

REVIEW PAPER

Exploiting phytochemicals for developing a ‘push–pull’ crop protection strategy for cereal farmers in Africa

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Abstract

Lepidopteran stemborers and parasitic weeds in the genus *Striga* are major constraints to efficient production of cereals, the most important staple food crops in Africa. Smallholder farmers are resource constrained and unable to afford expensive chemicals for crop protection. Development of a push–pull approach for integrated pest and weed management is reviewed here. Appropriate plants were discovered that naturally emit signalling chemicals (semiochemicals). Plants highly attractive for egg laying by stemborer pests were selected and employed as trap crops (pull), to draw pests away from the main crop. Of these, Napier grass, *Pennisetum purpureum* (Schumach), despite its attractiveness, supported minimal survival of the pests’ immature stages. Plants that repelled stemborer pests, notably molasses grass, *Melinis minutiflora* P. Beauv., and forage legumes in the genus *Desmodium*, were selected as intercrops (push). *Desmodium* intercrops suppress *Striga hermonthica* (Del.) Benth. through an allelopathic mechanism. Their root exudates contain novel flavonoid compounds, which stimulate suicidal germination of *S. hermonthica* seeds and dramatically inhibit its attachment to host roots. The companion crops provide valuable forage for farm animals while the leguminous intercrops also improve soil fertility and moisture retention. The system is appropriate as it is based on locally available plants, not expensive external inputs, and fits well with traditional mixed cropping systems in Africa. To date it has been adopted by more than 30 000 smallholder farmers in East Africa where maize yields have increased from ~1 t ha⁻¹ to 3.5 t ha⁻¹. Future directions for semiochemical delivery by plants including biotechnological opportunities are discussed.

Key words: Allelochemicals, cereals, push–pull, semiochemicals, stemborer, *Striga*.

Introduction

Plants, being at the base of food chains, have evolved a remarkable diversity of strategies to defend themselves against attack by antagonistic organisms including herbivores and parasitic plants. These involve both physical and chemical defences which have evolved as adaptations over a long history of exposure (Roades, 1983). Abundant evidence has accumulated to implicate secondary metabolites as defensive compounds in plant–plant, plant–herbivore, and plant–pathogen interactions (Harbone, 1978; Rosenthal and Janzen, 1979). Defence mechanisms against herbivores are broadly categorized as direct and indirect responses. Direct defence mechanisms are based on the plant secondary metabolites or defensive proteins that directly affect the

herbivore by toxic or otherwise deterrent properties, whereas indirect defences are based on the release of volatile plant signals that attract natural enemies of the herbivore (Gouinguene and Turlings, 2002). The benefits of indirect defence result in the reduction of subsequent herbivory and an increase in reproductive fitness (Bruce and Pickett, 2007). In recent years, indirect defences have been the subject of much attention because they might offer new strategies for crop protection. Here a combination of both defences has been discovered and exploited in Africa as explained in this review. With regards to weeds, the term allelopathy is used to refer to the effects of one plant on another through the production of secondary metabolites

(allelochemicals) and their release into the rhizosphere (Rice, 1984).

Africa faces serious and increasing problems in its ability to feed its rapidly growing population, and has the tragic distinction of being the only continent where per capita food production has been on the decline in the past two decades (Muchena *et al.*, 2005). The situation is particularly severe in sub-Saharan Africa (SSA) where almost 33% of the population (close to 200 million people) is undernourished. It is the only region in the world where hunger and poverty are projected to worsen over the next two decades unless drastic action is taken to improve agriculture and economic development (Kidane *et al.*, 2006). Approximately 80% of the population of SSA depends on agriculture for food, income, and employment. However, the agricultural sector is characterized by very low productivity, resulting in very high poverty levels and undernourishment. Increases in crop production are therefore needed to provide food security, stimulate economic growth, and alleviate poverty. Sustainable solutions are also needed to arrest environmental degradation over most of the region.

Biotic crop production constraints in sub-Saharan Africa

Cereals, principally maize, *Zea mays* (L.), sorghum, *Sorghum bicolor* (L.) Moench, finger millet, *Eleusine coracana* (L.) Gaertn., and rice, *Oryza sativa* (L.), are the most important food and cash crops for millions of rural farm families in SSA. Their production by smallholder farmers in the region is severely constrained by insect pests, particularly cereal stem borers in the families Noctuidae and Crambidae, and parasitic weeds in the genus *Striga* (Orobanchaceae) (Khan *et al.*, 2008a). Indeed, attack by either stem borers or *Striga* can completely destroy the yield of cereal crops.

