CURRENT STATUS AND FUTURE PROSPECTS FOR MANAGEMENT OF PARASITIC WEEDS (*STRIGA* AND *OROBANCHE*)

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ABSTRACT

The genera *Striga* and *Orobanche* include species that are serious constraints to the production of staple cereals or pulses in predominantly smallholder systems of sub-Saharan Africa, India and the Mediterranean Basin. The weeds are particularly problematic where soil fertility is low. The principal *Striga* species affect predominantly sorghum and maize production, while *Orobanche* affects a wide variety of dicotyledonous crops. The majority of control strategies depend on perturbing the interaction between parasite and host coupled with improving management practices, such as enhancing soil fertility. Recent advances in three approaches to control hold much promise for *Striga*: the use of fungal biocontrol agents; intercropping with the legume *Desmodium*; and sources of (partial) resistance in wild relatives of sorghum. In the longer term, molecular genetics offers several avenues towards the generation of resistant (or tolerant) crop genotypes and these techniques are summarised together with an assessment of current progress. We conclude that controlling parasitic weeds require knowledge of more than biology alone and the latter must be set in the appropriate socio-economic framework.

INTRODUCTION

More than 3000 species (*c.* 1%) of flowering plants are parasitic and depend either partially or completely on their host for water, carbon and nutrients (Press & Graves, 1995). A small number of genera parasitise crops and have the potential to be important weeds. Of these, the root hemiparasitic witchweeds (*Striga* species) and the root holoparasitic broomrapes (*Orobanche* species) are the most important. In this review, the current distribution of these weeds is described, together with their importance and range of impacts. Next, current control methods are briefly reviewed. Emphasis is placed on their constraints and limitations, since extensive accounts of the methods themselves appear elsewhere (see below). Finally, we consider the extent to which new approaches, including biotechnology, may contribute to the control of parasitic weeds by examining a number of strategies that have either been the subject of trials (ranging from controlled environment studies to on-farm studies) or offer the potential to control parasitic weeds in the future.

DISTRIBUTION AND IMPORTANCE OF ROOT PARASITIC WEEDS

The genera *Orobanche* and *Striga* include a number of species that are serious constraints to the production of staple cereals or pulses in the smallholder systems of the drier zones of the Mediterranean Basin, sub-Saharan Africa and India. *Orobanche* species are also important pests in high-input commercial farming in eastern and southern Europe (Parker & Riches, 1993).

Striga

Of the 28 species of *Striga* currently recognised as present in Africa, *S. asiatica*, *S. aspera*, *S. forbesii*, *S. gesnerioides* and *S. hermonthica* are of particular economic importance as crop pests (Mohamed *et al.*, 2001). With the exception of *S. gesnerioides*, which parasitises only dicotyledons, these species attack all the important tropical cereals, as summarised in Table 1. *S. asiatica*, the most widely distributed of the cereal witchweeds (see Cochrane & Press, 1997) and is common, particularly on maize and sorghum, on light sandy soils in the semi-arid areas of southern, central and eastern Africa in a range extending from the Northern Province of South Africa to Ethiopia and Sudan. Although not generally found in west Africa, it is a local problem on maize in some humid savanna areas of Cameroon, southern Nigeria and Togo where it may be an introduction (Agbobli, 1991). Outside of continental Africa, *S. asiatica* is a problem on Indian Ocean Islands, including on upland rice in Madagascar, and extends from Arabia and eastwards through much of south and east Asia in Pakistan, India, Thailand, Vietnam, and Indonesia to China (Parker & Riches, 1993). *S. hermonthica*, a serious pest of cereals especially in the Sahel of Africa, extends from Senegal to Ethiopia with southern limits in northern Namibia and the Lake Victoria Basin of Tanzania (Mohamed *et al.*, 2001). It thrives on a range of soil types and can be abundant on lighter sandy soils in west Africa and heavier clays in east Africa. *S. hermonthica* is thought to be the most important parasitic weed species on a world scale. More than 5 million ha of crops are infested in six countries of west Africa alone and the total area affected on the continent may be as much as 10 million ha (Sauerborn, 1991).

Table 1. The main cereal crops attacked by *Striga* species in Africa (based on Riches & Parker, 1995). XXX, widely and seriously affected; XX, seriously affected locally only; X, locally affected to a moderate degree; - not attacked.

