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Push-Pull: Chemical Ecology-Based Integrated Pest Management Technology

Zeyaur Khan¹ & Charles A. O. Midega¹ & Antony Hooper² & John Pickett²

Abstract Lepidopterous stemborers, and parasitic striga weeds belonging to the family Orobanchaceae, attack cereal crops in sub-Saharan Africa causing severe yield losses. The smallholder farmers are resource constrained and unable to afford expensive chemicals for crop protection. The push–pull technology, a chemical ecology-based cropping system, is developed for integrated pest and weed management in cereal–livestock farming systems. Appropriate plants were selected that naturally emit signaling chemicals (semiochemicals). Plants highly attractive for stemborer egg laying were selected and employed as trap crops (pull), to draw pests away from the main crop. Plants that repelled stemborer females were selected as intercrops (push). The stemborers are attracted to the trap plant, and are repelled from the main cereal crop using a repellent intercrop (push). Root exudates of leguminous repellent intercrops also effectively control the parasitic striga weed through an allelopathic mechanism. Their root exudates contain flavonoid compounds some of which stimulate germination of *Striga hermonthica* seeds, such as Uncinane B, and others that dramatically inhibit their attachment to host roots, such as Uncinane C and a number of di-C-glycosylflavones (di-CGFs), resulting in suicidal germination. The intercrop also improves soil fertility through nitrogen fixation, natural mulching, improved biomass, and control of erosion. Both companion plants provide high value animal fodder, facilitating milk production and diversifying farmers' income sources. The technology is appropriate to

smallholder mixed cropping systems in Africa. Adopted by about 125,000 farmers to date in eastern Africa, it effectively addresses major production constraints, significantly increases maize yields, and is economical as it is based on locally available plants, not expensive external inputs.

Keywords Cereal crops · Stemborer pests · Parasitic striga · Semiochemicals · Allelopathy

Introduction

Food insecurity continues to affect millions of Africa's poor and is likely to worsen with climate change and population growth. With per capita food production having declined in the past two decades (Muchena et al. 2005), the continent faces increasing problems in feeding its rapidly growing human population. Indeed almost 33 % of the population (close to 200 million people) in sub-Saharan Africa (SSA) alone is undernourished, with projections indicating that hunger and poverty will worsen over the next two decades unless drastic action is taken to improve agriculture and economic development. Agriculture remains the backbone of Africa's economy (Abate et al. 2000), and the means of livelihood for about 60 % of its people (FAO 2011). Thus, there can be no meaningful economic development in the continent without growth in agricultural productivity.

Cereal crops play a major role in smallholder farmers' livelihoods in SSA, with maize, *Zea mays* L., and sorghum, *Sorghum bicolor* (L.) Moench, being the most important food and cash crops for millions of rural farm families in the predominantly mixed crop–livestock farming systems of the region. In spite of the importance of cereal crops in the region, grain yields have continued to decline, with yields representing some of the lowest in the world

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(Cairns et al. 2013). Consequently, there is a widening gap between food supply and demand, with per capita production steadily declining (World Bank 2008). Efficient production of cereal crops is, therefore, central to addressing the food security challenge in the region.

Major Biotic Constraints to Cereal Production in SSA

One of the main causes of the chronic food insecurity witnessed in Africa is poor crop yields, largely caused by insect pests, weeds, and degraded soils. This is complicated further by the increasingly hot and dry weather conditions associated with climate change (Fischer et al. 2005; Jones and Thornton 2003).

Cereal cultivation by smallholder farmers in SSA is severely constrained by insect pests, particularly lepidopteran stemborers in the families Noctuidae and Crambidae, and parasitic weeds in the genus *Striga* (Orobanchaceae) (Khan et al. 2010). There is a complex of >20 economically important lepidopteran stemborers of cultivated cereals 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 30 % 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 socioeconomically important in cereal cultivation in much of SSA (Gethi et al. 2005; Gressel et al. 2004). *Striga* infests >40 % of arable land in SSA (Lagoke et al. 1991) and causes yield losses of up to 100 %. *Striga* is so ingeniously adapted to its environment and host plants (Bebawi and Metwali 1991) that it will germinate only 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) adding to its detrimental impact. *Striga* infestation results in a large reduction in host plant height, biomass, and eventual grain yield (Gurney et al. 1999). Unfortunately, *striga* infestation continues to extend to new areas in the region as farmers abandon heavily infested fields for new ones (Gressel et al. 2004; Khan 2002), a practice that is untenable due to consistent reduction in landholdings resulting from 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 Push-Pull Companion Cropping System for Stemborers and Striga Control

Use of companion cropping strategies to reduce the losses caused by stemborers and striga weed significantly increases cereal production and results in better nutrition and purchasing power for many cereal producers (Khan et al. 2014). Therefore, companion cropping involving an intercrop as a low-input system is potentially of great value in developing world agriculture where chemical inputs are not affordable, and where low-input agriculture is practised (Pickett et al. 2010).