There is a complex of >20 economically important lepidopteran stem borers of cultivated grasses in SSA (Maes, 1998), with the two most important species being the indigenous *Busseola fusca* (Füller) (Lepidoptera: Noctuidae) and exotic *Chilo partellus* Swinhoe (Lepidoptera: Crambidae). Attack by stem borers alone causes between 10% and 80% yield loss, depending on the pest population density and the phenological stage of the crop at infestation (Kfir *et al.*, 2002). On the other hand, there are at least 22 species of *Striga* in Africa, of which *Striga hermonthica* (Del.) Benth. and *Striga asiatica* (L.) Kuntze are the most socio-economically important in cereal cultivation in much of SSA (Gressel *et al.*, 2004; Gethi *et al.*, 2005). *Striga* infests >40% of arable land in SSA (Lagoke *et al.*, 1991) and causes yield losses of up to 100% (Hassan *et al.*, 1994). The effects of *Striga* are most severe in degraded environments, with low soil fertility and low rainfall, and in subsistence farming systems where there are few options for purchasing external inputs (Sauerborn *et al.*, 2003; Gurney *et al.*, 2006). In western Kenya, for example, it is estimated that 76% of land planted to maize and sorghum is infested with

S. hermonthica, causing annual losses estimated at US\$40.8 million (Kanampiu *et al.*, 2002).

Striga is so ingeniously adapted to its environment and host plants (Bebawi and Metwali, 1991) that it will only germinate in response to specific chemical cues present in host root exudates or certain non-host plants (Parker and Riches, 1993; Yoder, 1999). Seeds can remain dormant but viable in the soil for >10 years. *Striga* also causes 'phytotoxic' effects within days of attachment to its hosts (Frost *et al.*, 1997; Gurney *et al.*, 1999), the underlying mechanism of which has not yet been elucidated (Gurney *et al.*, 2006). *Striga* infestation results in a large reduction in host plant height, biomass, and eventual grain yield (Gurney *et al.*, 1999). Moreover, maize infested by *Striga* has recently been found to be more preferred for egg laying by stem borer moths than uninfested maize (Mohamed *et al.*, 2007), thereby aggravating its effects. Unfortunately, *Striga* infestation continues to extend to new areas in the region as farmers abandon heavily infested fields for new ones (Khan, 2002; Gressel *et al.*, 2004), a practice that is untenable due to consistent reduction in landholdings due to increases in human population.

Although insecticides and herbicides can help to alleviate these problems, complete control is seldom achieved. Moreover, the resource-constrained subsistence farmers in SSA cannot afford expensive chemicals. A large number of farmers, therefore, do not attempt to manage stem borers or *Striga*, resulting in high grain yield losses and food insecurity (Chitere and Omolo, 1993; Oswald, 2005).

Development of a mixed cropping push-pull system for stem borer and *Striga* control

A 'push-pull' strategy is a cropping system in which specifically chosen companion plants are grown in between and around the main crop. These companion plants release semiochemicals that (i) repel insect pests from the main crop using an intercrop which is the 'push' component; and (ii) attract insect pests away from the main crop using a trap crop which is the 'pull' component (Cook *et al.*, 2007). Such a system requires a good understanding of the chemical ecology of plant-insect interactions on the different crops. Candidate crops need to be systematically evaluated in field trials. While a push-pull system was being developed specifically for the control of cereal stem borers in smallholder maize production in Kenya, it was discovered that certain intercrops had further benefits in terms of suppression of *Striga* weed. This effect is just as important as stem borer control for achieving yield increases as *Striga* is a very serious weed in much of SSA. However, the mechanism underpinning this is an allelopathic effect of intercrop root exudates (non-volatile) in suppressing germination of *Striga* and hence only requires the intercrop component of the push-pull system.

The cereal stem borers are generally polyphagous, attacking a wide range of grasses in the families Poaceae, Cyperaceae, and Typhaceae (Khan *et al.*, 1997a; Polaszek

and Khan, 1998). Africa is home to thousands of grass species and, under natural conditions, stemborers attack these wild grasses (Mally, 1920) with which they have co-evolved. Because of the biodiverse nature of grass stands, there is a wide range of food resources that support many insect pests which often invade surrounding agro-ecosystems (Van Emden, 1990). The wild hosts act as pest reservoirs when crop hosts are not available. However, attractive wild hosts can be exploited as natural trap plants for stemborers (Khan *et al.*, 1997a; Schulthess *et al.*, 1997).

In an extensive field survey, >500 species belonging mainly to three grass families (Poaceae, Cyperaceae, and Typhinae) as well as some leguminous crops in different agro-ecological zones in Kenya were sampled, and stemborers associated with each species were recovered. The purpose of the survey was to identify appropriate species that could be used as intercrop (push) and trap crop (pull) components of the push-pull mixed cropping system. Species selected as potential intercrops had to be repellent to stemborers and reduce their populations on the main crop of maize. Candidate crops that fulfilled this criterion while also attracting natural enemies of the pests were ranked higher than crops which merely repelled the pest. Species selected as potential trap crops had to be preferred by stemborers to maize and other cereal crops for oviposition. The best trap crops were those which were attractive but did not support development of the immature stages of the stemborer pest.

These studies identified the most attractive plant species as putative trap crops (pull). It was observed that two poaceous plants, Napier grass, *Pennisetum purpureum* Schumach, and Sudan grass, *Sorghum sudanense* Stapf, both of which are forage crops, attracted considerably more oviposition by stemborer moths than maize (Khan *et al.*, 2000, 2006a). These two crops, despite being attractive, did not support development of the stemborer pest populations. Stemborer larvae did not survive on Napier grass because it produces a gummy substance that immobilizes the young larvae as they try to bore into the stem. Additionally, it has low nutritive value for the larvae (Khan *et al.*, 2007a). This made it a good choice for a trap crop. Although Sudan grass allowed development of the larvae, they had a very high parasitization rate, with up to 80% being killed on this plant species.