Species	Maize	Sorghum	Finger millet	Pearl millet	Upland Rice
S. asiatica	XXX	XXX	XX	XX	XX
S. aspera	XX	X	X	-	XX
S. forbesii	XX	XX	-	-	-
S. hermonthica	XXX	XXX	XX	XX	XX

The importance of *S. hermonthica* has increased in recent years as a consequence of increasing population pressure and more intensive cereal cropping, particularly of susceptible maize cultivars in the moist savanna of west Africa in place of more tolerant land races of pearl millet and sorghum. Table 1 represents the total range of crops attacked, but *S. hermonthica* is a highly variable species and not all these crops are necessarily attacked in all locations. Distinct host preference is seen in some areas of the Sahel where only pearl millet is attacked while sorghum is immune. Elsewhere, sorghum is attacked but millet very little if at all. This host preference may arise from differential responses of parasite populations to different germination stimulants in the host root exudates (Parker & Reid, 1979), although it is not possible to eliminate post-germination mechanisms.

S. aspera is distributed north of the equator in Africa, in the Sahelian and Sudanian regions from the Gambia and Senegal to southern Ethiopia (Mohamed *et al.*, 2001). It is closely related to *S. hermonthica* with which there is a high rate of inter-fertility (Aigbokhan *et al.*, 2000). The species has been reported to attack maize, sorghum, upland rice, fonio (*Digitaria exilis*) and sugar cane in west Africa (Parker & Riches, 1993). *S. forbesii* is of local importance, largely on maize, sorghum and sugarcane on relatively wet, moisture retentive soils in the Sudanian savannas extending from Senegal to Somalia and southwards through east and southern Africa.

Found throughout sub-saharran Africa and extending to Arabia and Asia, *S. gesnerioides* is the most widely distributed of all witchweed species. It has evolved a strong host-specificity among its populations (Mohamed *et al.*, 2001). Tobacco can be attacked in southern Africa by the *Nicotiana* strain (Wild, 1948) but it is the *Vigna* strain which is of most economic importance, because it attacks and causes extensive damage to cowpea (*Vigna unguiculata*) in the Sahelian and dry savanna zones of Mali, Burkina Faso, Niger, Nigeria and Cameroon (Parker & Riches 1993.

The witchweeds threaten the livelihoods of millions of smallholders throughout semi-arid Africa and parts of Asia. Continuous cropping and the extension of cultivation onto more marginal soils due to population pressure have resulted in the spread and intensification of the *Striga* problem (Parker, 1991; Shaxson & Riches, 1998). It has been estimated that 40% of the arable lands in sub-saharran Africa, accounting for 67% of the 73 million ha in cereal production in savanna zones, is infested with witchweeds (Mboob, 1989; Lagoke *et al.*, 1991). Accurate estimates of yield losses are compromised by the non-uniformity of natural infestations and by the difficulty of creating parasite-free areas with which to make a comparison. Published estimates include 21% annual loss of sorghum in northern Ghana and 6-10% for all cereals in Nigeria, Gambia and Benin due to *S. hermonthica* (Sauerborn, 1991). A survey of southern India estimated an average loss of sorghum yield to *S. asiatica* of 21% at infested sites (Vasudeva Rao *et al.*, 1989). In Malawi 4.5% of national maize production has been calculated to be lost due to *S. asiatica*, based upon field estimates of an average yield loss at infested sites of 28%, ranging from 10.5 to 59% (Kroschel *et al.*, 1996).

Orobanche

The genus *Orobanche* includes more than 100 species of which five are of most significance as crop weeds, mainly in the Mediterranean Basin. (Parker & Riches, 1993). These are *O. crenata*, a clearly defined species, the closely related *O. cernua* and *O. cumana* (combined by most taxonomists as the single species *O. cernua*) and the two species *O. ramosa* and *O. aegyptiaca*, which are difficult to distinguish and for practical purposes can perhaps be treated as one. Hosts include a range of pulse, oilseed and vegetable crops (Table 2). *O.*

crenata is especially important as a widespread parasite of faba bean, and to a lesser extent of lentil and chickpea, all around the Mediterranean. It also extends eastwards through the Middle East to Iran. The *O. cernua*/*O. cumana* complex has a restricted host range among crops in the Solanaceae and the Asteraceae. It is distributed mainly in the Middle East, southern Europe and north Africa, but also extends to Niger, Tanzania and Uganda, east to India and many former states of the USSR. It is troublesome as a pest of tomato and tobacco in Pakistan, India, Nepal, Iran, Arabia, Egypt and Italy. It has also been of great importance on sunflower crops in Bulgaria, Hungary, Russia, Turkey and the former Yugoslavia.

Table 2. The main host crops of *Orobanche* species (adapted from Parker & Riches, 1993). XXX, seriously attacked; XX, moderately attacked; X, lightly attacked.

