Journal of
Experimental
Botany
www.jxb.oxfordjournals.org

REVIEW PAPER

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

Zeyaur R. Khan[1], Charles A. O. Midega[1], Toby J. A. Bruce[2], Antony M. Hooper[2] and John A. Pickett[2],*

[1] International Centre of Insect Physiology and Ecology (ICIPE), PO Box 30772, Nairobi, Kenya
[2] Rothamsted Research, Harpenden, Herts AL5 2JQ, UK

* To whom correspondence should be addressed. E-mail: john.pickett@bbsrc.ac.uk

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 stemborers in the families Noctuidae and Crambidae, and parasitic weeds in the genus *Striga* (Orobanchaceae) (Khan *et al.*, 2008a). Indeed, attack by either stemborers or *Striga* can completely destroy the yield of cereal crops.

There is a complex of >20 economically important lepidopteran stemborers 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 stemborers 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 stemborer 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 stemborers 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 stemborer 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 stemborers 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 stemborer 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 stemborers 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 agroecosystems (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 onethird 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).
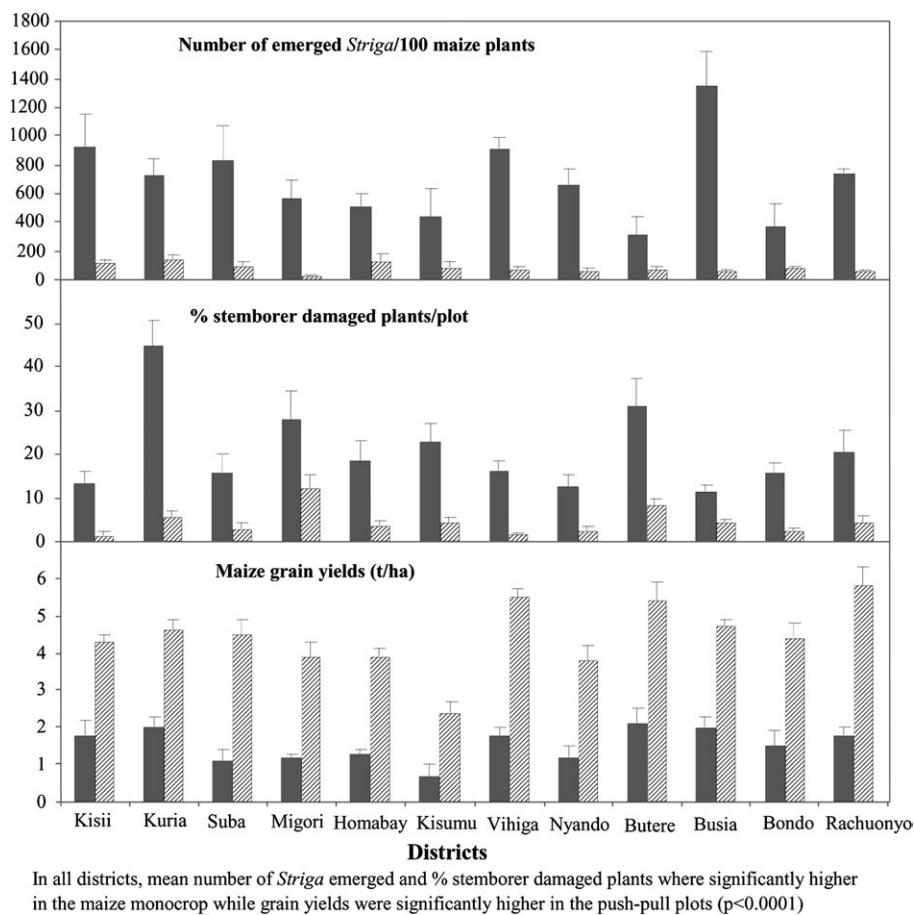
Fig. 1. Mean number of emerged *Striga hermonthica* per plot, proportion of stemborer-damaged plants per plot, and average maize grain yields (t ha^{-1}) from maize monocrop (shaded bars) and push–pull plots (striped bars) in different districts in western Kenya. Means represent data averages from 30 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 semiochemicals 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
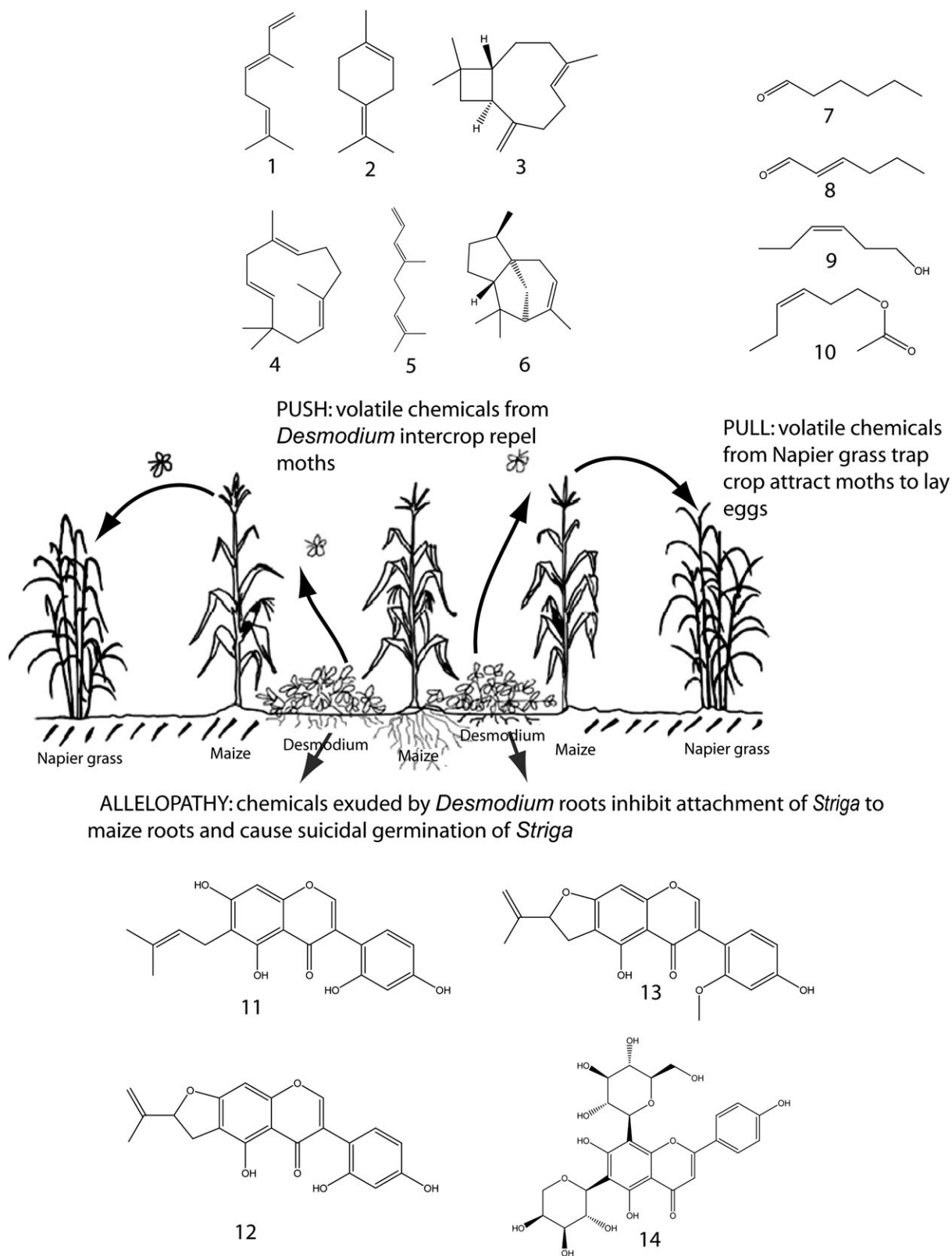
Fig. 3. How the push–pull system works: stemborer moths are repelled by intercrop volatiles while attracted to trap crop volatiles. Root exudates from the *Desmodium uncinatum* intercrop cause suicidal germination of *Striga* and inhibit attachment to maize roots. 1=(*E*)-β-ocimene; 2=α-terpinolene; 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 (uncinanone A); 12=4′′,5′′-dihydro-5,2′,4′-trihydroxy-5′′-isopropenylfurano-(2′′,3′′;7,6)-isoflavanone (uncinanone B); 13=4′′,5′′-dihydro-2′-methoxy-5,4′-dihydroxy-5′′-isopropenylfurano-(2′′,3′′;7,6)-isoflavanone (uncinanone 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 isoflavanones, 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 stemborers (Khan *et al.*, 2008a).