The least attractive plant species were identified as putative repellent intercrop species (push). Notably, the molasses grass, *Melinis minutiflora* P. Beauv, an indigenous poaceous plant with forage value, attracted no oviposition at all. Farmers in SSA practice polycropping where the main cereal crops are interplanted with legumes, and therefore legumes were also evaluated in these studies although they are not attacked by cereal stemborers. Two plants in the *Desmodium* genus, silverleaf, *D. uncinatum* DC and greenleaf, *D. intortum* (Mill) Urb, were shown to repel ovipositing stemborers (Khan *et al.*, 2000).

These putative 'push' and 'pull' plants were then tested under field conditions in western Kenya where plots of maize were grown either as monocultures or surrounded by

a 1 m border of Napier or Sudan grass to act as a trap crop. In plots with a border of Napier grass, although there was considerably more oviposition and early larval development in the trap crop compared with the maize, only 20% of the larvae survived on the Napier grass, whereas 80% survived through to adults on the maize. Sudan grass border contained eight times as many larvae as the maize, and stemborer numbers within the maize were reduced to one-third compared with the maize monoculture. Grain yields were significantly higher in these fields than in the monocultures, higher by ~1–1.5 t ha⁻¹ (Khan *et al.*, 1997a) (Fig. 1).

Planting *M. minutiflora* between each row of maize caused a dramatic reduction in stemborer infestation (Khan *et al.*, 2000), with a decrease in numbers of >80%. Indeed, there was a highly significant reduction in stemborers at the more practically useful ratio of one row of *M. minutiflora* to three or four of maize. A statistically significant effect could still be seen at a ratio of one row in 20 rows of maize. Intercropping maize with either *D. uncinatum* or *D. intortum* also gave similar results to maize-*M. minutiflora* intercrops (Khan *et al.*, 2000, 2006b).

While push-pull systems were being optimized for stemborer control, intercrops were systematically investigated. During this process a highly effective intervention against *Striga* spp. in cereals was discovered. It was noticed that maize intercropped with *D. uncinatum* or *D. intortum* suffered far less *Striga* infestation than maize in monoculture (Figs 1, 2). This effect was confirmed by further field testing and shown to be significantly greater than that observed with other legumes widely recommended as intercropping solutions to *Striga* problems, for example cowpea, *Vigna unguiculata* (L.) Walp., as were the concomitant yield increases (Khan *et al.*, 2002, 2007b).

Understanding semiochemistry of companion plants

The push-pull system is based on understanding and exploiting the rich botanical biodiversity in the African flora. The interactions with pests and weeds are based on semiochemicals released by the companion plants. The science underpinning these interactions is described here:

Semiochemistry of 'push' and 'pull' plants for stemborer control

Attraction of insects to plants and other host organisms involves detection of specific semiochemicals (natural signal chemicals mediating changes in behaviour or development) (Nordlund and Lewis, 1976; Dicke and Sabelis, 1988), or specific ratios of semiochemicals (Bruce *et al.*, 2005). Also, avoidance of unsuitable hosts can involve the detection of specific semiochemicals, or mixtures of semiochemicals, associated with non-host taxa (Hardie *et al.*, 1994; Pettersson *et al.*, 1994).

