Rhamphicarpa fistulosa, a widespread facultative hemi-parasitic weed, threatening rice production in Africa

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Summary

Rhamphicarpa fistulosa is a facultative hemi-parasitic plant of the Orobanchaceae family, adapted to wet soils. Apart from tropical Australia, it is only found in sub-Saharan Africa, where it is considered a minor weed in cereal crops such as rice. Due to this status, the species has received only sporadic attention. Recent field observations and encounters with rice farmers in several African countries showed that *R. fistulosa* is, however, a more serious and increasing production constraint than previously thought. Results from a systematic literature review and a global herbarium study support this. The species has a broad distribution over Africa (at least 35 countries from Madagascar to Senegal and from Sudan to South Africa) and a wide range in altitude (0–2150 m a.s.l.) and environment (waterlogged swamps to moist free-draining uplands). *Rhamphicarpa fistulosa* is relatively independent and persistent because of the presumably wide host range, the facultative nature of its parasitism and its prolific seed (estimated 100 000 seeds m^{-2} under moderate infestation levels). Finally, *R. fistulosa* causes severe yield losses (average 60%) and high regional annual economic losses (estimated US $175 million), while effective control options are scant and awareness of the species among important R&D stakeholders is almost absent. An integrated approach is advocated to assist the rice sector to reduce current *R. fistulosa*-inflicted losses and to prevent further spread of the species into new areas.

Keywords: rice vampire weed, inland valley, rain-fed lowland, parasitic plant, integrated weed management, subsistence farming, sub-Saharan Africa.

Introduction

Rhamphicarpa fistulosa (Hochst.) Benth. (Orobanchaceae) is an annual, facultative hemi-parasitic forb species (Hansen, 1975; Ouédraogo *et al.*, 1999). Although much less well known than other weedy members of Orobanchaceae, such as *Striga* Lour. spp., *Orobanche* L. spp. and *Phelipanche* Pomel spp., it is a widespread and common feature in the natural vegetation of ephemeral wetlands (e.g. Hansen, 1975; Cissé *et al.*, 1996; Deil, 2005; Müller & Deil, 2005; Müller, 2007), as well as in agro-ecosystems of tropical Africa, including cropping systems characterised by dryer soils (Ouédraogo *et al.*, 1999; Gworgwor *et al.*, 2001; Rodenburg *et al.*, 2011). The species is increasingly encountered and perceived as a noxious weed in rice.

Rice farmers and agricultural extension agents lack knowledge on effective management strategies for this species. This is mainly a result of the low awareness of its existence and consequently the low priority it has so far received for research and development (Schut *et al.*, 2014). Indeed, many knowledge gaps exist with respect to *R. fistulosa*. There is an urgent need to understand just how important the species is in terms of its distribution, invasiveness and agronomic and economic impacts. Secondly, effective management strategies should be developed that prevent the species' spread and reduce crop damage. Knowing the ecological and biological characteristics of the plant is of utmost importance for the development of such strategies. While researchers, mainly botanists, have studied and reported on *R. fistulosa* since 1835, when it was first described and named, the information is scattered and far from complete. A structured and co-ordinated approach is advocated to complete the missing information and increase our understanding of this species. To this end, we have reviewed all publicly available publications and herbarium specimens of this species. The objectives were to provide an overview of the current knowledge and understanding of the species' distribution, biology, ecology, invasiveness, agronomic and economic importance and management and to identify and prioritise research questions. The overall aim of this review was to alert decision and policy makers and stakeholders of the emerging problem caused by *R. fistulosa* and to prioritise and guide research and development efforts aimed (i) at the control of this species where it has already turned into a weed and (ii) at the prevention of spread into new areas.

What do we know about the plant species *R. fistulosa*?

Taxonomy, nomenclature and similarities to other species

Rhamphicarpa fistulosa is an angiosperm species of the *Lamiales* order, *Orobanchaceae* family (formerly *Scrophulariaceae*; Olmstead *et al.*, 2001) and the genus *Rhamphicarpa* (Bentham, 1835; Hochstetter, 1841; Bentham, 1846; Engler, 1895; Hansen, 1975; Philcox, 1990; Mielcarek, 1996; Fischer, 2004; Table 1). Its phylogenetic position is not yet completely confirmed, but the species *R. fistulosa* has been placed under the tropical clade of Orobanchaceae previously reported by Morawetz *et al.* (2010), with Fischer *et al.* (2012) showing its closest relatives being the genera *Sieversandreas* Eb. Fisch., *Bardotia* Eb. Fisch. Schäferh. & Kai Müll. and *Randamaea* Benth. The species *R. fistulosa* has a number of local names in many of the countries where it occurs as a weed in rice (see Table 1). Based on the species' parasitic nature and the most common host crop species, rice vampire weed is proposed as the common name of *R. fistulosa*.

Plants are erect and slender, simple-stemmed and (mostly) glabrous, with smooth needle-like pale green leaves, in opposite arrangement (Fig. 1A and B), and can reach up to 120 cm height, depending on locality (Philcox, 1990). The species is adapted to semi-aquatic environments, with large (air) spaces between the cortical cells of the root aerenchyma to facilitate air flow under submerged conditions (Neumann *et al.*, 1997; Ouédraogo *et al.*, 1999).

Mature plants are branched and may turn reddish (Fig. 1C). Flowers are white, cream, pale pink or pale blue (the white form is most common in Africa) (Fig. 1D) with long tubes (25–30 mm) that are straight or slightly curved (Hansen, 1975; Fig. 1A and D). The fruits are asymmetrical and neatly beaked (Fig. 1A and B), about the size of a small pea, that is 6–15 mm long and 4–7 mm broad, containing 100–250 dark brown seeds. Seeds are oval shaped, 0.2×0.55 mm, and the outer seed coat forms a reticulate network covered by prominent ridges (Fig. 1A; e.g. Mielcarek, 1996; Ouédraogo *et al.*, 1999) and weigh about 0.011 mg (Rodenburg *et al.*, 2011). For complete botanical descriptions, see Hansen (1975) and Ouédraogo *et al.* (1999).