Agronomic benefits of push–pull

Farmers adopting the push–pull system have reported significant control of both *Striga* and stemborers, 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 stemborer 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 *Striga hermonthica* 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/*Desmodium*	7.7 (1.8) b	1.0 (0.4) b
Rice/*Desmodium*/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/*Desmodium*	2.6 (0.5) a	2.4(0.2) a
Rice/*Desmodium*/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 herbivove-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 ~1 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.

References

Amudavi DM, Khan ZR, Wanyama JM, Midega CAO, Pittchar J, Hassanali A, Pickett JA. 2009*a*. Evaluation of farmers' field days as a dissemination tool for push–pull technology in western Kenya. *Crop Protection* **28,** 225–235.

Amudavi DM, Khan ZR, Wanyama JM, Midega CAO, Pittchar J, Nyangau IM, Hassanali A, Pickett JA. 2009*b*. Assessment of technical efficiency of farmer teachers in the uptake and dissemination of push–pull technology in Western Kenya. *Crop Protection* **28,** 987–996.

Arimura G, Ozawa R, Shimoda T, Nishioka T, Boland W, Takabayashi J. 2000. Herbivory-induced volatiles elicit defence genes in lima bean leaves. *Nature* **406,** 512–515.

Bebawi FF, Metwali EM. 1991. Witch-weed management by sorghum—Sudan grass seed size and stage of harvest. *Agronomy Journal* **83,** 781–785.

Birkett MA, Campbell CAM, Chamberlain K, *et al.* 2000. New roles for *cis*-jasmone as an insect semiochemical and in plant defense. *Proceedings of the National Academy of Sciences, USA* **97,** 9329–9334.

Birkett MA, Chamberlain K, Khan ZR, Pickett JA, Toshova T, Wadhams LJ, Woodcock CM. 2006. Electrophysiological responses of the lepidopterous stemborers *Chilo partellus* and *Busseola fusca* to volatiles from wild and cultivated host plants. *Journal of Chemical Ecology* **32,** 2475–2487.

Bradfield M, Stamp N. 2004. Effect of nighttime temperature on tomato plant defensive chemistry. *Journal of Chemical Ecology* **30,** 1713–1721.

Bruce TJA, Midega CAO, Birkett MA, Pickett JA, Khan ZR. 2010. Is quality more important than quantity? Insect behavioural responses to changes in a volatile blend after stemborer oviposition on an African grass. *Biology Letters* **6,** 314–317.

Bruce TJA, Pickett JA. 2007. Plant defence signalling induced by biotic attacks. *Current Opinion in Plant Biology* **10,** 387–392.

Bruce TJA, Wadhams LJ, Woodcock CM. 2005. Insect host location: a volatile situation. *Trends in Plant Science* **10,** 269–274.

Burke MB, Lobell DB, Guarino L. 2009. Shifts in African crop climates by 2050, and the implications for crop improvement and genetic resources conservation. *Global Environmental Change* **19,** 317–325.

Chamberlain K, Khan ZR, Pickett JA, Toshova T, Wadhams LJ. 2006. Diel periodicity in the production of green leaf volatiles by wild and cultivated host plants of stemborer moths, *Chilo partellus* and *Busseola fusca*. *Journal of Chemical Ecology* **32,** 565–577.

Chitere PO, Omolo BA. 1993. Farmers' indigenous knowledge of crop pests and their damage in western Kenya. *International Journal of Pest Management* **39,** 126–132.

Cook SM, Khan ZR, Pickett JA. 2007. The use of 'push–pull' strategies in integrated pest management. *Annual Review of Entomology* **52,** 375–400.

