Companion Cropping to Manage Parasitic Plants

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Abstract

Parasitic plants, through a range of infestation strategies, can attack crop plants and thereby require management. Because such problems often occur in resource-poor farming systems, companion cropping to manage parasitic plants is an appropriate approach. Many examples of companion cropping for this purpose have been reported, but the use of cattle forage legumes in the genus *Desmodium* as intercrops has been shown to be particularly successful in controlling the parasitic witchweeds (*Striga* spp.) that afflict approximately one quarter of sub-Saharan African cereal production. Through the use of this example, the development of effective companion crops is described, together with developments toward widespread adoption and understanding the underlying mechanisms, both for sustainability and ensuring food security, and also for exploitation beyond the cropping systems described here.

INTRODUCTION

With the first demonstration of gene-for-gene resistance in parasitic plant-plant interactions (46), the scene is set for the control of parasitic plants to be discussed in this review. In addition to the witchweeds (*Striga* spp.), originally in the Scrophulariaceae but now in the Orobanchaceae, together with the genera *Alectra* and *Orobanche*, other important genera of parasitic plants include *Cuscuta*, Cuscutaceae (dodders), and the mistletoe families, Viscaceae and Loranthaceae. This review will focus on the most destructive of the parasitic weeds from the genera *Striga* and *Orobanche* (**Table 1**). Economically important weeds from the genus *Striga* include *Striga gesnerioides*, an important pest of fabaceous crops such as cowpea [*Vigna unguiculata* (Fabaceae)] (46, 74), and *Striga asiatica* and *Striga hermonthica*, which are major pests of cereals, with 24% of sub-Saharan African maize [*Zea mays* (Poaceae)] being infested with *S. hermonthica*. *Striga* affects the lives of 100 million people in Africa and infests 40% of arable land in the savanna region, with infestations that have been so severe as to cause farmers to abandon their land (25). The broomrapes from the genus *Orobanche* are again important with fabaceous plants, but also for the sunflower (*Helianthus annuus*) and commercial crops in the Solanaceae. In the case of *Orobanche*, the threat to crops extends into North Africa and across southern Europe (56).

CONTROL STRATEGIES TO MANAGE PARASITIC PLANTS

Chemical Control Strategies

Although the infestation processes may vary between species, control is difficult with conventional herbicides because vascular connection to the host and much of the damage to the crop occurs prior to emergence. However, differential susceptibility to herbicides of the host plant and parasitic weed can be exploited where hosts can be bred with natural resistance, such as the case of imidazolinone-resistant maize, or genetically engineered resistance to the herbicide (71).

Biological Control

Biological control encompasses strategies from the gene to the whole organism, which can be antagonistic to the parasitic plant by a range of processes such as direct attack, or by interference with a part of the parasite's life cycle.

Genetic. Because the cropping situations predominantly attacked are low input, and herbicides are thereby not an option, control needs to be delivered not only by a low cost method but preferably sustainably, with minimum external inputs. Gene-for-gene resistance has been demonstrated for the *S. gesnerioides* association with *V. unguiculata* (46), and such an understanding has allowed tremendous practical developments against fungal pathogen attack. Therefore, increased efforts in delivering control by resistant cultivars can be made, and the tools of modern plant breeding and of heterologous gene transferral (GM) (61) will be valuable. The most resource-poor regions, which represent the bulk of farming in sub-Saharan Africa (2), will also require open-pollinating varieties rather than delivery by hybrid seed because of the need for annual expenditure to be minimized.

Conventional. Biological control (5, 55, 64) of parasitic weeds by conventional approaches, using organisms directly antagonistic to the parasite, is an option, but is usually more costly than is compatible with low-input farming in the developing world. The broomrape fly [*Phytomiza orobanchia* (Diptera: Agromyzidae)] and the *Striga* gall-forming weevils [*Smicronyx* spp. (Coleoptera: Curculinidae)] are insect biological controls, and although they target seed reproduction, destruction of seeds is not total and most of the damage to the host plant is complete before this stage. Early stages of parasitic weed development can be affected by one of many species of *Fusarium* specific to the weed, and this is currently under field

Table 1 Major parasitic weeds from the genera *Striga*, *Orobanche*, and *Alectra*

