Chapter 10
Exploiting Chemical Ecology for Developing Novel Integrated Pest Management Strategies for Africa

Zeyaur R. Khan, Charles A. O. Midega, Jimmy Pittchar, and John A. Pickett

Abstract Push-pull, a novel approach for integrated management of insect pests, weed and soil fertility, was developed through the exploitation of chemical ecology and agro-biodiversity to address agricultural constraints facing millions of resource-poor African farmers. The technology was developed by selecting appropriate plants that naturally emit signalling chemicals (semiochemicals) and influence plant-plant and insect-plant interactions. Plants highly attractive for egg laying by lepidopteran cereal stemborer pests were selected and employed as trap crops, to draw pests away from the main cereal crops. Among these, *Pennisetum purpureum* produced significantly higher levels of volatile cues (stimuli), used by gravid stem borer females to locate host plants, than maize (*Zea mays*) or sorghum (*Sorghum bicolor*). Despite its attractiveness to stemborer moths, *P. purpureum* supported minimal survival of the pests' immature stages. Plants that repelled stem borer moths, notably *Melinis minutiflora* and forage legumes in the genus *Desmodium*, were selected as intercrops, which also attracted natural enemies of the pests through emission of (E)-β-ocimene and (E)-4,8-dimethyl-1,3,7-nonatriene. *Desmodium* intercrop suppressed parasitic weed, *Striga hermonthica*, 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 the host roots. We identified and selected new drought- and temperature-tolerant trap [*Brachiaria* (*B. brizantha* × *B. ruziziensis*) cv. *mulato*] and intercrop plants (*Desmodium*, e.g. *D. intortum*) suitable for drier agroecologies. The new trap and intercrop plants also have appropriate chemistry in controlling stemborers, a new invasive pest, fall armyworms and parasitic striga weeds. Opportunities for semiochemical delivery by companion plants, including plant-plant signalling and early herbivory alert, are explored for developing future smart integrated pest management (IPM) strategies.

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R. Peshin, A. K. Dhawan (eds.), *Natural Resource Management: Ecological Perspectives*, Sustainability in Plant and Crop Protection,
https://doi.org/10.1007/978-3-319-99768-1_10

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Keywords Biodiversity and basic science · Chemical ecology · Push-pull technology · Novel pest management · Fall armyworm · Climate change

Abbreviations

BBSRC	Biotechnology and Biological Sciences Research Council
BIRE	Biological Interactions in The Root Environment
DFID	Department for International Development
FAW	Fall armyworm
GC-EAG	Coupled gas chromatography–electroantennography
GDP	Gross domestic product
HIPVs	Herbivore-induced plant volatiles
IPM	Integrated pest management
OPV	Open pollinated varieties
SDC	Swiss Agency for Development and Cooperation
SDG	Sustainable Development Goals
SSA	Sub-Saharan Africa

10.1 Introduction

Agricultural development in sub-Saharan Africa (SSA) is constrained by biophysical factors, low capacities and institutional and policy bottlenecks, while development assistance to agriculture has declined to only 4% of public expenditure (World Bank 2008; IFAD 2011). Although agriculture contributes to over 25% of the gross domestic product (GDP) and more than half of export earnings, the per capita food production in Africa has declined over the past two decades. Rural Africa is characterized by continuing stagnation and often deterioration, low crop and livestock productivity, low farm incomes and the rising vulnerability of resource-poor smallholder farmers, who constitute the majority and whose basic source of livelihood is agriculture (World Bank 2008). More than 265 million rural poors face higher levels of hunger and poverty. Longer-term development challenges include dependence on a few primary commodities, poor human capacity, increasing migration to urban areas, low employment, especially of the youth and women, and climate changes (World Bank 2007).

10.2 Low Agricultural Productivity and Other Compounding Effects in SSA

Several factors interrelated with the low productivity remain a concern, not least the environmental degradation of the natural resource bases, the human population pressure on productive resources, leading to food insecurity, undernutrition, poverty, high morbidity and human migrations. Intensive land use, without sustainable investments in soil fertility enhancement, has transformed most of the natural landscape characterized by a decline in the overall quality of soil and vegetation, reducing agricultural yields. Soil erosion further leads to land degradation. Land clearance for agriculture is causing serious deforestation (World Resources Institute 2007), and there is progressive depletion of soil nutrients, particularly of nitrogen and soil organic carbon (Solomon et al. 2010). African soils are poor in organic matter due to continuous cropping and poor farming practices and in need of an agronomic innovation that continuously improves soil health (Sanchez 2002; Oswald 2005; Rodenburg et al. 2005).

