CHAPTER 11

PLANT VOLATILES YIELDING NEW WAYS TO EXPLOIT PLANT DEFENCE

JOHN A. PICKETT[*,#], TOBY J.A. BRUCE[#],
KEITH CHAMBERLAIN[#], AHMED HASSANALI[##],
ZEYAUR R. KHAN[##], MICHAELA C. MATTHES[#],
JOHNATHAN A. NAPIER[#], LESLEY E. SMART[#],
LESTER J. WADHAMS[#] AND CHRISTINE M. WOODCOCK[#]

** Corresponding author. E-mail: john.pickett@bbsrc.ac.uk*
[#] *Rothamsted Research, Harpenden, Hertfordshire, AL5 2JQ, UK*
[##] *International Centre of Insect Physiology and Ecology, PO Box 30772, Nairobi, Kenya*

Abstract. When plants are damaged, they produce semiochemicals which can act as repellents for herbivorous pests and as attractants for organisms antagonistic to these pests, e.g., predators and parasitic wasps. Plants can also produce signals that warn other plants of impending attack. From this range of phenomena, it is possible to identify new ways to control pests. Although, in the past, we have needed to deploy such approaches by applying slow-release formulations of semiochemicals to crop plants, we can now use the plants themselves as a source of these semiochemicals. This may be achieved by using inducing agents, or a new range of natural product plant activators, to 'switch on' plant defence prior to attack. This paper considers the identification of new plant activators. In addition, practical use of plants releasing semiochemicals to ward off pest attack, to ensnare the attackers, and to attract beneficial insects that will attack the pests, is demonstrated by use of the stimulo-deterrent diversionary ('push-pull') strategy that has been developed for management of stem-borer moths in Africa.
Keywords: semiochemical; push-pull; non-host; electrophysiology; *cis*-jasmone; jasmonate

INTRODUCTION

We now know that attraction of insects to plants and other host organisms involves detection of specific semiochemicals (natural signal chemicals mediating changes in behaviour and development) (Nordlund and Lewis 1976; Dicke and Sabelis 1988), or specific ratios of semiochemicals. We have also learned, more recently, that the avoidance of unsuitable hosts can involve the detection of specific semiochemicals, or mixtures of semiochemicals, associated with non-host taxa (Hardie et al. 1994; Pettersson et al. 1994). During host alternation by many pest aphids, there can be repulsion away from a host that is not suitable for use at that developmental stage.

Marcel Dicke and Willem Takken (eds.), Chemical ecology: from gene to ecosystem, 161-173

For example, the winter, or primary, hosts of aphids can produce compounds that repel the spring morphs on their migration back to the summer, or secondary, hosts. Similar phenomena can be observed during colonization by a herbivorous insect, because the plant releases signals indicating that it is already infested and is therefore less suitable as a host. These signals can repel other incoming insects, but can also increase foraging by predators and parasitic wasps. The first interaction with the semiochemicals involved in these types of non-host recognition is usually on the insect antenna. Therefore, by using electroantennography (EAG) or single-cell recording (SCR) from individual olfactory neurons, coupled to high-resolution gas chromatography (GC), we can identify the compounds involved (Pickett et al. 1992).

SEMIOCHEMICALS AS REPELLENTS

Using plants upon which herbivores are feeding, and investigating, by GC-EAG or GC-SCR, the volatile compounds released, it is possible to identify a range of compounds that are electrophysiologically active and which may subsequently prove, in behavioural assays, to be repellents for insect pests. These compounds can also be effective in increasing foraging activity by predators and parasitoids that attack the pests. The compounds involved come from a wide range of biosynthetic pathways, but prominent amongst these are the isoprenoid and lipoxygenase pathways. For example, monoterpenes such as (*E*)-ocimene, and sesquiterpenes such as (-)-germacrene D, can be produced by plants and cause repellency to herbivores (Bruce et al. 2005). However, it is difficult to deploy these chemicals in the field as there is no long-lasting effect and the chemicals themselves are highly volatile and unstable. Heterologous expression of the genes associated with biosynthesis of these compounds has been attempted, but it is often very difficult to obtain useful expression rates, or at least expression that leads to useful production of these compounds (Aharoni et al. 2003). Recently, we have found that the heterologous expression of an (*E*)-β-farnesene synthase in *Arabidopsis thaliana* can be accomplished so that large amounts of (*E*)-β-farnesene are produced, which can affect aphids and their parasitoids (Beale et al. in prep.).