Genus	Approx. no. of species	Parasitic weed species	Major crop hosts	Distribution	Ref.
Striga	41	*S. hermonthica*	Cereal crops (Poaceae) including sorghum (*Sorghum bicolour*), pearl millet (*Pennisetum glaucum*), maize (*Zea mays*), rice (*Oryza sativa*)	Sub-Saharan Africa	15, 45, 56
		S. asiatica		Sub-Saharan Africa, Indian subcontinent	
		S. gesnerioides	Cowpea [*Vigna unguiculata* (Fabaceae)]	West and central Africa	
Orobanche	100	*O. crenata*	Faba bean [*Vicia faba* (Fabaceae)], Leguminosae	Southern Europe, west Asia	56, 62, 64
		O. cumana	Sunflower [*Helianthus annuus* (Asteraceae)]	Eastern Europe, eastern Mediterranean, North African coast	
		O. ramosa	Solonaceae, hemp [*Cannabis sativa* (Cannabaceae)]	Mediterranean, Chile, Cuba, Nepal, western Australia	
		O. aegyptiaca	All Solanaceae, rapeseed [*Brassica napus* (Brassicaceae)], chickpea [*Cicer arietinum* (Fabaceae)]	Eastern Mediterranean, Indian subcontinent.	
Alectra	30	*A. vogelli*	Cowpea, groundnut [*Arachis hypogaea* (Fabaceae)]	Sub-Saharan Africa	23, 64
		A. fluminensis	Sugarcane [*Saccharum officinarum* (Poaceae)]	Latin America	

evaluation, although input costs will be relatively high even if effective. Furthermore, these most highly selective agents have evolved not to eradicate their hosts, and we currently lack effective means by which eradicant generalists can be targeted specifically toward parasitic plants.

Companion cropping. Another form of biological control is companion cropping, usually involving an intercrop antagonistic to the parasitic plant, but trap crops are also an option. This low-input system is potentially of greatest value in developing world agriculture where chemical inputs are not possible for financial reasons and where other forms of low-input agriculture such as organic farming are practiced from choice.

Trap crops. Trap crops are crops that draw pests and diseases away from the main crop. Although trap crops have proved to be valuable when grown in conjunction with host crop plants for controlling insect pests (11), this has so far proved less valuable in parasitic plant control, where trap crops have been used in efforts to stimulate germination and clear parasitic weeds from the seed bank before planting.

Cover and fallow crops. Other forms of companion cropping, such as cover crops (25) and crops used in fallow or rotation (71), are not normally an option unless they have both effectiveness and, more importantly, economic value to the farmer in the specific growing system involved. Even green manures and nitrogen fixing crops that do not combine such value with specific mechanisms for controlling parasitic plants are unsuitable and will not be adopted by farmers into practice. The fallow crop sunhemp, [*Crotaria ochroleuca* (Fabaceae)] used in a maize rotation, invites consumption but cannot be recommended because of its toxic alkaloid content (71).

Trap crop: crop that will draw pests and diseases away from the main crop

Companion crop: crop grown in some way to benefit the main crop

Allelopathy: an effect on an organism by another; originally deleterious but now can include beneficial effects

Intercropping. For companion cropping, and specifically intercropping, where crop plant and intercrop are simultaneously cultivated in the same space, an obvious mechanism is provided by use of nonhost crops, for example, against *O. crenata*, which parasitizes legumes. The mechanisms by which parasitic weeds can be suppressed through companion planting often involve physical methods. These include smothering by cover crops to increase soil moisture and fertility (if nitrogen fixing) and decrease soil temperature, all of which may be antagonistic to weed development. A companion crop, a crop grown along with the main crop and provides the main crop with some benefit, that provides extra yields for the farmer is vital but these physical processes, although reducing parasitic weed damage, can also be detrimental to the yield of the protected crop by competition. An alternative mechanism exploiting the natural chemistry of plant-plant interactions is allelopathy. The subject was previously defined as a chemical produced by one organism that exerts a deleterious influence on another organism, such as a general toxic effect between competing plants. However, it is now considered to extend to chemical ecology in the rhizosphere, beneficial and symbiotic effects, other signaling, and physiological effects (6, 47).

Cereals such as oats [*Avena sativa* (Poaceae)] and the fabaceous plant fenugreek (*Triganella*) (14, 16) can release into their soil ecosystems (rhizosphere) chemicals antagonistic to parasitic weeds. Oats release avenacins, glycosylated triterpenes that may provide part of an allelopathic mechanism in suppression of *O. crenata* in legumes (9, 16, 17, 52). Genetic opportunities to exploit this are made possible by the elucidation of the avenacin biosynthetic gene cluster in oat (52). Fenugreek was also effective against *O. crenata* in legumes such as faba bean and pea (14), with the mechanism defined as allelopathic by the root exudation of a trioxazonane inhibiting weed germination (13). Chemically based plant-plant interactions through air also occur, and now that the mechanism of *Cuscuta* host plant location has been shown to involve volatile chemicals released from its host plant (63, 66), new intercropping strategies can be elucidated to deal with the extreme practical difficulties in dealing with such parasitic weeds (44).