Bentham (1835) was the first to describe a species within this genus, that is *Rhamphicarpa longiflora* Benth. Independently from this work, Hochstetter (1841) named the genus *Macrosiphon* and described two African species, *M. fistulosus* Hochst. and *M. elongatus* Hochst. These are currently considered synonyms of *Rhamphicarpa fistulosa* and *R. elongata* (Hochst.) O.J. Hansen respectively (Hansen, 1975). In total, 41 different names of species and subspecies (or varieties) have been given to plants presumed to belong to *Rhamphicarpa*, but many of them are no longer accepted. For instance, Hooker (1884) and van Steenis (1970) considered the African, Australian and Indian species to be different. The Australian plants were named *R. australiensis* Steen., but as van Steenis did not compare this species to the African or Caucasian species, this name was not widely acknowledged. In the literature prior to Staner's (1938) revision, many species that are currently considered to be part of the genus *Cycnium* were classified as *Rhamphicarpa*; For example, the hemi-parasitic *Cycnium veronicifolium* (Vatke) Engl. used to be called *Rhamphicarpa veronicifolia* Vatke (Fuggles-Couchman, 1935; Parker & Riches, 1993). The closely related genera *Rhamphicarpa* and *Cycnium* are distinguished based on the form of

Table 1 Taxonomy, scientific, common and local names of *Rhamphicarpa fistulosa*

Scientific name	*Rhamphicarpa fistulosa*	
Authors	Hochstetter (1841), Bentham (1835, 1846), Engler (1895)	
Common name	Rice vampire weed	
Family	*Orobanchaceae* (formerly: *Scrophulariaceae*)	
Tribe	*Buchnereae* (formerly *Gerardieae*)	
Order	Lamiales	
Class	Angiospermae – Dicotyledons	
Synonyms	*Macrosiphon elongatus* Hochst.	
	Rhamphicarpa longiflora (Indian species most related to *R. fistulosa*) Benth.	
	Macrosiphon fistulosus (synonym of *R. longiflora*) Hochst.	
	Rhamphicarpa australiensis Steenis	
Vernacular names	Tutari (*R. longiflora*)	– India – Maharashtra state (Marathi)
	Grassland trumpet or trumpet flower (*R. longiflora*)	– India (English)
	Kayongo	– Uganda – Namutumba District (Lusoga)
	Otcha, Do, Corico, Efri	– Benin – Dassa, Glazoué Districts (Idaatcha)
	Mbosyo	– Tanzania – Kyela District (Nyakusa)
	Ntengo ya nchele nchele	– Tanzania – Mbinga District (Nyasa)
	Mulungi	– Tanzania – Ifakara (Kisajala)
	Angamay	– Madagascar – Mid West (Malagasy)
	Mogogatau	– Zambia – North (Tswana)
	Loho Soukoh/Soukoh lô	– Cote d'Ivoire – North: Korhogo/Boundiali (Dioula/Senoufo)

Sources: Hochstetter (1841), Bentham (1835, 1846), Engler (1895), von Wettstein (1891), Steenis (1970), Hansen (1975), Ouédraogo *et al.* (1999), l'Herbier de Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar, Herbarium of the Department of Botany, University of Dar es Salaam, Muséum National d'Histoire Naturelle, Paris, France (SONNERAT).

the capsules and the presence of a beak on their capsules; that is, oblique ovoid capsules with beaks (*Rhamphicarpa*) compared with straight oblong capsules without a beak (*Cycnium*) (Staner, 1938). In fact, the genus name *Rhamphicarpa* is a combination from the Greek words for 'beak' or 'bill' and 'fruit'. Another distinctive feature is the stamen structure; that is stamens arising at two levels in the corolla tube with the style never exceeding the lower pair of stamens (*Cycnium*) compared with stamens equal in length with the style exceeding the stamens (*Rhamphicarpa*) (Philcox, 1990; Fischer, 1999; Leistner, 2005). *Rhamphicarpa fistulosa* can be confounded with *Cycnium recurvum* (Oliv.) Engl. (previously named *Rhamphicarpa recurva* Oliv. and *R. tenuisecta* Standl.), which has a similar appearance and overlapping distribution in parts of north-east and south-east Africa. However, the tube of the corolla of *C. recurvum* is about a third of that of *R. fistulosa*. Moreover, *C. recurvum* has a distinctly different habitat, favouring dry conditions (Mielcarek, 1996). There is, however, still no conclusive evidence that *Cycnium* and *Rhamphicarpa* are really separate genera. A recent molecular phylogenetic study, the first of this type to include *Rhamphicarpa*, seems to indicate a much closer lineage with the Madagascan genera *Radamaea*/*Sieversandreas* than with *Cycnium* (Fischer *et al.*, 2012). Further phylogenetic work will be necessary to definitively determine the closest relatives of *Rhamphicarpa*.

There are five other species accepted within *Rhamphicarpa*: *R. longiflora* Wight ex. Benth., *R. elongata* (Hochst) O.J. Hansen, *R. brevipedicellata* O.J. Hansen, *R. capillacea* A. Raynal and *R. medwedewii* Albov. The latter species is only found in the Caucasus. The species *R. fistulosa* is most often confused with *R. longiflora*, but they differ in distribution; that is, *R. longiflora* is only found in India. These two species can be distinguished by the form of the beak of their capsules: *R. fistulosa* has a straight beak, while the Indian *R. longiflora* has an oblique beak (Bentham, 1846). Hansen (1975) concluded that *R. fistulosa* is the correct name for the species occurring in New Guinea, Australia, Madagascar and Africa, while *R. longiflora* is the Indian species of this genus. This is still the currently accepted taxonomic division (Philcox, 1990; Mielcarek, 1996).

In Central Africa, *R. fistulosa* can be confounded with *R. capillacea*, which also has long white flowers and favours similar growth conditions (Raynal, 1970). *Rhamphicarpa capillacea* can be distinguished from the other *Rhamphicarpa* species by the leaves (entire for *R. capillacea* compared with pinnatisect for the others) and capsules (isodiametric for *R. capillacea* compared with variable and never isodiametric for the others) (Raynal, 1970; Hansen, 1975).

