Molecular Plant Pathology

MOLECULAR PLANT PATHOLOGY DOI: 10.1111/mpp.12058

Pathogen profile

The genus *Striga*: a witch profile

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SUMMARY

The genus *Striga* comprises about 30 obligate root-parasitic plants, commonly known as witchweeds. In particular, *S. hermonthica*, *S. asiatica* and *S. gesnerioides* cause immense losses to major stable crops in sub-Saharan Africa. Most *Striga* species parasitize grass species (Poaceae), but *Striga gesnerioides* has evolved to parasitize dicotyledonous plants. Aspects of phylogeny, economic impact, parasitic life style and molecular discoveries are briefly reviewed to profile one of the main biotic constraints to African agriculture.

Taxonomy: *Striga* Lour.; Kingdom Plant; Division Angiospermae; Clade Eudicots; Order Laminales; Family Orobanchaceae.

Important hosts: *Sorghum* Moench., maize (*Zea mays* L.), rice (*Oryza* L.), sugarcane (*Saccharum* L.), pearl millet [*Pennisetum glaucum* (L.) R. Br.], cowpea [*Vigna unguiculata* (L.) Walp.].

Disease symptoms: Stunted growth, drought-stressed-like appearance, in severe cases chlorosis and necrosis.

Economic importance: 1 billion $US per annum.

Disease control: Hand weeding, breeding, chemical control, intercropping with catch or trap crops.

Useful webpages: http://ppgp.huck.psu.edu; http://striga.psc.riken.jp

INTRODUCTION

Parasitic plants are a major threat to today's agriculture and provide an intriguing case of pathogenesis between species of relatively close evolutionary ancestry. Almost all crop species are potential hosts for parasitic plants, but severe disease outbreaks are usually restricted to certain host–pathogen combinations. The evolutionary strategy of exchanging autotrophy for dependence on host plants (parasitism) may seem odd, but it has proven to be evolutionarily successful for several plant species. Plant parasitism has arisen at least 12 times independently, generating more than 4000 parasitic dicotyledonous plant species (Westwood *et al*., 2010). Although some parasitic plants are still photosynthetically active (hemiparasitic), others are not, and depend entirely on a host (holoparasitic). The establishment of parasitism is essential for holoparasites and several hemiparasites, and therefore these species are called obligate parasites. Depending on which host organ is infected, parasitic plants are grouped into stem or root parasites. In both cases, the parasite connects to the host vascular system via a specialized feeding organ, the haustorium. Unlike the haustoria of plant-pathogenic fungi or oomycetes, plant haustoria are always multicellular organs with complex anatomies and multiple cell types (Mayer, 2006). The genus *Striga* consists of obligate hemiparasitic root parasites, some of which are serious agricultural pests (Parker, 2009). This pathogen profile aims to give readers a brief overview of the biology of *Striga* and how this relates to current control strategies.

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THE GENUS *STRIGA*—PLANT PARASITES AMONG PLANT PARASITES

'Striga' is the Latin word for 'witch'. Witchweed, Yan maemod (Thai), Buta (Kiswahili) and other common names for *Striga* often refer to the word 'witch', presumably because plants diseased by *Striga* display stunted growth and an overall drought-like phenotype long before *Striga* plants appear. *Striga* species are annual plants and most of their life cycle occurs underground. The genus *Striga* was previously grouped within the family Scrophulariaceae, but more recent analyses have placed *Striga* as a monophyletic group in the family Orobanchaceae Vent. The family Orobanchaceae contains the highest number of parasitic species (Bennett and Mathews, 2006). Although most Orobanchaceae species are root parasites, ranging from facultative hemiparasitic plants, such as *Triphysaria* Fisch. & C.A. Mey., to holoparasitic *Orobanche* L. (broomrapes), 12 known species in the genus *Lindenbergia* Lehm. are not parasitic (Bennett and Mathews, 2006; See Table S1). This offers an opportunity to study successive stages in plant parasitism within the relatively confined evolutionary boundaries of one plant family (Westwood *et al*., 2010). Parasitism is believed to have evolved once within this family and the divergence of the *Lindenbergia* linage predates this event. Specialization towards holoparasitism then followed in several genera independently, often leading to closely related species with different degrees of parasitism (Bennett and Mathews, 2006).

Approximately 30 *Striga* species have been described and most parasitize grass species (Poaceae). *Striga gesnerioides* (Willd.) Vatke is the only *Striga* species that is virulent to dicots (Mohamed and Musselman, 2008). *Striga* possibly originates from a region

between the Semien Mountains of Ethiopia and the Nubian Hills of Sudan (Atera and Itoh, 2011). This region is also the birthplace of domesticated sorghum (*Sorghum bicolor* L.), which is a major host species for several *Striga* species, including *S. hermonthica* (Delile) Benth. and *S. asiatica* (L.) Kuntze, and is believed to be the host on which monocot-parasitizing *Striga* species have evolved and spread throughout Africa and Asia (Vasudeva-Rao and Musselman, 1987).