For control of *Striga* spp., particularly *S. hermonthica*, in low-input cereals such as maize and sorghum (*Sorghum bicolor*) in sub-Saharan Africa, legumes have received most attention as companion plants. The legumes add nitrogen to the cereal nutritional cycle and also have value as food or animal forage. Among many examples are sesame [*Sesamum indicum* (Pedaliaceae)] (21) and groundnuts [*Arachis hypogaea* (Fabaceae)] (8, 43, 67). Most effective appears to be intercropping with cowpea, *V. unguiculata*, for example, in sorghum (7, 59) and in maize (50, 53). Farmer uptake is stimulated by the economic advantages of increased food yields in subsistence farming (48) and in the health potential where protein-rich edible beans are employed (51). Some nonhost intercrops such as sweet potato [*Ipomoea batatus* (Convolvulaceae)] (54) would present considerable competition to the maize itself. Although specific mechanisms have been claimed for some intercrops (12, 73), these still await elucidation beyond nitrogen nutrition. Legume shrubs (60) such as *Sesbania sesban* are reported to give *Striga* control, but negative effects through shading would need to be accommodated. The social conditions and cultural farming methods under which companion cropping is practiced can also be a major contributor (1, 58), but without efficacy and economic value, companion crops are unlikely to succeed. Ideally, an intercrop would be a perennial into which successive annual crops can be planted and that provides an efficient mechanism of parasitic plant control, while at the same time providing economic or at least on-farm value. This has been observed for the animal forage legume *Desmodium uncinatum* (Fabaceae), commonly known as desmodium or silverleaf, and for some other members of this genus that protect maize and other cereals by an allelopathic mechanism against *Striga*, including *S. hermonthica* and *S. asiatica*. Because of its extensive use in regions of East Africa and because there is substantially more mechanistic information than for other companion crops used to manage parasitic plants, this system will be used throughout the review to exemplify this approach to plant management.

USE OF THE COMPANION CROP *DESMODIUM* AGAINST THE PARASITES *STRIGA* SPP.

Development

Development of the system by which *Striga* parasitism is inhibited by *Desmodium* is here described from discovery, through the scientific demonstration of effectiveness to acceptance, as there is recognized added value to the farmer.

Initial discovery. Pest control measures involving companion cropping with intercrops antagonistic to the pest, combined with surrounding trap crops having a positive developmental effect on the pest, are termed stimulo-deterrent diversionary strategies, or push-pull (11). Such a system has been developed against a group of moths, Noctuidae and Crambidae, the larvae of which are cereal stem or stalk borers (20), and is being disseminated among resource-poor farmers in Africa. The intercrops are repellent to the ovipositing adults, but attractive to parasitic wasps that attack the larvae. The trap crop is highly attractive to the pest and, in addition, larval development is naturally arrested by a secretion from the leaves or is prevented by subsequent feeding of the plant material to livestock (27, 28, 33, 35, 36, 38).

In the course of developing this push-pull system, the farmers asked for consideration to be given to legumes with which to replace the best initial intercrop, the cattle forage molasses grass, *Melinis minutiflora* (Poaceae). Farmers' practice involves intercropping maize with edible legumes, and the advantage of companion cropping here is that the technology transfer into farming practice is facilitated by this already being an extensive activity in resource-poor farms. There is even specific linguistic terminology, e.g., "kilimo cha mchanganyiko" in Kiswahili. Work was undertaken to find such edible intercrops, but this proved difficult. However, it was possible to provide a different solution. Although not suitable for human consumption, cattle forage legumes from the *Desmodium* genus (silverleaf, *D. uncinatum*, and greenleaf, *D. intortum*) were found to be valuable in the field for repelling stem borer moths, although not as effective as *M. minutiflora* in attracting parasitoids (27, 42). *D. uncinatum* and *D. intortum* were introduced quickly because of farmer demand (26, 34, 35), particularly into the more arid regions of the Kenyan Lake Victoria Basin, as they survived conditions there well. This region benefited particularly from the ground cover provided by the *Desmodium* spp. and the nitrogen fixation of this nodulating crop. However, much of the region is infested by *S. hermonthica*, which can reduce maize yields to below the equivalent of one ton ha^{-1}. Where such high infestations of *S. hermonthica* occurred, with a one-to-one *Desmodium* intercrop, it was observed that *Striga* infestation of the maize was virtually eliminated (31) (**Figure 1**).