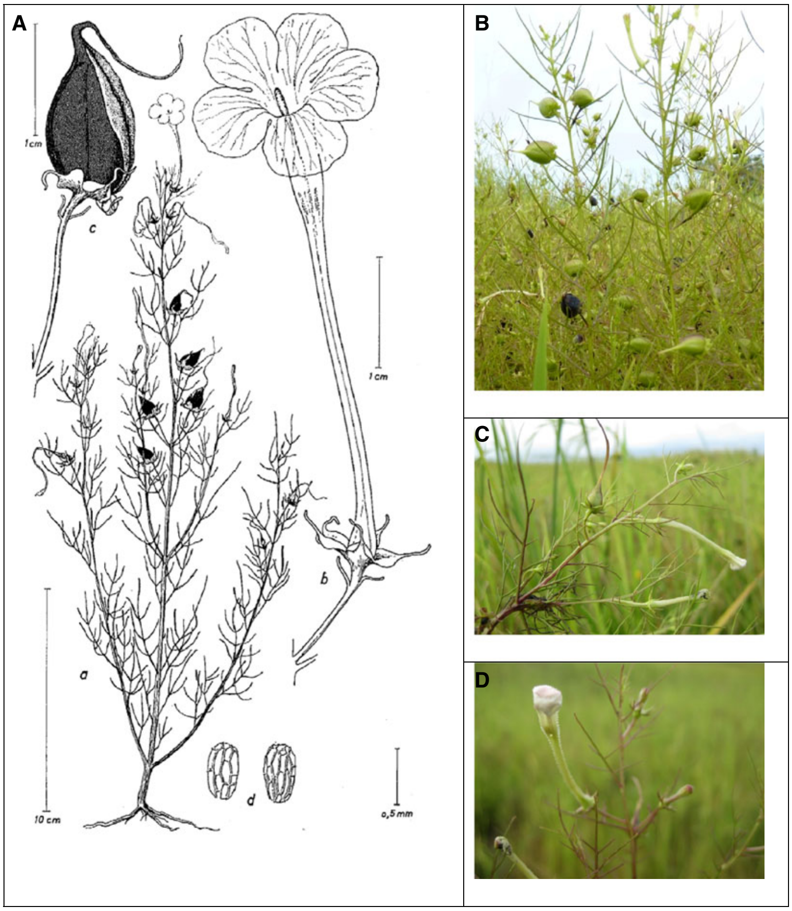

Fig. 1 (A) Drawing of *Rhamphicarpa fistulosa*, adapted from Hansen (1975), showing habit (a), flower (b), capsule (c) and seed (d); (B) *R. fistulosa* seed capsules, (C) close-up of the flower head with flowers and capsules at different stages and with reddish stem; (D) *R. fistulosa* flower during daytime. Photographs were taken by J Rodenburg.

Finally, *R. fistulosa* can be confounded with the *Striga* spp. that have an overlapping host range (mainly *Striga hermonthica* (Delile) Benth., *S. asiatica* (L.) Kuntze or *S. aspera* (Willd.) Benth.). The morphological differences between the species are obvious (e.g. Parker & Riches, 1993), but due to their parasitic nature and similarities in host crop ranges and geographic distribution, local names given by farmers are often the same for *R. fistulosa* and *Striga* spp. (e.g. 'Kayongo' in Uganda, 'Otcha' and 'Do' in Benin; Table 1). *Rhamphicarpa fistulosa* is sometimes even referred to as 'the *Striga* of rice', even though both *R. fistulosa* and *Striga* spp. parasitise rice. An important difference is that *Striga* spp. are usually found on rice grown in the free-draining uplands, whereas *R. fistulosa* mainly parasitises rice in the water-logged lowlands and hydromorphic zones, sometimes within the same upland–lowland continuum (Kabiri *et al.*, 2015).

A facultative root hemi-parasite

Rhamphicarpa fistulosa roots develop haustoria like other parasitic plants such as *Striga* spp. and *Orobanche* spp. (Parker & Riches, 1993; Press & Graves, 1995). While *Striga* species develop terminal and lateral haustoria, *R. fistulosa*, like other facultative parasites such as *Rhinanthus minor* L. (Seel *et al.*, 1993; Cameron & Seel, 2007) and *Buchnera hispida* Buch.–Ham. Ex. D. Don, (e.g. Neumann *et al.*, 1997, 1999), only develops lateral haustoria that bridge the parasite and host root xylem (Kuijt, 1969; Neumann *et al.*, 1998, 1999). About three to four weeks after sowing of the host plant, upon contact between the parasite and the host root, the parasite starts to develop haustoria. The haustorium initiation starts with the development of tiny hairs around the area of outgrowth, which sometimes facilitate the attachment of the parasite with the host root (Neumann *et al.*, 1998). If the host root and the parasite root are parallel to each other, the parasite root can develop multiple haustoria. Without a host in its vicinity, the parasite does not develop any haustoria, indicating that some morphogenic host root factors are involved in the host detection of the parasite. Upon establishment of a xylem-to-xylem connection, the parasite can extract host metabolites, nutrients and water from its host (e.g. Aly, 2013). In some cases, phenolic substances or lignins can be observed on the host roots where the parasite attempts to penetrate, indicating the existence of a host plant defence reaction (Neumann *et al.*, 1999). *Rhamphicarpa fistulosa* uses the C_3 pathway for CO_2 assimilation (Press *et al.*, 1987), but plants are pale green (both stem and leaves), which suggests a low chlorophyll content and consequently suboptimal CO_2 assimilation levels, explaining the species' need for host metabolites. The biomass accumulated by a parasitising *R. fistulosa* plant is usually much smaller than the biomass lost by the affected host plant (Rodenburg *et al.*, 2011). This would point to a phytotoxic mechanism, but the existence of such a pathological effect is not yet confirmed (Rodenburg *et al.*, 2010).

The host range of *R. fistulosa* has not yet been fully established. Apart from cereal crops such as maize, millet and rice (Bouriquet, 1933; Kuijt, 1969; Cissé *et al.*, 1996; Ouédraogo *et al.*, 1999), it has been reported to parasitise groundnut (*Arachis hypogaea* L.; Bouriquet, 1933) and cowpea (*Vigna unguiculata* (L.) Walp.), although the latter report concerned *R. veronicifolia* Vatke (= *Cycnium veronicifolium* (Vatke) Engl.) rather than *R. fistulosa* (Fuggles-Couchman, 1935). Supposedly it can also parasitise wild grasses (*Poaceae*) and members of the *Cyperaceae*, *Leguminosae* and *Labiatae* families (Bouriquet, 1933). Although other facultative hemi-parasites such as *Rhinanthus minor* are able to parasitise both grasses and legumes (Cameron & Seel, 2007), parasitic plant species typically parasitise either monocotyledons or dicotyledons; hence, these reports need to be confirmed.

