1 Introduction to Parasitic Plants

Abstract
Parasitic plants are generally little known by agriculturalists even though under some conditions they may be the most important factor in crop losses. Globally, they have their greatest impact on food crops of smallholder farming systems in Africa. Despite this, they are often treated simply as weeds, overlooking the fact that they do not just harm the crop indirectly through competition, but also directly through parasitism. Parasitic weeds connect to crop plants through a specialized structure, the haustorium. In fact, the presence of a haustorium is what defines a parasitic plant. Parasitism has arisen in 12 clades of angiosperms, yielding plants with a diversity of habits including herbs, vines, shrubs and even trees. Likewise, there is a range of parasite–host interactions. Some parasites will only germinate with a stimulant produced by the host. Some are specific in host selection, some are promiscuous with many different hosts, and some are not quite generalists but are not host specific. We include all known African parasites that attack crops, with emphasis on mistletoes, witchweeds, dodders and broomrapes, including their taxonomy, hosts, distribution and control measures.

1.1 Parasitic Plants as Weed Problems

Parasitism has been reported in 28 plant families, comprising nearly 4500 species, all exclusively dicotyledons (Heide-Jørgensen, 2013; Nickrent, 2020). When these plants parasitize other plants, either out of necessity or to increase their reproductive output (Shen *et al.*, 2006), the host plants can be severely damaged. When hosts are agricultural crops, parasitic plants can become important weed problems. A broad range of African crops suffer from parasitic weeds. Affected crops include staple food grains (e.g. maize, rice, sorghum, millet) and legumes (e.g. cowpea, faba beans, lentils), a diversity of vegetables (e.g. carrots, tomatoes, leek), oil crops (e.g. sunflower, linseed), fibre crops (e.g. flax, hemp), forage crops (e.g. lucerne, clover), many fruit-tree species (e.g. mango, guava, citrus) and plantation cash crops (e.g. cacao, coffee, tea, rubber).

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Parasitic plants can lead to severe yield losses, making them an important constraint to food security in many areas (Fig. 1.1). While quantitative information on yield losses from parasitic weeds is lacking for many parasite–host species combinations, available data emphasize just how serious these pathogens are. An assessment by Rodenburg *et al*. (2016a) showed that when *Striga asiatica* is not controlled, mean yield losses of upland rice are around 73%. For maize, the same parasite causes yield losses of 80% or higher when uncontrolled (Ransom *et al*., 1990; Rusinamhodzi *et al*., 2012). *Striga hermonthica* can cause yield losses of up to 84% (mean: 37%) in sorghum (Rodenburg *et al*., 2005) and up to 81% in maize (mean: 68%; Kim *et al*., 2002), depending on variety, infestation level and environmental conditions. *Rhamphicarpa fistulosa* causes yield losses of rice ranging from 24% to 73% (mean: 50%), again depending on the variety and infestation level (Rodenburg *et al*., 2016b). Field dodder, *Cuscuta campestris*, reduces yields of sesame by 67%, soybean by 48%, pigeon pea by 25% and groundnut by 18% (Mishra *et al*., 2007). *Alectra vogelii* inflicted yield losses in susceptible cowpea varieties that were reported to range from 30% to 66% (mean: 51%; Alonge *et al*., 2001) whereas *Striga gesnerioides* inflicted yield losses that ranged from 79% to 86% (mean: 81%; Alonge *et al*., 2005), but for both parasite species, these losses were reduced in some of the resistant and tolerant cowpea genotypes. Yield losses caused by broomrapes (*Orobanche* spp. and *Phelipanche* spp.) in faba bean, chickpea, tomato, potato and sunflower range from 5% to 100% (Abang *et al*., 2007).

No quantitative data exist on damage inflicted by mistletoe but assessment is based on field observations and farmer perceptions. Loranthaceae parasitism causes important shea tree yield reductions in Burkina Faso (Boussim *et al*., 2004). Damage to these and other economically important crops is generally increased by low soil fertility and drought stress, conditions facing many African smallholders.