In the 'push-pull' strategy, 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; Khan et al. 2010). Such a system requires a complete understanding of the associated chemical ecology of plant-insect and plant-plant interactions on the different crops. Candidate plants need to be systematically evaluated in laboratory and 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 (Khan et al. 2000). 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 inhibiting parasitism by striga and hence only requires the desmodium intercrop component of the push-pull system.

Selection of Push-Pull Companion Plants Most stemborers that attack cereal crops are polyphagous, and can utilize a wide range of grasses in the families Poaceae (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 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 that 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; Schulte et al. 1997). In an extensive field survey, >500 species belonging mainly to the family Poaceae in different agro-ecological zones in Kenya were

sampled, and stemborers associated with each species were recorded. 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 stemborer adult females and reduce their populations on the main crop of maize. The candidate crops that fulfilled these criteria 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 stemborers.

The field and laboratory studies identified the most attractive plant species as candidates for trap crops (pull). It was observed that two grass species, Napier grass, *Pennisetum purpureum* Schumacher, and Sudan grass, *Sorghum sudanense* Stapf, both of which are forage crops, attracted significantly 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 show high survival rates 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 candidates for repellent intercrop species (push). The molasses grass, *Melinis minutiflora* P. Beauv, an indigenous poaceous plant with forage value, attracted no stemborer oviposition at all but was highly attractive to larval parasitoid, *Cotesia sesamiae* (Khan et al. 1997b). 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 %, much of it due to increased action of parasitoids. 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 still could be seen at a ratio of one row in 20 rows of maize.

Farmers in SSA practice polycropping where the main cereals are interplanted with legumes, and therefore, legumes also were 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). While push–pull systems were being optimized for stemborer control, it was noticed that maize intercropped with *D. uncinatum* or

D. intortum suffered far less parasitic striga infestation than maize in monoculture. 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 corresponding yield increases (Khan et al. 2002, 2006b, 2007b). The impact of *Desmodium* on the emergence of striga originally was shown to be caused by *Desmodium* root exudates in pot experiments (Khan et al. 2002). Maize was grown in pots of striga infested soil and irrigated with water that had percolated through *Desmodium* roots. This was sufficient to prevent striga attachment and emergence of the parasite showing that the protection mechanism was due to the root exudates. Plot experiments demonstrated that physical factors such as the addition of nitrogen fertilizer and the use of ground shading did impact striga parasitism but this was not as effective as *Desmodium* (Khan et al. 2002).

Semiochemistry of Push-Pull Technology

The push–pull system is based on understanding and exploiting the chemical ecology and biodiversity of companion plants (Table 1). The interactions with pests and weeds are based on semiochemicals released by the companion plants. The science underpinning these interactions, which is described here, is vital in discovering and understanding the underlying mechanism of the trap and repellent companion plants. 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 then were eluted from the polymer with a solvent, and the samples were 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. The GC peaks consistently associated with EAG activity were tentatively identified by GC coupled-mass spectrometry (GC-MS), and identity was confirmed using authentic samples. Some of the active compounds identified from both maize and the Napier grass trap crop included octanal, nonanal, naphthalene, 4-allylanisole, eugenol, and linalool. Each of these compounds was shown to have positive activity in behavioral tests that investigated oviposition onto an artificial substrate treated with the individual compounds (Khan et al. 2000).