Striga asiatica is morphologically similar to *S. hirsuta* Benth., *S. lutea* Lour. and *S. elegans* Benth., and therefore they are grouped into one *Striga* cluster. A few *S. asiatica* races or ecotypes occur outside Africa, mainly in Asia (Mohamed and Musselman, 2008). Because the evolutionary relationship between African and Asian *S. asiatica* populations is not well understood, the populations are often treated separately. *Striga hirsuta*, *S. lutea* and *S. elegans* are not considered to be serious agricultural pests (Mohamed and Musselman, 2008). *Striga asiatica* is autogamous like most *Striga* species, but *S. hermonthica* and *S. aspera* (Willd.) Benth. are obligate outcrossers and occasionally hybridize (Mohamed and Musselman, 2008). Allogamy probably contributes to the genetic variation between subpopulations of *S. hermonthica*, and also restricts spread outside the geographical distribution of available pollinators (Berner *et al*., 1997).

A recent phylogenetic analysis using six chloroplastic loci has suggested a closer relationship of *S. gesnerioides* to *S. aspera* and *S. hermonthica* than *S. asiatica* to *S. hermonthica* and *S. aspera*, despite the similar host specificities of *S. asiatica*, *S. hermonthica* and *S. aspera*. *Striga gesnerioides* is morphologically distinct relative to other *Striga* species (Estep *et al*., 2012). The haustoria differ especially in size and morphology from those of monocot-parasitizing *Striga* species. The haustoria of *S. gesnerioides*, in contrast with those of other *Striga* species, such as *S. hermonthica*, exhibit a branched vascular system and lack the so-called hyaline body (Ba, 1979), which is a specialized tissue surrounding the xylem bridge connecting the vascular systems of host and parasite.

THE IMPACT—DISTRIBUTION AND HOST RANGE

Striga is an 'Old World' parasite, and several species were already recognized as cereal pests in Africa and India at the beginning of the last century. Roughly 80% of the described *Striga* species are endemic to Africa, nine species are found outside Africa and three species, *S. curvilflora* Benth., *S. multiflora* Benth. and *S. parviflora* Benth., are present on the Australian continent (Berner *et al*., 1995). *Striga* species are predominantly found on open grasslands and savannahs in semi-arid tropical regions. Infestations are more pronounced in infertile soils, but *S. asiatica* can grow in a wide range of different soils (Cochrane and Press, 1997). An increase in monoculture in some parts of Africa has led to reduced soil fertility, thus further worsening the situation with regard to *Striga* infestations (Berner *et al*., 1997). In addition to the presence of host-derived germination stimulants, temperature is an important factor affecting the distribution of *Striga*, as prolonged exposure to high temperatures and humid conditions is required to break seed dormancy in *Striga* (Ejeta and Gressel, 2007).

An estimated cereal production area of 50 million hectares, approximately the size of Spain, shows different levels of *Striga* infestation in Africa (Westwood *et al*., 2010). In total, 25 African countries reported *Striga* infestations in 2005 (De Groote *et al*., 2008). The socioeconomic consequences are difficult to measure, but a few estimations have suggested that *Striga* affects the life of more than 100 million people in Africa and causes economic damage equivalent to approximately 1 billion $US per year (Labrada, 2008; Waruru, 2013). Host plants include sorghum, millet, maize, upland rice, sugarcane, cowpeas—representing the most important stable crops grown by subsistence farmers in affected areas. Farmers have reported losses between 20% and 80%, and are eventually forced to abandon highly infested fields (Atera and Itoh, 2011). The extent of yield losses cannot be explained solely by competition for nutrients and water (Berner *et al*., 1995). When disease progresses, very severe symptoms, such as water-soaked leaf lesions, chlorosis, necrosis and leaf desiccation, occur (Berner *et al*., 1997). An unknown phytotoxin has been proposed to at least partially contribute to the disease phenotype, but still awaits biochemical identification. Interestingly, *Striga* extracts are rich in secondary metabolites and find broad use in traditional medicine, especially as a result of their antimicrobial activity (Koua and Babiker, 2011).

Only five *Striga* species are currently of economic importance, with *S. hermonthica* causing by far the most serious damage to sub-Saharan cereal production, followed by *S. asiatica*, *S. gesnerioides* and, to a far lesser extent, *S. aspera* and *S. forbesi* Benth. (Parker, 2009). Facultative parasitic plants of the sister genus *Buchnera* L. are sometimes mistaken for *Striga*, but cause far less damage on host plants such as sorghum, maize or millet (Berner *et al*., 1997). The obligate parasitic species *Alectra vogeli* (Benth., Orobanchaceae) is commonly also referred to as yellow witchweed and, similar to *S. gesnerioides*, is a major biological constraint to cowpea production in eastern and southern Africa (Musselman, 1980).