Crop	*O. aegyptiaca* *O. ramosa*	*O. cumana*	*O. cernua*	*O. crenata*
Lettuce	X	-	-	X
Sunflower	XX	XX	-	X
Cabbage	XX	-	-	-
Mustard	XX	-	-	-
Rape seed	XX	-	-	-
Cucumber	XX	-	-	-
Melon	XX	-	X	-
Squash	XX	-	-	-
Chickpea	X	-	-	XX
Faba bean	X	-	-	XXX
Lentil	X	-	-	XX
Pea	X	-	-	X
Eggplant	XXX	-	XX	-
Pepper	X	-	-	-
Potato	XX	-	X	-
Tobacco	XXX	-	XXX	-
Tomato	XXX	-	XX	X
Carrot	X	-	XX	-
Celery	X	-	X	-
Parsnip	X	-	-	-

In addition to the Mediterranean Basin, *O. ramosa* extends to central Europe, the Middle East and northern Africa and as an introduction to other regions including South Africa, Australia, Cuba and several sites in Central America and USA. It was first detected in Chile in 1986 and is now a serious threat to tomato production (Diaz & Norambuena, 2001). Infestations have also become a problem in recent years in oilseed rape in Western France (Gibot-Leclerc *et al.*, 2001). Holm *et al.*, (1979) list the species as a principal or serious weed in Egypt, Jordan, Lebanon, Italy, Turkey, Hungary, Nepal and Cuba.

The closely related *O. aegyptiaca*, which has a similar host range, is less widely distributed, occurring mainly in southestern Europe, northeastern Africa, the Middle East and southern areas of the former Soviet Union, Afghanistan, Pakistan, north India and Nepal. According to Holm *et al.* (1979) it is a major weed in Jordan, Iran, Arabia, Afghanistan and common in Iraq, Pakistan and Turkey. An additional species, which is regarded as a weed, is *O. minor*. Although this is rarely recorded as a major problem it is widespread, especially in temperate areas of the world and has been introduced from northern Europe to many other parts of the world including South Africa, Australia and New Zealand. It has recently been reported from clover fields in Oregon, USA where eradication strategies are under evaluation (Colquhoun *et al.*, 2001).

As with the witchweeds, areas of infestation and yield losses attributable to *Orobanche* species are poorly documented. *O. cernua* (*O. cumana*) has been a problem in sunflower growing areas of eastern Europe for many decades, indeed breeding for resistance had begun in Russia by 1912 (Pustovoit, 1976). Past reports have suggested that over 1 million ha have been affected, with estimates of 20,000 ha in each of Spain and China, 10,000 ha in Greece and over 200,000 in Turkey (Parker, 1994). Some 40,000 ha of tobacco has been reported to be infested by *O. cernua* in India, with overall yield losses estimated at 24-52% (Krishnamurthy *et al.*, 1977). By the early 1990s some 63% or 200,000 ha of the area planted to faba bean in Morocco, Portugal, Spain and Syria was estimated to be infested by *O. crenata* (Sauerborn, 1991). On a regional basis the overall loss in seed yield has been estimated at 5.4% in Spain and 12% in Morocco (Aber, 1984; Mesa Garcia *et al.*, 1984). Losses due to *O. ramosa* and *O. aegyptiaca* in tomato, tobacco and vegetable crops are thought to be as high as 10-50% (Riches & Parker, 1995). Losses of 16-32% in yield of tobacco in Cuba reduced the crop value by 20-50%, while yield reductions of 21-29% have been reported for tomato in California (Cordas, 1973). As a result of mounting losses farmers may decide to stop growing susceptible crops on infested fields. In Tunisia, for example Zermane *et al.* (2001) reported that 76% of farmers interviewed in an *O. crenata* infested region had abandoned faba bean production.

CURRENT MANAGEMENT SOLUTIONS

A variety of methods for controlling parasitic weeds exists and there have been a number of informative and comprehensive reviews in the last decade, for example, Parker (1991), Gressel (1992), Parker & Riches (1993) and Eplee & Norris (1995). Most control strategies work by perturbing the life cycle of the parasite or interfering with its interaction with the host and are build around an understanding of physiological and metabolic interactions between host and parasite (see Stewart & Press, 1990; Press *et al.*, 1999). It is also important to consider socio-economic factors that affect the implementation and efficacy of a particular control strategy. With regard to *Striga*, high technology methods were developed in the USA as a consequence of accidental introduction of the parasite to the Carolinas as a contaminant of imported maize grain in the early 1950s. The potential impact of witchweed on cereal production in the USA was enormous, with estimates in the order of a 10% reduction in total yield of maize, sorghum and sugar cane together with an annual control cost of >$1 billion (1982 data). The fear arising from these predictions led to the development of a vigorous and successful eradication programme, using herbicides and soil fumigation with ethylene gas, which triggers germination of *Striga* seed (see below). However, such techniques are not transferable to African farming systems, where they would be both economically unfeasible and impracticable, and low technology methods still prevail today.

