similar set-ups and treatments, mineral fertilisers (NPK or DAP), locally sourced organic soil amendments (rice husks or cattle manure) and combinations of organic fertilisers with half the dose of mineral fertilisers were tested. While *S. asiatica* was suppressed by fertilisers (most effectively by NPK or DAP and urea), the opposite response was observed with the facultative *R. fistulosa* (Fig. 5; Tippe et al., 2020). Fig. 5 presents the results obtained in one of the years showing a range of *R. fistulosa* infection levels. Compared to the no-fertiliser control treatment, parasite biomass generally increased after fertiliser application, in particular when mineral fertiliser was combined with organic soil amendments. From a crop production perspective fertiliser application would however still be interesting as rice productivity increased with fertilisers, despite associated increased *R. fistulosa* infestations. The use of rice husks, or cattle manure with half the recommended level of DAP and urea, proved good and affordable options in that regard (Fig. 5). Rice husks (with or without DAP and urea supplementation) was also the preferred soil fertility amendment among *R. fistulosa* affected lowland rice farmers in Tanzania (Tippe et al., 2017a). In follow-up experiments, under more environment-controlled greenhouse conditions, the stimulating effect of (mineral) fertilisers on *R. fistulosa* plants was confirmed but the parasite could only benefit from the increased nutrient availability when they

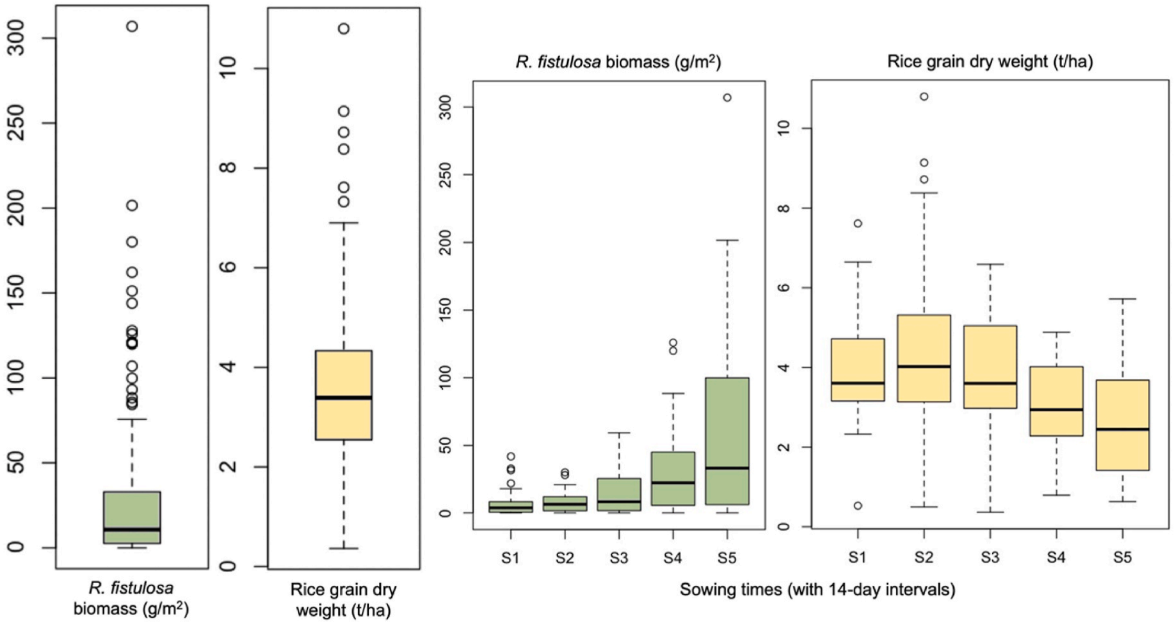


Fig. 4. Range of *R. fistulosa* biomass (g/m^2) rice yields (t/ha) obtained across sowing times (S1–S5; with 2 week intervals) and (left two box plots) and for each specific sowing time (right two panes). Source: (Tippe et al., 2017b).

were parasitizing a host (Rodenburg et al., 2023). Biomass accumulation of independently growing *R. fistulosa* plants remained at the same level across nutrient application treatments. Also, across nutrient application treatments the total biomass accrued by host and parasite together was always lower than that of the parasite-free host plants (Fig. 5B; Rodenburg et al., 2023).