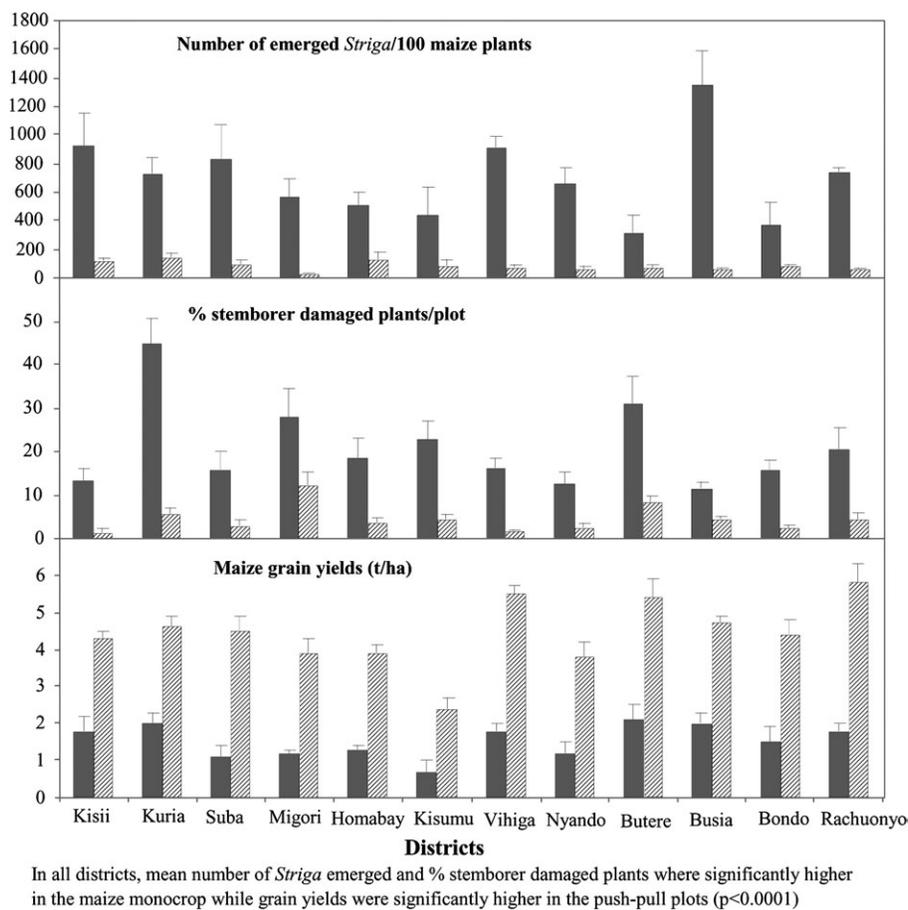


Fig. 1. Mean number of emerged *Striga hermonthica* per plot, proportion of stemborer-damaged plants per plot, and average maize grain yields (t ha^{-1}) from maize monocrop (shaded bars) and push-pull plots (striped bars) in different districts in western Kenya. Means represent data averages from 30 farmers' fields per district over three cropping seasons (long and short rains 2007, and long rains 2008).

The underlying semiochemistry of the push and pull companion plants was investigated. This was considered essential for maintaining sustainability in the event that new planting material releases different volatiles from the plants originally investigated. Volatile compounds released by the trap plants, Sudan grass, Napier grass, and other highly attractive hosts were captured by absorption onto a porous polymer. The volatiles were then eluted from the polymer with a solvent and the samples subjected to gas chromatographic (GC) analysis coupled directly to a preparation from the moth antenna [an electroantennogram (EAG)], to enable identification of semiochemicals likely to have attractant activity at the levels released by the plant. GC peaks consistently associated with EAG activity were tentatively identified by GC coupled-mass spectrometry (GC-MS) and identity was confirmed using authentic samples. Six active compounds were identified from both maize and the Napier grass trap crop: octanal, nonanal, naphthalene, 4-allylanisole, eugenol, and linalool. Each of these compounds was shown to have positive activity in behavioural tests that investigated oviposition onto an artificial substrate treated with the individual compounds (Khan *et al.*, 2000).

Further studies showed that trap plants produced significantly higher amounts of attractive compounds than maize and sorghum (Birkett *et al.*, 2006). Moreover, emission varied over the day-night cycle so that it was highest at the time when moths are most active. The green leaf volatiles, mainly hexanal, (E)-2-hexenal, (Z)-3-hexen-1-ol, and (Z)-3-hexen-1-yl acetate, from the trap plants, principally *P. purpureum* and *Hyparrhenia tamba*, showed an ~100-fold increase in the first hour of the scotophase (night) (Chamberlain *et al.*, 2006). This coincides with the period at which stemborer moths seek host plants for oviposition (Päts, 1991). Although similar changes in emission over the diurnal cycle were observed with *S. bicolor* and two out of three cultivars of *Z. mays*, the magnitude of increase was 10 times less than in the trap crop. This provided an explanation for why Napier grass was preferred to maize by stemborer moths for oviposition (Fig. 3).

For the intercrop it was found that volatiles were released that play a role in both direct and indirect defence. *Melinis minutiflora* constitutively emits volatiles that repelled female stemborer moths but attracted parasitoids, principally foraging female *Cotesia sesamiae* Cameron



Fig. 2. Cereal production biotic constraints addressed by the push–pull system: (a) *Striga hermonthica* weed; (b) maize grown alone damaged by *Striga*; (c) stemborer larva inside a stem; (d) maize intercropped with *Desmodium uncinatum* and not damaged by *Striga*.

(Hymenoptera: Braconidae) (Khan *et al.*, 1997b). Further behavioural studies confirmed that the active compounds found specifically in *M. minutiflora*, but not in the trap plants, comprised (*E*)-ocimene, (*E*)-4,8-dimethyl-1,3,7-nonatriene, β -caryophyllene, humulene, and α -terpinolene (Khan *et al.*, 1997b, 2000; Pickett *et al.*, 2006) (Fig. 3). In response to attack by herbivores, plants produce semi-chemicals called herbivore-induced plant volatiles (HIPVs) which act to repel pests and attract their natural enemies (see review by Khan *et al.*, 2008b). Compounds such as ocimene and the nonatriene are semiochemicals produced during damage to maize plants by herbivorous insects (Turlings *et al.*, 1990, 1995). The nonatriene was demonstrated to be responsible for the increased parasitoid foraging in the intercropped plots (Khan *et al.*, 1997b), indicating that intact plants such as *M. minutiflora* with an inherent ability to release such stimuli could be used in development of new crop protection strategies. *Desmodium* spp. were also shown to produce similar compounds (Khan *et al.*, 2000). Indeed further studies have shown that they enhance stemborer larval and pupal parasitoid activity when intercropped with maize, and its flowers are highly attractive to *C. sesamiae* (Midega *et al.*, 2009).