Striga and *Orobanche* seeds germinate in response to specific chemical cues that are present in the root exudate of host (together with some non-host) species. The active molecules are sequiterpene lactones (known as strigolactones) with a complex stereochemistry (see, e.g., Zwanenburg & Reizelman, 2001). A number of analogues have been produced that have the potential to stimulate the germination of *Striga* seed in the absence of a host, but to date, production costs and instability in the rhizosphere have prevented them being used in control programmes. Production of natural germination stimulants differs between cultivars and there has been much interest in the generation of low germination stimulant (*lgs*) producing lines. Ejeta *et al.* (2000) have successfully introgressed the *lgs* gene into high yielding broadly adapted sorghum varieties that are being used in several African countries (Ejeta *et al.*, 2000), such as the so-called Purdue lines.

Good management practices can go some way towards alleviating the impact of the weed. Some of these practices revolve around improvement of soil fertility, for example, through crop rotation, the use of nitrogen fertilisers (and manure) and intercropping. Increasing soil fertility not only stimulates the growth of the host but also adversely affects germination, attachment and subsequent development of the juvenile *Striga* plants (Cechin & Press, 1993a,b; Pieterse & Verkleij, 1991). However, this approach has only limited success, largely attributable to socio-economic factors: financial constraints prevent the use of adequate nitrogen fertilisation; farmers often have insufficient access to manure; and education and training in the management of *Striga*, particularly with regard to the spread of seed, is still rudimentary. Further, increasing pressure to produce more food for a rapidly expanding population can lead to greater use of marginal lands for farming. Such areas may already be infested with *Striga*, or have been previously abandoned, or be of poor soil nutrient status. Although a relatively large number of intercropping studies has been conducted, their impact on the alleviation of parasitic weeds is variable, at best. However, recently, it has been shown that some species (*Desmodium* spp.) may act as control agents through allelopathetic effects in the rhizosphere (Khan *et al.*, 2001) and this approach is discussed further below.

Other control methods involve crop rotation. This can both prevent the production of further *Striga* seed and also allow the density already in the soil seed bank to decline, although several years are often required before a significant improvement in yield is apparent. Some species (trap crops or false hosts, e.g., cotton) may accelerate these processes by stimulating the germination of *Striga* seed but then not allow successful attachment and development of the parasite to the root system of the plant. Of less use are catch crops, species that act as successful hosts but that are destroyed before the parasite sets seeds. In summary, rotation methods have only achieved limited success and farmers are increasingly unable to sustain rotations over a longer enough periods of time to yield significant results.

Herbicides have had only limited impact on *Striga* control in developing countries, principally because much of the damage to the crop occurs before the parasites emerge above ground. *Striga* affects host performance in two ways, first through source-sink interactions (competition for carbon and nutrients) and second through an additional so-called 'phytotoxic' interaction, the metabolic basis of which is unknown (see Press *et al.*, 1999). The latter occurs shortly after attachment, can result from only one or two infections on a host plant, and is quantitatively much more significant in terms of its impact on host productivity than source-sink impacts (Gurney *et al.*, 1999). Herbicides, particularly glyphosate, have been more widely used to control *Orobanche*, where they are probably more effective than on *Striga*, since the impacts of *Orobanche* are primarily controlled through source-sink interactions (Hibberd *et al.*, 1998). A challenge is to identify the concentration of herbicide required to inhibit a target process *in vitro*. This varies among species but in the case of parasitic weeds should be facilitated by the fact that parasitic weeds tend to accumulate solutes from the host, thus resulting in lower application rates. The development of herbicide resistant crops provides further opportunities for using herbicides and this approach is explored further below.

Thus, there is an urgent need for biologists to identify control strategies consistent with the socio-economic status of subsistence farmers. The best way forward is to identify or develop genotypes of major crops that are either tolerant or resistant (immune) to *Striga*. There appear to be remarkably few sources of resistance among the very large numbers of sorghum and maize genotypes screened to date. However, there are now a limited number of cultivars, particularly of sorghum, that appear to show some tolerance or partial resistance to *Striga*, and these are dealt with further below.

RECENT ADVANCES IN EXISTING APPROACHES

Here we review some recent advances that have been made with existing technologies, which have the potential to make a significant impact on the control of parasitic weeds in the short-medium term.