The above management practices alone and in combination were also tested on farms with farmers. Based on these tests and evaluation of farmers' preferences, the combination of early sowing, the late maturing but parasite-tolerant traditional cultivar Supa India and the application of rice husks with half the recommended level of DAP fertiliser as soil amendments would comprise a potentially effective and suitable integrated *R. fistulosa* management approach (Tippe et al., 2017a).

Clearly the number of effective prevention methods against the facultative parasitic weed *R. fistulosa* is small, in particular compared to the range of options to prevent infection by the obligate parasitic weed Striga spp. (Rodenburg and Bastiaans, 2024). On the other hand, while Striga spp. can only be addressed by preventive measures, the life-cycle of *R. fistulosa* also offers a window for curative weed management. Depending on availability of resources and access to agrochemical supply markets, the use of post-emergence herbicides could for instance be considered. Good results have been obtained with 2,4-D (Ouédraogo et al., 2017).

6. Institutional and innovation system context

The above findings illustrate that tangible *R. fistulosa* control options are available. However, farmers have varying awareness of control options. In Benin, farmers and even agricultural extension services had very limited ideas on how to control this parasitic weed, apart from hand weeding and herbicide application (N'Cho et al., 2014). Here, most of the affected farmers are women who are also often obliged to work in the more marginal rice growing locations. In Tanzania, in a district (Kyela) where *R. fistulosa* infestations were found adjacent to *S. asiatica* infested fields, and where influence of past research and extension was notable, farmers had knowledge of a wide range of control options, whereas in more remote district (Songea), where *R. fistulosa* was the only parasitic weed, farmers had a much more limited understanding on how to address this parasitic weed (Tippe et al., 2017a). Even when farmers were aware of control options, such as in Kyela (Tanzania), a range of obstacles prevented these farmers from implementing this knowledge. Most important constraints to the application of control options, perceived by farmers, were the high costs and/or the lack of local availability or a lack of actual technical knowledge on the correct application of required inputs. These obstacles were mainly associated with herbicide use and corroborates findings of an African wide study on herbicide availability and use by rice farmers (Rodenburg et al., 2019). Limited access or availability of seeds, was mentioned as an obstacle for the use of resistant or tolerant rice cultivars, and transport challenges were preventing farmers from using organic soil amendments (Tippe et al., 2017a). The above shows that the technical questions regarding *R. fistulosa* management are only part of the challenge that needs to be resolved. The remainder of this parasitic weed challenge is comprised of constraints at the institutional or even political level, as was already observed by Schut et al. (2015b). A study conducted on this type of constraints, among *R. fistulosa* (and *Striga* spp.) affected rice farmers and associated actors and organisations in Benin and Tanzania demonstrated that the majority of constraints to (and opportunities for) innovations were related to the general functioning of the crop protection, or even agricultural, systems in place in these countries (Schut et al., 2015a). These kinds of constraints would need to be addressed to improve parasitic weed control at the farm level. Among the most important generic constraints to successful implementation of *R. fistulosa* management are (farmers') access to credits, information and training, and quality inputs (Schut et al., 2015a). These access issues were also identified by other studies conducted among *R. fistulosa* affected rice farmers in Benin (N'Cho et al., 2014) and Tanzania (Tippe et al., 2017a). Improving collaboration (among farmers, agricultural extension and crop protection services) and raising awareness of both the problem and potential solutions, were identified as two of the main opportunities for improved parasitic weed management at the local level.