Allelopathy of intercrops for Striga control

Although the phenomenon of allelopathy has been well documented, its potential in weed control has only recently been embraced and demonstrated (Olofsdotter *et al.*, 2002). Previous studies of allelopathy in this context have primarily focused on toxic activity. To elucidate the mechanism of *Striga* suppression by *Desmodium* intercrops, a number of potential mechanisms were investigated. These included effects of increased available nitrogen in the soil, shading, and allelopathic effects associated with chemicals released from the *Desmodium* roots (Khan *et al.*, 2000, 2002). These factors were studied in field and screenhouse trials in western Kenya using *D. uncinatum* (Khan *et al.*, 2002). Although soil shading and addition of nitrogen fertilizer showed some degree of reduction against *S. hermonthica* infestation, there was stronger evidence for a putative allelopathic mechanism. A highly significant reduction in *S. hermonthica* infestation was observed in screenhouse studies when an aqueous solution, eluting from pots in which *D. uncinatum* plants were growing, was used to irrigate pots of maize planted in soil seeded with high levels of *S. hermonthica*. Growth of the parasitic weed was almost

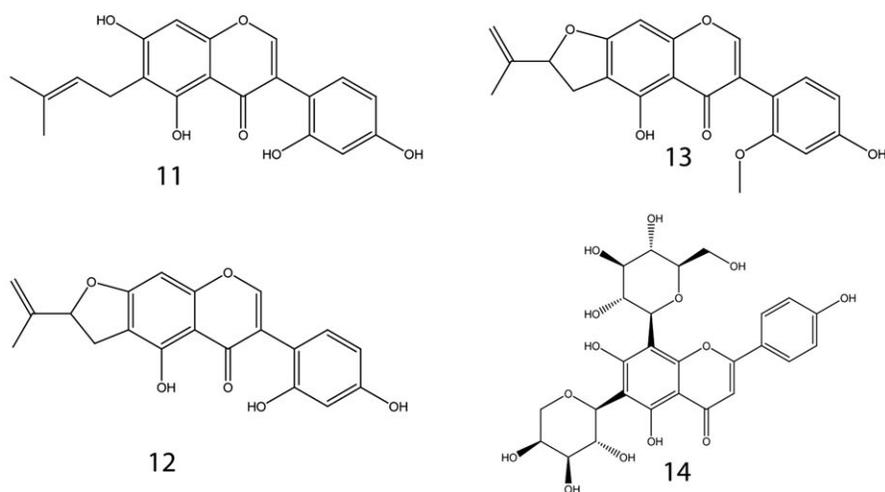
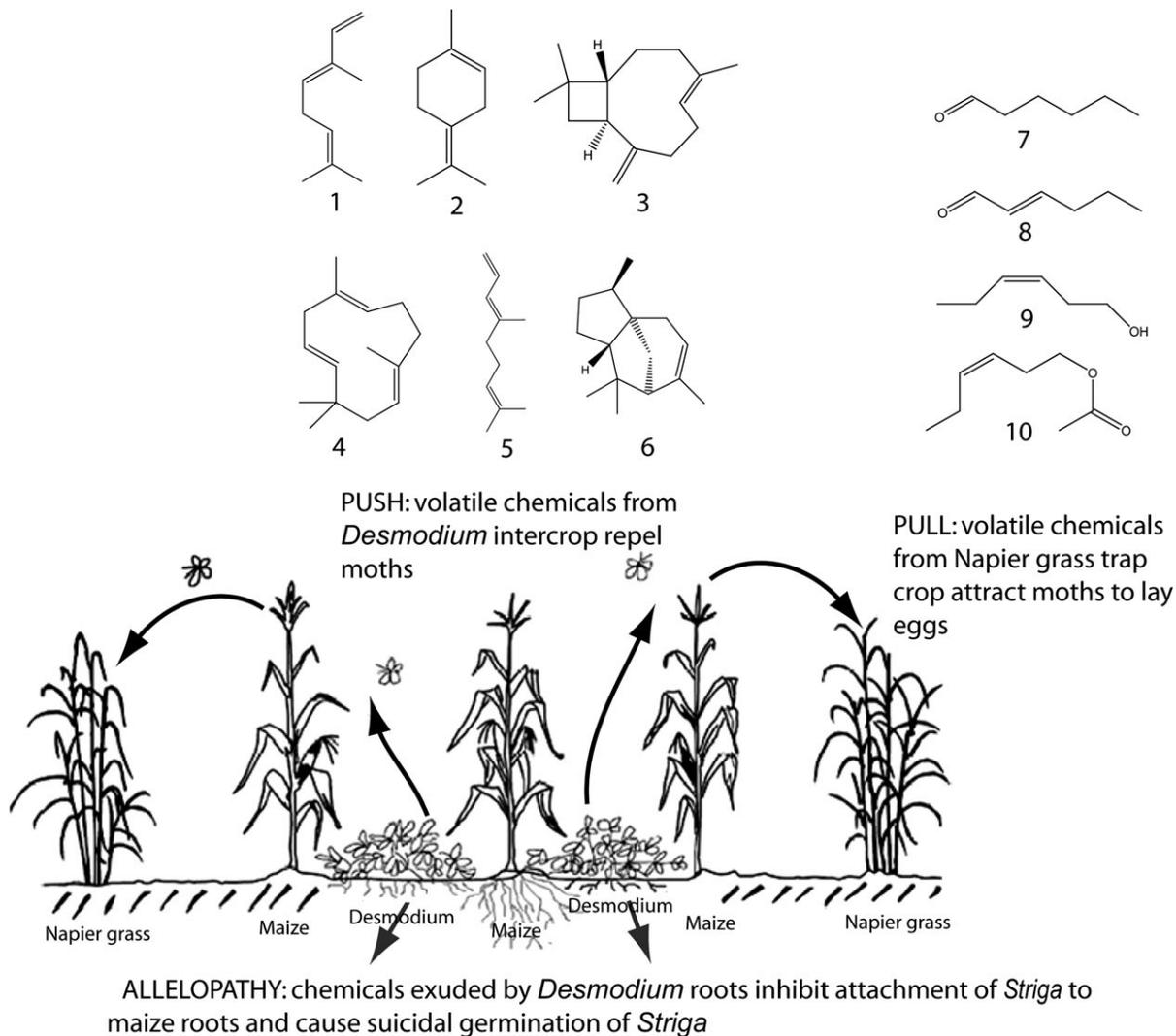