The above yield-loss estimates are field- or crop-scale measurements. The extent of the parasitic weed problem in Africa cannot be truly assessed without quantitative information on the spread of the different parasite species across croplands and their economic impact at a national and regional scale. The data on parasitic weed distribution and economic impact in Africa are scarce, however, and are mainly associated with those parasites that impact the region's cereal production. Maize cropland infested by *Striga* spp. (chiefly *Striga hermonthica* and *S. asiatica*) in sub-Saharan Africa is estimated at 2.3 million ha and the concomitant annual economic losses are estimated at US$383 million (Woomer *et al*., 2008). The area of rainfed rice infested by parasitic weeds (*Striga hermonthica*, *S. asiatica*, *S. aspera* or *Rhamphicarpa fistulosa*) is estimated at 1.34 million ha (about 19% of the total area under rainfed rice) resulting in a total estimated annual economic impact of at least US$111 million (Rodenburg *et al*., 2016a). The total annual loss caused by *S. hermonthica*, one of the main parasitic weeds in cereals in Africa, is roughly estimated to be more than US$1 billion (Parker, 2009). For Africa, no quantitative economic impact data are available on any of the stem parasites described in this book.

Fig. 1.1. Farmers in parasitic-weed-infested field crops in Africa. (A) Rice field infested by *Striga hermonthica* (purple-flowered plants) in Côte d'Ivoire. (B) Rice field infested by *Rhamphicarpa fistulosa* (reddish plants among the rice) in Uganda.

1.2 What is a Parasitic Plant?

Although parasitic plants are often thought of as weeds, they are part of a guild of highly unique plants, the parasitic angiosperms. An understanding of their biology is essential for effective control and management. Parasitic plants are amazingly specialized, with remarkable adaptations for their heterotrophic existence. Their habits are diverse, including herbaceous plants, vines, shrubs and trees. Some appear innocuous, with no external evidence of their parasitic nature. Others lack chlorophyll or even leaves and stems, existing only within the bodies of other plants until they flower. Parasitic plants' reproductive strategies also vary widely, from the tiny (1 mm) flowers of some mistletoes to the metre-wide flowers of *Rafflesia* species – the largest flower in the world. Unique among African parasitic plants is the rainforest tree *Okoubaka aubrevillei* (Santalaceae), a rare but widely distributed tree in Western and Central Africa, much sought after for its purported medicinal value. It is the largest parasitic plant in the world and little studied. Veenendaal *et al*. (1996) present the only data from experimental work on host selection and host damage. In their study, they found that *O. aubrevillei* caused morbidity and death in seedlings of *Pericopsis elata*, a leguminous rainforest tree. The authors suggest that *O. aubrevillei* favours such nitrogen-fixing trees and that the role of parasitism is to reduce competition at the seedling stage.

What this diverse coterie of plants share is a haustorium. Simply put, if a haustorium is present, the plant is a parasite. It is the defining feature of this group of organisms. The haustorium is the morphological and physiological bridge between host and parasite. This structure is the conduit for water and dissolved materials, such as nutrients and metabolites, but also proteins and pathogens (Yoshida *et al*., 2016) as well as genetic material transported from the host into the parasite or from the parasite into the host. Non-parasitic weeds compete with crop plants for water and nutrients in the soil, whereas parasitic weeds obtain these resources directly from host plants. Farmers are sometimes surprised to learn that some of the weeds in their crops, in particular the ones with green leaves such as witchweeds, are also parasites. Knowing the parasitic behaviour is, however, essential to understanding control measures.

1.3 Categories of Parasitic Weeds

There are roughly four different categories of parasitic plants (Table 1.1). Parasitic plants can be distinguished by the presence or absence of chlorophyll. Those that produce chlorophyll (and therefore have some photosynthetic activity) are termed hemiparasites (also known as semiparasites), and this category comprises about 90% of all parasitic plant species (Heide-Jørgensen, 2013). Those that lack chlorophyll (and therefore are not green and are totally dependent upon their host for nutrition and water) are termed holoparasites. Another distinction among parasites is with germination. Obligate parasites require the presence of a host to germinate and initiate a haustorium. Facultative parasites, on the other hand, can germinate without a host (see Kabiri *et al*., 2016).