7. Future research

The host range of *R. fistulosa* is still not completely established. Houngbedji and Gibot-Leclerc (2015) reported field observations with jute mallow (*Corchorus olitorius* L. also known as tossa jute), soybean, and groundnut plants being infected by this parasite. This could be

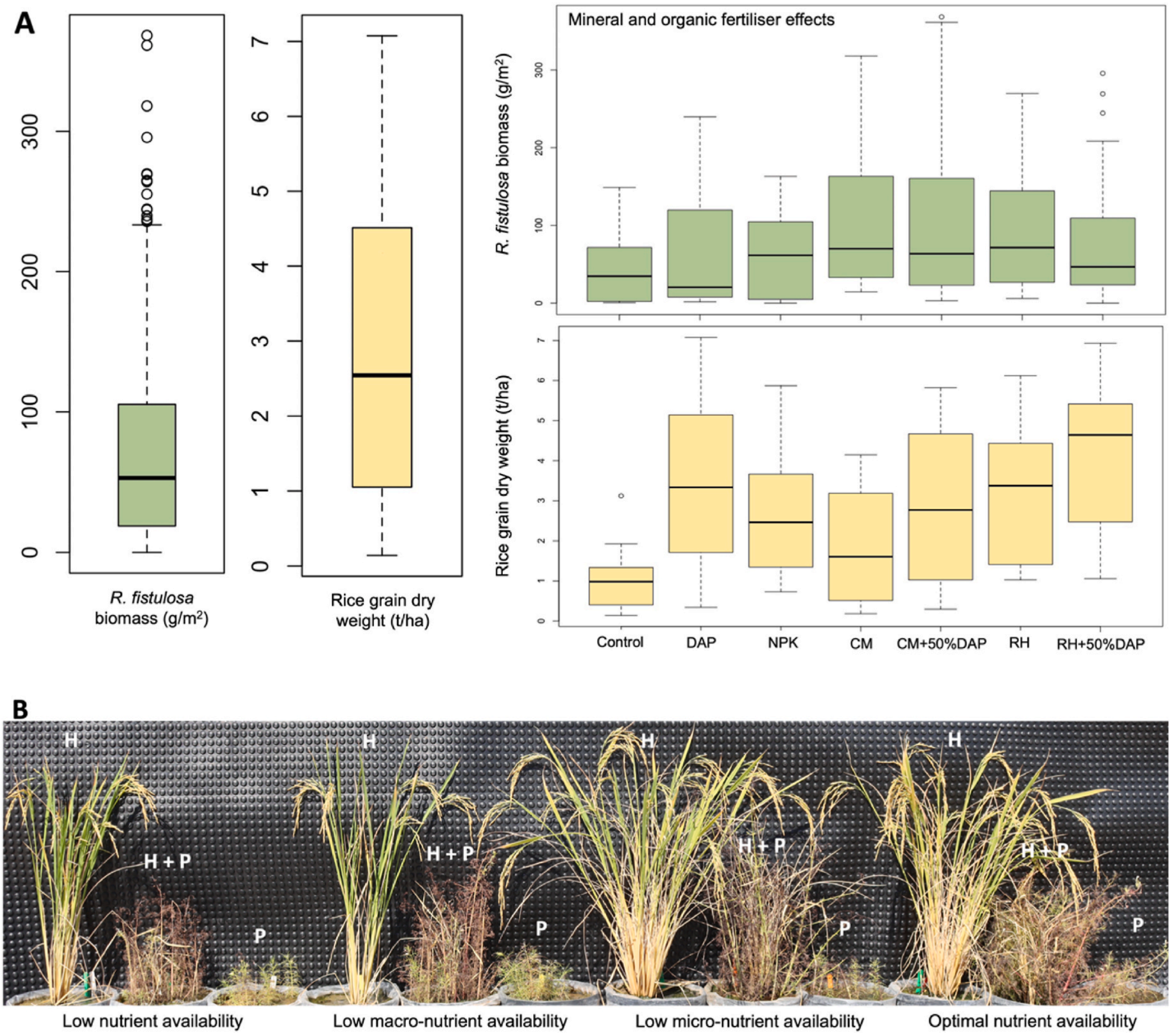


Fig. 5. Range of *R. fistulosa* biomass (g/m^2) and rice yields (t/ha) obtained across fertiliser treatments (A: left two box plots) and effect of mineral (DAP + urea or NPK) and/or organic (cattle manure, CM; rice husks, RH) fertilisers on *Rhamphicarpa fistulosa* biomass and rice yields (A: right upper and lower box plots, respectively) and effects of nutrient availability on the parasite with (H + P) and without (P) a host and on the host, with and without (H) the parasite (B). (Source for 5B: Tippe et al., 2020; Rodenburg et al., 2023).

confirmed *in vitro* and, more importantly, expanded to explore the wider range of host plant species. Apart from the question whether *R. fistulosa* is able to attach and parasitise a particular host plant species outside the current range of known hosts, it would need to be investigated whether host preference could be established as well. Can *R. fistulosa* obtain similar fitness advantages from different host species, or is there a differentiation therein? In a recent greenhouse experiment with rice and maize, the *R. fistulosa* plants parasitizing maize were clearly more robust and accumulated more biomass than those parasitizing rice (Rodenburg, personal observation). This would indicate that parasite fitness is indeed host-plant dependent. Also, is *R. fistulosa* virulence host-plant species dependent or not? In other words does it have similar effects on different host plant species (across a range of genotypes) or are there clear differences between species. An additional question that would merit further research is whether specific ecotypes of *R. fistulosa* exist and whether there are virulence differences between these ecotypes. For other parasitic weed species, e.g., *Striga gesnerioides* (Lane et al., 1996), *Alectra vogelii* (Riches et al., 1992) and *Phelipanche ramosa* (Stojanova et al., 2019), distinct races (ecotypes or strains) have been identified. Zossou et al. (2016) identified the existence of