Fig. 3. How the push–pull system works: stemborer moths are repelled by intercrop volatiles while attracted to trap crop volatiles. Root exudates from the *Desmodium uncinatum* intercrop cause suicidal germination of *Striga* and inhibit attachment to maize roots. 1=(*E*)- β -ocimene; 2= α -terpinolene; 3= β -caryophyllene; 4=humulene; 5=(*E*)-4,8-dimethyl-1,3,7-nonatriene; 6= α -cedrene; 7=hexanal; 8=(*E*)-2-hexenal; 9=(*Z*)-3-hexen-1-ol; 10=(*Z*)-3-hexen-1-yl acetate; 11=5,7,2',4'-tetrahydroxy-6-(3-methylbut-2-enyl)isoflavanone (uncinane A); 12=4'',5''-dihydro-5,2',4'-trihydroxy-5''-isopropenylfurano-(2'',3'')-(7,6)-isoflavanone (uncinane B); 13=4'',5''-dihydro-2'-methoxy-5,4'-dihydroxy-5''-isopropenylfurano-(2'',3'')-(7,6)-isoflavanone (uncinane C); and 14=di-C-glycosylflavone 6-C- α -L-arabinopyranosyl-8-C- β -D-glucopyranosylapigenin (part of this figure is adapted from an illustration in a brochure, 'The Quiet Revolution: Push–Pull Technology and the African Farmer'. Gatsby Charitable Foundation, 2005).

completely suppressed, whereas extensive infestation occurred with the control eluate (Khan *et al.*, 2002). Further studies demonstrated that this involved a germination stimulant for *S. hermonthica* and also an inhibitor for radical development (Khan *et al.*, 2000, 2002).

Three isoflavonones, 5,7,2',4'-tetrahydroxy-6-(3-methylbut-2-enyl)isoflavanone (uncinanone A), 4'',5''-dihydro-5,2',4'-trihydroxy-5''-isopropenylfurano-(2'',3'';7,6)-isoflavanone (uncinanone B), and 4'',5''-dihydro-2'-methoxy-5,4'-dihydroxy-5''-isopropenylfurano-(2'',3'';7,6)-isoflavanone (uncinanone C), were isolated from the root exudates of *D. uncinatum* (Tsanuo *et al.*, 2003; Hooper *et al.*, 2010) (Fig. 3). Isolated fractions containing uncinanone B induced germination of *Striga* seeds while fractions containing uncinanone C inhibited radical growth, representing the first example of a newly identified potential allelopathic mechanism to prevent *S. hermonthica* parasitism.

Recently another key post-germination inhibitor, di-C-glycosylflavone 6-C- α -L-arabinopyranosyl-8-C- β -D-glucopyranosylapigenin, also known as isoschaftoside, as well as other C-glycosylflavones have been characterized from a more polar fraction of *D. uncinatum* root exudates and solvent extracts (Pickett *et al.*, 2007; Hooper *et al.*, 2009) (Fig. 3), and full chemical elucidation of other allelopathic agents is ongoing. The combined effect of germination stimulants and post-germination inhibitors represents a novel and highly efficient mechanism of suicidal germination of *S. hermonthica* seeds. It thus provides a novel means of continual *in situ* reduction of the *Striga* seed bank in the soil, even in the presence of graminaceous host plants. Indeed the density of *S. hermonthica* seeds steadily decreases after every cropping season in maize–*Desmodium* intercrops, while in maize monocrop plots it steadily rises (Khan *et al.*, 2008c; Vanlauwe *et al.*, 2008). *Desmodium*-based intercrops thus represent one of the very few examples of use of allelopathy for weed control (Hooper *et al.*, 2009; Pickett *et al.*, 2010). More than 30 000 small-scale farmers in eastern Africa are now using it for controlling *S. hermonthica*, in addition to its role in the push–pull strategy for control of cereal stem borers (Khan *et al.*, 2008a).

Agronomic benefits of push–pull

Farmers adopting the push–pull system have reported significant control of both *Striga* and stem borers, resulting in significant increases in grain yields, by at least 2 t ha⁻¹ per season (Khan *et al.*, 2008a), in many cases tripling maize yields (Fig. 1). Moreover, farmers often cited additional benefits including improvement in soil fertility, fodder, and milk productivity (Khan *et al.*, 2008d), resulting in significantly higher revenue, gross benefits, and returns to land and labour than their conventional cropping systems (Khan *et al.*, 2008e; De Groote *et al.*, 2010). The technology thus has the potential to improve the livelihoods of smallholder farmers and rural families while improving environmental sustainability. In addition, it opens up

significant opportunities for smallholder growth and represents a platform technology around which new income generation and human nutritional components, such as livestock keeping, can be added.