Confirmation of the unique value of *Desmodium*. Considerable global effort has been directed at control of *S. hermonthica* and *S. asiatica*, with very little success in terms of technologies suitable for resource-poor farming. Although claims have been made for intercropping with nonhost plants, particularly other legumes (7, 8, 67, 72), it was necessary to investigate whether *D. uncinatum* was acting by a novel mechanism in addition to the provision of ground cover and nitrogen to the cereal crop. This was achieved by field trials employing six replicates in a 6 × 6 quasicomplete Latin square design (65), with treatments comprising maize alone, ground cover provided by maize stalks and leaves, added nitrogen fertilizer, *D. uncinatum*, and *D. uncinatum* plus fertilizer. Two seasons' work demonstrated unequivocally that there was a qualitatively different and significantly greater effect with the *D. uncinatum* intercrop compared to the

Figure 1

Maize cultivated with an intercrop of *Desmodium intortum* to control the witchweed *Striga hermonthica*, showing improvements in height, stature, and color of the maize crop. (*a*) Maize and *Desmodium* intercrop; (*b*) maize grown as a monocrop. (Pictures taken at the *icipe* Thomas Odhiambo Campus, Mbita Point, Kenya).

other systems, confirming an allelopathic effect in addition to ground cover and nitrogen input (29). These ongoing trials continue to confirm a powerful allelopathic effect against *S. hermonthica* (Z.R. Khan, unpublished results). Further field trials demonstrated that the effect with *Desmodium* spp. is qualitatively different from intercropping with other legumes, for example, *V. unguiculata*, greengram, *Vigna radiate*, and *C. ochroleuca* (32, 41), which had all been previously proposed as control intercrops.

To confirm the allelopathic mechanism of *D. uncinatum*, water was passed through the root system in pots and then into soil containing seeds of *S. hermonthica* and maize. The aqueous eluate from soil in which *D. uncinatum* was growing again showed an extremely effective reduction in the infestation of maize by *S. hermonthica*, with or without inoculation with *Rhizobium* spp. (inoculum CB 627, whose taxonomy is ambiguous and has not yet been assigned a species by molecular sequencing, supplied by the International Livestock Research Institute, Nairobi, Kenya) found in association with wild *D. uncinatum*.

Initial studies on the mode of action of *D. uncinatum* root exudate allelochemicals collected from hydroponics on *S. hermonthica* in vitro suggested that, although there was a stimulation to germinate, the subsequent development prior to vascular attachment to the host, measured by a reduction in radicle length, was also affected (29, 75).

After the discovery of the control of *S. hermonthica* by *Desmodium* spp. in the field in 1998, take-up by farmers was rapid (30). In addition to control of *Striga*, which can raise maize yields in the worst affected areas from under one to approximately six tons ha^{-1} (although generally, yields of maize will double), there were other demonstrable advantages relating to enhanced nutrition through *Desmodium* producing cattle forage, soil conservation by increasing soil nitrogen and moisture through ground cover, and, because of its value as animal forage, to dairy and livestock production (30). The socioeconomic aspects of this will be discussed below in the Technology Transfer section.

Social acceptance. The use of companion crops is already widespread in farming practices in sub-Saharan Africa, where the main parasitic weed, *S. hermonthica*, is a major threat to food production. This greatly facilitates technology transfer. However, an understanding of the way the *D. uncinatum* intercrop can be used against the parasitic plant needed to be established among the resource-poor farming community. This was achieved by farmers visiting demonstration plots on field station farms. On seeing the benefits of *D. uncinatum* intercropped with maize to control *S. hermonthica*, seed for *D. uncinatum* had to be made available on a precommercial scale to be passed on within the farming community. Bioassays were established by which seed from multiplication plots could be assessed for its performance in controlling *S. hermonthica*. Throughout the process of transfer from field station to farm trials and through to farming practice, instruction through direct contact with field-based scientists and a growing number of extension workers was needed to establish *D. uncinatum* as a perennial crop.