different genetic groups within specimen collected in Benin and Senegal (both West Africa), but were cautiously avoiding to label them as different ecotypes because different groups were identified within the same location. Field observations point at differences in colour and robustness between *R. fistulosa* plants in West Africa and in East Africa, with populations observed in East Africa comprised of (possibly more) robust plants turning red brown upon maturity, whereas those in West Africa stay green (Rodenburg, personal observation). This could indicate the existence of different races (ecotypes), but could also be driven by differences in edaphic conditions or host plant genotype.

Answers to the above questions would provide valuable clues for location specific and cropping-system specific management recommendations. For instance, would crop rotations or intercropping, where possible given the hydrological field characteristics, be a potential management option and with which crop species? Would management recommendations, for instance regarding cultivar choice, need to be adapted to a particular ecotype or would more generic recommendations suffice? Based on their finding of genetic diversity within *R. fistulosa* populations, Zossou et al. (2016) already suggested to study whether this also implies a diversity in virulence, that could potentially complicate the recommendations towards the use of resistant rice cultivars.

Whilst a number of low-input management options have been identified (most promisingly: resistant/tolerant cultivars and early crop establishment), more research would be warranted to broaden the range of feasible options and to investigate effective integrated management strategies combining these options. Based on the light requirements for seed germination, any soil tillage or soil coverage measures that prevent seed exposure to light could be explored as potential additional *R. fistulosa* management option. Inversion tillage, burying *R. fistulosa* seeds at depths where light does not infiltrate would be effective. Given the short seed longevity and the waterlogged soil conditions during the season, seeds that are buried are not likely to remain viable until the next inversion tillage when they are unintentionally but unavoidably be brought closer to the surface again.