Degen T, Dillmann C, Marion- PF, Turlings TC. 2004. High genetic variability of herbivore-induced volatile emission within a broad range of maize inbred lines. *Plant Physiology* **135,** 1928–1938.

De Groote H, Vanlauwe B, Rutto E, Odhiambo, GD, Kanampiu F, Khan ZR. 2010. Economic analysis of different options in integrated pest and soil fertility management in maize systems of Western Kenya. *Agricultural Economics* (in press).

De Moraes CM, Mescher MC, Tumlinson JH. 2001. Caterpillar-induced nocturnal plant volatiles repel conspecific females. *Nature* **410,** 577–580.

Dicke M, Sabelis MW. 1988. Infochemical terminology: based on cost-benefit analysis rather than origin of compounds? *Functional Ecology* **2,** 131–139.

Engelberth J, Alborn HT, Schmelz EA, Tumlinson JH. 2004. Airborne signals prime plants against insect herbivore attack. *Proceedings of the National Academy of Sciences, USA* **101,** 1781–1785.

Frost DL, Gurney AL, Press MC, Scholes JD. 1997. Striga hermonthica reduces photosynthesis in sorghum: the importance of stomatal limitations and a potential role for ABA? *Plant, Cell and Environment* **20,** 483–492.

Gethi JG, Smith ME, Mitchell SE, Kresovich S. 2005. Genetic diversity of *Striga hermonthica* and *Striga asiatica* populations in Kenya. *Weed Research* **45,** 64–73.

Glinwood R, Pettersson J, Ahmed E, Ninkovic V, Birkett M, Pickett J. 2003. Change in acceptability of barley plants to aphids after exposure to allelochemicals from couch-grass (*Elytrigia repens*). *Journal of Chemical Ecology* **29,** 261–274.

Gouinguené SP, Turlings TC. 2002. The effects of abiotic factors on induced volatile emissions in corn plants. *Plant Physiology* **129,** 1296–1307.

Gressel J, Hanafi A, Head G, Marasas W, Obilana AB, Ochanda J, Souissi T, Tzotzos G. 2004. Major heretofore intractable biotic constraints to African food security that may be amenable to novel biotechnological solutions. *Crop Protection* **23,** 661–689.

Gurney AL, Press MC, Scholes JD. 1999. Infection time and density influence the response of sorghum to the parasitic angiosperm *Striga hermonthica*. *New Phytologist* **143,** 573–580.

Gurney AL, Slate J, Press MC, Scholes JD. 2006. A novel form of resistance in rice to the angiosperm parasite *Striga hermonthica*. *New Phytologist* **169,** 199–208.

Hamilton ML, Caulfield JC, Pickett JA, Hooper AM. 2009. C-Glucosylflavonoid biosynthesis from 2-hydroxynaringenin by *Desmodium uncinatum* (Jacq.) (Fabaceae). *Tetrahedron Letters* **50,** 5656–5659.

Harbone JB. 1978. *Biochemical aspects of plant and animal co-evolution*. New York: Academic Press.

Hardie J, Isaacs R, Pickett JA, Wadhams LJ, Woodcock CM. 1994. Methyl salicylate and (–)-(1*R*,5S)-myrtenal are plant derived repellents for black bean aphid, *Aphis fabae* Scop. (Homoptera: Aphididae). *Journal of Chemical Ecology* **20,** 2847–2855.

Hassan R, Ransom JK, Ojeim J. 1994. The spatial distribution and farmers' strategies to control *Striga* in maize: survey results from Kenya. In: Jewell D, Waddington S, Ransom JK, Pixley K, eds. *Proceedings of the Fourth Eastern and Southern Africa Regional Maize Conference*. CIMMYT: Harare, 250–254.

Hassanali A, Herren H, Khan ZR, Pickett JA, Woodcock CM. 2008. Integrated pest management: the push–pull approach for controlling insect pests and weeds of cereals, and its potential for other agricultural systems including animal husbandry. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363,** 611–621.

Hooper AM, Hassanali A, Chamberlain K, Khan Z, Pickett JA. 2009. New genetic opportunities from legume intercrops for controlling *Striga* spp. parasitic weeds. *Pest Management Science* **65,** 546–552.