Biocontrol

A number of fungi and insects have been identified with the potential to control parasitic weeds, but few, if any, have shown sufficient potential to allow adoption by farmers. Further work is required to identify suitable agents and to explore their efficacy with regard to interactions with (micro) climate, longevity, virulence and method of application. One of the most promising developments is the use of a *Fusarium oxysporum* isolate for control of *S. hermonthica* that was identified from a survey of native fungi of West Africa (Savard *et al.*, 1997; Ciotola *et al.*, 1995). A pot study demonstrated that the isolate prevented the emergence of *S. hermonthica* and resulted in a 400% increase in the dry weight of the sorghum host. The fungus acts by inhibiting germination of *S. hermonthica* in the vicinity of sorghum roots, through production of fusaric acid and dehydrofusaric acid. More recently, Ciotola *et al.* (2000) have evaluated liquid fermentation systems for production of large numbers of chlamydospores using materials that would be locally available to subsistence farmers. In field trials, chlamydospore powder harvested from small-scale fermenters reduced *S. hermonthica* emergence by 92% and complete inhibition of *S. hermonthica* emergence occurred when the chlamydospore powder was added to the soil or applied as a seed dressing to sorghum.

There are several reports in the literature of mycoherbicidal pathogens that attach *Orobanche* species (see, e.g., Amsellem *et al.*, 2001a,b), however few, if any, of these are currently in use. Amsellem *et al.* (2001b) demonstrate that a *Fusarium arthrosporioides* strain and *F. oxysporum* strain are capable of controlling *O. aegyptiaca*, *O. cernua*, and *O. ramosa* but not *O. cumana*, without affecting any of the vegetable and legume crops examined.

Insects have also received some attention as biocontrol agents. For example, Norambuena *et al.* (2001) describe the control of *O. ramosa* on tomato and potato, particularly, by the dipteran *Phytomyza orobanchia* in Chile. The insect has been previously used in eastern and central Europe (see Parker, 1991). The insect was introduced to Chile in 1998/99 following collection in Morocco. It is indigenous to the Mediterranean Basin, where it feeds either on the seed capsules of the parasite or mines the shoot. Progress with this control agent is still at the research phase, where emphasis is being placed on the rearing and field release of the organism.

Intercropping: the use of *Desmodium*

The importance of the genus *Desmodium* (Fabaceae) for the control of *Striga* was discovered as part of study on the control of stem borers. Khan *et al.* (2001) report the development of a 'push-pull' strategy for minimising stem borer damage to maize and sorghum, involving the use of plant species that act as trap crops to attract the insects away from the cereal plants and/or intercrops that repel the pests. Among the latter, *Desmodium uncinatum* and *D. intortum* were also found to suppress the development of *S. hermonthica*. The mechanisms that underpin successful intercropping are varied, and the balance between facilitation and competition may be very sensitive to environmental conditions, which will vary markedly through space and time. However, typical mechanisms that are purported to underpin successful polyculture systems, such as impacts on shading, water relations or soil nutrient status, do not explain the action of *Desmodium*. The plant is thought to act through a complex web of allelochemicals that are released into the rhizosphere, the identity of which are under investigation (J.A. Pickett, personal communication). In addition to these allelopathic effects, the nitrogen-fixing ability of *Desmodium* has the potential to improve soil fertility and the plant also provides excellent forage. The use of *Desmodium* offers great potential as part of an integrated control system for the control of *Striga*.

Wild relatives as sources of resistance

Despite extensive cereal screening programmes, there appears to be a lack of resistance to *Striga* species among germplasm pools of cultivated sorghum and maize. Many groups have examined the extent to which land races, wild relatives and related species contain traits that confer resistance (or tolerance) to *Striga*. The ultimate goal of such studies would be to introduce these traits into cultivated lines, using either traditional breeding methods and/or molecular genetic techniques. Many of the research programmes are summarised in Haussmann *et al.* (2000) and Fer *et al.* (2001). For example, Rich *et al.* (2001) screened 78 wild sorghums, many of which differed markedly in their susceptibility to *S. asiatica.* 16 potential low germination stimulators were identified, together with 18 that were described as low haustorial initiators. In addition, one accession of *Sorghum veticilliflorum* and two of *Sorghum drummondii* prevented germination and tubercle formation.

Fewer sources of resistance have been identified in wild relatives of maize. However, Gurney *et al.* (2001) report partial resistance in *Tripsacum*, a wild relative of maize, in response to *S. hermonthica.* The parasite establishes vascular continuity on the grass, although growth of *S. hermonthica* is arrested at an early stage of development. Histological analysis of the haustorium demonstrated poor tissue differentiation, with the hyaline body, a metabolically active region of cells surrounding the xylem core, being largely absent. Studies are underway to determine the heritability of this trait using crosses between *Tripsacum* and maize.