This situation, driven further by a significantly increased demand for food because of population growth, urbanization and changing food consumption patterns, raises the need for sustainable intensification of production systems (Pretty et al. 2011), which includes both the management of pests and soil health and the reduction of land degradation. Effects of climate changes are expected to have greater impacts on sustainable agricultural development in SSA with production constraints expected to increase during the next few decades, as agriculture intensifies to meet the extra food demand by the growing population. The resource-constrained smallholder farmers living in arid and semiarid regions, who practise mixed crop–livestock systems, are particularly badly affected. SSA is projected to have more than 500 million food insecure people by 2020.

Cereals remain the major food and cash crops for the majority of the resource-poor smallholders in SSA, grown alongside livestock in mixed farming systems. Production of main cereals, maize, *Zea mays*, and sorghum, *Sorghum bicolor*, is severely reduced by a complex of biotic constraints, namely, stemborer pest complexes, parasitic striga weeds and more recently fall armyworm invasion, as well as abiotic factors, such as water stress and degraded soils. The most economically significant insect pests are Lepidopteran stemborers of the families Noctuidae and Crambidae, e.g. the indigenous *Busseola fusca* (Noctuidae) and the invasive *Chilo partellus* (Crambidae), as well as the fall armyworm (FAW) *Spodoptera frugiperda* (Lepidoptera: Noctuidae) (Midega et al. 2018). Over 20 stemborer species attack cultivated gramineae in SSA (Kfir et al. 2002), causing between 30% and 80% yield losses of cereal crops (Kfir et al. 2002).

10.2.1 A New Challenge: The Fall Armyworm Invasion in Africa

In addition, losses of up to 100% to maize and other crops have been reported by smallholder farmers (<2 ha), due to the recent FAW invasion of Africa (Midega et al. 2018). FAW is a native pest in tropical and sub-tropical Americas (Todd and Poole 1980). More than 28 countries in Africa are already affected, and the pest is extending rapidly to other countries (Goergen et al. 2016; Cock et al. 2017). The pest adds to the diversity of Lepidopterans of cereal crops and signals increased about its

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negative impacts on agricultural production and food security in Africa. FAW invasion has adverse economic impacts on smallholder farmers as it directly increases their capital costs through increased labour and inputs needed, specialised knowledge required to deal with the pest, the inability of agricultural systems to respond to sudden invasions and the overall effect of higher production costs and yield losses on household incomes.

FAW is a polyphagous pest with a wide host range of economically important grasses such as maize, rice, sorghum and sugarcane, as well as other crops, including cabbage, beet, peanut, soybean, alfalfa, onion, cotton, pasture grasses, millet, tomato, potato and cotton. It is prolific, ovipositing egg masses in batches of 100–200 eggs (Sparks 1979; Johnson 1987; CABI 2017). Eggs hatch in 2 to 4 days under optimum temperatures. Adult moths can survive 2 to 3 weeks during which females mate multiple times, producing up to 1000 eggs each. Their larval stages have six instars, the first of which is most voracious, consuming the most plant material. The larvae eat different parts of the plant, mainly young whorls, ears and tassels, depending on the larval age, stage of development and the host plant type. On maize, young larvae eat leaves at night, leaving a 'window pane' effect, and hide in the plant funnel during the day. Larval feeding often kills the growing point, causing 'dead heart'. At the reproductive stage of maize, the larvae also attack reproductive organs, feeding on tassels and/or boring into the ears (Midega et al. 2018). The larger caterpillars also act as cutworms by entirely sectioning the stem base of maize plantlets. As larvae grow older, they hide inside the funnel, limiting the effect of pesticide applications and natural enemies. FAW is a sporadic and long-distance migratory pest whose adult moths are able to fly over 100 km in a single night (Goergen et al. 2016). It has a significant economic impact, up to 100% crop loss (CABI 2017), finding most farming communities ill prepared to manage the invasive pest.

Single control methods are relatively costly, unsustainable or ineffective. A number of control methods have been tried, including:

i) Application of pesticides (chemical control)
ii) Use of microbial organisms that attack FAW in its native range, for example, *Beauveria bassiana* and *Spodoptera frugiperda* multiple *nucleopolyhedrovirus* (SfMNPV)
iii) Use of predatory insects and parasitic wasps (parasitoids)
iv) Use of genetically modified crops containing Bt genes that are resistant to FAW
v) Mass trapping of male moths using pheromones, preventing them from mating
vi) Integrated pest management (IPM) – a combination of methods minimizing pesticides use (CABI 2017)

Past management of FAW has mainly relied on application of synthetic chemical pesticides, with dismal results, depending on farmers' knowledge, consistency of use, purchasing power and choice of pesticide products (Midega et al. 2018). Although chemical insecticides have been shown to provide control of the pest (Young 1979), cases of resistance to some key a.i. have been reported (Yu 1992; Al-Sarar et al. 2006). Dispersion of FAW larvae lower into the maize plant canopy keeps them out of reach of topical insecticide applications (Cook et al. 2004, Midega

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et al. 2018). Moreover, pesticides are not affordable for the vast majority of smallholder famers in Africa, and their incorrect use has resulted in poisoning farmers and the environment, as well.