Hooper AM., Tsanuo MK, Chamberlain K, Tittcomb K, Scholes J, Hassanali A, Khan ZR, Pickett JA. 2010. Isoschaftoside, a C-glycosylflavonoid from Desmodium uncinatum root exudate, is an allelochemical against the development of Striga. *Phytochemistry* **71,** 904–908.

Kanampiu F, Friesen D, Gressel J. 2002. CIMMYT unveils herbicide-coated maize seed technology for *Striga* control. *Haustorium* **42,** 1–3.

Karban R, Maron J, Felton GW, Ervin G, Eichenseer H. 2003. Herbivore damage to sagebrush induces resistance in wild tobacco: evidence for eavesdropping between plants. *Oikos* **100,** 325–332.

Kfir R, Overholt WA, Khan ZR, Polaszek A. 2002. Biology and management of economically important lepidopteran cereal stemborers in Africa. *Annual Review of Entomology* **47,** 701–731.

Khan ZR. 2002. Cover crops. In: Pimentel D, Ed. *Encyclopedia of pest management*. USA: Marcel Dekker, Inc., 155–158.

Khan ZR, Ampong-Nyarko K, Chilishwa P, et al. 1997*b*. Intercropping increases parasitism of pests. *Nature* **388,** 631–632.

Khan ZR, Amudavi DM, Midega CAO, Wanyama JM, Pickett JA. 2008*d*. Farmers' perceptions of a 'push–pull' technology for control of cereal stemborers and *Striga* weed in western Kenya. *Crop Protection* **27,** 976–987.

Khan ZR, Chilishwa P, Ampong-Nyarko K, Smart LE, Polaszek A, Wandera J, Mulaa MA. 1997*a*. Utilisation of wild gramineous plants for the management of cereal stemborers in Africa. *Insect Science and its Application* **17,** 143–150.

Khan ZR, Hassanali A, Overholt W, Khamis TM, Hooper AM, Pickett AJ, Wadhams LJ, Woodcock CM. 2002. Control of witchweed *Striga hermonthica* by intercropping with *Desmodium* spp., and the mechanism defined as allelopathic. *Journal of Chemical Ecology* **28,** 1871–1885.

Khan ZR, James DG, Midega CAO, Pickett JA. 2008*b*. Chemical ecology and conservation biological control. *Biological Control* **45,** 210–224.

Khan ZR, Midega CAO, Amudavi DM, Hassanali A, Pickett JA. 2008*a*. On-farm evaluation of the 'push–pull' technology for the control of stemborers and *Striga* weed on maize in western Kenya. *Field Crops Research* **106,** 224–233.

Khan ZR, Midega CAO, Hassanali A, Pickett JA, Wadhams LJ. 2007*b*. Assessment of different legumes for the control of *Striga hermonthica* in maize and sorghum. *Crop Science* **47,** 728–734.

Khan ZR, Midega CAO, Hutter NJ, Wilkins RM, Wadhams LJ. 2006*a*. Assessment of the potential of Napier grass (*Pennisetum purpureum*) varieties as trap plants for management of *Chilo partellus*. *Entomologia Experimentalis et Applicata* **119,** 15–22.

Khan ZR, Midega CAO, Njuguna EM, Amudavi DM, Wanyama JM, Pickett JA. 2008*e*. Economic performance of 'push–pull' technology for stemborer and *Striga* weed control in smallholder farming systems. *Crop Protection* **27,** 1084–1097.

Khan ZR, Midega CAO, Pickett JA, Wadhams LJ, Hassanali A, Wanjoya A. 2006*c*. Management of witchweed, *Striga hermonthica*, and stemborers in sorghum, *Sorghum bicolor*, through intercropping with greenleaf desmodium, *Desmodium intortum*. *International Journal of Pest Management* **52,** 297–302.

Khan ZR, Midega CAO, Wadhams LJ, Pickett JA, Mumuni A. 2007*a*. Evaluation of Napier grass (*Pennisetum purpureum*) varieties for use as trap plants for the management of African stemborer (*Busseola fusca*) in a 'push–pull' strategy. *Entomologia Experimentalis et Applicata* **124,** 201–211.