Striga hermonthica is widespread in sub-Saharan Africa, and is found throughout West Africa to Ethiopia, Uganda and Kenya in East Africa (Fig. 1A; Mohamed *et al*., 2001). Occurrences of *S. hermonthica* have also been reported from south-east Africa. *Striga hermonthica* is particularly harmful to sorghum, maize and millet, but is also increasingly being found in sugarcane and rice fields (Atera and Itoh, 2011). Upland rice is becoming more and more important for African agriculture, not least because it can sustain more people per crop area than can maize or sorghum (Atera and Itoh, 2011). In an ongoing effort to breed New Rice for Africa

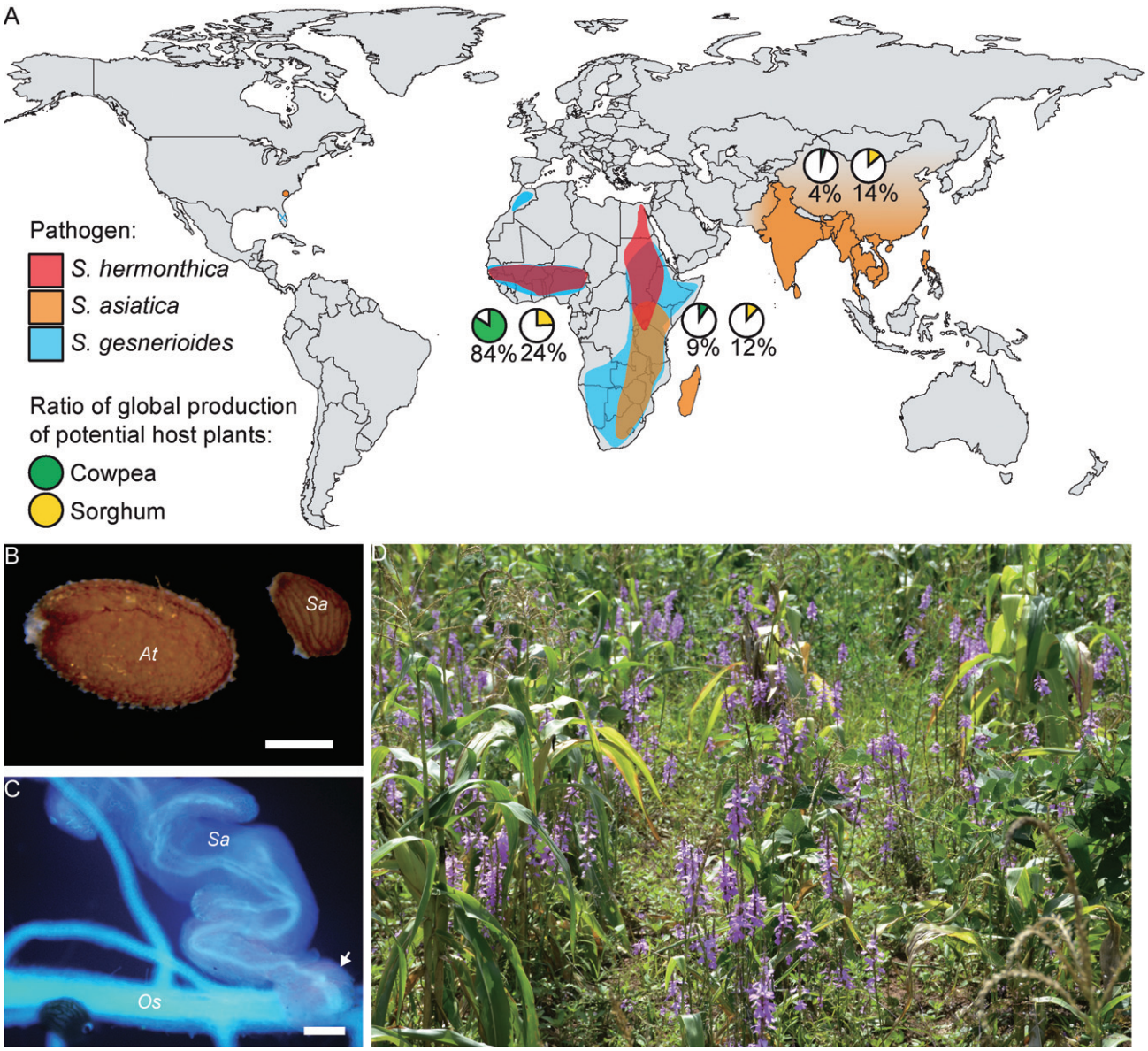

Fig. 1 (A) Global distribution of the economically most destructive *Striga* species and two major host plants, cowpea and sorghum, according to Mohamed and Musselman (2008) and Musselman (1980). The relative production of sorghum and cowpea in West Africa, East Africa and South-East Asia is based on values published by the Food and Agriculture Organization of the United Nations (FAO, http://www.fao.org/corp/statistics/en) for 2011. (B) *Striga asiatica* (*Sa*) seed next to an *Arabidopsis thaliana* (*At*) seed. (C) Two-week-old *S. asiatica* (*Sa*) haustorium (arrow) on rice (*Oryza sativa*, *Os*). (D) *Striga hermonthica*-infested sorghum field in Kismu (Kenya, December 2012). (B, C) Scale bars represent 200 μm.