10.2.2 The Need for Integrated Pest Management (IPM) of Stemborers and Fall Armyworm

Suitable and cost-effective integrated pest management (IPM) strategies need therefore to be developed, specifically for smallholder farmers in Africa (Midega et al. 2018). However, most available literature on FAW control relates to agricultural systems in its native Americas, which differ from those in Africa. Therefore, control methods that have been effective in FAW native habitats may not be effective in Africa. However, evidence from Latin America indicates that an IPM approach may be necessary in which pesticides use is minimised and alternative approaches, such as exploiting the pest's natural enemies and crop monitoring, be consistently applied (CABI 2017). Climatic conditions in Africa support prolific reproduction of FAW, which is expected to result in increasingly severe damage to crops (Goergen et al. 2016), as the invasive pest is likely to have few natural enemies. Conventional control methods have limited effectiveness, as explained above, notably the difficultly in application of pesticides and development of resistance by the pest to some insecticides and transgenic technologies such as Bt-maize. Therefore, an integrated management approach for fall armyworm that fits within the mixed cropping nature of the African farming systems is necessary, for the resource constrained farmers. Thus, an IPM technology like the push-pull (www.push-pull.net) that exploits natural processes, including the use of natural enemies, appears as the most promising (see paragraph 3).

10.2.3 Parasitic Striga Weeds

Parasitic weeds in the genus *Striga* (Scrophulariaceae), commonly known as striga, further severely constrain cereal production in SSA (Oswald et al. 2001; Khan et al. 2014). There are at least 22 species of *Striga* of which *Striga hermonthica* and *Striga asiatica* have been identified as the most socio-economically important in cereal cultivation, in much of SSA (Gressel et al. 2004; Gethi et al. 2005). Striga infestation weakens host cereal plants by competing for and absorbing its supply of moisture, photosynthates and minerals (Tenebe and Kamara 2002). The weed quickly adapts to its environment (Bebawi and Metwali 1991) and germinates in response to specific chemical cues present in root exudates of its hosts or certain non-host plants (Yoder 1999, Parker and Riches 1993). Striga roots mesh with the host root system and also injects phytotoxins into roots (Frost et al. 1997, Gurney et al. 1999; Gurney et al. 2006). Striga infestations cause significant reductions in host plant height, biomass and grain yields (Gurney et al. 1999). Striga weed

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parasitization causes up to 100% cereal yield losses. Conditions such as degraded environments, low soil fertility, higher soil temperature and low rainfall (Gurney et al. 2006) exacerbate striga attacks in subsistence farming systems.

10.2.4 Unsustainable Pest and Weed Control Methods

Research and extension institutions in Africa often recommend the use of insecticides and herbicides in management of stemborers, FAW and striga, respectively, with dismal results. This is complicated by the resource-constrained nature of subsistence farmers in the region, impeding their ability to afford expensive chemicals. Insecticide use in Africa is limited, largely due to shortage of information, inaccessibility of appropriate and effective products and associated high costs (Midega et al. 2018). Transgenic plant technologies such as Bt maize have been tried (Frizzas et al. 2014). However, development of field resistance by stemborers and FAW to transgenic crops has been documented, including resistance to Cry1F maize in Puerto Rico (Storer et al. 2010). Majority of smallholders therefore do not attempt to manage stemborers, FAW or striga and consequently suffer high grain yield losses and food insecurity (Chitere and Omolo 1993; Oswald 2005; Midega et al. 2018).

Sustainable management of pests, weeds and resource degradation therefore needs sustainable intensification that maximizes soil quality and crop productivity, adopting a systems approach (social, economic and environmental) to agricultural development and developing solutions based on integrated analyses of specific agroecosystem conditions and farmer practices (IAASTD 2009; Pinstrup-Andersen 2010). Significant and sustainable increases of productivity require a more holistic approach, reflecting the multifunctionality of agriculture, which integrate a variety of resource-conserving technologies and practices – i.e. IPM, integrated soil fertility management (ISFM) and livestock integration (Pretty et al. 2006). In order to manage the production constraints, approaches that are compatible with the polycultural nature of low-input farming systems in Africa need to be developed by understanding the intricate biological interactions within ecosystems, farm landscapes and socioeconomic conditions of smallholder farmers. One such approach is the ‘push-pull’ technology which is compatible with African socio-economic conditions as it does not rely on high external inputs, but biological management of local bio-resources.