When the intercropping system is introduced on-farm, rows of maize (75 cm apart) are intercropped with *D. uncinatum* (also 75 cm apart). In the first year, plots are hand-weeded early and again after five weeks to establish the matrix. The intercropping system is then managed by clipping back the desmodium. At the end of the season, after maize harvest, the desmodium is allowed to grow on, flower, and set seed. Initially, the seed was threshed by use of wooden mallets, but farm involvement, specifically by female farmers, demonstrated that this was better achieved by rubbing the seed on the lower quern stone with a cast-off plastic sandal sole. Winnowing is achieved conventionally by blowing away the chaff. An alternative method of propagation was established by the farmers themselves, initially in central Kenya, where, by observing the physical similarity between *Desmodium* spp. and *Ipomoea batatus*, they developed vegetative propagation (S. Njihia, unpublished report; **http://www.push-pull.net/Vines_brochure.pdf**). As well as the sale or

Table 2 Average (± SE) number of emerged *Striga hermonthica* plants, crop plant height (cm), and grain yields (tons ha^{-1}) from plots of maize, sorghum, and finger millet planted in sole stands (monocrop) or intercropped with *Desmodium* in a push-pull strategy in western Kenya

Crop	Cropping system	No. of emerged *Striga* per 100 crop plants	Plant height (cm)	Grain yields (tons ha^{-1})
Maize[a]	Monocrop	351.5(35.5)	125.9(4.1)	2.2(0.1)
	Push-pull (*with D. uncinatum*)	59.4(9.3)	196.1(3.1)	4.1(0.1)
Sorghum[b]	Monocrop	639.7(46.8)	90.6(0.2)	0.85(0.1)
	Sorghum-*D. intortum* intercrop	66.5(22.4)	145.7(11.1)	1.65(0.1)
Finger millet[c]	Monocrop	1422.1(673)	94.4(5.5)	0.4(0.1)
	Finger millet-*D. intortum* intercrop	10.1(1.7)	102.7(1.1)	0.9(0.1)

In all cases, *Striga hermonthica* counts were significantly lower, whereas plant height and grain yields were significantly higher, in the push-pull, sorghum-*Desmodium intortum*, and finger millet-*D. intortum* intercrops than in the monocrop plots.
[a]Means comprise data averages of 200 farmers' fields in 10 districts in western Kenya over seven cropping seasons (data extracted from Ref. 31).
[b]Means comprise data averages of 10 farmers' fields in western Kenya over two cropping seasons (data extracted from Ref. 35).
[c]Means comprise data averages from on-station plots at *icipe* Thomas Odhiambo campus in western Kenya over four cropping seasons (data extracted from Ref. 49).

use of seed, cut desmodium is a nutritious cattle forage for stall-fed cattle and has allowed an increase in dairy cow numbers, with individual farmers able to afford a dairy cow for the first time. The nutritional content of the forage legume has allowed exotic breeds of high milk-yielding cows to be introduced to the area, improving nutritional status of the population and income generation (24, 26). The Desmodium is perennial and so, in subsequent seasons, it is cut back for forage before maize is planted and again clipped after three and six weeks, along with hand weeding the plot, and a furrow is made in the remaining Desmodium root mass for sowing of the maize.

From the outset, very large improvements in grain yield were obtained (**Table 2**) and the approach was set for wider dissemination. However, essential to this process, and one of the main lessons to be learned from this success story, was the need for scientific input, both to overcome technical problems and to meet the challenge set by using such a low-input but knowledge-intensive system sustainably.

Problems and Challenges

In addition to ensuring sustainability of the companion cropping approach to controlling parasitic plants by providing a mechanistic understanding of the mode of action, a science base provides the means for solving problems as they arise. This includes reliable mass production of seed or planting material for the companion crops. When the *Desmodium* spp. crop is allowed to flower after the cereal is harvested and prior to setting seed, a large number of flower-feeding beetles were reported by farmers in certain regions of western Kenya. Farmers and extension workers reported that this damage could result in up to 50% reduction in the expected seed yield of 60–80 tons ha^{-1} equivalent. These beetles were identified as blister beetles (Coleoptera: Meloidae) in the genera *Mylabris* and *Coryna*. A PhD studentship was established collaboratively between *icipe* and the University of Pretoria in South Africa, and a cheap selective trap was created for these pests, using visual and flower-derived chemical attractants (Z.R. Khan, unpublished results). As soon as the trap is in local production and wide-scale farmer deployment is achieved, attempts will be made to find a market for the blister beetles that produce useful natural products, such as cantharidin, which may be used to treat skin complaints.

Ideally, local commercial enterprises would deal with aspects of providing the availability of seed and vegetatively propagated planting material but, in serving such resource-poor farmers who do not normally purchase agricultural inputs, there are problems. Vegetative propagation, achieved by allowing the Desmodium vines to have contact with the soil until sufficient rooting has developed for planting, is ideal for technology transfer from farmer to farmer, either involving a small payment or goods in kind. This transaction does not require repetition, as *Desmodium* spp. are crops grown perennially. However, although it is the most important approach in the dissemination of this technology, commercial seed production has required a guarantee that any excess seed will be purchased back by the development program. So far, this has not been necessary, but further capacity building is needed for this commercial route to work extensively enough for field-scale dissemination. Nonetheless, production of desmodium seed by small-scale farmers and women's groups has been commercialized through the Western Seed Company in Kenya and, in this process, has received full registration from the Kenya Plant Health Inspectorate Service (KEPHIS).