STRESS-RELATED SEMIOCHEMICALS

Methyl salicylate has been identified as a stress-related plant semiochemical, and most insects that we have examined, including some haematophagous insects, show strong electrophysiological responses to this compound. The cereal aphids *Rhopalosiphum padi*, *Sitobion avenae* and *Metopolophium dirhodum* have, in an olfactory organ (the primary rhinarium) on the sixth antennal segment, a specific olfactory neuron for methyl salicylate (Pettersson et al. 1994). This compound, as predicted, is associated with avoidance of cereal crops treated with a slow-release formulation of the material. Thus, in spring field trials, methyl salicylate applied to wheat significantly reduced (by 30-40%) the overall number of aphids colonizing the crop (Pettersson et al. 1994). Methyl salicylate is biosynthetically related to salicylic acid, a signal of systemically acquired resistance (Lucas 1999). This may indicate that the plant is upregulating defence pathways associated with hormonal activity of salicylate and could thereby present difficulties for colonization by herbivores. However, in these trials, the effect was short-lived and the formulation needed to continue to release to provide ongoing field activity.

INDUCTION OF PLANT DEFENCE BY METHYLATED PLANT HORMONES

In addition to direct effects on herbivores, methyl salicylate has been shown, when applied aerially to plants, to induce defence against fungal pathogens (Shulaev et al. 1997). However, a great deal of attention has been directed towards the jasmonate pathway (Figure 1), which is part of the lipoxygenase pathway referred to above. Again, jasmonic acid can act internally as a plant hormone associated with a damage/stress response but, when methylated (i.e., methyl jasmonate, Figure 1), can be released by the plant and, whether naturally or not, will certainly have an effect on intact plants by upregulating defence-related and other genes (Farmer and Ryan 1990; Doughty et al. 1995; Karban et al. 2000; Preston et al. 2002). Unfortunately, a large number of genes are influenced and this can have a deleterious effect on plant development and yields for agricultural crops. Although methylation converts plant hormones such as salicylate and jasmonate to volatile compounds with potential for external signalling, there are other possible mechanisms. From the jasmonate pathway, such an alternative was discovered initially by looking at the chemical ecology of host alternation in aphids.

SEEING *CIS*-JASMONE IN A NEW WAY

When we were studying the host alternation semiochemistry of the lettuce aphid, *Nasonovia ribis-nigri*, we found, as predicted from the above hypothesis, that the spring migrants were repelled by their winter hosts (members of the Saxifragiaceae, e.g., the blackcurrant, *Ribes nigrum*) and that these semiochemicals could act as repellents for such migrants searching for the summer host, lettuce, *Lactuca sativa* (Asteraceae). However, the mixture of semiochemicals contained *cis*-jasmone, which is also involved in the jasmonate pathway (Figure 1). It has been suggested that *cis*-jasmone is a metabolic product of jasmonate and represents a sink for this pathway (Koch et al. 1997), but the behavioural response from *N. ribis-nigri* was very pronounced with this compound alone. A specific olfactory neuron was identified which responded exclusively to *cis*-jasmone, with virtually no response from methyl jasmonate at orders of magnitude greater stimulus concentrations, even though *cis*-jasmone and methyl jasmonate have a close structural resemblance (Figure 1) (Birkett et al. 2000). *cis*-Jasmone was also found to be a repellent for the damson-hop aphid *Phorodon humuli*, taxonomically very different in terms of having a *Prunus* species (Rosaceae) as its primary host and, as a secondary host, the hop *Humulus lupulus* (Cannabiaceae). It was also found that *cis*-jasmone increased attraction and searching behaviour by an aphid predator, the seven-spot ladybird, *Coccinella septempunctata*.