Avoidance of unsuitable hosts by herbivores involves detection of specific semiochemicals, or mixtures of semiochemicals, associated with non-host taxa, with some plants

Table 1 Key compounds involved in stemborer and striga control emitted by intercrop and trap plants in the push–pull cropping system

Pull semiochemistry		Compound	Source	Method for ID	Target	Activity
	o	Octanal	Maize (<i>Zea mays</i>)	GC-EAG, GC-MS, co-elution with standards	Stemborer moths (adults)	Host cue attractant
	o	Nonanal	Napier grass (<i>Pennisetum purpureum</i>)			
	o	Naphthalene				
	o	4-allylanisole				
	OH	Eugenol				
	OH	(<i>E</i>)-Ocimene	<i>Melinis minutiflora</i>	GC-EAG, GC-MS, co-elution with standards	Stemborer moths * <i>Cotesia sesamiae</i>	Repellent Attractant
	o	(<i>E</i>)-4,8-dimethyl-1,3,7-nonatriene	<i>Desmodium</i> spp.			
	OH	Humulene				
	H	-Caryophyllene				
	H	-Terpinolene				
	H	-Cedrene				
	Structure	Compound	Source	Method for ID	Target	Activity
	o	Orobanchol	<i>D. uncinatum</i> <i>D. incanum</i>	Root exudate isolation. NMR spectroscopy	<i>Striga</i>	Germination stimulation
	OH o	Orobanchol acetate		Root exudate. LC-MRM-MS		
	o					
	OAc o					
	o	Uncinanone B				
	OH o	6-C-galactosyl-8-C-glucosylapigenin	<i>D. uncinatum</i> <i>D. intortum</i> <i>D. incanum</i>	Root exudate LCMS, structure verified through isolated natural product standard.	<i>Striga</i>	All glycosides are present in whole root exudate that inhibit <i>Striga</i> parasitism
	OH o	6,8-di-C-glucosylapigenin (vicenin-2)	<i>D. ramosissimum</i>			
	OH o	6-C-glucosyl-8-C-galactosylapigenin				
OH o	6-C-galactosyl-8-C-arabinosylapigenin					
OH o	6-C-arabinosyl-8-C-glucosylapigenin (isoschaftoside)				‡Inhibits radicle growth at picomolar concentrations <i>in vitro</i>	
OH o	6-C-arabinosyl-8-C-galactosylapigenin					
OH o	Uncinanone C	<i>D. uncinatum</i>	Root exudate isolation. NMR spectroscopy	<i>Striga</i>	Radicle inhibitor	

being avoided because they release signals indicating that they are already infested and are, therefore, less suitable as hosts (Pickett et al. 2006). Electrophysiological and behavioral studies with molasses grass revealed that it produced active compounds responsible for its repellence to stemborer moths. These comprised (E)-ocimene, (E)-4,8-dimethyl-1,3,7-nonatriene (DMNT), (β)-caryophyllene, humulene, and α -terpinolene (Table 1). It is noteworthy that (E)-ocimene and DMNT belong to a group of semiochemicals referred to as herbivore-induced plant volatiles (HIPVs) since they are produced during damage to plants by herbivorous insects (Turlings et al. 1990). These compounds often act as foraging cues for parasitoids, and are repellent to ovipositing stemborers (Khan et al. 2000). Molasses grass is thus treated as a non-host because it produces semiochemicals typically emitted by a highly infested maize plant. *Desmodium* also produced (E)-ocimene and DMNT, together with large amounts of other sesquiterpenes, including α -cedrene (Khan et al. 2000), and effectively repelled stemborer moths and attracted the pest's natural enemies (Midega et al. 2009). The combined effects of the trap and repellent intercrops results in significant reductions in stemborer colonization, translated in reduced damage to the maize and significant improvements in grain yields (Midega et al. 2015a, 2015b).

Initial experiments using the root exudates from *Desmodium uncinatum* demonstrated that the germination of *Striga hermonthica* was not inhibited but was stimulated as it was by maize root exudates. Flavonoid compounds were found in the root exudates that possessed germination stimulation activity (uncinanone C) and recently strigolactones also have been identified that have previously been reported to stimulate germination of striga (Boumeester and Charnikhova, personal communication). However, the subsequent development of germinated striga plants, the extension of the radicle, was inhibited by another isoflavanone named uncinanone B (Tsanuo et al. 2003). Subsequent studies on the chemical composition of the root exudates of *D. uncinatum* showed that the main active components of the exudate were the more polar C-glycosylflavones (CGFs) and di-C-glycosylflavones (di-CGFs), specifically vitexin and isoschaftoside (6-C-arabinosyl-8-C-glucosylapigenin). Field experiments demonstrated that the related species *D. intortum* also inhibited striga parasitism, and its root exudate also contained isoschaftoside as well as another di-CGF, vicenin-2 (6,8-di-C-glucosylapigenin). As a result of these discoveries, the effects of the di-CGF isoschaftoside on pre-germinated *S. hermonthica* were studied and, at concentrations found in hydroponic solutions, showed significant inhibition of radicle growth in vitro at ecologically relevant concentrations (Hooper et al. 2010) leading us to propose isoschaftoside as important in the striga inhibiting trait.