The relation between *R. fistulosa* germination and growth and (soil) exchangeable potassium or soil pH levels could be further explored, following findings by Houngbedji et al. (2020) and Tippe et al. (2020). But also relations with other nutrients (including micro-nutrients) and soil chemical traits could be more systematically investigated as these could potentially lead to improved fertiliser recommendations for *R. fistulosa* affected farmers, with potential changes in composition, timing and delivery, resulting in reduced overall input requirements.

8. Conclusions

In the past three decades, a steep increase in problems with the facultative parasitic weed *Rhamphicarpa fistulosa* in rainfed lowland rice systems in Africa has been observed. Research on this species has only really picked up during the past ten years. These recent research efforts have generated many valuable insights in the genetics, germination biology, environmental and ecological contexts. Moreover, these studies have shown how widespread the distribution of the species is and to what extent it impacts crop yields at farm levels and production and economies at the national and regional level. It has been shown that problems with *R. fistulosa* in smallholder rice systems are embedded in the wider crop protection and agricultural systems of the affected countries, showing that resolving this problem requires improvements in stakeholder communications and collaborations as well as in institutional and political arrangements. Importantly, for affected smallholder farmers a number of feasible and affordable control options are identified, such as resistant/tolerant cultivars and recommendations for early crop establishment. Future research would need to increase the range of control measures for affected farmers and also investigate necessary local applications, adaptations and combinations of these measures.

CRediT authorship contribution statement

Jonne Rodenburg: Writing – review & editing, Writing – original draft, Visualization, Funding acquisition, Conceptualization. **Lammert Bastiaans:** Writing – review & editing, Writing – original draft, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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References

Bouriquet, G., 1933. Une Scrophulariacée parasite du riz à Madagascar. Revue de Pathologie Végétale et d'Entomologie Agriculture de France 20, 149–151.

Cissé, J., Camara, M., Berner, D.K., Musselman, L.J., 1996. *Rhamphicarpa fistulosa* (Scrophulariaceae) damages rice in Guinea. In: Moreno, M.T., Cubero, J.I., Berner, D. K., Joel, D., Musselman, L.J., Parker, C. (Eds.), Advances in Parasitic Plant Research: 6th Parasitic Weeds Symposium, Cordoba, Spain, pp. 518–520.

Cochrane, V., Press, M.C., 1997. Geographical distribution and aspects of the ecology of the hemiparasitic angiosperm Striga asiatica (L.) Kuntze: a herbarium study. J. Trop. Ecol. 13, 371–380.

Diagne, A., Amovin-Assagba, E., Futakuchi, K., Wopereis, M.C.S., 2013. Estimation of cultivated area, number of farming households and yield for major rice-growing environments in Africa. In: Wopereis, M.C.S., Johnson, D.E., Ahmadi, N., Tollens, E., Jalloh, A. (Eds.), Realizing Africa's Rice Promise. CABI, Wallingford, Oxfordshire, UK, pp. 35–45.

Dugje, I.Y., Kamara, A.Y., Omoigui, L.O., 2006. Infestation of crop fields by Striga species in the savanna zones of northeast Nigeria. Agric. Ecosyst. Environ. 116, 251–254.

Gbèhounou, G., Assigbé, P., 2003. *Rhamphicarpa fistulosa* (Hochst.) Benth. (Scrophulariaceae): new pest on lowland rice in Benin. Results of a survey and immediate control possibilities. Annales des Sciences Agronomique du Bénin 4, 89–103.

Gworgwor, N.A., Ndahi, W.B., Weber, H.C., 2001. Parasitic weeds of North-eastern region of Nigeria: a new potential threat to crop production. The BCP Conference. British Crop Protection Council, Farnham, England.

Hansen, O.J., 1975. The genus *Rhamphicarpa* Benth. emend. Engl. (Scrophulariaceae). A taxonomic revision. Bot. Tidsskr. 70, 103–125.

Houngbedji, T., Dessaint, F., Nicolardot, B., Perronne, R., Gibot-Leclerc, S., 2020. Abundance of Rhamphicarpa fistulosa in rainfed lowland rice fields in the Savannah region of Togo: moderate influence of physico-chemical characteristics of soils. Weed Res. 60, 385–391.