(NERICA), several NERICA lines have been tested for *Striga* resistance. Some cultivars show good resistance to *S. hermonthica* and *S. asiatica*. Susceptible NERICA varieties display biomass reduction of up to 81% when infected with either *S. hermonthica* or *S. asiatica* (Cissoko *et al*., 2011). Notably, even resistant varieties showed a biomass reduction of 46% with *S. hermonthica* and 24% with *S. asiatica* in this study. In addition, some susceptible rice varieties perform better than others, a phenomenon called 'tolerance'. Tolerance is so far the only genetic resource for resistance against *Striga* in maize (Cardoso *et al*., 2011). Ideally, breeding for *Striga* resistance or tolerance should be linked with other favourable traits, such as high yield and drought resistance. Drought is the major constraint to agriculture in semi-arid zones. Promising results were obtained in sorghum when both traits, *Striga* and drought resistance, were combined by classical breeding. This effort was internationally recognized when Professor Gebisa Ejeta received the World Food Prize in 2009 (http://www.worldfoodprize.org).

Striga asiatica is the most widespread *Striga* species (Fig. 1A), with a geographical distribution ranging from South Africa to East Africa and from the Arabian Peninsula to Far East Asia, including India and Pakistan (mainly on sorghum and millet), Cambodia, China, Thailand (maize in the 1970s), Vietnam, Malaysia, Indonesia and the Philippines (mainly on rice) (Musselman, 1980). Asian *S. asiatica* occurs mainly in the form of two morphotypes: white-flowered *S. asiatica*, which is found in India and Pakistan, and a yellow-flowered race which is predominant in Thailand and Indonesia (Vasudcva Rao, 1984). African *S. asiatica* plants have mainly red flowers. *Striga asiatica* infestation is less severe in Asia relative to Africa. Until the start of the 1990s, African *S. asiatica* was mainly restricted to South and Central Africa (Mohamed and Musselman, 2008). Although *S. asiatica* is now increasingly being found in other parts of Africa, it is most problematic south of the Equator in East and South Africa (Fig. 1A). Tanzania marks a transition zone between *S. hermonthica* and *S. asiatica*, with *S. asiatica* becoming more problematic in countries such as Tanzania, Malawi, Mozambique and Madagascar (Parker, 2009). In addition to numerous previous studies of host specialization (for a review, see Musselman, 1980), a study in Benin has discovered a high degree of host specialization within 14 analysed *S. asiatica* populations (Botanga *et al*., 2002). For example, some *S. asiatica* isolates collected from wild grass species are unable to successfully parasitize sorghum and maize plants, which are susceptible to other *S. asiatica*. In addition, a significant linear relationship between genetic and geographical distance was observed. Mostly unstudied populations of *S. asiatica* can be found outside the usual distribution, for example in the Nile delta. *Striga asiatica* was also accidentally introduced to North and South Carolina (USA) in the 1950s (Hood *et al*., 1998). The US population of *S. asiatica* is highly monomorphic, which strongly supports the theory of a single introduction event from Africa. An immense effort costing about 250 million $US was undertaken to eradicate *S. asiatica* from the USA. Although *Striga* currently does not pose a high risk for modern high-input agricultural systems, such as those in the south-eastern USA, it remains a significant problem for African farmers with no or only limited access to fertilizers, herbicides and modern mechanical tillage equipment (Berner *et al*., 1997). The introduction of new farming systems into rural societies takes time, such that hand weeding often remains the only technique to control *Striga*.

Striga gesnerioides is extremely widespread on the African continent (Mohamed *et al*., 2001). It is mainly a problem to cowpea farming in West Africa (Mali, Burkina Faso, Niger and Benin) and also to tobacco plantations in Zimbabwe. Cowpea is one of the most important food legumes in semi-arid regions, and is considered to be a subsistence crop in sub-Saharan Africa. *Striga gesnerioides* was also introduced to Florida, USA, in 1979. Based on the genetic variation observed in US strains, a single introduction effect is also most likely for *S. gesnerioides* (Musselman, 1980). Other *Striga* species are of lesser economic importance, but locally can cause significant yield losses. For example, *S. angustifolia* (Don) Saldhana has been reported to infect sorghum, rice and sugarcane in India, and *S. aspera* causes significant losses on maize plantations in Nigeria, Cameroon, Ivory Coast and Ethiopia and on rice plantations in Ivory Coast and Senegal (Kroschel, 1993).

THE PARASITIC LIFE CYCLE OF *STRIGA*

Parasitic plants have evolved specific traits which allow parasitism or reflect the consequences of adaptation to a parasitic life style. Critical stages in the life of an obligate root parasite are as follows: (i) the identification of a suitable host, thus coupling germination and seedling growth with the presence and direction of a potential host; (ii) gain of access to the host's nutrients and water supply; this process involves the production of a functional haustorium; (iii) completion of the life cycle on the host; this includes the establishment of parasitism and its maintenance until seeds are set.

Germination—location of a host root

Striga and other root-parasitic plants have evolved highly efficient strategies to ensure successful reproduction. Key strategies include the dispersal of an enormous amount of tiny seeds (Fig. 1B) of high longevity to establish an extremely persistent seed bank. These dust-like seeds are easily dispersed by wind, crop seeds, water and people. In addition, *Striga* seeds can survive for more than 10 years before germination (Atera and Itoh, 2011). Germination is linked to the presence of a nearby host, because the endosperm of *Striga* seeds can sustain growth/life only for the first 3–7 days (Berner *et al*., 1995). Within that time, *Striga* must successfully establish a parasitic relationship with the host plant or otherwise die. This aspect was successfully exploited during an *S. asiatica* eradication programme in the USA, when so-called 'suicide germination' was induced by fuming farmland with ethylene to trigger *Striga* germination in the absence of host plants (Parker, 2009).