Adaptation of Push-Pull Technology to Climate Change

The push-pull technology is effective under a range of different agro-ecologies and with a range of cereal crops, including the more drought tolerant sorghum and finger millet (Khan et al. 2006c; Midega et al. 2010). This makes the technology and its associated benefits relevant currently to 300 million people in SSA, with this number rapidly rising. Indeed a number of studies have demonstrated that the technology yields significantly higher economic returns than other pest and soil fertility management options (De Groote et al. 2010; Khan et al. 2008; Midega et al. 2014), even without factoring the environmental benefits of the technology. However, the companion plants used in conventional push-pull are rainfall and temperature limited. Therefore, to extend these benefits to drier areas and ensure the technology's long-term sustainability in view of the increasingly dry and hot conditions associated with climate change, alternative drought tolerant plants were sought for the push-pull. Thus icipe, Rothamsted Research (United Kingdom), and African partners in Ethiopia, Kenya, and Tanzania, screened about 400 grass species from which 21 drought tolerant species were initially selected. Out of these, *Brachiaria cv. mulato II* was chosen as the trap plant for the climate adapted push-pull given also its ability to control stemborers, farmers' preference for it as livestock fodder, and commercial availability of its seed that would allow faster dissemination and up-take. Our studies indicate insignificant effect of drought stress on relative attractiveness of *Brachiaria cv. mulato II* to stemborer moths for oviposition (Chidawanyika et al. 2014). Additionally, drought stress only minimally alters secondary metabolism in *Brachiaria cv. mulato*, with emission of key volatile organic compounds necessary for stemborer host location such as (Z)-3-hexenyl acetate not significantly affected (Chidawanyika 2015). *Brachiaria spp.* have been observed to support minimal survival of stemborer larvae (Midega et al. 2011), with these rates not affected by drought stress (Chidawanyika et al. 2014). *Brachiaria* has a suitable characteristic of a border plant that would support populations of natural enemies within season and when the cereal crop is not in season. The full semiochemical mechanisms of stemborer control by the new companion plants is currently being elucidated with the aim of providing both sustainability and quality assurance as more companion plants are being selected for new agro-ecologies.

Additionally, drought tolerant species of *Desmodium* that emit volatiles that repel stemborers, fix nitrogen to improve soil fertility, produce high biomass but have low growth habit that cover the soil and improve soil health were identified. From a collection of 43 accessions collected from dry and hot areas in Africa and other arid environments, greenleaf (*D. intortum*) was observed to be more drought tolerant and was chosen as the intercrop species for immediate integration

into a climate adapted push-pull. Greenleaf desmodium *D. intortum* was chosen given its known ability to control striga and stemborers (Khan et al. 2007b), coupled with commercial availability of its seed that would enable its wider testing by farmers within the target areas. *Desmodium intortum* is more drought tolerant, wilts less, and fixes more atmospheric nitrogen than the silverleaf desmodium (Whitney 1966). Recent studies have demonstrated the beneficial effect of the combined use of *Brachiaria* and greenleaf *Desmodium* in the control of stemborers and striga, resulting in significantly increased grain yields (Khan et al. 2014; Midega et al. 2015a). This ensures long-term sustainability of the technology and has expanded the geographical appeal of push-pull technology into the drier areas of eastern Africa, including Tanzania, and Ethiopia. *Desmodium intortum* also has a relatively higher nitrogen-fixing ability, over 300 kg N/ ha/year under optimum conditions (Whitney 1966), than *D. uncinatum*, and is, therefore, more appropriate as an intercrop for the drier areas with more degraded environments vulnerable to further climate change. Therefore, in the climate-adapted push-pull technology, which is currently practiced by more than 54, 000 farmers in Ethiopia, Kenya, Tanzania, and Uganda, uses *Brachiaria* cv Mulato II a border crop while *D. intortum* is used as an inter-crop, in areas with mean annual rainfall of less than 700 mm and mean daily temperatures more than 30 °C, indicating effective control of cereal stemborers and striga, with concomitant increases in grain yields in both sorghum and maize (Midega et al. 2015a). Recent studies indicate other highly drought-tolerant desmodium of African origin, such as *D. ramosissimum* and *D. incanum* are also able to effectively suppress striga under drier agro-ecologies in eastern Africa, suggesting relative stability of allelochemical production and release into the rhizosphere by these plants (Hooper et al. 2015; Midega et al. 2016, in press).