Reproduction and seed biology

Flowers are white and fragrant, only open at dusk and usually last only one night, after which they fall off (Cissé *et al.*, 1996). Plants growing without a host develop fewer flowers (often just one or very few) than plants having successfully established a parasitic relationship with a suitable host (Ouédraogo *et al.*, 1999). The reproductive biology of *R. fistulosa* is unclear. Some reports mention cross-pollination by night moths (Parker & Riches, 1993; Cissé *et al.*, 1996; Ouédraogo *et al.*, 1999), perhaps mainly due to the shape of the corolla that is compatible with hawk-moth pollination (e.g. Fischer *et al.*, 2012) and the fact that the flowers only open between sunset and sunrise. However, viable seeds have been produced in the absence of such insects in controlled screen house environments (A van Ast, pers. comm.). The species may produce well over 1000 small seeds per plant. As densities above 100 plants per m^2 are not unusual (N'cho *et al.*, 2014), seed production may easily exceed 100 000 seeds per m^2.

Little is known about seed longevity under natural conditions, but according to Gbèhounou and Assigbé (2004), seeds are short-lived (approximately 1 year). Seeds of *R. fistulosa* have a dormancy period of six months and require water and daylight for germination (Ouédraogo *et al.*, 1999). Contrary to other parasitic Orobanchaceae, seeds of *R. fistulosa* do not require pre-conditioning for germination (A van Ast, pers. comm.). Moreover, in contrast to obligate parasitic plants (e.g. *Striga* spp.), the seeds of the facultative hemi-parasitic *R. fistulosa* do not need a host-derived stimulant for germination (Ouédraogo *et al.*, 1999; Gbèhounou & Assigbé, 2004). Germination occurs within about 4 days, when the conditions are favourable. Two to three days after germination, the green cotyledons emerge, after which the seedling starts to develop leaves. *Rhamphicarpa fistulosa* usually has a low initial growth rate (J Rodenburg, pers. obs.).

Flowering and maturity times seem to vary with growing conditions. Ouédraogo *et al.* (1999) reported initiation of flowering around 140 days after sowing (DAS) in trials in Burkina Faso, but an earlier onset of flowering (around 70–100 DAS) has been observed in trials in Benin and Tanzania (J Rodenburg, pers. obs.). Plants of *R. fistulosa* can continue growth and reproduction beyond the harvest of the crop, provided that there is enough residual soil moisture.

Where and under what conditions can we find *R. fistulosa*?

Biotic and abiotic environment

Rhamphicarpa fistulosa thrives in wet and semi-aquatic environments in forest and savannah zones (e.g. Cissé *et al.*, 1996). It can grow in peaty soils over rock substratum, on or between rocks in shallow, slow running streams, but more frequently in grassy swamps, temporary or permanently flooded areas such as inland valley swamps and poorly drained rain-fed lowland rice fields (Hansen, 1975; Philcox, 1990; Ouédraogo *et al.*, 1999). In areas where rice, the most common host of *R. fistulosa,* is grown along the upland–lowland continuum, the weed is only found in the lower, seasonally flooded zones (Kabiri *et al.*, 2015), although recently, we have observed it on higher parts as well (J Rodenburg, pers. obs.). Soils favouring *R. fistulosa* are generally poor in N, P and K with relatively high silt content (Ouédraogo *et al.*, 1999; Kabiri *et al.*, 2015), which would imply a high degree of salinity tolerance. The exact range of salinity tolerated needs to be confirmed.

Fungi (i.e. *Fusarium* spp., *Sclerotium rolfsii*) and bacteria (i.e. *Stenotrophomonas maltophilia*, *Bacillus pumilus*, *B. megaterium*) have been observed as pathogenic to *R. fistulosa* (Sikirou *et al.*, 2002a). The species is also attacked by beetles and caterpillars. The Nymphalid caterpillar *Junonia* spp. has frequently been observed on *R. fistulosa* plants and is able to feed on all the above-ground plant tissue (J Rodenburg, pers. obs.). The Coleoptera (beetle) *Smicronyx* spp. (Curculionidae) has also been observed to cause foliar damage to *R. fistulosa* plants and to lay eggs in the seed capsules (Sikirou *et al.*, 2002a). The larvae of these beetles feed on the immature seeds in the capsule and make the capsule look swollen (J Rodenburg, pers. obs.).

Rhamphicarpa fistulosa has been observed to co-occur with other parasitic weeds, such as *Alectra vogelii* Benth., *Striga asiatica*, *S. aspera* and *S. hermonthica* in Guinea (Cissé *et al.*, 1996), *Striga aspera* in Burkina Faso (Sallé *et al.*, 1994), *Striga asiatica* in Tanzania (Johnson *et al.*, 1998; Kayeke *et al.*, 2010; Kabiri *et al.*, 2015) and Madagascar (M Cissoko & A P Andrianaivo, pers. comm.), and *S. hermonthica* in Mali, Burkina Faso (Sallé *et al.*, 1994) and Uganda (J Rodenburg, pers. obs.). *Rhamphicarpa fistulosa* is, however, rarely observed with any of these species in the same crop, due to its distinct environmental niche (Kabiri *et al.*, 2015).

The species has been indicated as characteristic of the West African class of mud vegetation: *Rhamphicarpo fistulosae-Hygrophiletea senegalensis* (Deil, 2005; Müller & Deil, 2005). Observed associated wild plant or weed species are: *Parahyparrhenia annua* (Hack.) W. D. Clayton, *Sacciolepis microcorra* Mez., *Panicum* spp. or wild rice (*Oryza* spp.) in Senegal, Burkina Faso and Mali (Ouédraogo *et al.*, 1999) and *Ammania auriculata* Willd., *Oryza longistaminata* A. Chev. & Roehr., *Scleria vogelii* C. B. Clarke, *Fimbristylis littoralis* Gaudich. and *Mariscus longibracteatus* Cherm. in a field survey in southern Tanzania (Kabiri *et al.*, 2015). Whether or not any of these plants are also parasitised by *R. fistulosa* is not known.