Houngbedji, T., Dessaint, F., Nicolardot, B., Shykoff, J.A., Gibot-Leclerc, S., 2016. Weed communities of rain-fed lowland rice vary with infestation by Rhamphicarpa fistulosa. Acta Oecologica-International Journal of Ecology 77, 85–90.

Houngbedji, T., Gibot-Leclerc, S., 2015. First report of *Rhamphicarpa fistulosa* on Peanut (*Arachis hypogaea*), soybean (*Glycine max*), and tossa jute (*Corchorus olitorius*) in Togo. Plant Dis. 99, 1654–1655.

Houngbedji, T., Pocanam, Y., Shykoff, J., Nicolardot, B., Gibot-Leclerc, S., 2014. A new major parasitic plant in rice in Togo: *Rhamphicarpa fistulosa*. Cah. Agric. 23, 357–365.

Jamil, M., Charnikhova, T., Houshyani, B., van Ast, A., Bouwmeester, H.J., 2012. Genetic variation in strigolactone production and tillering in rice and its effect on Striga hermonthica infection. Planta 235, 473–484.

Joel, D.M., 2013. Functional structure of the mature haustorium. In: Joel, D.M., Gressel, J., Musselman, L.J. (Eds.), Parasitic Orobanchaceae - Parasitic Mechanisms and Control Strategies. Springer, Heidelberg, pp. 25–60.

Johnson, D.E., Riches, C., Camara, M., Mbwaga, A.M., 1998. *Rhamphicarpa fistulosa* on rice in Africa. Haustorium: Parasitic Plants Newsletter 33, 2–3.

Kabiri, S., Rodenburg, J., Kayeke, J., Van Ast, A., Makokha, D.W., Msangi, S.H., Irakiza, R., Bastiaans, L., 2015. Can the parasitic weeds *Striga asiatica* and *Rhamphicarpa fistulosa* co-occur in rain-fed rice? Weed Res. 55, 145–154.

Kabiri, S., Rodenburg, J., van Ast, A., Bastiaans, L., 2017. Slavery in plants: how the facultative hemi-parasitic plant Rhamphicarpa fistulosa can completely dominate its host. Ann. Appl. Biol. 171, 353–363.

Kabiri, S., Rodenburg, J., van Ast, A., Pflug, S., Kool, H., Bastiaans, L., 2021. Impact of the facultative parasitic weed *Rhamphicarpa fistulosa* (Hochst.) Benth. on photosynthesis of its host *Oryza sativa* L. J. Plant Physiol. 262, 153438.

Kabiri, S., van Ast, A., Rodenburg, J., Bastiaans, L., 2016. Host influence on germination and reproduction of the facultative hemi-parasitic weed Rhamphicarpa fistulosa. Ann. Appl. Biol. 169, 144–154.

Kuijt, J., 1969. The Biology of Parasitic Flowering Plants. University of California Press, Berkeley.

Lane, J.A., Moore, T.H.M., Child, D.V., Cardwell, K.F., 1996. Characterization of virulence and geographic distribution of Striga gesnerioides on cowpea in West Africa. Plant Dis. 80, 299–301.

Mallamaire, A., 1949. Diseases, parasitic plants and weeds of cultivated rice in West Africa. Agron. Trop. 4, 77–80.

Mohamed, K.I., Musselman, L.J., Riches, C.R., 2001. The genus *Striga* (Scrophulariaceae) in Africa. Ann. Mo. Bot. Gard. 88, 60–103.

N'Cho, S.A., Mourits, M., Rodenburg, J., Demont, M., Oude Lansink, A., 2014. Determinants of parasitic weed infestation in rainfed lowland rice in Benin. Agric. Syst. 130, 105–115.