10.3 Development of the ‘Push-Pull’ Technology

The push-pull technological innovation was developed by the International Centre of Insect Physiology and Ecology (ICIPE) to significantly increase cereal and livestock productivity, by addressing the interrelated problems caused by the above

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biotic constraints (notably insect pests and weeds), soil and environmental degradation, lack of livestock fodder, loss of biodiversity, increasing temperatures and water stress, through improved management strategies (Khan et al. 2014; Midega et al. 2015b). The technology is a polycropping innovation that holistically combines resource-conserving principles of IPM and ISFM, by using natural processes and locally available bio-resources (Cook et al. 2007; Hassanali et al. 2008). It was developed for smallholder farming systems based on the traditional African diversified cereal-legume-fodder intercropping practice. In this method, the perennial intercrop maintains continuous soil cover and provides live mulching, thus conserving soil moisture and improving arthropod abundance and biodiversity as well as the food web of natural enemies of stemborers (Khan et al. 2002, 2006a; Midega et al. 2015a).

The technology effectively controls the major insect pests of cereals in SSA, i.e. lepidopteran stemborers and FAW (Midega et al. 2018), and the devastating parasitic striga weeds, both of which can cause total yield loss to cereals (Khan et al. 2014). The technology relies on understanding natural biochemical processes and their underlying chemical ecology, agro-biodiversity and plant-plant and insect-plant interactions (Cook et al. 2007; Khan et al. 2014; Pickett and Khan 2016). It deploys inter- and trap crops in a mixed cropping system (Khan et al. 2006b) which release behaviour-modifying stimuli (plant chemicals) to manipulate the distribution and abundance of stemborers and beneficial insects.

ICIPE initially conducted a series of studies on the behaviour and chemical ecology of plants, insect pests and their natural enemies in order to identify companion plants that would naturally manipulate the behaviour of insects, while delivering additional benefits to the farmers (Khan et al. 2014). A stimulo-deterrent cropping strategy, known as 'push-pull', was thus developed by exploiting phytochemicals released by two sets of carefully chosen companion plants. These consist of repellent and trap plants, intercropped in between and planted around the main cereal crops (Khan et al. 2010). The intercrops, (e.g. *Desmodium* spp.) emit semiochemicals that repel ('push') insect pests from the main crop while attracting their natural enemies. The trap plant [e.g. Napier grass, *Pennisetum purpureum* or *Brachiaria* (*B. brizantha* × *B. ruziziensis*) cv. Mulato], grown as a border crop, attracts ('pull') the insect pests away from the main crop (Cook et al. 2007; Khan et al. 2010). The *Desmodium* intercrop was found to effectively suppress parasitic striga weeds (Khan et al. 2002). In a long-term research, ICIPE later established that the underpinning mechanism was an allelopathic effect of *Desmodium* root exudates which caused abortive germination of Striga seeds, thus preventing root-to-root attachment to the host plant and progressively depleting its seed bank. Furthermore, this strategy was found to improve soil health by fixing atmospheric nitrogen, improving carbon sequestration and conserving soil moisture (Midega 2015a; CABI 2017).

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10.3.1 Exploiting Semiochemistry of Companion Plants for Stemborer Control

Cereal stemborers are polyphagous herbivores that feed on a range of host plants, including uncultivated grasses that serve as reservoirs (Khan et al. 1997a). Herbivorous arthropods are attracted to their host plants through olfactory detection of specific attractive semiochemicals which mediate changes in their behaviour or development (Nordlund and Lewis 1976; Dicke and Sabelis 1988) or to specific ratios of semiochemicals (Bruce et al. 2005) emitted by host plants or organisms, as well. Semiochemicals or their blends emitted by non-host plants conversely cause avoidance of those chemical compounds by the insects (Hardie et al. 1994).

Development of ‘push-pull’ was based on field surveys of more than 500 grass species (Poaceae, Cyperaceae and Typhaceae), as well as some leguminous crops in different agroecological zones in East Africa. Attractive and antagonistic plant species for use as trap and repellent intercrops, respectively, were thus identified. Potential trap crops were selected from plant species that were attractive but did not support development of the larval stages of the stemborer pest. Napier grass, *Pennisetum purpureum*, a forage crop, was found to produce significantly higher amounts of volatile organic compounds (VOCs) that attracted gravid stemborer females more than maize or sorghum (Birkett et al. 2006). The production of VOCs by Napier grass was found to be 100-fold in the first hour of nightfall (scotophase) (Chamberlain et al. 2006), the period during which stemborer moths seek host plants for oviposition (Päts 1991). This strategy influences the oviposition preference by gravid stemborer females. However, about 80% of the stemborer larvae did not survive (Khan et al. 2006a; 2007), as Napier grass produced a sticky sap which mechanically trapped them, exposing them to natural elements and enemies and causing high mortality. This resulted in significant reductions in stemborer infestation in maize, increasing yields by up to 1.5 t ha^{-1} (Khan et al. 2000).