Geographic distribution

The genus *Rhamphicarpa* is spread over four subareas: (i) sub-Saharan Africa and Madagascar, (ii) India, (iii) New Guinea and tropical Australia and (iv) the Caucasus. It is not clear yet how the genus could have spread to such discontinuous and remote places. It was hypothesised by Hansen (1975) that the genus *Rhamphicarpa* originated in Africa and that *R. fistulosa* represents the ancestral stock, as this species is the most widely distributed and the only taxon that is found in more than one subarea. From Africa, the genus may have spread to other areas, while subsequent environmental changes (e.g. in climate) may have caused a break-up of the original distribution to the currently observed discontinuous subareas.

Rhamphicarpa fistulosa is a very widespread species in tropical Africa (Staner, 1938; Müller, 2007). Combining a literature study with a search in national and international herbaria and our own field observations, we retrieved 392 observations, 378 of which can be traced back to geo-coordinates and 348 of which seemed to be unique individual observations/specimens. They are collected from 35 countries (Table 2), and the distribution of the species' observations is shown in Fig. 2. From two countries, the Gambia and Egypt, we only found a reference in the literature (i.e. Mielcarek, 1996), but no actual herbarium specimen or concrete observation with a name or geo-reference to the location. Liberia, Sierra Leone, Equatorial Guinea, Eritrea, Somalia and Comoros are the most remarkable absentees of the list of countries where *R. fistulosa* was observed, as these countries are located within the species' distribution zone. Apart from the possibility that this species does indeed not occur in these countries, the absence of any herbarium record may simply be a symptom of an incomplete national flora inventory or a weak national research infrastructure, which may be a result of recent turbulent histories, characterised by political instability and armed conflicts. The altitude of collections or observations ranged from 2 to 1750 m a.s.l. (average: 536 m), the latitude ranged from −28.72 to 19.25 degrees, and the longitude ranged from −16.85 to 49.97 degrees (Fig. 2). Previously, *R. fistulosa* distribution in Africa was assumed to be restricted to sub-Saharan regions, below 17°N, but our herbarium and literature search provided indications that the species can be found in more northern parts of Africa, as well. Outside Africa, it is reported in New Guinea and Australia (USDA, 2013), notably the northern tropical areas of Queensland (Martin, 2000).

Means of spread

Rhamphicarpa fistulosa seeds are minute and can adhere to crop seeds harvested from infested fields; if these seeds are then marketed, they can be introduced to previously uninfested fields when they are sown. Other likely means of introduction are through flood water, as *R. fistulosa* is mostly found along streams or in temporary flooded areas, and by wild or domesticated animals, for example free-roaming cattle in infested fields. The latter is a commonly observed a feature in the agricultural systems where *R. fistulosa* constitutes a weed problem (J Rodenburg, pers. obs.). Seeds are transported in the fur or hooves of the animals or ingested by animals feeding on crop residues at one place and deposited in their droppings in another place. Such means of dispersal is believed to be over relatively short distances, that is the typical distances these cattle cover. Although no published studies are available on seed dispersal for *R. fistulosa*, the above-mentioned processes have been reported as

Table 2 Rain-fed rice area, yields, total production and *Rhamphicarpa fistulosa*-inflicted economic losses in African countries where *R. fistulosa* was reported, sorted in decreasing order of magnitude

Country	Total area of rain-fed lowlands rice systems (ha)*	Average estimated yield from rain-fed lowlands (t ha^{-1})†	Estimated milled rice production from rain-fed lowlands (tonnes)‡	Estimated minimum annual economic loss caused by *R. fistulosa* (US $)§	Estimated maximum annual economic loss caused by *R. fistulosa* (US $)§
Nigeria	1 032 935	3.02	1 871 678	17 293 049	123 521 778
Tanzania	677 806	1.89	768 632	7 101 643	50 726 023
Madagascar	322 688	1.71	331 078	3 058 937	21 849 551
Cote d'Ivoire	314 863	1.61	304 158	2 810 212	20 072 945
Guinea	381 756	1.10	251 95	2 327 931	16 628 082
Mali	134 851	2.85	230 595	2 130 545	15 218 177
Ghana	129 533	1.16	90 155	832 971	5 949 795
Mozambique	73 954	1.89	83 864	774 845	5 534 611
Uganda	72 109	1.89	81 772	755 515	5 396 533
Burkina Faso	61 743	1.71	63 348	585 296	4 180 685
Guinea-Bissau	47 521	1.89	53 889	497 896	3 556 403
Chad	37 734	1.89	42 790	395 354	2 823 958
Cameroon	19 635	3.2	37 699	348 315	2 487 966
Senegal	43 948	1.22	32 170	297 229	2 123 061
Malawi	28 338	1.89	32 135	296 909	2 120 775
Togo	27 876	1.89	31 611	292 068	2 086 200
Benin	23 552	1.83	25 860	238 930	1 706 642
Gambia	25 231	1.28	19 377	179 034	1 278 816
DRC	28 021	0.88	14 795	136 697	976 405
Zambia	11 775	1.89	13 353	123 371	881 224
Burundi	7778	1.89	8820	81 493	582 094
Angola	6036	1.89	6845	63 242	451 726
Niger	4727	1.89	5360	49 527	353 762
Ethiopia	2811	1.89	3188	29 452	210 371
Sudan	1438	1.89	1631	15 066	107 618
Congo	1008	1.89	1143	10 561	75 437
CAR	2731	0.53	868	8024	57 314
South Africa	572	1.89	649	5993	42 808
Kenya	414	1.29	320	2961	21 147
Gabon	258	1.89	293	2703	19 308
Zimbabwe	145	1.89	164	1519	10 852
Total	3 523 787	1.79	4 410 201	40 747 288	291 052 067

*Estimates from Diagne *et al*. (2013a).

†Estimates for 18 countries derived from Diagne *et al*. (2013a); where national yield figures are not provided, the average yield from the 18 countries (1.89 t ha^{-1}) was used.

‡rice area multiplied by paddy yield per area and a paddy to milled rice conversion factor of 0.6.