Khan ZR, Midega CAO, Wanyama JM, Amudavi DM, Hassanali A, Pittchar J, Pickett JA. 2009. Integration of edible beans (*Phaseolus vulgaris* L.) into the push–pull technology developed for stemborer and *Striga* control in maize-based cropping systems. *Crop Protection* **28,** 997–1006.

Khan ZR, Pickett JA, Hassanali A, Hooper AM, Midega CAO. 2008*c*. *Desmodium* species and associated biochemical traits for controlling *Striga* species: present and future prospects. *Weed Research* **48,** 302–306.

Khan ZR, Pickett JA, Van Den Berg J, Wadhams LJ, Woodcock CM. 2000. Exploiting chemical ecology and species diversity: stemborer and *Striga* control for maize and sorghum in Africa. *Pest Management Science* **56,** 957–962.

Khan ZR, Pickett JA, Wadhams LJ, Hassanali A, Midega CAO. 2006*b*. Combined control of *Striga* and stemborers by maize–*Desmodium* spp. intercrops. *Crop Protection* **25,** 989–995.

Kidane W, Maetz M, Dardel P. 2006. *Food security and agricultural development in sub-Saharan Africa: building a case for more public support*. Rome: FAO.

Lagoke STO, Parkinson V, Agunbiade RM. 1991. Parasitic weeds and control methods in Africa. In: Kim SK, ed. *Combating Striga in Africa*. Proceedings of an International Workshop organized by IITA, ICRISAT and IDRC, 22–24 August 1988. IITA, Ibadan, Nigeria, 3–14.

Maes K. 1998. Pyraloidea: Crambidae, Pyralidae. In: Polaszek A, ed. *African cereal stem borers: economic importance, taxonomy, natural enemies and control*. Wallingford, UK: CAB International, 87–98.

Mally CW. 1920. The maize stalk borer *Busseola fusca* (Fuller). *Bulletin of the Department of Agriculture of South Africa* **3,** 111.

Matusova R, Rani K, Verstappen WA, Franssen CR, Beale MH, Bouweester HJ. 2005. The strigolactone germination stimulants of the plant-parasitic *Striga* and *Orobanche* spp. are derived from the carotenoid pathway. *Plant Physiology* **139,** 920–934.

Midega CAO, Khan ZR, Amudavi DM, Pittchar J, Pickett JA. 2010. Integrated management of *Striga hermonthica* and cereal stemborers in finger millet (*Eleusine coracana* (L.) Gaertn.), through intercropping with *Desmodium intortum*. *International Journal of Pest Management* **56,** 145–151.

Midega CAO, Khan ZR, van den Berg J, Ogol CKPO, Bruce TJ, Pickett JA. 2009. Non-target effects of the 'push–pull' habitat management strategy: parasitoid activity and soil fauna abundance. *Crop Protection* **28,** 1045–1051.

Mohamed HM, Khan ZR, Mueke JM, Hassanali A, Kairu E, Pickett JA. 2007. Behaviour and biology of *Chilo partellus* (Swinhoe) on *Striga hermonthica* (Del.) Benth. infested and uninfested maize plants. *Crop Protection* **26,** 998–1005.

Muchena FN, Onduru DD, Gachini GN, de Jager A. 2005. Turning the tides of soil degradation in Africa: capturing the reality and exploring opportunities. *Land Use Policy* **22,** 23–31.

Nordlund DA, Lewis WJ. 1976. Terminology of chemical releasing stimuli in intraspecific and interspecific interactions. *Journal of Chemical Ecology* **2,** 211–220.

Olofsdotter M, Jensen LB, Courtois B. 2002. Improving crop competitive ability using allelopathy—an example from rice. *Plant Breeding* **121,** 1–9.

Oswald A. 2005. *Striga* control technologies and their dissemination. *Crop Protection* **24,** 333–342.

Parker C, Riches CR. 1993. *Parasitic weeds of the world: biology and control*. Wallingford, UK: CAB International.

Päts P. 1991. Activity of *Chilo partellus* (Lepidoptera: Pyralidae): eclosion, mating and oviposition time. *Bulletin of Entomological Research* **81,** 93–96.