Conversely, the fodder intercrops, *Melinis minutiflora* and legumes in the genus *Desmodium* (commonly known as desmodium) similarly repelled stemborer moths and provided effective control of these pests in intercrops with maize (Khan et al. 1997b, 2000). Both the *Desmodium* genus (silverleaf, *D. uncinatum*, and greenleaf, *D. intortum*) were found to produce repellent volatile semiochemicals during the damaging stage to plants of herbivorous insects, which repelled the stemborer moths (Khan et al. 2001). Also the intercropping of maize with silverleaf desmodium, *D. uncinatum*, was serendipitously found to suppress the emergence of the parasitic striga weed *S. hermonthica*, through allelopathic mechanism of the *Desmodium* root exudates, produced independently of the presence of striga. Blends of secondary metabolites produced by activities in the root exudates of *Desmodium* spp., concomitantly with striga seed germination stimulatory isoflavanones, were found to directly interfere with *Striga* parasitism. This combined effect reduced the striga seed bank in situ through efficient suicidal germination even in the proximity of graminaceous host plants (Tsanuo et al. 2003). Additional benefits were provided by *Desmodium* spp. in terms of increased availability of nitrogen and soil shading.

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Controlling both stemborers and striga resulted in significant yield increases, from an average of 1–3.5 t ha^{-1} (Khan et al. 2006a; 2008). Other *Desmodium* spp. similarly controlled both stemborers and striga weeds (Khan et al. 2006b). *Desmodium* thus became the intercrop of choice for most smallholder farmers in Eastern Africa, where both constraints affect cereal production. Other African adapted *Desmodium* spp. were also tested and found to have similar effects on stemborers and striga (Khan et al. 2006b). They have been evaluated to be incorporated as intercrops in adapted push-pull systems with maize, sorghum and millets (Midega et al. 2015b). The effectiveness of push-pull technology in pest control delivered through both direct and indirect effects is described in Fig. 10.1.

Innate, direct plant defence systems are deployed by plants to protect themselves from pests. These include production of toxins, digestion inhibitors and semiochemicals repellent to herbivorous insects (Kessler and Baldwin 2001). The trap and repellent plants exert direct effects on both adult and developing stages of cereal stemborers (Midega et al. 2015a). The VOCs mediate the behaviour of gravid stemborer moths, which are diverted to the border crop thus protecting the main crop from the pest. The main physiologically active compounds responsible for attractiveness of the trap crop to the gravid stemborer moths, i.e. hexanal, (E)-2-hexenal, (Z)-3-hexen-1-ol and (Z)-3-hexen-1-yl acetate, were identified using coupled gas chromatography–electroantennography (GC–EAG) on the antennae of stemborers (Khan et al. 2000).

Molasses grass was discovered to emit active compounds similar to those that are produced by plants damaged by herbivorous insects, known as herbivore-induced plant volatiles (HIPVs) (Turlings et al. 1990a, b, 1995). Identified compounds included (E)-ocimene and (E)-4,8-dimethyl-1,3,7-nonatriene (DMNT). These compounds are associated with a high level of stemborer colonisation and also attract parasitoids, natural enemies of stemborers, and are responsible for

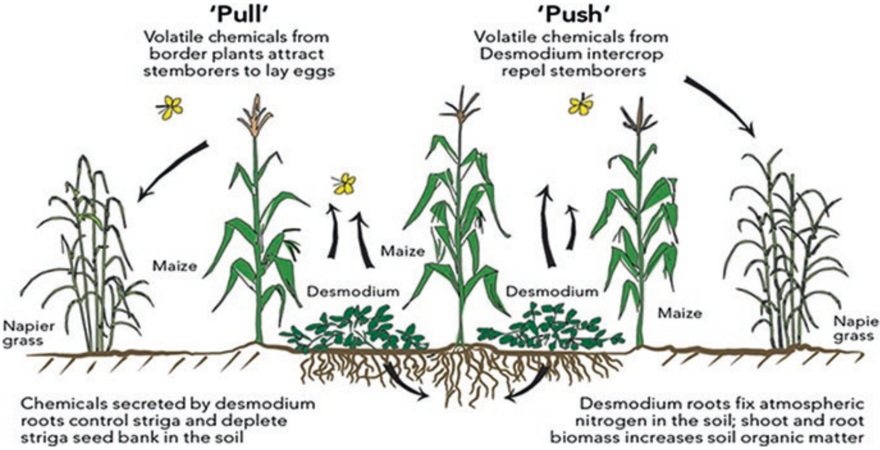

Fig. 10.1 How the push-pull system works: stemborer moths are repelled by intercrop volatiles while attracted to trap crop volatiles. Root exudates from the desmodium intercrop cause suicidal germination of striga and inhibit attachment to host cereal roots

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repelling ovipositing stemborers (Khan et al. 2000). Molasses grass naturally produces high levels of HIPVs and therefore is not preferred as host. It typically produces semiochemicals emitted by a highly infested maize plant.