§Milled rice production multiplied by the estimated proportion of *R. fistulosa*-infested lowlands (22%), the estimated proportion of infested fields in infested lowlands (72%), the estimated minimum or maximum *R. fistulosa*-inflicted yield loss in these infested fields (14 and 100%, respectively) and the most current world rice price (June 2014: US $416.64 per tonne). Based on the average yield loss (60%), the annual economic loss would be $175 million.

possible contamination pathways for other parasitic weeds (Jacobsohn *et al*., 1987; Berner *et al*., 1994).

What is the impact of *R. fistulosa* on rice in Africa?

Agronomic impact

In north-eastern Nigeria (Adamawa, Borno, Jigawa, Bauchi, Gombe and Yobe states), *R. fistulosa* occurred in 48% of the 65 surveyed locations (each sampling area was 1 km^2, comprising both farmland and natural vegetation) and was classified as 'abundant' (Gworgwor *et al*., 2001). In neighbouring Benin, an estimated 22% of the inland valleys where rice is grown were infested by *R. fistulosa* (Rodenburg *et al*., 2011), and in another survey in Benin, *R. fistulosa* was found in 72% of the rice fields in an infested inland valley (N'cho *et al*., 2014). When *R. fistulosa* invades a rice crop, resulting yield losses are generally high. The weed will parasitise the rice, removing metabolites, water and nutrients from it and presumably exerting a negative effect on its hormone regulatory system. The result is stunted growth of rice and reduced grain pro-

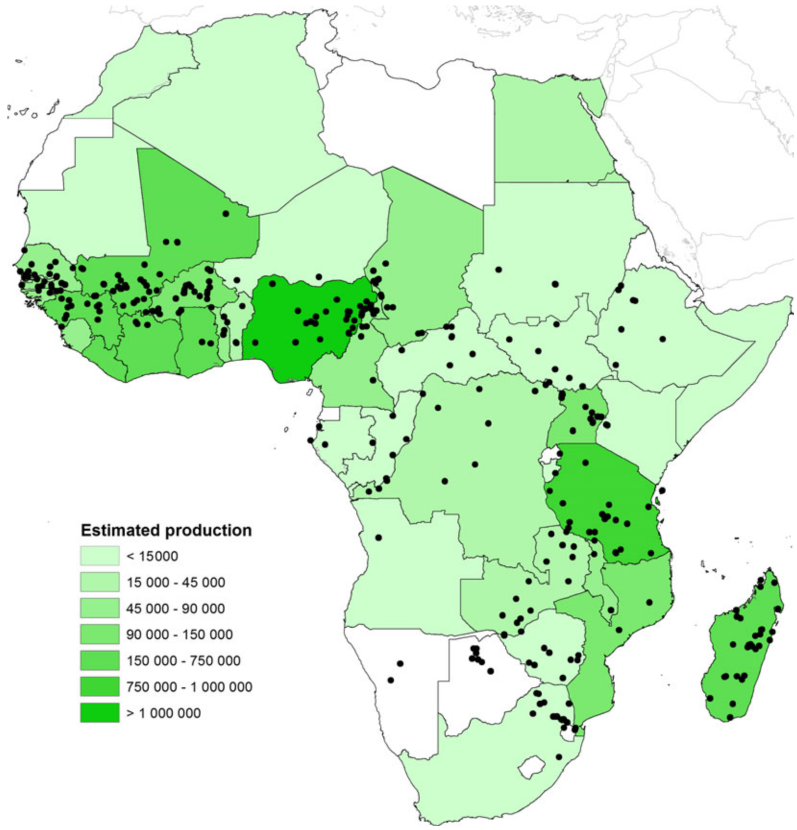

Fig. 2 Distribution of *Rhamphicarpa fistulosa* in Africa, based on the literature (see References), national and international herbaria (see Acknowledgements) and field observations of the authors and co-workers. Locations where *R. fistulosa* has been observed or herbarium specimen have been collected are indicated by black dots; national paddy production (tonnes) estimates from rain-fed lowland rice (derived from area and yield figures provided by Diagne *et al.*, 2013a), which may be impacted by *R. fistulosa*, are indicated by shading (see legend).

duction. In *R. fistulosa*-infested rice fields, yield losses can be as high as 100%, as observed in Benin (Sikirou *et al.*, 2002a; Gbèhounou & Assigbé, 2003) and in Tanzania (Kayeke *et al.*, 2010). The effect of *R. fistulosa* is also obvious from some of the local names it received from farmers, for example 'Efri' meaning 'killing' (Rodenburg *et al.*, 2011), 'Otcha' referring to 'viper' (poisonous snake) and 'Do' meaning 'crop killer' (Table 1; Gbèhounou & Assigbé, 2003). Pot experiments showed a range of 14–78% *R. fistulosa*-inflicted grain losses, depending on rice variety and infestation level, while in infested fields in Benin, rice farmers estimated the average yield losses at 60% (Rodenburg *et al.*, 2011). This average is much higher than estimated yield losses caused by non-parasitic weeds. For comparison, in a large survey held among rice farmers from 21 African countries, farmers growing rice in rain-fed lowlands who indicated weeds to be a problem, estimated weed-inflicted yield losses in rain-fed lowland rice around 36%, with a maximum average estimate of 43% in Kenya and 40% in Cote d'Ivoire (Diagne *et al.*, 2013b).

Economic impact

Of the 35 countries where the species is found, at least 31 have rainfed lowland rice production systems, which, based on the most recent and accurate estimations (see Diagne *et al.*, 2013a; data on Sudan and South Sudan are combined) annually produce about 7.35 M tonnes of paddy (4.41 M tonnes of milled rice), worth around US $1.84 billion. If *R. fistulosa* can be found in 22% of the rice grown inland valleys, and in 72% of the rice fields in such valleys, and given an average *R. fistulosa*-inflicted yield loss of 60% (ranging from 14% to 100%), the current annual economic losses in sub-Saharan Africa are estimated at US $175 million (with a range from US $41 to 291 million; see Table 2). This is 9.5% of the total estimated value of the regional rain-fed lowland rice production. This estimate will become more accurate, once additional data are available.