The work to isolate and purify all the active compounds in the drought-tolerant desmodium root exudates and fully elucidate their effects on striga suppression is in advanced stage. The success of the climate-adapted push-pull in farmers' fields led to the goal of finding different *Desmodium* species that possess the same inhibitory chemistry but with suitable agronomic properties for use in different agroecologies, in particular species that are drought tolerant or resilient to the stresses expected through climate change. The species chosen were identified through phenotypic screening (Midega et al. 2016, in press) as *D. intortum*, *D. ramosissimum*, and *D. incanum*. To study their root exudate profiles, the plants were grown in hydroponic solution for three months, and over time, as the plants matured, the root exudate profiles that varied between species early in their growth, became similar (Hooper et al. 2015). Initially, the di-CGF isoschaftoside was prominent in the root exudates but after three months, the root exudate blend comprised a number of other di-CGFs that included isoschaftoside, although this was not a major component in

mature plants (Table 1). In addition to these C-glycosylflavones, esters of di-C-glycosylflavones, deduced as ferulates or synapinates by molecular weight, were also found. The crude root exudates were tested in pot experiments similarly to the original work in identifying exudate activity, and demonstrated that the chemicals in the root exudate again were responsible for striga inhibiting activity (Hooper et al. 2015).

New Opportunities for Advancing Push-Pull Technology

Early Herbivory Alert Herbivore attack often triggers the production of HIPVs that serve as foraging cues for natural enemies antagonistic to the pests, in what is referred to as indirect defense (Turlings et al. 1990). This often occurs as a result of feeding by the larval stages of the pests. Because the natural enemies are attracted as a result of the damage to plants, such biological control approaches are generally not very effective in reducing pest damage in farmers' fields, and, therefore, activity of the natural enemies does not prevent crop yield losses. Defenses elicited by the presence of eggs would benefit plants more as they enable defense to be switched on early, before damage is caused to the plant by larvae (Bruce et al. 2010; Hilker and Meiners 2006). Earlier, we observed an unusual phenomenon where oviposition by *C. partellus* on signal grass, *Brachiaria brizantha* (Hochst. ex A. Rich.) Stapf., resulted in suppression of the main green leaf volatile (Z)-3-hexenyl acetate, 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). Consequently, the ratio of other compounds relative to (Z)-3-hexenyl acetate was increased in plants exposed to *C. partellus* oviposition, making the volatile blend more attractive to *C. sesamiae*, than that of plants without oviposition. Our observation of *B. brizantha* signals suggested there was an opportunity for exploiting early herbivory to enhance pest management. Our follow-up studies showed that some open pollinated varieties of maize and maize landraces of Latin American origin had increased emission of defense semiochemicals in response to *C. partellus* oviposition, a trait that was not present in standard commercial varieties (Tamiru et al. 2011). This increased emission of HIPVs resulted in an attraction of both the egg and larval parasitoids, representing an effective tritrophic response drawing in natural enemies before damage is caused to the crop. Subsequently, we have shown this trait to be present in the locally adapted African open pollinated varieties (OPVs) (Tamiru et al. 2012). The majority of smallholder farmers in Africa (about 80 %) grow these local varieties (Odendo et al. 2001) for their adaptation to local agro-ecologies, including their resilience to some of the biotic and abiotic stresses, and because they can replant the seeds (Aquino et al. 2001). Such 'smart' maize cultivars that

respond to oviposition represent an opportunity to make better use of indirect defense traits and, therefore, their use in the push-pull approach not only enhances the stemborer control efficiency of the technology but also improves its ecological effectiveness. The mechanism by which potential 'smart' maize indirect defense can be initiated through use of the chemical elicitors identified from the egg laying process is, therefore, an area of importance to the project.