Similarly, *Desmodium* was also found to produce (E)-ocimene and DMNT, and large amounts of other sesquiterpenes, including alpha-cedrene (Khan et al. 2000), thus effectively repelling stemborer moths and attracting their natural enemies (Midega et al. 2009). Furthermore, a significant increase in parasitism of stemborer larvae by the indigenous parasitoid, *Cotesia sesamiae* (Hymenoptera:Braconidae), was observed in maize fields intercropped with molasses grass in western Kenya (Khan et al. 2000). It was caused by the same semiochemicals produced by molasses grass, which repelled female stemborer moths. Attraction of female parasitoid *C. sesamiae* to DMNT was confirmed in a Y-tube olfactometer bioassay, under field conditions (Khan et al. 1997b, 2000). Similarly, intercropping maize with *Desmodium* resulted in significant increase of stemborer larval and pupal parasitoid activity (Midega et al. 2014).

The push-pull cropping system seems to attract an abundance of generalist predators like ants, earwigs and spiders which prey on the stemborer immature stages (Midega et al. 2006), contributing to reduce the pest populations. The synchronized effects of the trap crops and repellent intercrops result in significant reductions in stemborer colonisation and mortality, reduced crop damage and significant improvements in grain yields. The same mechanism is thought to be responsible for reduction of FAW populations under the push-pull system (Midega et al. 2018). ICIPE is investigating the semiochemical mechanisms that prevent FAW pests from attacking crops, under the push-pull system.

In spite of Napier grass being preferred to maize for oviposition by gravid moths, it did not support the development of stemborer larvae (Khan et al. 2006a). Further investigations established that the high mortality of stemborer larvae on the grass was due to innate defence mechanism in the grass, which produces sticky sap upon injury inflicted by feeding larvae. The sap traps the young larvae and impedes their mobility, both directly exposing the larvae to the elements. Indirect mortality is caused by generalist natural enemies such as spiders that are often prevalent in Napier grass fields/strips (Midega et al. 2008). Moreover, Napier grass slows the development rates of larvae because of its poor nutritional qualities (Khan et al. 2006a).

The *Desmodium* intercrop controls the parasitic striga through a variety of mechanisms including increased availability of nitrogen, soil shading and allelopathic root exudation that happens independently of the presence of striga (Khan et al. 2002). Root exudates of different *Desmodium* legume species studied contain a complex array of plant secondary compounds that simultaneously stimulate germination and subsequently inhibit Striga radicle growth. Some of the identified compounds, including 4″,5″-dihydro-5,2′,4′-trihydroxy-5″-isopropenylfurano-(2″,3″;7,6)-isoflavanone, stimulate germination of striga seeds. At the same time, other compounds, including 4″,5″-dihydro-2′-methoxy-5,4′-dihydroxy-5″-isopropenylfurano-(2″,3″;7,6)-isoflavanone, inhibit the growth of the *Striga* root haustoria (Tsanuo et al. 2003). In maize–*Desmodium* intercrops under field conditions, both *Desmodium* and maize root exudates stimulate striga germination, but

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subsequent development of striga root haustoria was disrupted by a second group of compounds in the root exudates. This abortive germination is mediated by this combined allelopathic mechanism by which *Desmodium* prevents parasitism and continuously removes striga seed bank from the soil, in situ (Tsanuo et al. 2003). Multilocation field studies across several ecosystems have confirmed that *Desmodium* effectively control striga and result in significant yield increases in maize (Khan et al. 2008, 2014), sorghum (Khan et al. 2006b), finger millet (Midega et al. 2010) and upland rice (Pickett et al. 2010).