Social impact

Infestation by *R. fistulosa* can be considered a *poor-man*'s problem. The parasitic weed is primarily problematic on marginal arable land, that is on low fertility and poorly drained soils, where water cannot be controlled (e.g. N'cho *et al.*, 2014). These are the typical crop production conditions of resource-poor subsistence farmers, with a high proportion of female farmers (N'cho *et al.*, 2014; Rodenburg *et al.*, 2014). The weed has clear negative economic impacts and requires the farmer to invest valuable time for weeding (S. N'cho, pers. comm.). Weeding is often performed by women and children and consumes time that could otherwise be invested in family welfare and education (Ogwuike *et al*., 2014). Sometimes heavily infested fields are abandoned by the farmer (e.g. Rodenburg *et al*., 2011).

Little is known about the economic, social or environmental value of *R. fistulosa*. The species has been observed locally (in central Benin) being used as an insect repellent. Fresh plants were burned in a portable stove to produce smoke that was believed to repel (biting) insects such as mosquitoes (J. Rodenburg, pers. obs.). The plant was also reported to have medicinal uses in Machipi (near Ifakara), Kilombero District, Tanzania (EAH, 2013).

How can we stop the future spread of *R. fistulosa* and reduce current damage?

Prevention

As with other parasitic weeds of the Orobanchaceae family, the spread of *R. fistulosa* via their minute seeds can be prevented through basic phytosanitary measures. This means that any possible vectors that move seeds from an infested area should be controlled as much as possible (e.g. Rubiales *et al*., 2009; Goldwasser & Rodenburg, 2013). Farm implements should be cleaned before using them in another field. Cattle movement between contaminated and clean fields should be avoided. Fields should be bunded to prevent seed movement from one field to another in water following uncontrolled floods and crop seeds should be cleaned before sowing. To prevent a seedbank build-up in a given field in a contaminated area, the crop should be regularly weeded (at least before flowering), so that weeds are removed from the field, both during the season and between seasons during any fallow period.

Control

The main weed management practices by rice farmers in Benin, Cote d'Ivoire and Tanzania with parasitic weed infested rice fields (including *R. fistulosa* and *Striga* spp.) are, in decreasing order of frequency: hand weeding, hand-hoe weeding, soil fertility management, herbicide use, water control, use of clean seeds, transplanting and the use of resistant or tolerant rice varieties (S. N'cho pers. comm.).

Rhamphicarpa fistulosa can be controlled with the post-emergence herbicide 2,4-D (Gbèhounou & Assigbé, 2003). Fertiliser has a proven suppressive effect on *R. fistulosa* and a positive effect on rice yields of *R. fistulosa*-infected plants (Sikirou *et al*., 2002b; Rodenburg *et al*., 2011). Resource-poor rice farmers could use rice husks, which are often freely available, as it may reduce negative effects of *R. fistulosa* infestation on yield (Kayeke *et al*., 2013). Genetic variation in resistance and tolerance levels (Rodenburg *et al*., 2011), as well as in weed competitiveness (Rodenburg *et al*., 2009), was observed among adapted lowland rice cultivars, and these could be useful in *R. fistulosa*-infested rice fields. For resource-poor farmers, the availability of improved rice varieties may, however, be limited. It is also hypothesised that improved water management, enabling either drainage or continuous flooding, can reduce *R. fistulosa* abundance (Parker & Riches, 1993; Parker, 2012). Permanently flooded conditions, starting at the early stages of the crop, will contribute to reduced *R. fistulosa* plant numbers (van 't Klooster, 2011). Indeed, *R. fistulosa* has never been reported in irrigated rice systems where water is fully controlled. As *R. fistulosa* is particularly problematic in direct seeded rice (Johnson *et al*., 1998), transplanting is also likely to have a positive effect on rice performance in infested fields (Gbèhounou & Assigbé, 2003). It will give the crop a time advantage over the weed, thereby rendering it more competitive. It has the additional advantage of facilitating hand weeding, the spot application of post-emergence herbicides or the use of a rotary weeder (e.g. Rodenburg & Johnson, 2009). Timing of planting is also reported to be important (Langeloo, 2013; Rodenburg *et al*., 2013). However, whether or not early or late sowing is advantageous most probably depends on the local environmental conditions, in particular the hydrology and rainfall distribution. Exact relationships between environmental conditions, timing and parasitism should therefore be further investigated. An integrated management strategy against *R. fistulosa*, combining any of the above measures, is generally considered the most effective and sustainable solution (e.g. Sallé *et al*., 2000; Kayeke *et al*., 2010; Goldwasser & Rodenburg, 2013).

Discussion

Rhamphicarpa fistulosa: an increasing problem

Rhamphicarpa fistulosa is a widespread and rather common species of natural wetland vegetation in Africa (e.g. Deil, 2005; Müller & Deil, 2005; Müller, 2007). Sallé *et al*. (1994) observed the species to occur more frequently in natural vegetation than in crops. Indeed, for parasitic plants in general, the natural geographical range is usually much larger than their geographical range as a weed (Raynal Roques, 1994). This also seems to be the case for *R. fistulosa*. From the aforementioned herbarium study, many of the specimens were collected from national parks and nature reserves or otherwise uncultivated areas. From only 10% of the specimens or observations, we are sure that the plants were found in a rice field. We estimate that of the remaining 90% of specimens for which it was not indicated whether it was found in a rice crop, about 50% were collected from locations with at least a close vicinity to rice production sites and about 40% was likely not close to a rain-fed rice production area.

We hypothesise that when the natural habitats of *R. fistulosa* are turned into agricultural production sites, with a suitable host grown as a monoculture in a high density, the spontaneously occurring population of the species can rapidly increase, transforming the species into an agricultural pest (Bouriquet, 1933; , Akoegninou *et al*., 1999; Gbèhounou & Assigbé, 2003). The only major staple crop that can be grown across the range of environments where *R. fistulosa* is observed, that is from hydromorphic to waterlogged soils, is rice. Rice is an increasingly important crop in sub-Saharan Africa. To keep pace with the increasing regional rice consumption, about 30 million tons more rice will be needed by 2035 (Seck *et al*., 2012). Part of the increase in production will likely come from expansion into areas previously unused for agriculture. Low-lying areas, such as inland valleys, with a relatively favourable hydrology and soil fertility, constitute high-potential areas for rice production and are likely to be increasingly exploited for that purpose (Rodenburg *et al*., 2014). Intensification of rice production in these ecosystems may be threatened by infestations of *R. fistulosa* (Johnson *et al*., 1998). Given its widespread distribution, the species is poised to become an even more serious parasitic weed throughout the continent.