Table 1.1. Parasitic plant species reported to be weed problems in African agriculture.

Parasitism and common name	Family	Genus	Species	Main crop hosts	Chapter[a]
Stem parasites					
Obligate hemiparasites					
Mistletoe	Loranthaceae				
		Tapinanthus	*T. bangwensis*	Guava, other tree crops	2
			T. belvisii	Tree crops	2
		Erianthemum	*E. dregei*	Tree crops	2
		Phragmanthera	*P. capitata*	Tree crops	2
			P. incana		2
	Viscaceae				
		Viscum	*V. cruciatum*	Tree crops	2
			V. anceps		2
			V. engleri		2
			V. rotundifolium		2
Love vine	Lauraceae				
		Cassytha	*C. filiformis*	Mango, cashew, other tree crops	3
Dodder	Convolvulaceae				
Field dodder		***Cuscuta***	***C. campestris***	Vegetables, tree crops, forage crops	4
			C. epilinum	Flax	4
Fringed dodder			*C. suaveolens*		4
			C. hyalina		4
Eastern dodder			*C. monogyna*	Tree crops	4
Lucerne dodder			*C. epithymum*	Forage crops, lucerne	4
			C. pedicellata	Vetch, lentil, arugula	4
			C. planiflora	Lucerne	4
Australian dodder			*C. australis*	Lucerne	4
Chinese dodder			*C. chinensis*	Various	4
			C. kilimanjari	Cassava, ornamental shrubs	4

Continued

Table 1.1. Continued.

Parasitism and common name	Family	Genus	Species	Main crop hosts	Chapter[a]
Root parasites					
Facultative hemiparasites					
Rice vampire weed	Orobanchaceae				
		Rhamphicarpa	***R. fistulosa***	Rice, maize	5
			R. brevipedicellata		5
			R. capillacea		5
			R. elongata		5
			R. veronicaefolia		5
Hairy buchnera	Orobanchaceae				
		Buchnera	*B. hispida*	Cereals	6
NA	Orobanchaceae				
		Micrargeria	*M. filiformis*	Rice	11
		Sopubia	*S. parviflora*	Rice	11
Thesium	Santalaceae/ Thesiaceae				
		Thesium	*T. humile*		11
			T. resedoides		11
Obligate hemiparasites					
Witchweed	Orobanchaceae				
Red witchweed		***Striga***	***S. asiatica***	Sorghum, millet, maize, rice, sugarcane	7
Witchweed			*S. aspera*	Cereals, fonio, sugarcane	7
Purple witchweed			***S. hermonthica***	Sorghum, millet, maize, rice, sugarcane	7
Cowpea witchweed			***S. gesnerioides***	Cowpea, sweet potato, tobacco	7
Giant maize witchweed			*S. forbesii*	Cereals, sugarcane	7
NA			*S. passargei*	Cereals	7
NA			*S. brachycalyx*	Cereals	7
Alectra	Orobanchaceae				

		Alectra	***A. vogelii***	Cowpea, groundnut	8
			A. picta	Pulses	8
			A. sessiliflora	Pulses	8
			A. orobanchoides	Sunflower, tobacco	8
Obligate holoparasites					
Broomrape	Orobanchaceae				
Bean broomrape		*Orobanche*	*O. crenata*	Faba bean, bean, chickpea	9
Sunflower broomrape			***O. cumana*** syn. ***cernua***	Sunflower, tobacco, tomato, aubergine	9
Small broomrape			*O. minor*	Tobacco, lettuce, forage legumes	9
Stinking broomrape			*O. foetida*	Pulses	9
Egyptian broomrape		*Phelipanche*	*P. aegyptiaca*	Potato, tomato, melons	9
Branched broomrape			***P. ramosa***	Potato, tomato, aubergine, tobacco, cole crops	9
Thonningia	Balanophoraceae				
		Thonningia	*T. sanguinea*	Tree crops including rubber, coffee and cacao	10

Species in bold are the most economically important.
[a]Chapter in this volume where the species is discussed.
NA = no widely accepted common name available.