The germination of *Striga* depends on the perception of germination stimulants released by host roots. In order to be responsive to germination stimulants, *Striga* seeds must go through a phase of moisture and high temperatures for 7–14 days, called 'conditioning'. If, during that time, no germination stimulant is perceived, *Striga* seeds fall into a secondary dormancy (Cardoso *et al*., 2011). Several germination stimulants have been isolated and include strigolactones, dihydrosorogoleone, sesquiterpene, kinetin, coumarin, jasmonate, ethylene and fungal metabolites (reviewed in Cardoso *et al*., 2011). Strigolactones are certainly the best studied and extremely potent inducers of *Striga* germination. Strigolactones are associated with the negative regulation of root

and shoot branching (tillering). They also induce hyphal branching of arbuscular mycorrhizal (AM) fungi, presumably to attract them in low-nutrient environments (Xie and Yoneyama, 2010). Major discoveries in biosynthesis and perception have been made in recent years, and key players have also been predicted to be present in *Striga* (Cardoso *et al*., 2011; Yoshida and Shirasu, 2012). Strigolactones have been shown to induce the germination of *Striga* at concentrations as low as 10^{-16} M (Musselman, 1980). The first strigolactone was interestingly isolated from the root exudates of a nonhost plant, cotton (Cook *et al*., 1966); indeed, the use of nonhost plants producing high levels of *Striga* germination stimulants is a promising strategy in *Striga* control. In particular, intercropping with the legume *Desmodium* has been proven to be successful in some parts of Africa (Khan *et al*., 2006). Alternatively, low strigolactone-producing host plants reduce *Striga* germination and thus infection (Umehara *et al*., 2008). Low *Striga* germination stimulant activity is controlled in sorghum by one single recessively inherited gene, *lgs* (*low germination stimulant*) (Satish *et al*., 2012). Lines showing low germination-inducing activity have been shown to have good tolerance towards *S. asiatica* and *S. hermonthica*, but tolerance mediated by low strigolactone production is less reliable when the *Striga* seed pool in the soil is high (Atera and Itoh, 2011).

Haustorium development

The radical tip grows chemotropically towards potential host roots after germination. On contact, *Striga* radicals stop growing, attach to host roots, form a haustorium and penetrate into the root cortex of potential hosts. Most plants, including many nonhost plants, do not resist attachment and penetration. An exception to this is *Phtheirospermum japonicum* (Thunberg) Kanitz, a hemiparasitic plant commonly found in East Asia and relatively closely related to *Striga*. The root exudate from *P. japonicum* is able to induce the germination of *S. hermonthica*, but *S. hermonthica* radicals rarely penetrate to *P. japonicum* roots (Yoshida and Shirasu, 2009). It is currently unknown whether *P. japonicum* actively inhibits the attachment of *Striga* or whether it is lacking a factor required for *Striga* penetration.

Within 12 h of attachment, reorganization of the *S. asiatica* meristem is initiated. Essential for this step is the perception of haustoria-inducing factors. Several naturally occurring haustoria-inducing factors have been isolated and their mode of action is best studied by following 2,6-dimethoxy-*p*-benzoquinone (DMBQ; Chang and Lynn, 1986). DMBQ is a product of lignin oxidation and decarboxylation of phenolic acids found in plant cell walls. The current model of DMBQ perception is mainly based on work performed on *S. asiatica* and *Triphysaria versicolor* Fisch. & C.A. Mey. (Bandaranayake *et al*., 2010; Keyes *et al*., 2000). In summary, this model proposes that DMBQ is released from host cell walls and eventually enters parasite cells. The NAD(P)H-dependent quinone reductase QR1 reduces DMBQ to produce an unstable semiquinone intermediate, which is required for haustorium development. *Triphysaria QR1* is transcriptionally up-regulated in response to host root extracts and *QR1* knock-down roots are compromised in haustoria formation. A second quinone reductase (QR2) does not respond to host root extracts, but to DMBQ, and could act as a parallel detoxification pathway. A balance between the detoxification and accumulation of the haustorium-inducing semiquinone might create an equilibrium-dependent threshold mechanism, whereby a continuous exposure to DMBQ is required for haustoria formation.

In addition to chemical signals, a thigmotropic response is required for *Striga* to produce morphologically normal haustoria (Wolf and Timko, 1991). Within 24 h after contact, rapid cell division of the radical tip stops and a hypertrophic growth phase begins (Hood *et al*., 1998). Penetration of the host epidermis is mediated by the elongation of distal cells in the protoderm or epidermis and underlying ground tissue, followed by rounds of periclinal and anticlinal divisions of these cells, leading to growth into the cortex of host plants. When the host endodermis is reached, the most distal cells of the haustorium elongate and divide, thus forming a palisade arrangement of cells. Break through the endodermis is often delayed, but, once accomplished, vascular connections are established. In general, penetration is completed 48–72 h after contact with a host root (Hood *et al*., 1998). A detailed scanning electron microscopy study by Dorr (1997) showed that invading *Striga* cells perforate the host vascular system using a specialized structure, the osculum. Interestingly, no phloem-to-phloem connections have been observed between *Striga* and host plants. Once xylem-to-xylem connections are established, the cotyledons of *Striga* enlarge and break free from the seed coat within 24 h (Hood *et al*., 1998).