N'Cho, S.A., Mourits, M., Rodenburg, J., Lansink, A.O., 2019. Inefficiency of manual weeding in rainfed rice systems affected by parasitic weeds. Agric. Econ. 50, 151–163.

Neumann, U., Sallé, G., Weber, H.C., 1998. Development and structure of the haustorium of the parasite *Rhamphicarpa fistulosa* (Scrophulariaceae). Bot. Acta 111, 354–365.

Niang, A., Becker, M., Ewert, F., Dieng, I., Gaiser, T., Tanaka, A., Senthilkumar, K., Rodenburg, J., Johnson, J.M., Akakpo, C., Segda, Z., Gbakatchetche, H., Jaiteh, F., Bam, R.K., Dogbe, W., Keita, S., Kamissoko, N., Mossi, I.M., Bakare, O.S., Cisse, M., Baggie, I., Ablede, K.A., Saito, K., 2017. Variability and determinants of yields in rice production systems of West Africa. Field Crops Res. 207, 1–12.

Ouédraogo, O., Kaboré, I., Kaboré, T., Boussim, I.J., 2017. Effets de traitements herbicides sur *Rhamphicarpa fistulosa* (Hochst.) Benth. une plante parasite facultative. Journal of Applied Biosciences 119, 11983–11992.

Ouédraogo, O., Neumann, U., Raynal Roques, A., Sallé, G., Tuquet, C., Dembélé, B., 1999. New insights concerning the ecology and the biology of *Rhamphicarpa fistulosa* (Scrophulariaceae). Weed Res. 39, 159–169.

Ouedraogo, O., Neumann, U., Raynal-Roques, A., Salle, G., Tuquet, C., Dembele, B., 1999. New insights concerning the ecology and the biology of Rhamphicarpa fistulosa (Scrophulariaceae). Weed Res. 39, 159–169.

Press, M.C., Smith, S., Stewart, G.R., 1991. Carbon acquisition and assimilation in parasitic plants. Funct. Ecol. 5, 278–283.

Riches, C.R., Hamilton, K.A., Parker, C., 1992. Parasitism of grain legumes by Alectra species (Scrophulariaceae). Ann. Appl. Biol. 121, 361–370.

Rodenburg, J., Bastiaans, L., 2024. Differences in the ecology of witchweed and vampireweed: implications for rice farming in Africa. Plants People Planet. https://doi.org/10.1002/ppp3.10491.

Rodenburg, J., Cissoko, M., Dieng, I., Kayeke, J., Bastiaans, L., 2016a. Rice yields under *Rhamphicarpa fistulosa*-infested field conditions, and variety selection criteria for resistance and tolerance. Field Crops Res. 194, 21–30.

Rodenburg, J., Demont, M., Zwart, S.J., Bastiaans, L., 2016b. Parasitic weed incidence and related economic losses in rice in Africa. Agric. Ecosyst. Environ. 235, 306–317.

Rodenburg, J., Dümmer, R., Ho, Y.-H., Bastiaans, L., 2023. Fertilization benefits the facultative parasitic plant *Rhamphicarpa fistulosa* while gains by the infected host *Oryza sativa* are marginalized. Ann. Bot. https://doi.org/10.1093/aob/mcad190.

Rodenburg, J., Johnson, J.M., Dieng, I., Senthilkumar, K., Vandamme, E., Akakpo, C., Allarangaye, M.D., Baggie, I., Bakare, S.O., Bam, R.K., Bassoro, I., Abera, B.B., Cisse, M., Dogbe, W., Gbakatchetche, H., Jaiteh, F., Kajiru, G.J., Kalisa, A., Kamissoko, N., Sekou, K., Kokou, A., Mapiemfu-Lamare, D., Lunze, F.M., Mghase, J., Maiga, I.M., Nanfumba, D., Niang, A., Rabeson, R., Segda, Z., Sillo, F.S., Tanaka, A., Saito, K., 2019. Status quo of chemical weed control in rice in sub-Saharan Africa. Food Secur. 11, 69–92.