Intuitively, it seems that the most serious parasitic weeds would be holoparasites. And indeed, species of *Orobanche* and *Phelipanche* are well-known pathogens of a variety of crops. But in Africa, the most serious parasitic weeds are the witchweeds, which are obligate hemiparasites in the genus *Striga*. A further broad distinction can be made between categories of parasitic weeds in terms of where they parasitize their hosts. Around 40% of parasitic plants attack stems, whereas others are restricted to roots. These are simply referred to respectively as stem parasites and root parasites.

1.4 Parasitic Plant Research

The modern science of parasitic plants was launched in 1969 by the publication of Job Kuijt's magisterial biology of parasitic plants (Kuijt, 1969). This drew attention to a group of plants known chiefly for their bizarre morphology. A decade earlier, in-depth studies on physiology, biochemistry and control were stimulated by the discovery of *Striga asiatica* (red witchweed) in North and South Carolina (USA) in the 1950s. The parasite quickly developed as a serious pathogen of maize in these states, prompting extensive work on the biology, control and containment of this species. As a result, after many years of work, the elegant, complex germination biology of witchweed and other parasites has been elucidated and parasitic plant research expanded worldwide, leading to a surge in publications on parasitic plants.

Following Kuijt's treatment, a series of books on parasitic plants has appeared, for example Parker and Riches (1993), Press and Graves (1995), Heide-Jørgensen (2008) and Joel *et al.* (2013). These volumes deal with parasitic angiosperms as a whole. Less exhaustive discussions of parasitic plants are summarized in Těšitel (2016), Nickrent and Musselman (2017), and Texeira-Costa and Davis (2021). Reviews of groups of parasites we cover in this book can be found in their respective chapters.

As the number of publications suggests, an appraisal and review of research would be a large undertaking, beyond the scope of this book. As examples, two highlights stand out: first, phylogenetic studies, well reviewed in Nickrent (2020) documenting the evolution of parasitism in 12 clades of angiosperms; and second, the germination biology of parasites, especially root parasites. This has resulted in the discovery of a new group of plant hormones, the strigolactones. These growth regulators are now known to be widespread in angiosperms. A helpful review of strigolactones is provided by Xie *et al.* (2010).

The heightened level of research in parasitic plants is now a worldwide phenomenon. In 1957, in response to the discovery of witchweed in the USA, an exhaustive review of the world literature on witchweed was published as a detailed annotated bibliography (McGrath *et al.*, 1957). It had 298 references, including non-peer-reviewed entries. A November 2022 Web of Science search (all peer reviewed) for *Striga* yielded 1801 strikes. Similarly, an extensive review of *Cuscuta* in 1994 (Dawson *et al.*, 1994) had 303 references, the Web of Science search for *Cuscuta* gave 1271, and for *Orobanche* (including *Phelpanche*) (broomrapes) about 1585. Of course, not all the references concern agriculture or even biology. Studies on these plants have expanded beyond agronomic interest to phylogenetic research, physiology, herbal medicines, ecology and more.