Plant Signaling Plants can respond to HIPVs emitted by neighboring plants adjusting their metabolism to increase their resistance to herbivores by becoming either 'repellent' to the herbivore or more attractive to the natural enemies (Birkett et al. 2000). Such plants have a higher expression of resistance genes and defense-related plant compounds (Arimura et al. 2000). We have demonstrated that intact plants such as molasses grass constitutively release similar defense semiochemicals without activity of herbivores (Khan et al. 2000, Tigist unpublished), and can induce defense responses in neighboring maize plants. Recently, it has been observed that local African OPVs 'Nyamula' and 'Jowi', when exposed to molasses grass volatiles, become significantly attractive to the stemborer larval parasitoid, *C. sesamiae* and less attractive to *C. partellus* moths (Midega et al. 2015b). Similarly *B. brizantha* also was found when exposed to *C. partellus* eggs to signal to the maize open pollinated varieties Nyamula and Jowi and the land race Cuba 91 causing these plants to release volatile attractant signals also for the parasitoid *Cotesia sesamiae* including the tetranorterpene DMNT or TMTT (Magara et al. 2015). Studies currently are underway to understand the effects, and biochemical pathways involved, of defense inducing volatiles of molasses grass as this will enable exploitation of this trait in development of new plant protection systems based on switching on of inherent plant defenses, either through companion cropping or synthetic variants of the active compounds mediating these responses.

Understanding early herbivory alert and plant-plant signaling will enable their full exploitation in development of future push-pull strategies with these traits. We are currently identifying companion plants with the ability to induce defense against insect attack in cereal crops for possible use in the push-pull technology, or for development of other companion cropping-based approaches to enhance natural plant defense.

Summary and Future Directions

The push-pull system effectively addresses the constraints to cereal production faced by the farmers and is an appropriate system because it uses locally available companion plants rather than expensive imported inputs. Although the technology was originally devised to control insect pests it has

multiple benefits in controlling striga weeds, improving soil fertility, and providing livestock fodder in a truly integrated system. It is, thus, a novel IPM approach that was developed with full participation of the target farmers and is modelled alongside their practice of multiple cropping thereby enhancing its acceptance. It is currently used by about 125,000 small-holder farmers in eastern Africa and has been adapted for drier areas vulnerable to climate change by identifying and incorporating drought tolerant trap and repellent plants. This has made the technology more resilient in the face of climate change as rainfall becomes increasingly unpredictable. Moreover, the technology is being made 'smarter' through identification and incorporation of cereal crops with defense systems against stemborer pests that are inducible by egg deposition by the pests. Companion plants that are able to signal defense systems of the neighboring smart cereals also are being identified. Accompanying these are efforts to elucidate full mechanisms of these responses. Chemical ecology-based IPM solutions, which are environmentally sustainable and low cost, like push-pull, are urgently needed to address the real and increasing dangers of food insecurity, and for a real Green Revolution in Africa without causing any ecological and social harm.

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References

- Abate T, van Huis A, Ampofo JKO (2000) Pest management strategies in traditional agriculture: an African perspective. *Annu Rev Entomol* 45:631–659
- Aquino P, Carrion F, Calvo R, Flores D (2001) Selected maize statistics. CIMMYT 1999–2000. World maize facts and trends. Meeting world maize needs: Technological opportunities and priorities for the public sector (ed. by P.L. Pingali), pp. 45–57. CIMMYT, Mexico
- 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. *Agron J* 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. *Proc Natl Acad Sci U S A* 97:9329–9334
- 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. *Biol Lett* 6:314–317
- Cairns JE, Hellin J, Sonder K, Araus JL, MacRobert JF, Thierfelder C, Prasanna BM (2013) Adapting maize production to climate change in sub-Saharan Africa. *Food Secur* 5:345–360