In contrast, sources of resistance are more readily available among cowpea germplasm collections. As a result of international collaboration with a systematic conventional breeding programme undertaken at the International Institute of Tropical Agriculture, Nigeria, resistance to both *Striga gesnerioides* and *Alectra vogelii* has been transferred from a land race cowpea, collected in Botswana, into high yielding cultivars. Two have now been released for general cultivation in Nigeria (Singh, 2000) and are being widely field tested in West Africa.

THE USE OF NEW TECHNOLOGIES AND MOLECULAR GENETIC APPROACHES

An understanding of the mechanisms underlying both the detrimental effects of parasitic plants on susceptible hosts, and resistance to these parasites may benefit greatly from the application of genomic, proteomic and metabolomic technologies, ultimately leading to the design of novel strategies for their control. Some of the molecular techniques that are currently being used, or which have the potential to increase our understanding of the interaction between parasitic plants and their hosts, are discussed below. Clearly, in order to exploit modern molecular genetic techniques, there is a need to identify crop genotypes that behave differentially when challenged with *Striga* or *Orobanche*. These will include some of the materials described above (e.g. crop genotypes and wild relatives) as well as species that are used as model systems, e.g. *Arabidopsis thaliana.*

Linkage mapping

The use of molecular markers such as restriction fragment length polymorphisms (RFLPs) or simple sequence repeats (SSRs) has allowed a large number of randomly distributed polymorphic loci to be mapped in single populations, and low and medium resolution maps have been constructed for numerous plant species over the last 15 years. These maps can be used for locating newly cloned genes and to facilitate characterisation of genes underlying both simply and quantitatively inherited traits.

Melake-Berhan *et al.* (2000) crossed an accession of a wild relative of maize, *Zea diploperennis* (teosinte), with a susceptible maize cultivar. Backcross progeny from this study were then selected that showed resistance to *S. hermonthica* in greenhouse and field studies and, over the next three years, mapping populations were generated. DNA was isolated from 24 selected resistant *Z. diploperennis* backcrosses ($BC4S_2$ lines), two susceptible inbreds and the original *Z. diploperennis* accession. Screening SSR and RFLP markers to determine which of the $BC4S_2$ lines showed the highest polymorphism with the susceptible inbred lines and to look for markers from teosinte that might be common among the selected lines but absent in the susceptible parents is currently in progress. Using similar approaches *S. hermonthica* resistance genes have recently been mapped in rice (Bennetzen *et al.*, 2000) and sorghum (Ejeta, 2000; Haussmann *et al.*, 2000). Ultimately, the identification of markers closely linked to loci conferring resistance to *Striga* can be used to transfer these traits into elite lines using marker assisted breeding. This approach is still in its infancy and to date materials derived from such an approach have yet to make a significant impact at the farmer level.

Insertional mutagenesis and the use of model organisms

Arabidopsis thaliana (Brassicaceae) is a small flowering plant that is widely used as a model organism in plant biology. It is not of major agronomic significance, but it offers important advantages for basic research in genetics and molecular biology. It has a small genome, the sequence of which was published in December 2000. Extensive genetic and physical maps of all 5 chromosomes are available, the species has a rapid life cycle and is easily transformed. In addition, there are a large number of mutant lines and genomic resources available to the scientific community. Thus, for those parasitic weeds that interact with *Arabidopsis*, the potential exists to determine the molecular nature of the interaction, and hence to understand how it may be perturbed. *A. thaliana* is a susceptible host for *Orobanche* species (Goldwasser *et al.,* 2000), but exhibits non-host resistance to *Striga hermonthica* and *S. asiatica* (Vasey, Press & Scholes, unpublished data).

One approach to identifying host genes which are important in mediating the germination, attachment and subsequent development of a parasite, or which may be important in conferring resistance, is to disrupt the function of the gene and to examine the effect of this on the interaction. Insertional mutagenesis is a means of disrupting gene function and is based on the insertion of foreign DNA into the gene of interest. In *Arabidopsis* this involves the use of either transposable elements (Parinov *et al.*, 1999) or T-DNA (Krysan *et al.,* 1999). If the foreign DNA inserts into the coding region of the gene, it induces a mutation by preventing the proper expression of that gene. In addition, it also acts as a marker for subsequent identification of the mutation, since knowledge of the T-DNA or transposon tag sequence enables probes and PCR primers to be designed, allowing amplification of sequences adjoining the insertion (Liu & Whittier, 1995; Hui *et al.*, 1998). In this way disrupted genes can often be identified with reference to published gene sequences.