Despite the thousands of studies by scientists around the world, smallholder farmers in Africa have profited little by the effort and expense put into understanding parasitic weeds. Control, either by reducing infestations or by reducing the impact on the host, is seldom realized by the farmer whose management of the parasites affects daily existence. It has been previously observed by Schut *et al*. (2015a) that research on parasitic weeds in Africa has mainly focused on understanding the biology, ecology and distribution of the parasites, and on the development and testing of strategies for managing them, with some efforts on understanding the socio-cultural dimension (e.g. Vissoh *et al*., 2008; N'cho *et al*., 2014) and economic impact of parasitic weeds (e.g. N'cho *et al*., 2017, 2019). The institutional and political dimensions of parasitic weeds and the innovations to address them have not received the same structural attention. While farmers frequently participate in parasitic weed research (e.g. Schulz *et al*., 2003; Emechebe *et al*., 2004; Abang *et al*., 2007; Tippe *et al*., 2017), the private sector, civil society organizations and government representatives are less often involved (Schut *et al*., 2015b). For research on parasitic weeds to benefit smallholder farmers, involving a broader range of stakeholders and considering broader dimensions than just the crop or farm is deemed necessary (Rodenburg *et al*., 2015).

1.5 Parasitic Weeds in African Agricultural Systems

Parasitic weed infestation, in particular by species of the Orobanchaceae, constitutes one of the most important and complex agricultural production constraints in Africa (e.g. Vurro *et al*., 2010; Waddington *et al*., 2010). The problem is important because staple crops such as maize, rice, sorghum and millet are important hosts of a number of the parasitic weed species (e.g. *Striga hermonthica*, *S. asiatica*, *Rhamphicarpa fistulosa*) and because these species are widely distributed (e.g. Rodenburg *et al*., 2016b). Hence, the parasitic weed problem greatly affects food security in the region.

The problem is complex because of the ingenious biology of plant parasitism (see Shen *et al*., 2006; Spallek *et al*., 2013; Těšitel, 2016). Many weedy species of parasitic plants have a wide host range, and their germination and reproductive biology render them highly successful in annually cropped environments. The problem is also difficult because most of the affected crops in Africa are predominantly grown by smallholder farmers. Although smallholder farming systems in Africa are highly diverse in their resources, environments, challenges and opportunities (e.g. Tittonell *et al*., 2010), the majority of farmers struggle with adverse environmental conditions and limited access to productive agricultural land, production resources, information and services. These conditions render the control of parasitic weeds an even more difficult task.

Parasitic weed infection and damage is often associated with and aggravated by adverse biophysical conditions such as poor soil fertility and drought. The weeds present technological challenges because the number of feasible, effective and affordable control measures is limited (e.g. Tippe *et al*., 2017; Silberg *et al*., 2020) or farmers are unaware of them. The affordability, accessibility and awareness of control strategies are a direct function of the socio-cultural, economic, institutional and even political dimensions shaping this problem; agricultural extension services in rural Africa are often poorly staffed, poorly equipped and ill-informed on parasitic weed problems and ways to address them, and communications between farmers and extension and crop protection services are often suboptimal (Schut *et al*., 2015b). Therefore, addressing the problem of parasitic weeds in Africa, by technological and organizational control strategies, requires not only a thorough understanding of the biology and ecology of the important species but also a better understanding of the social, economic and institutional environments where these weeds are problems. Such research and development endeavours need to involve a range of stakeholders, including social and natural science researchers, farmers, extension services, and public and private crop health services. The control strategies arising from such a transdisciplinary research approach should match the resource availability and farming practices of the farmers who need to implement them and should be effectively communicated to them and be locally available at an affordable price or input level.

The present work deals with parasitic plants that are current or potential agricultural pests (Table 1.1). Although it is beyond the scope of this book to note them all, parasitic species that are not currently a problem in Africa possess – at least theoretically – the ability to become weedy and cause crop damage in the future. There are examples of indigenous parasitic plants becoming pathogens in agriculture and forestry (e.g. *Thonningia sanguinea* on rubber, coffee and other crops in Western Africa; Imarhiagbe and Aigbokhan, 2019). Knowledge on biology and control of those species representing current parasitic weed problems in Africa, as well as on the socio-economic and institutional environments of farming systems where these problems are embedded, could prepare us for future outbreaks. The hope of the authors is that this contribution will increase the awareness of these plants as parasitic pathogens – especially those that are currently lesser known – ultimately to aid the smallholder farmer in Africa.

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