We assume, based on the descriptions of its habitat (Hansen, 1975) and our own observations in the field, that *R. fistulosa* will in particular invade rain-fed lowland rice growing environments. However, the species was shown to have a relatively broad ecological niche (Kabiri *et al*., 2015), and we have recently observed it in the undulating landscape of Namutumba District (Ivukula village) in Uganda on the top of a hill in a free-draining upland rice field. In the same district, it has been found in maize fields as well. Ouédraogo *et al*. (1999) also reported this species in agro-ecosystems other than rain-fed lowlands. Hence, *R. fistulosa* seems to have a reasonably high degree of ecological plasticity.

Rhamphicarpa fistulosa remains a relatively unknown species among local extension and research (Schut *et al*., 2014) and therefore often goes unnoticed (as we observed in Benin, Cote d'Ivoire, Madagascar, Senegal, Tanzania and Uganda). The species is also easily overlooked because the flowers are only opening at sunset (Cissé *et al*., 1996). The actual extent of the problem of *R. fistulosa* in rain-fed lowland rice in sub-Saharan Africa is therefore expected to be largely underestimated. Recent observations in West Africa indicate the species is spreading. Rodenburg *et al*. (2011) observed an increase in the number of infested inland valleys growing rice over a period of about 10 years. In Cote d'Ivoire, farmers indicated an observed general increase of the species in the period 2008–2012 (S N'cho, pers. comm.). In Senegal in 2008, *R. fistulosa* was observed in a rice field in the Casamance, south of the Gambia (J Rodenburg, pers. obs.), where it had not been observed previously during annual surveys from 1985 to 1996 (Ouédraogo *et al*., 1999). For the farmer of the aforementioned highly infested upland rice field in Ivukula, Namutumba District, Uganda, *R. fistulosa* was a completely new species three years ago when he observed the first invasive individuals. Similarly in Madagascar (Tsiroanomandidy, Bongolava region), farmers indicated new infestations of *R. fistulosa* in their rice fields during recent years (M Cissoko and A P Andrianaivo, pers. comm.).

Future research topics

Since its description by Bentham in 1835, the taxonomy, biology, ecology and agronomic importance of *Rhamphicarpa fistulosa* has been only infrequently studied. The species therefore remains relatively unknown and many knowledge gaps still need to be filled. Increased awareness and knowledge is required for the development and implementation of control strategies to prevent the species from becoming a more important constraint to food production in sub-Saharan Africa. Ten important research topics are listed below:

Within the domain of invasive plant ecology and environmental studies, (i) the invasiveness of *R. fistulosa* needs to be studied to ascertain whether the distribution is increasing, stable or decreasing. Furthermore, (ii) the main distribution mechanisms and the history of the spread of the genus over the discontinuous subareas would need to be clarified. Related to that, (iii) the altitude and environmental plasticity need to be confirmed, as well as the soil chemical ranges of the *R. fistulosa* habitat, with special focus on salinity and acidity tolerances. These all seem to be important parameters to infer the likely spread of the species. Next, within the economic science domain, (iv) our *best-bet* economic loss estimate of US $175 million per year should be revised using updated figures on *R. fistulosa* incidences and yield losses in rain-fed rice systems per country with local rice prices and using solid spatial and economic models. This is important for priority setting of research and developments efforts, as well as for raising awareness of the problem. Within the domain of taxonomy, plant physiology and crop sciences, (v) the host–parasite and damage mechanisms need to be elucidated, as it remains unclear whether this can purely be defined as a sink-source relation or whether *R. fistulosa* negatively affects the host plant hormone balance and through that, the host metabolism and growth, as with *Striga* spp. Another fundamental issue, (vi) the distinction between *Cycnium* and *Rhamphicarpa*, requires further study, probably using molecular analyses. Next, (vii) the parasitic nature, the biology and ecology of other species of the genus *Cycnium* and *Rhamphicarpa* should be investigated, as other species from these families could potentially emerge as important parasitic weeds as well, (viii) the host range of *R. fistulosa* (and other parasitic species of *Rhamphicarpa* and *Cycnium*) needs to be confirmed, as it will determine whether crop rotations, inter- or relay cropping are useful control methods, and which species should then be used. Related to that, (xi) feasible control strategies for rice farmers need to be further investigated and developed. In particular, the timing of crop and weeding operations and soil fertility management seems to be promising avenues to explore further. Another potentially interesting control option is the use of resistant or tolerant host crop varieties. To explore and use this option (x) the host resistance and tolerance mechanisms and responsible genes need to be identified and possibly transferred to adapted cultivars.

Conclusions

Rhamphicarpa fistulosa (rice vampire weed) is a widespread facultative hemi-parasitic weed, threatening rice production in Africa. Based on a literature and herbarium study, we conclude that *R. fistulosa* is an important rice production constraint in some areas, particularly in subsistence rice production systems, and poses a strong threat for rice production in other areas in Africa. The species has a broad distribution over tropical Africa, occurring in at least 35 countries geographically spread from eastern Madagascar to western Senegal and from Sudan to South Africa. In addition to the wide geographic range, *R. fistulosa* has been observed at widely varying altitudes, from sea level to an estimated 1750 m a.s.l., and under a range of ecological conditions, from waterlogged swamps to (moist) free-draining uplands. Combined with a presumably wide host range, the facultative nature of its parasitism and prolific seed production, the plant has a putative high degree of ecological plasticity. While the weed has very significant effects on rice productivity when present, farmers and even extension services are generally unaware of effective and affordable control options. Despite the wide distribution and severe economic consequences (an estimated annual loss of US $175 million), awareness of the species among research, extension and development stakeholders is largely lacking.

A systematic and integrated approach is advocated to assist farmers and other stakeholders in affected areas to reduce current losses due to this parasitic weed and to prevent future spread into other areas. Important knowledge gaps concerning the species' taxonomy, biology, ecology, parasitic nature, invasiveness and economic impact need to be filled. This will enable informed development of effective integrated control and prevention strategies and form the necessary bedrock for increasing the awareness among a wider range of stakeholders and actors within research, development, education and policy domains.

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