More recently, farmers have begun integrating edible beans into the push–pull system, further increasing the technology's appeal to them (Khan *et al.*, 2009). During the last 6 years, the technology has been disseminated to farmers through a series of interventions (Khan *et al.*, 2008d; Amudavi *et al.*, 2009a, b), including mass media, information bulletins, farmer-to-farmer learning methods such as field days, farmer teachers, farmer field schools and drama, and public meetings. The technology has also been extended to sorghum and finger millet where intercropping with *Desmodium* effectively controls both *S. hermonthica* and stem borer infestations, resulting in significant increases in grain yields (Khan *et al.*, 2006c, 2007b; Midega *et al.*, 2010; Pickett *et al.*, 2010). Recently field trials have shown dramatic effects on *Striga* control (Pickett *et al.*, 2010) with concomitant increase in grain yield of upland NERICA rice through intercropping with *D. uncinatum* (Table 1).

Biodiversity and plant chemistry: additional opportunities for future plant protection

Early herbivory trait

One of the main defence mechanisms plants have evolved against attacking organisms involves an increase in volatile emission that appears to function as a 'cry for help' to

Table 1. Mean number of emerged *Striga hermonthica* and rice grain yields (t ha⁻¹) from upland rice plots planted either as sole stands or intercropped with *Desmodium uncinatum*

Means represent data averages of six replications, each 6 m by 6 m plots over two cropping seasons.

Treatment	Cropping seasons	
	Short rains 2008	Long rains 2009
Mean <i>Striga hermonthica</i> counts (30 hills plot ⁻¹)		
Rice monocrop	148.2 (27.6) a	102.7(42.1) a
Rice/nitrogen	140.2 (35.2) a	54.3 (23.7) a
Rice/ <i>Desmodium</i>	7.7 (1.8) b	1.0 (0.4) b
Rice/ <i>Desmodium</i> /nitrogen	9.3 (2.3) b	0.8 (0.4) b
$F_{3, 20}$	32.9	27.4
P	<0.0001	<0.0001
Mean rice grain yield (t ha ⁻¹)		
Rice monocrop	0.75 (0.1) b	0.4 (0.1) b
Rice/nitrogen	0.99 (0.2) b	0.5 (0.1) b
Rice/ <i>Desmodium</i>	2.6 (0.5) a	2.4(0.2) a
Rice/ <i>Desmodium</i> /nitrogen	2.9 (0.3) a	2.7(0.3) a
$F_{3, 20}$	12.5	66.4
P	<0.0001	<0.0001

a and b denote where there is a statistically significant difference ($P < 0.05$).

attract natural enemies in tritrophic interactions in response to insect attack (Whitfield, 2001; Turlings and Ton, 2006), and to repel further colonization by the herbivore itself (e.g. De Moraes *et al.*, 2001). However, such biological control approaches are generally not very effective in reducing pest damage in farmers' fields because the 'cry for help' comes after damage has already been inflicted on the plants, and therefore activity of the natural enemies does not prevent crop yield losses. Recently, an unusual phenomenon was observed where an African forage grass, *Brachiaria brizantha* (Hochst. ex A. Rich.) Stapf., responds to oviposition by *C. partellus* through suppression of the main green leaf volatile (Z)-3-hexenyl acetate (Z3HA), used in host location by the pest, thereby making the plant 'invisible' to ovipositing stemborer females and thus preventing further egg laying by them (Bruce *et al.*, 2010). Despite this suppression, the ratio of other compounds relative to Z3HA was increased in plants exposed to *C. partellus* oviposition, making the volatile blend more attractive to an indigenous larval parasitic wasp, *C. sesamiae*, than that of plants without oviposition. Attraction of the larval parasitoids is particularly advantageous as it makes them available immediately after the eggs hatch and before larvae begin to feed on and damage the plants. This is a useful trait that *B. brizantha* has evolved and uses to defend itself against pests, and there is an urgent need to identify and develop cereal varieties that exhibit similar traits to protect themselves against insect pests. Studies show considerable intraspecific variation, in both quantity and quality, of the odour released by different maize varieties (Degen *et al.*, 2004). Moreover, varietal and genotypic differences in herbivore-induced volatile emissions have been recorded for several plant species. Indeed, a similar trait has recently been observed in maize landraces that alter volatile emission as a result of oviposition by stemborer moths and attract both egg and larval parasitoids (ZR Khan *et al.*, unpublished data), and screening of more varieties is ongoing to select those that can switch on their defence systems early in the chain of pest attack events.