Atanasova *et al.* (2001) screened 20-25 plants from 101 T-DNA insertion *A. thaliana* lines for resistance to *Orobanche aegyptiaca* with the aim of identifying genes which are putatively involved in controlling the production of germination stimulants or haustorial initiation factors. A small number (eight) of T-DNA insertion lines were found that had very few, or no parasite attachments. This was attributed to perturbation of host signalling pathways that trigger parasite seed germination and haustorial induction, since once seeds were triggered to germinate artificially, the parasite was able to invade the root. Sequences of the genes adjacent to the T-DNA borders of the insert were obtained by PCR, and the sequence information was searched for similarity in computer databases in order to identify putative gene function. Some of the disrupted genes showed high sequence homology to known proteins involved in signal transduction pathways that operate in response to microbial challenge, or participate in biosynthetic pathways that contribute towards the production of secondary plant metabolites such as alkaloids. This work provides the first steps towards a better understanding of the molecular basis of host-parasite signalling prior to establishment of cellular integration and illustrates the value of this type of study. If such signalling pathways can be perturbed in crop plants it may allow the development of resistant materials that can be subsequently used in the field.

A similar approach can be taken with maize, although here only naturally occurring transposons can be employed to disrupt gene function. Grimanelli *et al.* (2000) constructed a large collection of transposon-induced mutations in a genome of maize adapted to African conditions using the Mutator type of transposable elements. More than 8000 F_2 families have been screened in the field in Kibos, western Kenya, for the occurrence of tolerance/resistance to *S. hermonthica* (assessed as lack of emergence of the parasite above ground). Following a three year screening programme, a small number of lines that consistently appear to show field resistance to *S. hermonthica* have been identified. These lines are now being studied in the laboratory to elucidate the physiological and molecular basis of this tolerance/resistance.

Comparative genome mapping studies have shown that there is a great deal of genome synteny between rice, sorghum and maize (Moore *et al.*, 1995; Merlake-Berhan *et al.*,1993; Whitkus *et al.*, 1992). It is, therefore, possible that identification of the function of genes which alter the susceptibility of maize to *S. hermonthica* will also shed light on the role of the corresponding gene in other cereal hosts.

Gene expression and function - transcript profiling

Following penetration of host roots by parasitic angiosperms during a susceptible interaction, changes in host gene expression will occur. Some genes or gene families will be induced by infection whilst others will be repressed. A knowledge of such changes in host gene expression will not only increase our understanding of the molecular basis of susceptibility but may allow the identification of genes that can be used to genetically engineer resistance to *Striga* or *Orobanche* in a wide variety of crop species.

In the last 10 years a number of techniques have been developed that allow the detection of differentially expressed members of individual gene families. These include cDNA-AFLP (Bachem *et al.*, 1996), SAGE (serial analysis of gene expresion) (Velculescu, 1995) and cDNA and oligonucleotide microarrays. For an in depth review of the technical aspects and advantages and disadvantages of such techniques see Kuhn (2001). These techniques have been used to identify plant defense-related genes from *A. thaliana* infected with the fungal pathogen *Peronospora parasitica* (van der Biezen *et al.*, 2000) and from potato infected with the potato cyst nematode (Qin *et al.*, 2000). They offer a novel approach to the investigation of the molecular basis of susceptibility and resistance to parasitic angiosperms.

In a recent study cDNA-AFLP has been used to profile changes in gene expression in roots of marigold undergoing non-host resistance to *S. asiatica* (Gowda *et al.*, 1999) and has lead to the identification and subsequent cloning of several gene products. Among these was a 917 bp cDNA encoding a 211 amino acid protein with significant homology to proteins encoded by disease resistance genes from other plant species. The cDNA was used to isolate a nuclear gene designated NRSA-1 for non-host resistance to *S. asiatica*. NRSA-1 is a member of a small gene family in marigold consisting of two to four members. RNA gel blot analysis showed that NRSA-1 transcripts accumulated to high levels in roots around the site of *Striga* invasion within 120 h after parasite attachment, consistent with a predicted role in defence. Studies to determine whether overexpression of NRSA-1 in *Striga* susceptible hosts and non-host backgrounds leads to the activation of defence-related gene expression and a corresponding enhancement of resistance to *Striga* remains to be seen.