Rodenburg, J., Morawetz, J.J., Bastiaans, L., 2015. *Rhamphicarpa fistulosa*, a widespread facultative hemi-parasitic weed, threatening rice production in Africa. Weed Res. 55, 118–131.

Rodenburg, J., Tippe, D.E., Touré, A., Irakiza, R., Kayeke, J., Bastiaans, L., 2022. From rice-like plants to plants liking rice: a review of research on weeds and their management in African rice systems. Field Crops Res. 276, 108397.

Rodenburg, J., Zossou-Kouderin, N., Gbèhounou, G., Ahanchede, A., Touré, A., Kyalo, G., Kiepe, P., 2011. *Rhamphicarpa fistulosa*, a parasitic weed threatening rain-fed lowland rice production in sub-Saharan Africa - a case study from Benin. Crop Protect. 30, 1306–1314.

Schut, M., Rodenburg, J., Klerkx, L., Hinnou, L.C., Kayeke, J., Bastiaans, L., 2015a. Participatory appraisal of institutional and political constraints and opportunities for innovation to address parasitic weeds in rice. Crop Protect. 74, 158–170.

Schut, M., Rodenburg, J., Klerkx, L., Kayeke, J., van Ast, A., Bastiaans, L., 2015b. RAAIS: rapid Appraisal of Agricultural Innovation Systems (Part II). Integrated analysis of parasitic weed problems in rice in Tanzania. Agric. Syst. 132, 12–24.

Senthilkumar, K., Rodenburg, J., Dieng, I., Vandamme, E., Sillo, F.S., Johnson, J.-M., Rajaona, A., Ramarolahy, J.A., Gasore, R., Abera, B.B., Kajiru, G.J., Mghase, J., Lamo, J., Rabeson, R., Saito, K., 2020. Quantifying rice yield gaps and their causes in Eastern and Southern Africa. J. Agron. Crop Sci. 206, 478–490.

Stojanova, B., Delourme, R., Duffé, P., Delavault, P., Simier, P., 2019. Genetic differentiation and host preference reveal non-exclusive host races in the generalist parasitic weed Phelipanche ramosa. Weed Res. 59, 107–118.

Tippe, D.E., Bastiaans, L., van Ast, A., Dieng, I., Cissoko, M., Kayeke, J., Makokha, D.W., Rodenburg, J., 2020. Fertilisers differentially affect facultative and obligate parasitic weeds of rice and only occasionally improve yields in infested fields. Field Crops Res. 254.

Tippe, D.E., Rodenburg, J., Schut, M., van Ast, A., Kayeke, J., Bastiaans, L., 2017a. Farmers' knowledge, use and preferences of parasitic weed management strategies in rain-fed rice production systems. Crop Protect. 99, 93–107.

Tippe, D.E., Rodenburg, J., van Ast, A., Anten, N.P.R., Dieng, I., Kayeke, J., Cissoko, M., Bastiaans, L., 2017b. Delayed or early sowing: timing as parasitic weed control strategy in rice is species and ecosystem dependent. Field Crops Res. 214, 14–24.

Waddington, S.R., Li, X.Y., Dixon, J., Hyman, G., de Vicente, M.C., 2010. Getting the focus right: production constraints for six major food crops in Asian and African farming systems. Food Secur. 2, 27–48.

Yoneyama, K., Awad, A.A., Xie, X.N., Takeuchi, Y., 2010. Strigolactones as germination stimulants for root parasitic plants. Plant Cell Physiol. 51, 1095–1103.

Zossou, N., Adoukoneou-Sagbadja, H., Fonceka, D., Baba-Moussa, L., Sall, M., Ahanchede, A., Sinsin, B., 2016. Genetic diversity of rice vampireweed (*Rhamphicarpa fistulosa*) populations in rainfed lowland rice in West Africa. Weed Sci. 64, 430–440.