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

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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 effective-ly 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 Uncinanone B, and others that dramatically in-hibit their attachment to host roots, such as Uncinanone C and a number of di-C-glycosylflavones (di-CGFs), resulting in suicid-al 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.

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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 sys-tems 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

(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 ex-udates 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 Schumach, 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 ce-real crops are interplanted with legumes, and therefore, le-gumes 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).

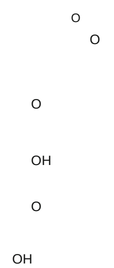
Semiochemistry of Push-Pull Technology

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).

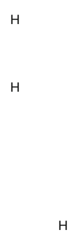
Avoidance of unsuitable hosts by herbivores involves detection of specific semiochemicals, or mixtures of semiochemicals, associated with non-host taxa, with some plants

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

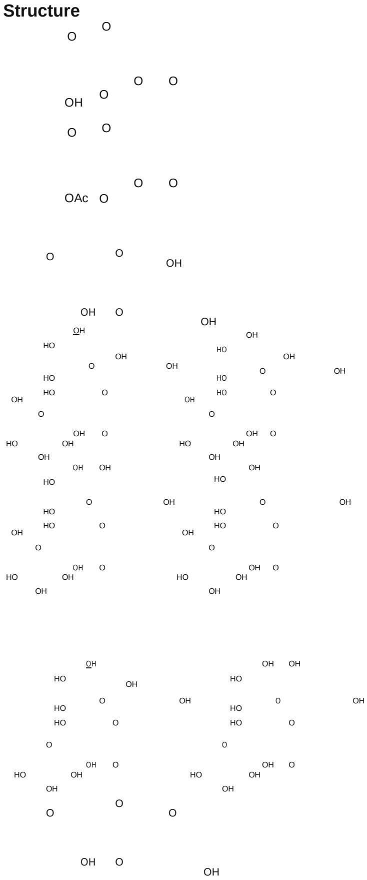
Pull semiochemistry

Structure	Compound	Source	Method for ID	Target	Activity
	Octanal Nonanal Naphthalene 4-allylanisole Eugenol Linalool	Maize (*Zea mays*) Napier grass (*Pennisetum purpureum*)	GC-EAG, GC-MS, co-elution with standards	Stemborer moths (adults)	Host cue attractant

Push semiochemistry

Structure	Compound	Source	Method for ID	Target	Activity
	(*E*)-Ocimene	*Melinis minutiflora*	GC-EAG, GC-MS, co-elution with standards	Stemborer moths	Repellent
	(*E*)-4,8-dimethyl-1,3,7-nonatriene	*Desmodium* spp.		**Cotesia sesamiae*	Attractant
	Humulene				
	-Caryophyllene				
	-Terpinolene				
	-Cedrene				

***Striga* inhibition**

Structure	Compound	Source	Method for ID	Target	Activity
	Orobanchol	*D. uncinatum* *D. incanum*	Root exudate isolation. NMR spectroscopy Root exudate. LC-MRM-MS	*Striga*	Germination stimulation
	Orobanchol acetate				
	Uncinanone B				
	6-*C*-galactosyl-8-*C*-glucosylapigenin	*D. uncinatum* *D. intortum* *D. incanum* *D. ramosissimum*	Root exudate LCMS, structure verified through isolated natural product standard.	*Striga*	All glycosides are present in whole root exudate that inhibit *Striga* parasitism
	6,8-di-*C*-glucosylapigenin (vicenin-2)				
	6-*C*-glucosyl-8-*C*-galactosylapigenin				
	6-*C*-galactosyl-8-*C*-arabinosylapigenin				
	6-*C*-arabinosyl-8-*C*-glucosylapigenin (isoschaftoside)				‡Inhibits radicle growth at picomolar concentrations *in vitro*
	6-*C*-arabinosyl-8-C-galactosylapigenin				
	Uncinanone C	*D. uncinatum*	Root exudate isolation. NMR spectroscopy	*Striga*	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 ac-tive 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 her-bivorous 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 sesquiter-penes, including α-cedrene (Khan et al. 2000), and effec-tively 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 reduc-tions 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 de-velopment of germinated striga plants, the extension of the radicle, was inhibited by another isoflavanone named unicinanone B (Tsanuo et al. 2003). Subsequent studies on the chemical composition of the root exu-dates 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 concen-trations 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 differ-ent 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 num-ber 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 com-panion 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 sustainabil-ity in view of the increasingly dry and hot conditions associ-ated with climate change, alternative draught 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 spe-cies from which 21 drought tolerant species were initially selected. Out of these, Bracharia 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 attrac-tiveness 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 mini-mal 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 with-in 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 com-mercial 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, there-fore, 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 technol-ogy, 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 ef-fective control of cereal stemborers and striga, with concom-itant 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 elu-cidate 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 agro-nomic properties for use in different agroecologies, in partic-ular 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 demonstrat-ed that the chemicals in the root exudate again were responsi-ble 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, there-by making the plant 'invisible' to ovipositing stemborer fe-males and thus preventing further egg laying by them (Bruce et al. 2010). Consequently, the ratio of other compounds rel-ative 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 oviposi-tion. 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 se-miochemicals 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 semio-chemicals 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 ex-posed 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 ex-posed 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 attractants signals also for the parasitoid Cotesia sesamia including the tetranorterpenes DMNT or TMTT (Magara et al. 2015). Studies currently are underway to understand the ef-fects, 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 com-panion cropping or synthetic variants of the active compounds mediating these responses.

Understanding early herbivory alert and plant-plant signal-ing will enable their full exploitation in development of future push-pull strategies with these traits. We are currently identi-fying 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 technol-ogy 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 enhanc-ing 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 incor-porating 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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