Pettersson J, Pickett JA, Pye BJ, Quiroz A, Smart LE, Wadhams LJ, Woodcock CM. 1994. Winter host component reduces colonization by bird cherry-oat aphid, *Rhopalosiphum padi* (L.) (Homoptera: Aphididae), and other aphids in cereal fields. *Journal of Chemical Ecology* **20,** 2565–2574.

Pickett JA, Bruce TJA, Chamberlain K, Hassanali A, Khan ZR, Matthes MC, Napier JA, Smart LE, Wadhams LJ, Woodcock CM. 2006. Plant volatiles yielding new ways to exploit plant defence. In: Dicke M, Takken W, eds. *Chemical ecology: from gene to ecosystem*. The Netherlands: Springer, 161–173.

Pickett JA, Hamilton ML, Hooper AM, Khan ZR, Midega CAO. 2010. Companion cropping to manage parasitic plants. *Annual Review of Phytopathology* (in press).

Pickett JA, Khan ZR, Hassanali A, Hooper AM. 2007. Chemicals involved in post-germination inhibition of *Striga* by *Desmodium*: opportunities for utilizing the associated allelopathic traits. In: Ejeta G, Gressel J, eds. *Integrating new technologies for Striga control: towards ending the witch-hunt*. Singapore: World Scientific, 61–70.

Polaszek A, Khan ZR. 1998. Host plants. In: Polaszek A, ed. *African cereal stem borers: economic importance, taxonomy, natural enemies and control*. Wallingford, UK: CAB International, 3–10.

Rice EL. 1984. *Allelopathy*, 2nd edition. New York: Academic Press.

Roades DF. 1983. Herbivore population dynamics and plant chemistry. In: Denno RF, McClure MS, eds. *Variable plants and herbivores in natural and managed systems*. New York: Academic Press, 155–220.

Rosenthal GA, Janzen DH. 1979. *Herbivores: their interaction with secondary plant metabolites*. New York: Academic Press.

Sauerborn J, Kranz B, Mercer-Quarshie H. 2003. Organic amendments mitigate heterotrophic weed infestation in savannah agriculture. *Applied Soil Ecology* **23,** 181–186.

Schulthess F, Bosque-Perez NA, Chabi-Olaye A, Gounou S, Ndemah R, Georgen G. 1997. Exchange of natural enemies of lepidopteran cereal stemborers between African regions. *Insect Science and its Application* **17,** 97–108.

Tsanuo MK, Hassanali A, Hooper AM, Khan ZR, Kaberia F, Pickett JA, Wadhams L. 2003. Isoflavanones from the allelopathic aqueous root exudates of *Desmodium uncinatum*. *Phytochemistry* **64,** 265–273.

Turlings TC, Loughrin JH, McCall PJ, Röse US, Lewis WJ, Tumlinson JH. 1995. How caterpillar damaged plants protect themselves by attracting parasitic wasps. *Proceedings of the National Academy of Sciences, USA* **92,** 4169–4174.

Turlings TCJ, Scheepmaker JWA, Vet LEM, Tumlinson JH, Lewis WJ. 1990. How contact experiences affect preferences for host-related odors in the larval parasitoid *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae). *Journal of Chemical Ecology* **16,** 1577–1589.

Turlings TC, Ton J. 2006. Exploiting scents of distress: the prospect of manipulating herbivore-induced plant odours to enhance the control of agricultural pests. *Current Opinion in Plant Biology* **9,** 421–427.

Van Emden HF. 1990. Plant diversity and natural enemy efficiency in agroecosystems. In: Mackauer M, Ehler LE, Roland J, eds. *Critical issues in biological control*. Andover, UK: Intercept, 63–80.

Vanlauwe B, Kanampiu F, Odhiambo G, De Groote H, Wadhams LJ, Khan ZR. 2008. Integrated management of *Striga hermonthica*, stemborers, and declining soil fertility in western Kenya. *Field Crops Research* **107,** 102–115.

Whitfield J. 2001. Making crops cry for help. *Nature* **410,** 736–737.

Yoder JI. 1999. Parasitic plant responses to host plant signals: a model for subterranean plant–plant interactions. *Current Opinion in Plant Biology* **2,** 65–70.