Mechanisms of *Striga Hermonthica* Control by *Desmodium Uncinatum*

The details of the mechanisms by which *D. uncinatum* as a companion crop controls *S. hermonthica* have not been fully elucidated. However, as published originally in 2002 (29), *D. uncinatum* causes germination of *Striga*, but the next phase of radicle development and attachment to the host vascular system through the haustorium attachment organ is almost completely prevented in the field after a good stand of *D. uncinatum* has been established. Laboratory studies on the mechanism (J.D. Scholes, personal communication) have not yet revealed the exact nature of how the infestation process is prevented, and it could possibly include induction of defense in the host plant by *D. uncinatum*. At the practical level, the germination stimulant effect caused by *D. uncinatum* together with the maize host plant, followed by the prevention of host infestation, results in suicidal germination (40, 70) of *Striga*. This means that, in addition to controlling these parasitic plants, the seed bank is rapidly depleted, thereby clearing the region of parasitic plants within approximately six years (40). Although the mechanism is not fully elucidated, it has been possible to use *S. hermonthica* seed germination, and the reduction in seed radicle length development after germination in bioassay-guided fractionation of root exudates and extracts from *D. uncinatum*, to identify germination stimulants and some inhibitory principles. Thus, compounds responsible for inducing germination include uncinanone B (**1**) (**Figure 2**). Analogous isoprenylated isoflavanones have also been characterized that, by oxidation, yield the isopropenylfurano structure given (70). A closely related compound, uncinanone C (**2**) (**Figure 2**), showed some radicle growth inhibitory effects on *Striga* (70). However, the most inhibitory fraction was more hydrophilic and yielded a di-*C*-glycosylated flavone (57), confirmed by further

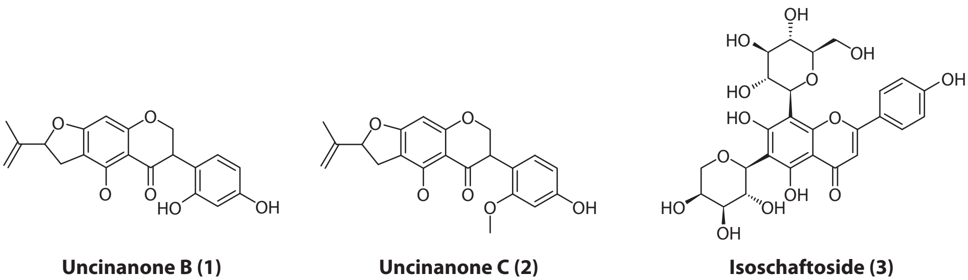

Figure 2

Flavonoids isolated from *Desmodium uncinatum* having biological activity toward *Striga hermonthica*.

Push-pull technology: to employ companion intercrops to push away pests and diseases, together with a trap crop

studies as 6-*C*-α-L-arabinopyranosyl-8-*C*-β-D-glucopyranosylapigenin (isoschaftoside) (**3**) (**Figure 2**). *C*-glycosylation, rather than the more usual *O*-glycosylation of flavones, would be responsible for higher stability in the rhizosphere and biological availability, which can account for the potent activity against infestation of maize by *S. hermonthica*. Nonetheless, continuous release into the rhizosphere takes place, as has been demonstrated by monitoring hydroponic production, and because maize develops within the *D. uncinatum* root mass, the presence of this inhibitory compound is ensured (75). Because of the farmers' demand for legumes producing edible beans for human consumption, understanding the biosynthesis of isoschaftoside (**3**) could allow production through breeding, or more particularly GM, in such plants or even in the cereals themselves.

Technology Transfer

After the development phase, various pathways have been investigated for technology transfer or adoption of companion cropping against *S. hermonthica* in maize and other cereals. These pathways include storylines on the radio through the daily agricultural serial Tembea na Majira, pictorial pamphlets featuring local languages, and farmers' meetings (barazas). However, farmer-farmer transfer mechanisms for this technology are most effective, and after nuclei of farmers are created, horizontal transfer is greatest (3). The push-pull technology is highly knowledge-intensive, and some farmers have been used in extension work as model examples of Desmodium companion planting, being assigned the role of farmer-teachers. The high level of technical efficiency shown by these farmer-teachers has resulted in more uptake and dissemination of the push-pull technology in western Kenya (4). Reasons for nonadoption, although mainly attributed to lack of *D. uncinatum* seed, include lack of knowledge of the technology as the second most important feature.