Switching on the plant defence system through companion cropping

Plants can respond to herbivore-induced volatiles emitted by neighbouring plants when damaged by adjusting their metabolism to increase their resistance to herbivores (Karban *et al.*, 2003). Plants exposed in this way are then avoided by herbivores (Glinwood *et al.*, 2004) because expression of resistance genes and hence defence-related plant compounds is higher (Arimura *et al.*, 2000). Exposure to HIPVs also primes the plant's defences to future attack (Engelberth *et al.*, 2004). Additionally, attractiveness of an uninfested plant to natural enemies increases after exposure to volatiles released from infested plants (Birkett *et al.*, 2000). Undamaged *M. minutiflora* constitutively releases the volatile cues associated with damaged maize [primarily (E)-4,8-dimethyl-1,3,7-nonatriene] that repel stemborer

pests (Khan *et al.*, 1997b). Very recently, it has been observed that volatiles emitted by intact molasses grass induce a defence response in the neighbouring maize plants, leading to production of similar 'cry for help' cues that attract larval parasitoids, without being damaged (ZR Khan *et al.*, unpublished data). Molasses grass is presently being used in the push-pull technology in some parts of Kenya, where *Striga* is not a problem, to control stemborer pests (Hassanali *et al.*, 2008). Understanding the effects, and biochemical pathways involved, of defence-inducing volatiles of *M. minutiflora* holds an important key to development of new plant protection systems based on switching on of inherent plant defences, through either companion cropping or synthetic variants of the active compounds.

Biotechnological opportunities against Striga

Another possibility for future crop protection would be to transfer the biosynthetic pathway for the allelochemicals that control *Striga* from *Desmodium* into other crops. Smallholder farmers in Africa plant food legumes as the intercrops of choice. However, such legumes do not provide potent suppression of *Striga* spp. observed with *Desmodium* spp. (Khan *et al.*, 2002, 2007b). Although root exudates of edible legumes already show significant levels of *Striga* germination stimulation caused by strigolactones derived from the carotenoid pathway (Matusova *et al.*, 2005), they are not able to exert effective *Striga* control. Therefore, studies are needed to identify pathways and genes responsible for the powerful *Striga*-controlling effects of *Desmodium* spp. The genes responsible for these traits could then be transferred into food legumes. A prerequisite for effective transfer of the allelochemical pathway into food legumes is to identify the active molecules and the genes responsible for their production. Progress is being made towards this (Tsanuo *et al.*, 2003; Khan *et al.*, 2008c; Hamilton *et al.*, 2009), although full confirmation of the active compounds and associated genes has not yet been achieved. The concentration of the purified compounds that show biological activity will be compared with the concentrations found in root exudates from hydroponics or soil to ascertain whether they are active at ecologically relevant concentrations (Hooper *et al.*, 2009, 2010). Once the active ingredients in *Desmodium* root exudates are fully defined, it will be possible to evaluate and select legumes, particularly those that have co-evolved with *Striga*, for similar allelochemicals and associated *Striga*-controlling traits comparable with those of *Desmodium* spp. Conventional breeding could be used to select and enhance the traits in the food legumes if they could be found or, alternatively, genes could be transferred directly from *Desmodium* by transforming plants.

Conclusions and future outlook

The push-pull system is a novel cropping system for controlling stemborers and *Striga* weed in smallholder

cereal farming systems in Africa (Cook *et al.*, 2007). It involves attracting stemborers with trap plants (pull) whilst driving them away from the main crop using a repellent intercrop (push). Chemicals released by the intercrop roots induce abortive germination of *Striga* seeds, providing very effective control of this noxious weed. The companion plants provide high value animal fodder, facilitating milk production and diversifying farmers' income sources. Furthermore, soil fertility is improved and soil erosion prevented. The technology is appropriate as it is based on locally available perennial plants, not expensive external inputs, and fits well with traditional mixed cropping systems in Africa. To date it has been adopted by more than 30 000 smallholder farmers in East Africa where maize yields have increased from $\sim 1 \text{ t ha}^{-1}$ to 3.5 t ha^{-1} , achieved with minimal inputs. While the number of farmers already using push-pull is considerable, there is much scope for further expansion. The system is proven to increase yields in situations where stemborers and *Striga* are a problem. It is estimated that a further 30 000 000 farmers could benefit if they were to adopt the push-pull system.

Plant chemistry is influenced by environmental factors such as temperature (Bradfield and Stamp, 2004), and there is evidence of increasingly hot and dry conditions associated with climate change (Burke *et al.*, 2009). Therefore, to ensure that push-pull technology continues to impact food security positively in the region over the longer term, new drought-tolerant trap and intercrop plants need to be found. These should have the appropriate chemistry in terms of stemborer attractancy for the trap component and stemborer repellence and *Striga* suppression, and ability to improve soil fertility and soil moisture retention, for the intercrop component. In addition, they should provide other ecosystem services such as biodiversity improvement and conservation and organic matter improvement.

The work to isolate and purify all the active compounds in the *Desmodium* root exudates and fully elucidate their effects on *Striga* suppression is ongoing. Elucidation of the underlying mechanism will allow quality assurance of intercrops in terms of assessment of whether they have the required chemistry. Once underpinning biosynthetic pathways are established it should become possible to develop or transfer relevant biochemical traits involved to edible legumes, such as cowpeas. There is also a possibility of eventually transferring these traits to cereal crops themselves as this would provide greater flexibility to farmers and contribute even more to stabilizing and improving cereal production in the poorest farming regions. Similarly, opportunities for exploiting early herbivory in plant defence and elucidating the underlying mechanisms of plant-to-plant communication between molasses grass and maize are being explored. Another aim is to establish the biochemical pathways of production of the induced defence chemicals in the plants as explained above. This will enable its full exploitation in crop protection and in the development of future cereal varieties with these traits.

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