- Chidawanyika F (2015) Effects of drought on the production of ectrophysiologically active biogenic volatiles important for cereal pest management. University of the Witwatersrand, South Africa pp. 172 pp (Ph.D. Dissertation)
- Chidawanyika F, Midega CAO, Bruce TJA, Duncan F, Pickett JA, Khan ZR (2014) Oviposition acceptance and larval development of *Chilo partellus* stem borers in drought-stressed wild and cultivated grasses of East Africa. *Entomol Exp Appl* 151:209–217
- Chitere PO, Omolo BA (1993) Farmers' indigenous knowledge of crop pests and their damage in western Kenya. *Intern J Pest Manage* 39: 126–132.
- Cook SM, Khan ZR, Pickett JA (2007) The use of 'push-pull' strategies in integrated pest management. *Annu Rev Entomol* 52:375–400
- 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. *Agric Econ* 41:471–482
- FAO (2011) The status of food insecurity in the world. Food and agriculture organization, Rome
- Fischer G, Shah M, Tubiello F, van Velthuis H (2005) Socioeconomic and climate change impacts on agriculture: An integrated assessment, 1990 – 2080. *Philos Trans R Soc B* 360:2067–2083
- 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 Environ* 20: 483–492
- Gethi JG, Smith ME, Mitchell SE, Kresovich S (2005) Genetic diversity of *Striga hermonthica* and *Striga asiatica* populations in Kenya. *Weed Res* 45:64–73
- Gressel J, Hanafi A, Head G, Marasas W, Obilana AB, Ochanda J, Souissi T, Tzozos G (2004) Major heretofore intractable biotic constraints to African food security that may be amenable to novel biotechnological solutions. *Crop Prot* 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 Phytol* 143:573–580
- Hilker M, Meiners T (2006) Early herbivore alert: Insect eggs induce plant defense. *J Chem Ecol* 32:1379–1397
- 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
- Hooper AM, Caulfield JC, Hao B, Pickett JA, Midega CAO, Khan ZR (2015) Isolation and identification of *Desmodium* root exudates from drought tolerant species used as intercrops against *Striga hermonthica*. *Phytochemistry* 117:380–389
- Jones PG, Thornton PK (2003) The potential impacts of climate change on maize production in Africa and Latin America in 2055. *Glob Environ Chang* 13:51–59
- Kfir R, Overholt WA, Khan ZR, Polaszek A (2002) Biology and management of economically important lepidopteran cereal stem borers in Africa. *Annu Rev Entomol* 47:701–731
- Khan ZR (2002) Cover crops. In: Pimentel D (ed) *Encyclopedia of pest management*. Marcel Dekker, Inc., USA, pp. 155–158
- Khan ZR, Chilishwa P, Ampong-Nyarko K, Smart LE, Polaszek A, Wandera J, Mulaa MA (1997a) Utilisation of wild gramineous plants for the management of cereal stem borers in Africa. *Insect Sci Appl* 17:143–150
- Khan ZR, Ampong-Nyarko K, Chilishwa P, et al. (1997b) Intercropping increases parasitism of pests. *Nature* 388:631–632
- Khan ZR, Pickett JA, Van Den Berg J, Wadhams LJ, Woodcock CM (2000) Exploiting chemical ecology and species diversity: Stem borer and *Striga* control for maize and sorghum in Africa. *Pest Manag Sci* 56:957–962
- 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. *J Chem Ecol* 28:1871–1885
- Khan ZR, Midega CAO, Hutter NJ, Wilkins RM, Wadhams LJ (2006a) Assessment of the potential of Napier grass (*Pennisetum purpureum*) varieties as trap plants for management of *Chilo partellus*. *Entomol Exp Appl* 119:15–22
- Khan ZR, Midega CAO, Pickett JA, Wadhams LJ, Hassanali A, Wanjoya A (2006b) Management of witchweed, *Striga hermonthica*, and stem borers in sorghum, *Sorghum bicolor*, through intercropping with greenleaf desmodium, *Desmodium intortum*. *Int J Pest Manag* 52:297–302
- Khan ZR, Pickett JA, Wadhams LJ, Hassanali A, Midega CAO (2006c) Combined control of *Striga* and stem borers by maize–*Desmodium* spp. intercrops. *Crop Prot* 25:989–995
- Khan ZR, Midega CAO, Wadhams LJ, Pickett JA, Mumuni A (2007a) Evaluation of Napier grass (*Pennisetum purpureum*) varieties for use as trap plants for the management of African stem borer (*Busseola fusca*) in a 'push-pull' strategy. *Entomol Exp Appl* 124: 201–211
- Khan ZR, Midega CAO, Hassanali A, Pickett JA, Wadhams LJ (2007b) Assessment of different legumes for the control of *Striga hermonthica* in maize and sorghum. *Crop Sci* 47:728–734
- Khan ZR, Midega CAO, Njuguna EM, Amudavi DM, Wanyama JM, Pickett JA (2008) Economic performance of 'push-pull' technology for stem borer and *striga* weed control in smallholder farming systems. *Crop Prot* 27:1084–1097
- Khan ZR, Midega CAO, Bruce TJA, Hooper AM, Pickett JA (2010) Exploiting phytochemicals for developing a push–pull crop protection strategy for cereal farmers in Africa. *J Exp Bot* 61: 4185–4196
- Khan ZR, Midega CAO, Pittchar J, et al. (2014) Achieving food security for one million sub-Saharan African poor through push-pull innovation by 2020. *Philos Trans R Soc B* 369:20120284
- 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; 1988 August 22–24. IITA, Ibadan, pp. 3–14
- Maes K (1998) Pyraloidea: Crambidae, Pyralidae. In: Polaszek, A, ed. *African cereal stem borers: Economic importance, taxonomy, natural enemies and control* Wallingford: CAB International, 87–98.
- Magara HJO, Midega CAO, Otieno AA, Ogol CKPO, Bruce TJA, Pickett JA, Khan ZR (2015) Signal grass (*Brachiaria brizantha*) oviposited by stem borer (*Chilo partellus*) emits herbivore-induced plant volatiles that induce neighbouring local maize (*Zea mays*) varieties to recruit cereal stem borer larval parasitoid *Cotesia sesamiae*. *Int J Sci Basic Appl Res* 19:341–375
- 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 Prot* 28: 1045–1051
- Midega CAO, Khan ZR, Amudavi DA, Pittchar J, Pickett JA (2010) Integrated management of *Striga hermonthica* and cereal stem borers in finger millet (*Eleusine coracana* (L.) Gaertn.), through intercropping with *Desmodium intortum*. *Int J Pest Manag* 56: 145–151
- Midega CAO, Khan ZR, Pickett JA, Nylin S (2011) Host plant selection behaviour of *Chilo partellus* and its implication for effectiveness of a trap crop. *Entomol Exp Appl* 138:40–47
- Midega CAO, Salifu D, Bruce TJA, Pittchar J, Pickett JA, Khan ZR (2014) Cumulative effects and economic benefits of intercropping maize with food legumes on *Striga hermonthica* infestation. *Field Crop Res* 155:144–152