Many nonhost plants allow the penetration of *S. hermonthica* and the early events of haustorium formation. Although infection is mainly terminated in the cortex of *Lotus japonicus* (Regel) K. Larsen, *S. hermonthica* reaches the stele in *Arabidopsis* and cowpea, but fails to develop beyond the six-leaf-pair stage (Yoshida and Shirasu, 2009). Nonhost resistance in lettuce, marigold and cowpea against *S. asiatica* is typically established in the cortex within 72 h post-infection (Hood *et al*., 1998). Resistance to *S. hermonthica* and *S. asiatica* in rice (*Oryza sativa* L.) cultivar Nipponbare also occurs post-attachment (Gurney *et al*., 2006). Using an inbred line between Nipponbare and the susceptible rice line Kasalath, Gurney *et al*. (2006) located seven putative quantitative trait loci (QTLs), which explained 31% of the overall resistance phenotype. Although resistance to monocot-infecting *Striga* seems to be polygenetic, two types of resistance are known in cowpea towards *S. gesnerioides*: a hypersensitive reaction (HR)-type response, causing the death of the parasite within 3–4 days, and a second type of resistance, allowing *S. gesnerioides* to establish xylem-to-xylem connections, but not supporting further

growth of the parasite (Li and Timko, 2009). The former type of resistance is race specific and mediated by the *RSG3-301* gene product in cowpea cultivar B301 against *S. gesnerioides* race 3. Li and Timko (2009) cloned the RSG3-301 gene and showed that it encodes a coiled-coil nuclear-binding site leucine-rich repeat (CC-NBS-LRR) type of resistance (R) protein. CC-NBS-LRR proteins are known to confer resistance to a wide variety of plant pathogens in many other plant species.

It is currently unknown which *Striga* genes are required to successfully infect susceptible host plants. Haustorium development uses cellular processes similar to organogenesis processes known in other autotrophic plants. For example, cycline promoter B1 is activated within 24 h after DMBQ treatment in *P. japonicum*, and localized auxin and ethylene accumulation are important for haustoria formation in *T. versicolor* (Ishida *et al*., 2011; Tomilov *et al*., 2005).

Haustoria constitute the interface between host and parasite. Although all parasitic plants develop haustoria, haustoria differ anatomically between different species. Although *Striga* lacks phloem-to-phloem connections, direct connections between sieve elements of *Orobanche crenata* (Forsk.) and *Vicia narbonensis* (L.) were observed by electron microscopy (Dorr and Kollmann, 1995). The transmission of phloem-localized viruses or RNA molecules has been reported for several parasitic plants, but not for *Striga* species (Leblanc *et al*., 2012). However, interspecies plasmodesmata between *S. gesnerioides* and pea (Dorr, 1996) raise the possibility of symplastic transport of nutrients and signalling molecules between *Striga* and host plants. The movement of DNA molecules across graft junctions also occurs via cell-to-cell movement and does not involve phloem connections (Stegemann and Bock, 2009). So far, there is no direct evidence of mRNA transit between *Striga* species and host plants. However, host-induced silencing of β-glucuronidase (GUS) gene expression in *T. versicolor* and the identification of several horizontal gene transfer (HGT) events between *S. hermonthica* and monocot hosts suggest that mRNA and other RNA molecules could travel between host and root parasite (Tomilov *et al*., 2008; Yoshida *et al*., 2010b). A degenerated poly-A sequence in a horizontally transferred *S. hermonthica* gene, *ShContig9483,* supports an mRNA-related origin (Yoshida *et al*., 2010b). A putative homologue of *ShContig9483* was found in *S. gesnerioides* but not *Orobanche minor* Sm., suggesting that this HGT event might have occurred after the genera split, but presumably before *S. gesnerioides* evolved host specificity towards dicot plants. Mechanisms underlying the integration of host genes into the germline of parasitic plants remain elusive. Nevertheless, HGT has also been reported in several other parasitic plants and seems to be more frequent in parasitic plants than in nonparasitic plants (Leblanc *et al*., 2012). It remains to be shown whether and to what extent RNA molecules travel between *Striga* and host plants and, if so, whether these molecules can function *in trans*.