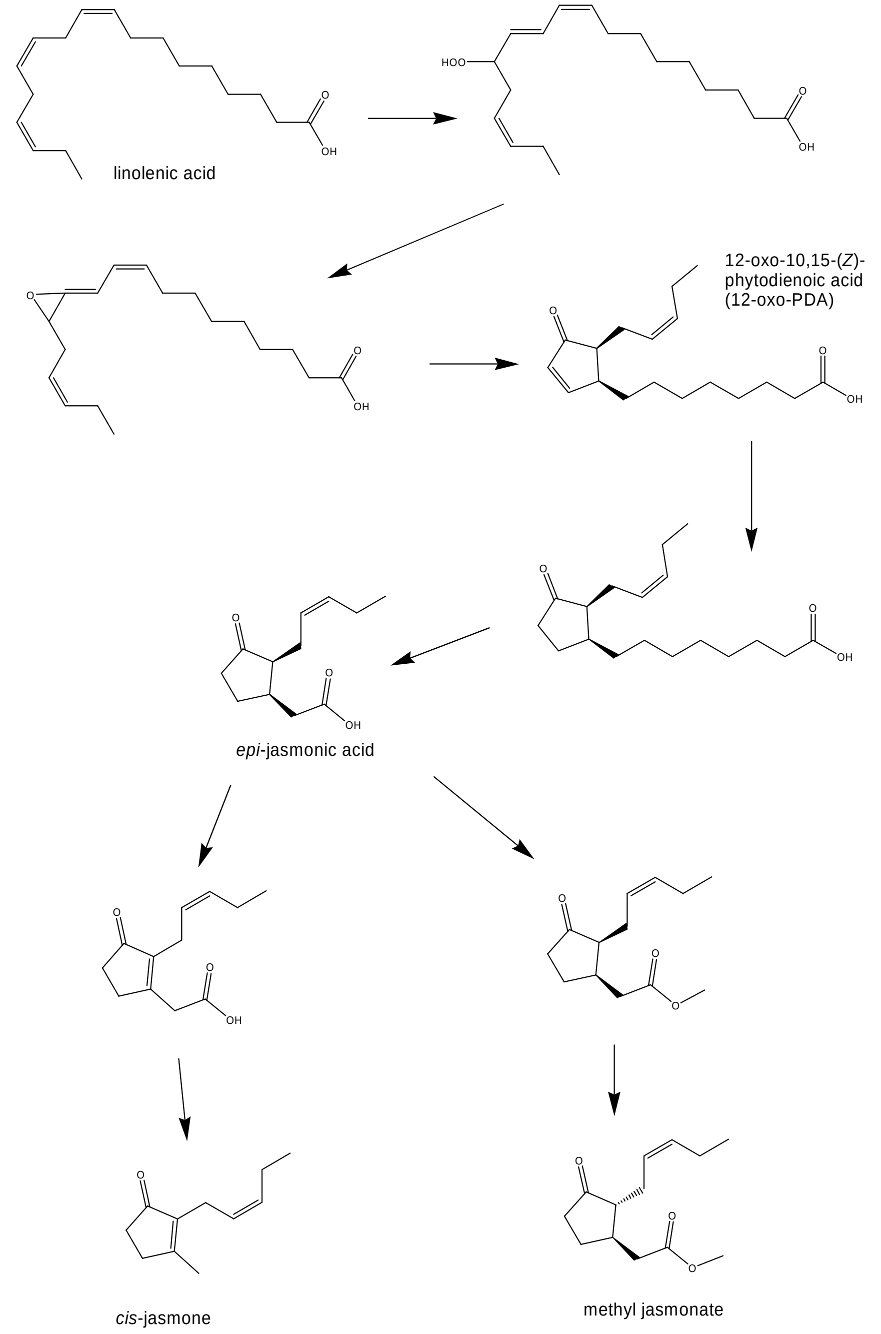


Figure 1. *Biosynthesis of methyl jasmonate and putative route to cis-jasmone*

INDUCTION OF DEFENCE BY *CIS*-JASMONE

Because of *cis*-jasmone's relationship with the jasmonate pathway, we decided to investigate whether aerial application of *cis*-jasmone could influence the defence of intact plants. This was achieved by placing low levels of *cis*-jasmone over bean plants contained in bell jars. The plants were tested for residual *cis*-jasmone, which was found to be completely absent after 24h. After a total of 48 h, these and control plants were placed in a wind tunnel and the effect on an aphid parasitoid, *Aphidius ervi*, was investigated. In both dual- and single-choice experiments, there were, respectively, threefold and twofold increases in oriented flight towards the *cis*-jasmone-treated plants, with both results being highly significant statistically (Birkett et al. 2000). One of the compounds showing induced release as a consequence of the *cis*-jasmone treatment was (*E*)-ocimene, which is known to be partly responsible for the response by *A. ervi* (Du et al. 1998). Although this compound was also induced by methyl jasmonate, the effect was short-lived and had disappeared 48 h after the initial treatment. However, the effect with *cis*-jasmone remained for 8 days (Birkett et al. 2000).