Underpinning such technology transfer must be of benefit to the farmer, and a socio-economic analysis including gross benefits and the return to labor must show enhanced rewards (26). Regardless of the region, although each has its own variations, the push-pull system with Desmodium outperforms maize intercropped with edible beans or a maize monocrop. It was possible to determine the benefits realized by farmers following adoption of the push-pull technology in the various districts in Kenya (31), with the decrease in *S. hermonthica* infestation generally being the main criterion. Although production costs were significantly higher in the first cropping year because of the establishment of perennial stands of *D. uncinatum*, these reduced to lower than in the maize-bean intercrop, even in the second year in most districts (34). As stated above, farmers originally expressed a wish for an edible bean having the *S. hermonthica* controlling trait. However, in the meantime, it has proved possible to combine use of *D. uncinatum* against *S. hermonthica* in maize with the production of edible beans (*Phaseolus vulgaris*) either by sowing beans in between plants in the maize rows or by putting them in the same planting hole as the maize seed; the edible beans are harvested earlier than the maize, as is the traditional practice (37) (**Figure 3**). Integration of beans into the push-pull technology provides an additional crop, a protein source, for the farmers and does not compromise the *S. hermonthica* control efficacy of *D. uncinatum*, yielding the same economic benefits. Where labor is easily available, farmers are advised to plant maize and beans in separate holes to avoid the risk of competition for moisture and nutrients where these might be limiting the yield.

Diversification to Other Cropping Systems

Use of *Desmodium* spp. against parasitic plants attacking cereals may be more general (see **Table 2**) and has been demonstrated using *D. intortum* against *S. hermonthica* in sorghum (32, 35). *D. intortum* also gave excellent control of *S. hermonthica* in finger millet, *Eleusine coracana* (49), which has high susceptibility to *S. hermonthica*.

Figure 3

Striga hermonthica control using *Desmodium uncinatum* as an intercrop, with maize and beans planted in the same rows.

Non-irrigated or upland rice is becoming more popular as a crop, and in some regions of Africa, for example, Uganda, NERICA (New Rice for Africa) is promoted for this. The main varieties of NERICA are very badly affected by *S. hermonthica*, indigenous to many of the regions now attempting to grow non-irrigated rice. However, with an undersowing of *D. uncinatum*, there is an immediate doubling of rice yields in areas highly infested with *S. hermonthica* (Z.R. Khan, unpublished results) (**Figure 4**).

With regard to other parasitic plants, in South Africa, *D. intortum* was reported to control effectively *S. asiatica* infesting sorghum (68). There is also evidence from initial studies in Tanzania that *S. asiatica* is controlled in maize in arid coastal regions by *D. intortum* (B. Pallangyo, unpublished report). Against *Orobanche* spp. infesting tomatoes, *Lycopersicon esculentum*, there is evidence of protection by drought tolerant *D. dichotomum* of African origin (A.G.T. Babiker, personal communication).

Biochemistry and Prospects for Biotechnology

An understanding of the biochemistry and related plant molecular genetics by which the inhibitory compounds released into the rhizosphere by *D. uncinatum* control *S. hermonthica* offers opportunities for exploiting these traits in more commercially or socially valuable companion crops (40). It would also be possible, by heterologous gene expression, to transfer these traits to the cereal crops themselves to create a new range of GM cereals. These would preferably be delivered as open-pollinating varieties

Figure 4

Striga hermonthica control using *Desmodium uncinatum* intercropped with New Rice for Africa (NERICA).

so that the farmers most afflicted by these parasitic plants could collect seed themselves and not have to buy hybrid seed seasonally (39). It would be assumed that, in each of these scenarios, sufficient of the necessary germination stimulants would occur from the background genetics of the legumes and cereals created with or without GM, so that the full suicidal germination mechanism was present (40). The main inhibitory compound obtained from *D. uncinatum*, isoschaftoside (**3**) (**Figure 2**), appears to be biosynthesized by *C*-glycosylation of apigenin. However, by using substrates isotopically labeled with deuterium, it has been demonstrated that 2-hydroxynaringenin (**4**) is the substrate (**Figure 5**) (19). In this work, it was proposed that the mechanism involves the open chain enol tautomer (**Figure 5**). There is now evidence (M.L. Hamilton, unpublished results) that the initial *C*-glucosylation is followed by an analogous *C*-arabinosylation, with the stereochemistry of substitution fixed as 8-*C*-glucosyl-6-*C*-arabinosyl at the dehydration step to isoschaftoside (**3**) (19). Currently, the protein fractions responsible are being purified for partial amino acid sequence determination by mass spectrometry, prior to attempts to clone the associated genes by degenerate PCR primers relating to the partial amino acid sequences. Full genomic sequences already available for legumes, including *V. unguiculata*, *Medicago truncatula*, and *Lotus japonicus*, could be searched for evidence of these genes being present (22). However, there is only one report of a characterized plant *C*-glycosyltransferase (10), despite these metabolites being found in more than 50 angiosperm families. As a result, there are no specific motifs for elucidating whether a glycosyltransferase sequence may encode an enzyme that glycosylates at an