Establishment of parasitism and life cycle completion

After xylem-to-xylem connections have been established, *Striga* grows upwards and adventitious roots are produced. These adventitious roots are able to form lateral (secondary) haustoria on the same or other host plants. Facultative hemiparasitic plants, such as *Triphysaria* or *Phtheirospermum*, produce exclusively lateral haustoria. Secondary haustoria are believed to be evolutionarily older than primary or terminal haustoria (Westwood *et al*., 2010). Under natural conditions, host plants are usually parasitized by several *Striga* plants, and the parasites quickly become a metabolic sink for photoassimilates and nutrients. Nitrogen levels are at least twice as high in *Striga* as in host plants (Agabawi and Younis, 1965). Depletion of nitrogen almost certainly affects host physiology and provokes lower host photosynthesis rates, which are frequently associated with *Striga* infections. Several photosynthetic parameters are reduced in sorghum plants infected with *S. hermonthica*, including the electron transport rate through photosystem II and photochemical quenching (Rodenburg *et al*., 2008). Frost *et al*. (1997) have shown that the negative effect on photosynthesis correlates with reduced stomatal conductance, which is possibly the consequence of elevated abscisic acid (ABA) levels of sorghum plants infected by *S. hermonthica*. Not only ABA, but also other plant hormones, such as cytokines and gibberellic acid levels, are altered in sorghum plants infected with *Striga* relative to control plants (Musselman, 1980; Taylor *et al*., 1996). It is not known whether *Striga* manipulates host hormone homeostasis directly and how these changes contribute to parasitism.

After emergence from the soil, *Striga* plants begin to photosynthesize. However, the low CO_2 fixation and high dark respiration rates of *S. asiatica* result in a negative carbon gain over the 24-h period, thus making *Striga* still host dependent when growing above ground (Press *et al*., 1987). In addition, *Striga* leaves are characterized by a degenerated palisade cell layer and a relatively small number of chloroplasts per cell. Low photosynthesis in *Striga* is supported by transcriptome data from RNA isolated from the above-grown *S. hermonthica* tissue. A relatively low expression of chlorophyll biosynthesis- and photosynthesis-related genes was observed when compared with the expression of these genes in the facultative hemiparasitic plant *T. versicolor* (Wickett *et al*., 2011). The high transpiration rates of *Striga* suggest that most host photoassimilates are obtained by transpirational pull, explaining why high humidity is inhibitory to *Striga* growth. Indeed, *Striga* stomata show high conductance and respiration rates and little response to dark-induced closure (Press *et al*., 1987). Relative to the host plant, *Striga* has a disadvantageous leaf surface ratio and might compensate for this with higher stomatal conductance (Press *et al*., 1987). Surprisingly, when water depletion was investigated under controlled experimental conditions of *Striga*-infected maize plants, no significant increase

in water use was observed until the very late stage of infection (63 days post-infection) (Taylor and Seel, 1998). Before that time, maize plants had already established disease symptoms and showed stunted growth. However, in the final stage of infection, maize plants used nearly 50% more water than control plants.

The fact that disease symptoms appear before *Striga* emerges illustrates how ineffective the biocontrol of above ground-grown *Striga* by hand weeding or herbicides is likely to be. Nevertheless, these techniques are important to avoid the reproduction of *Striga*. *Striga asiatica* and *S. hermonthica* flower about 4 weeks after emergence. *Striga gesnerioides* has been reported to flower earlier (Berner *et al*., 1995). Inflorescences are arranged in spikes or racemes, each carrying several flowers. Flower colour varies between species and sometimes within species from blue and pink (e.g. *S. hermonthica* and *S. gesnerioides*) to white, yellow or red (e.g. *S. asiatica*). After pollination, seeds mature within 4 weeks in seed pods, which contain 250–500 dust-like seeds of 200–300 μm in size. Under optimal conditions, each *Striga* plant can produce up to 50 000–500 000 seeds (Berner *et al*., 1995). When the seed pods crack, seeds are spread into the soil and quickly build up in numbers. *Striga* seeds require a certain time of after-ripening, about 6 months at elevated temperatures. According to Berner *et al*. (1997), this could be an adaptation to prevent germination during the last rains of the seasons, when no hosts are in the field.

NEXT-GENERATION *STRIGA* RESEARCH

In recent years, efforts have been undertaken to elucidate the molecular events underlying *Striga* infections using next-generation and conventional sequencing technology (Yoshida *et al*., 2010a). For example, comparative studies on repetitive regions in five *Striga* species generated a total of about 2200 Sanger sequence reads and about 10 000 454 reads (Estep *et al*., 2012). Partially assembled and identified repeats were most similar to the most closely related plant species. Overall, the authors came to the conclusion that the analysed *Striga* genomes have a rather typically complex angiosperm genome. Estimated haploid genome sizes range from 615 Mb for *S. asiatica* to 1425 Mb for *S. hermonthica* and 2460 Mb for *S. forbesii*, suggesting several polyploidization events. Polyploidization is also an important factor for speciation in the sister genus *Orobanche* (Schneeweiss *et al*., 2004). No evidence of large transfers of repetitive DNA regions from the host genomes was observed, which is in contrast with the observed HGT events between monocot genes and *S. hermonthica* (Yoshida *et al*., 2010b), and favours the hypothesis that HGT events originate from mRNA species rather than from large pieces of genomic DNA.

Next-generation sequencing technology has led to an increase in available transcriptional data for *S. hermonthica* and related species. For example, Wickett *et al*. (2011) analysed sequence data obtained from Illumina short reads of mRNA isolated from above-ground tissue of three Orobanchaceae species: the facultative hemiparasite *T. versicolor*, *S. hermonthica* and *Phelipanche aegyptiaca* (pers.) Pomel. The expression of photosynthesis-related genes was much lower in *S. hermonthica* than in *Triphysaria*, and no expression of these genes was detected in *Phelipanche*. This study also revealed that chlorophyll *a* synthesis gene expression was conserved and detectable in all three species, even in the nonphotosynthetically active *Ph. aegyptiaca*.