The analysis of the effects of biotic or abiotic stresses on the regulation of gene expression have traditionally focused on only one or a few genes at a time. However, the development of cDNA and oligonucleotide microarrays allows the measurement of expression levels of thousands of genes in parallel and serves as an important tool in functional genomics (for technical details see Kuhn, 2001). Such an approach allows the co-ordinated changes in gene expression which take place in tissues exposed to environmental signals or biotic agents to be profiled simultaneously and can also reveal putative roles for genes with no known function.

At present, high density microarrays are only available commercially for the model plant *A. thaliana* although custom microarrays can be produced either commercially by companies such as Affymetrix or in a number of research laboratories. Microarrays have been used successfully to profile changes in the expression pattern of *Arabidopsis* expressed sequence tags (ESTs) following inoculation of *Arabidopsis* with the incompatible fungal pathogen *Alternaria brassicola* (Schenk *et al.*, 2000) and 1300 *Arabidopsis* genes under drought and cold stress (Seki *et al.*, 2001). In addition, a custom microarray of 2032 lima bean cDNAs was used to examine changes in gene expression in lima bean leaves that were exposed to volatiles released from neighbouring leaves infested with spider mites (Arimura *et al.*, 2000). At present, there are no published studies of the use of microarrays to study the impact of angiosperm parasites on host gene expression although a number of studies are in progress.

Plant functional genomics couples the generation of mutant and transgenic plants with the global analysis of changes in gene expression. However, it is important to remember that these methods do not provide direct information about how a change in mRNA or protein is coupled to a change in biological function. As a result of a complex network of regulatory interactions at all levels in plant cells, a change in one level in the complex network does not necessarily lead to a particular change in function or phenotype (Fiehn, 2000).

However, transcript profiling, together with the newly emerging technology of metabolite profiling may offer a direct link between a gene sequence and the function of a metabolic network in plants. It is possible, in the future, that these techniques will greatly increase our understanding to the complex interactions between parasitic angiosperms and their hosts.

The use of mutants or transgenic plants: herbicide resistant cereals

As illustrated above, transgenic plants can be used to test specific hypotheses, for example, whether over expression of the NRSA-1 gene from marigold in susceptible cereal hosts can confer resistance to *Striga*. There is also a wealth of transgenic plants (and also mutants) which have characterised lesions in numerous metabolic, developmental or defense pathways. Such plants can be used in a directed approach to test hypotheses relating to the effect of a specific lesion on the infection process and development of the parasite, or in the control of *Striga*.

Gressel *et al.* (1996) and Kanampiu *et al.* (2000) report the use of maize mutants with acetolactate synthase (ALS) target-site resistance in the control of *Striga*, coupled with applications of imidazolinone and sulphonylurea herbicides. ALS is an enzyme that is responsible for the biosynthesis of key amino acids and hence survival. Post-emergent spraying delayed development of the parasite (Abayo *et al.*, 1998), although as noted above, *Striga* exerts its impacts prior to emergence above ground. Studies with maize seeds coated with either Mg-imazapyr or pyrithiobac-Na were more promising, and revealed a marked depression in rates of *S. hermonthica* emergence and, importantly, reduced the impact of the parasite on grain yield. The authors argue that given the high frequency of mutations conferring resistance to ALS-inhibiting herbicides, significant numbers of resistant *Striga* plants are likely to emerge within 3-5 years of treatment, making hand-weeding an essential component of the control strategy. The economics of the method are such that it would be affordable to subsistence farmers. Current studies are generating materials more suited to local conditions and elucidating the precise formulations and management practices necessary to enable farmers to apply the technique. This control strategy also has the potential to control other parasitic weeds such as *Orobanche* and *Alectra*.

CONCLUSION

Advances in understanding, and controlling, interactions between parasitic weeds and their hosts have lagged behind those involving other pests and pathogens. Rapid advances in molecular genetics should allow the balance to be redressed, resulting in the production of materials that offer resistance to *Striga* and *Orobanche*. In the short term, there are a number of promising techniques, which do not involve the use of transgenic materials, that could be adapted to effect improved control of these weeds. In the industrial developed world, the introduction of genetically modified crops has been seen by many as a major risk to well-being. Virtually no research has been undertaken on the applicability of this technology to poorer developing countries, where the technology could make a major contribution towards the alleviation of poverty and food insecurity (not only in the context of parasitic weeds but also other biotic and abiotic stresses). However, a number of concerns exist, such as ownership of genetic resources by the private sector, and it remains to be seen how power relations between different interested parties (e.g. farmers, NGOs, companies and governments) will be played out. There is a need to determine the impact of new technologies on cultural, religious and spiritual beliefs and their impact on structures of families, farms and the economy as a whole. In conclusion, controlling parasitic weeds require knowledge of more than biology alone and the latter must be set in the appropriate socio-economic framework.

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