-
- Midega CAO, Bruce TJA, Pickett JA, Pittchar JO, Murage A, Khan ZR (2015a) Climate-adapted companion cropping increases agricultural productivity in East Africa. *Field Crop Res* 180:118–125
- Midega CAO, Bruce TJA, Pickett JA, Khan ZR (2015b) Ecological management of cereal stemborers in African smallholder agriculture through behavioral manipulation. *Ecol Entomol* 40(Suppl. 1):70–81
- Midega CAO, Wasonga CJ, Drinkwater LE, Hooper AM, Pickett JA, Khan ZR (2016) Drought tolerant *Desmodium* species effectively suppress parasitic weeds, improve grain yields and soil health in smallholder African farming systems. *Agric Ecosyst Environ* (in press)
- 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
- Odendo M, De Groot H, Odongo OM (2001) Assessment of farmers' preferences and constraints to maize production in moist mid-altitude zone of Western Kenya. Paper Presented at the 5th International Conference of the African Crop Science Society (ed. by H. Malika), pp. 1–12. Nigeria, African Crop Science Society, Kampala
- Oswald A (2005) *Striga* control technologies and their dissemination. *Crop Prot* 24:333–342
- Parker C, Riches CR (1993) *Parasitic weeds of the world: Biology and control*. CAB International, Wallingford
- Pickett JA, Bruce TJA, Chamberlain K et al (2006) Plant volatiles yielding new ways to exploit plant defence. *Chemical ecology: From gene to ecosystem* (ed. by M. Dicke and W. Takken), pp. 161–173. Springer, Wageningen
- Pickett JA, Hamilton ML, Hooper AM, Khan ZR, Midega CAO (2010) Companion cropping to manage parasitic plants. *Annu Rev Phytopathol* 48:161–177
- Polaszek A, Khan ZR (1998) Host plants. In: Polaszek A (ed) *African cereal stem borers: Economic importance, taxonomy, natural enemies and control*. CABI, Wallingford, pp. 3–10
- Schulte 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 Sci Appl* 17:97–108
- Tamiru A, Bruce TJA, Woodcock CM, et al. (2011) Maize landraces recruit egg and larval parasitoids in response to egg deposition by a herbivore. *Ecol Lett* 14:1075–1083
- Tamiru A, Bruce T, Midega CAO, et al. (2012) Oviposition-induced volatile emissions from African smallholder farmers' maize varieties. *J Chem Ecol* 38:231–234
- 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 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). *J Chem Ecol* 16:1577–1589
- 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*. Intercept, Andover, pp. 63–80
- Whitney AS (1966) Nitrogen fixation by three tropical forage legumes and the utilization of legume-fixed nitrogen by their associated grasses. *Herbage Abstr* 38:143
- World Bank (2008) *World development report 2008: Agriculture for development*. The World Bank, Washington, District of Columbia
- Yoder JI (1999) Parasitic plant responses to host plant signals: a model for subterranean plant–plant interactions. *Curr Opin Plant Biol* 2:65–70