Next-generation sequencing technology will almost certainly provide detailed transcriptional information for *Striga* at different stages of infection and on different hosts, and will allow the simultaneous detection of host and pathogen transcriptomes. So far, host transcriptome data are mainly based on microarray studies or similar methods. Hiraoka *et al*. (2009) used a suppression subtractive hybridization strategy of mRNA isolated from *Lotus japonicus* to investigate differences when infected with *S. hermonthica* (resistant) or *Ph. aegyptiaca*. Several jasmonic acid-regulated genes showed higher expression, with some being systemically induced. The incompatible interaction with *S. hermonthica* was characterized by higher expression of genes in the biosynthetic pathway for vestitol. Vestitol is a phytoalexin with insect repellent activity. It is not clear whether vestitol concentrations indeed rise after *Striga* infection and whether vestitol is phytotoxic to *S. hermonthica*, but the up-regulation of defence-associated genes suggests that *S. hermonthica* is actively recognized as a pathogen and elicits a defence response in *L. japonicus*. The accumulation of cytotoxic material is also probably the cause of nonhost resistance to *S. hermonthica* in *Tripsacum dactyloides*, a wild relative of maize. In contrast with *Z. mays*, haustoria formation is impaired on *T. dactyloides* plants by an unknown factor. This factor is also able to suppress haustoria formation on *Z. mays*, when *Striga* plants are attached to *T. dactyloides* at the same time (Gurney *et al*., 2003).

Microarray analysis on cowpea cultivar B301 challenged with either a virulent (SG4z) or avirulent (SG3) race of *S. gesnerioides* has provided further insight into the transcriptional response during the early stages of plant parasitism. Infected tissue, sampled 6 days post-infection with SG3, was enriched with genes associated with apoptosis, programmed cell death and responses to biotic and abiotic stresses (Huang *et al*., 2012). At a later stage (13 days post-infection), enhanced expression of defence-related genes and genes involved in lignification processes was observed. At the same time, the expression of multiple defence-related genes, including genes associated with lignification and secondary cell wall modifications, was repressed in compatible interactions with SG4z. SG4z-infected plants also showed higher expression of genes coding for proteins involved in the cellular transport of nitrogen and sulphur.

A similar tendency was observed in rice, when one susceptible rice variety (IAC 45) and one resistant variety (Nipponbare) were infected with *S. hermonthica* and analysed 2, 4 and 11 days after

infection using whole-genome microarrays (Swarbrick *et al*., 2008). The incompatible interaction between *S. hermonthica* and Nipponbare showed enhanced expression of defence-related genes, such as genes encoding pathogenesis-related (PR) proteins, WRKY transcription factors and pleiotropic ABC transporters, whereas the compatible (susceptible) interaction was characterized by large-scale down-regulation of genes associated with growth regulation, metabolism, biogenesis of cellular components and cell division. Several genes coding for nutrient transporters, enzymes involved in amino acid metabolism, were up-regulated at the same time in the susceptible rice cultivar.

Overall, these data, although sometimes very difficult to compare, draw a common picture, in which *Striga* is actively recognized by resistant plants and triggers a defence-like response. This response appears to be very similar to that observed for other nonhost or race-specific resistance responses to other plant pathogens. It also shows that *Striga* actively manipulates host transcription to foster parasitism by either up-regulating host genes associated with nutrient supply or by down-regulating defence-related genes. It is not known how *Striga* manipulates transcription in host plants. Avirulence gene products are interesting candidates, but difficult to isolate as a result of limited genetic resources in parasitic plants. Ultimately, candidate genes will need to be tested *in planta*. Several hairy root transformation systems for members of the Orobanchaceae family, including *T. versicolor*, *P. japonicum* and *Ph. Aegyptiaca*, are available (Fernandez-Aparicio *et al*., 2011; Ishida *et al*., 2011; Tomilov *et al*., 2007).

SUMMARY AND PERSPECTIVES

Many genes essential for plant parasitism are yet to be identified and characterized. The identification of these genes will eventually help to answer fundamental questions in plant-parasitic interactions, such as: Which genetic modifications are required to enable a parasitic life cycle? What is the role of HGT in parasitic plant–plant interactions? Which parasite gene products are recognized by resistant plants and which gene products help to resist being detected by the host immune system? Which molecules are exchanged at the haustorium interface? What is the molecular basis of tolerance and can all this information be used to breed *Striga*-resistant crops? Ongoing whole-genome sequence projects of parasitic plants and related nonparasitic species, such as *Lindenbergia philippensis* (Cham. & Schltdl.) Benth. (http://ppgp.huck.psu.edu), will certainly provide new insights into the evolution of *Striga* species and facilitate the identification of genes important for plant parasitism.

ACKNOWLEDGEMENTS

TS and MM are supported by grants from the Japanese Society for Promotion of Science (JSPS) and KS by MEXT KAKENHI 24228008. The authors thank Satoko Yoshida and Luke Braidwood for helpful comments on the manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1 Overview of *Striga* species and related Orobanchaceae species discussed in the main text.