10.4 Climate Smart Push-Pull Technology

Climate change is anticipated to have far-reaching effects on sustainable agricultural development in SSA. Anticipated changes include increased frequency and intensity of plant abiotic stressors, e.g. unpredictable and erratic rainfall amounts and patterns, as well as flooding (Hoerling and Kumar 2003) and higher temperatures and droughts (Burke et al. 2009). Further and more serious land degradation, increased pest and weed pressure, increased incidences of crop failure and general increases in food and nutritional insecurity are expected for resource poor farmers, in many parts of SSA. There is therefore a need to build system adaptability to protect cropping systems from climate variability and to improve their resilience to climatic shocks. As majority of smallholder African farmers rely on rainfed agriculture, it became imperative to adapt the conventional push-pull system to withstand increasingly warmer and drier conditions. The trap and intercrops used in conventional push-pull were increasingly vulnerable to rainfall and temperature variations, as the initial system was developed for subhumid tropical conditions with an average rainfall of 800–1200 mm and moderate temperatures (15 to 30 °C).

Adaptation of the push-pull strategy for hotter and drier agroclimatic conditions has improved system resilience and adaptability needed to mitigate climate change effects (Khan et al. 2014). Using a series of studies under controlled and on-farm conditions, the push-pull technology has been adapted to drier agroecologies by selecting and incorporating new drought-tolerant trap (*Brachiaria* cv. mulato) and intercrop (drought-tolerant species of *Desmodium*, e.g. *D. intortum*) plants. These were tested and validated under farmers' conditions and incorporated into the push-pull technology.

The selection of new *Desmodium* intercrops was based on drought tolerance, appropriate chemistry to effectively control both stemborer and striga weeds, the ability to improve soil fertility and soil moisture retention as well as the ability to significantly improve yields of maize and sorghum (Khan et al. 2014, 2016; Midega et al. 2015b). *Brachiaria* cv. mulato II (*B. ruziziensis* × *B. decumbens* × *B. brizantha*) was the preferred trap plant in the climate adapted push-pull, because of its ability to control stemborers, high preference by farmers as livestock fodder and the commercial availability of its seed. In addition, drought stress significantly limited the relative attractiveness of *Brachiaria* cv mulato II to stemborer moths for oviposition

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(Chidawanyika et al. 2014). Furthermore, drought stress only minimally alters secondary metabolism in the plant and does not significantly affect emission of key VOCs necessary for stemborer host location (Chidawanyika 2015). An important attribute is that *Brachiaria* spp. allow for only minimal survival of stemborer larvae (Midega et al. 2015b) and have a suitable characteristic of a border plant that supports populations of natural enemies within and out of the cereal cropping season.

The climate-adapted companion plants (both trap and repellent plants) also generate high-quality livestock fodder over long periods of drought. They also improve biodiversity, soil conservation and organic matter among other ecosystem services (Midega et al. 2015b). There is potential for further adaptation of the push-pull technology through incorporation of even more drought-tolerant African-adapted *Desmodium* species such as *D. incanum*, *D. repandum* and *D. ramosissimum*, which exhibit the right chemistry and ability to control the identified constraints and improve cereal crop yields (Hooper et al. 2015; Midega et al. 2017).

10.4.1 Climate-Adapted Push-Pull Effectively Controls Fall Armyworm

Multilocational field surveys show that the climate-adapted push-pull technology effectively controls the invasive FAW (Midega et al. 2018). The control mechanism involves the diversionary 'push and pull' tactics previously found to be effective against stemborers. Additional action by natural enemies, i.e. parasitic wasps and generalist predators, such as ants, earwigs and spiders, complements the stimulo-deterrent action to reduce FAW invasion of crops under push-pull. Studies have shown that the damage caused by fall armyworm is reduced by up to 100% with the technology, resulting in significant improvements in grain yields.

ICIPE evaluated the functionality of climate-adapted push-pull using drought-tolerant Greenleaf *D. intortum* and *Brachiaria* sp. as inter and border crops, respectively, in FAW management through direct field observations and farmers' perceptions in Kenya, Uganda and Tanzania. Data were collected from a diverse sample of farmers in different agroecologies on the number of FAW larvae on maize, the percentage of maize plants damaged by the larvae and maize grain yields. Similarly, farmers' perceptions of the impact of the technology on the pest were assessed. There were highly significant reductions in infestation by fall armyworm larvae and plant damage in climate-adapted push-pull, compared to maize monocrop plots. Reductions of 82.7% in the average number of larvae per plant and 86.7% in plant damage per plot were observed in climate-adapted push-pull, compared to maize monocrop fields. Similarly, maize grain yields were significantly higher, approximately 2.7 times, in the climate-adapted push-pull fields. Farmers rated the technology significantly effective in reducing FAW infestation and plant damage rates. These results demonstrate that the technology is also effective in controlling FAW and represents a solution that can be immediately deployed for management of the invasive pest.