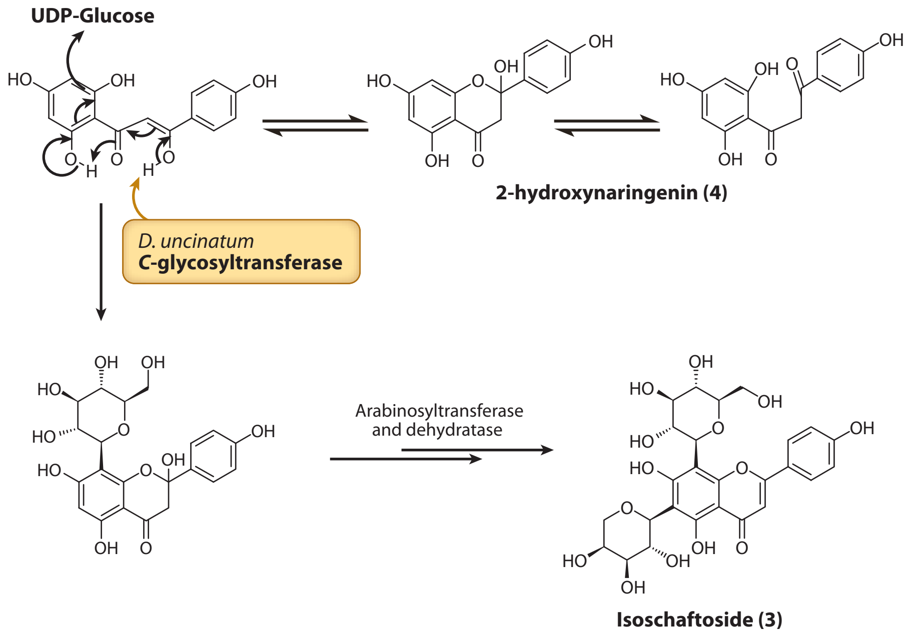

Figure 5

Proposed biosynthetic pathway for isoschaftoside (**3**) from 2-hydroxynaringenin (**4**) in *Desmodium uncinatum*.

O-, *N*-, *S*-, or *C*-position (R. Edwards, personal communication). The creation of a *C*-glycosyl bond in this case may be possible because of the reduced energy of the transitional state by the charge sharing exhibited in **Figure 5**. Nonetheless, evidence for the presence of such genetics in plants other than *Desmodium* could be exploited by breeding for a more pronounced version of this trait, or by genetic engineering to increase substrate availability and conversion to isoschaftoside (**3**). Already, vitexin, 8-*C*-glucosylapigenin, has been detected in various legumes and cereals, e.g., pearl millet (*Pennisetum glaucum*) (22), and it may be that only the final parts of the biosynthetic pathway would need to be incorporated by GM. These traits are *C*-arabinosylation and control of dehydration to allow multiple glycosylation and produce the desired regiochemistry.

SUMMARY POINTS

1. Although companion cropping is currently a tool for low-input agriculture, the sustainability of this approach could increase its value as agriculture intensifies sustainably (69). However, for both types of use to be reliable, mechanisms underpinning the role by which the companion crop controls the parasitic plant must be fully elucidated.
2. In addition to the value of the companion crop in weed or pest management, in this case for controlling parasitic plants, the companion crop should itself have commercial value, or at least social value.

3. For companion cropping to be efficient, the farmer must have complete ownership of the technology, apply it rigorously, and have sufficient knowledge of the underlying mechanisms so as not to depart from essential practices within the technology. Such knowledge-intensive technologies need to be disseminated in ways more sophisticated than simply buying a product with limited instructions, e.g., hybrid seed or a pesticide, or by copying new practices for the growing of new crops simply by observation or the acquisition of planting material.
4. Companion cropping could expand rapidly into intensifying agricultural production systems for use beyond the control of the specific parasitic plants discussed here and include the more general control of weeds, pathogens, and other organisms antagonistic to food and industrial crop production.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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Errata

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