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10.5 New Opportunities in Exploiting Chemical Ecology and Biodiversity

In constitutive indirect plant defence, the herbivorous attack triggers production of herbivore-induced plant volatiles (HIPVs) that provide foraging cues for natural enemies, antagonistic to the pests (Turlings et al. 1990a, b). This reaction is usually triggered by pest larval stage feeding, and therefore the natural enemies are only attracted following the damage to plants. This aspect has in part limited effectiveness of biological control in reducing pest damage in farmers' fields. Ideally, responses to egg deposition on the plants should thus elicit defences that are beneficial before the larvae cause any damage to plants (Hilker and Meiners 2006; Bruce et al. 2010). Maize landraces and some selected locally adapted African open pollinated varieties (OPVs) showed promise by having this desirable trait. Oviposition by *C. partellus* on these plants was observed to induce defence responses leading to attraction of both egg and larval parasitoids, as well as their reduced attractiveness for further oviposition (Tamiru et al. 2011, 2012). Remarkably, this trait is absent in élite maize hybrids, implying that it must have been lost during the breeding processes that selected for other desirable qualities such as higher yields.

Early production of HIPVs confers adaptive value to the plant and generates also selection pressure on the parasitoids to respond to such signals, because it enhances their foraging efficiency and improvement of ecological fitness. Some selected maize varieties with the early herbivory trait have now been incorporated in the push-pull system, conferring the added benefit of providing biological control of stemborers at oviposition, the earliest stage of attack. There is further opportunity to study the molecular basis of egg-induced semiochemical production with a view to develop molecular markers that can be used in advanced selection of crop varieties and introgression of these traits into mainstream commercial hybrid maize varieties (Tamiru et al. 2015).

There is emerging evidence that plants can respond to HIPVs produced by neighbouring plants, adjusting their metabolism to increase resistance to herbivores by becoming either antagonistic to foraging herbivores or more attractive to their natural enemies (Birkett et al. 2006). Such plants have thus a higher expression of resistance genes and defence-related plant compounds (Arimura et al. 2000). In controlled experiments, maize planted next to molasses grass was found to produce similar semiochemicals as those under attack by stemborer larvae, becoming more attractive to both egg and larval parasitoids and less attractive to stemborer moths for oviposition (Midega et al. 2015a). This suggests that semiochemicals produced by molasses grass provide aerial signals inducing resistance in the neighbouring undamaged plants. Furthermore, the latter are 'primed' to respond more quickly or aggressively to future stemborers attacks. Further research is being undertaken to identify the key compounds within the HIPVs that induce and/or prime these responses in a variety of plants. Early production of HIPVs as a crop protection strategy may have potential for deployment against the newly invasive FAW in Africa.

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10.6 Conclusion

The push-pull IPM system effectively exploits the science and knowledge of chemical ecology to address the key constraints to cereal production, faced by resource-poor smallholder farmers in SSA. It is an appropriate system because it uses locally available companion plants, rather than expensive external inputs. It is modelled on both the polycropping and mixed nature of smallholder farming systems, practised in Africa. It therefore allows integration with livestock through the fodder provided by the companion plants. These provide the stimulo-deterrent functionality of the technology, with trap plants attracting and trapping the gravid stemborer moths and the intercrop providing the push to the moths as well as attraction of natural enemies. The technology has been adapted for drier areas vulnerable to climate changes, by identifying and incorporating drought-tolerant trap and repellent plants. This has made the technology more resilient in the face of climate changes, as rainfall becomes increasingly unpredictable and temperatures increase. Moreover, the technology is being made ‘smarter’ through identification and incorporation of cereal crops with innate defence systems against stemborer pests, which include early production of HPIVs induced by egg pest deposition. Companion plants that can signal defence systems of the neighbouring smart cereals are also being identified. Deployment of inductive HPIVs as a crop protection strategy could have tremendous potential as a cost-effective solution against the more economically devastating FAW in Africa. The push-pull technology is being adopted by an increasing number of farmers in Africa, now estimated to be in excess of 170,000, because it is highly relevant to their needs and results compatible with their farming systems. Further efforts are being intensified to expand the technology to millions of farmers who need it in Africa.

Acknowledgements We gratefully acknowledge financial support to ICIPE provided by the following organizations and agencies: the European Union, Biovision Foundation, UK Department for International Development (DFID), Swedish International Development Cooperation Agency, the Swiss Agency for Development and Cooperation (SDC) and the Kenyan Government. The views expressed herein do not necessarily reflect the official opinion of these donors. The studies within the push-pull program are conducted in collaboration with Rothamsted Research of the UK, which receives grant-aided support from the UK Biotechnology and Biological Sciences Research Council (BBSRC), with additional funding provided under the Biological Interactions in the Root Environment (BIRE) initiative. Various roles played by all partners and collaborators, including farmers, are greatly acknowledged too.

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