CIS-JASMONE AS AN ACTIVATOR OF GENE EXPRESSION

Bean plants treated with *cis*-jasmone, and also with methyl jasmonate as a positive control, were investigated by differential gene display. However, it was not possible to find genes for expressing the semiochemicals induced during the *cis*-jasmone treatment (Birkett et al. 2000). For example, the gene for (*E*)-ocimene synthase could not be located. It was therefore decided to change plants and to use the model plant *Arabidopsis thaliana*, for which there is full genomic sequence information and associated microarrays. Such microarrays were analysed (Matthes et al. 2003) by treatment with *cis*-jasmone and methyl jasmonate. A number of genes were found to be upregulated and this was confirmed by Northern blotting and other studies (Matthes et al. 2003). Currently, we are trying to use *A. thaliana* knockout mutants, over-expression in *A. thaliana* and heterologous expression in other systems to study, more easily, the biochemistry of gene products where the genes appear to be coding for enzymes that could be involved in defence or the persistent effect of *cis*-jasmone. For example, there are a number of cytochromes P450 and isoprenoid genes. In addition, there are genes that may be associated with the biosynthesis of *cis*-jasmone, and these include *OPR1* (Schaller et al. 2000; Schaller 2001) and a thiamine-diphosphate cofactor synthase gene (Vander Horn et al. 1993). It has also been possible to isolate the promoter sequence from some of these genes and to fuse this to the reporter luciferase, so that, when the plants are treated with *cis*-jasmone, this enzyme is produced and, on adding luciferin, the plants emit light. A considerable amount of work still needs to be done until we know how *cis*-jasmone is recognized by the plant and which genes are responsible for the long-term defence that we have found.

PRACTICAL USE OF *CIS*-JASMONE

Whilst we continue to investigate the molecular basis of *cis*-jasmone plant activation as a means of providing transgenic delivery of these types of crop protection approaches (Pickett and Poppy 2001), we have been looking at elite cereal cultivars for high levels of activation with *cis*-jasmone. A target for increased production is 6-methyl-5-hepten-2-one, one of a number of compounds (Quiroz et al. 1997) produced when *R. padi* attacks cereals and which causes repulsion of this aphid from normally attractive wheat seedlings. We also know that 6-methyl-5-hepten-2-one is an important foraging cue for the aphid parasitoid *A. ervi* (Du et al. 1998). The biosynthesis of 6-methyl-5-hepten-2-one has been reported (Demyttenaere and De Pooter 1996) as an oxidation product of isoprenoids by microbes. However, we have found that, in certain elite wheat cultivars, there is an upregulation of this compound with *cis*-jasmone. We also found that, as a consequence of this and other effects, there is repellency for the cereal aphid *S. avenae* in the olfactometer when the wheat cultivar has been treated with *cis*-jasmone (Bruce et al. 2003b). This has been followed through in the field where, in three seasons out of four, we have had statistically reduced levels of cereal aphids on winter wheat one month after *cis*-jasmone, as an emusifiable concentrate, was applied (Bruce et al. 2003b). Although we have been unable to do similar work on aphid parasitoids in the field, because of climatic problems, we have shown, in simulated field trials on wheat seedlings treated with *cis*-jasmone, that there is a statistically significantly increase in foraging by *A. ervi* (Bruce et al. 2003a).

SIGNALLING BY INTACT PLANTS

When barley plants are placed alongside certain weeds such as thistles (*Cirsium* spp.) in a convection-driven wind tunnel, they can become less attractive to aphids (Glinwood et al. 2004). Furthermore, it was shown that, if different cultivars of barley are similarly used as the ‘inducing’ and ‘recipient’ plants in such an experiment, then there can also be a reduction in aphid settling (Pettersson et al. 1999). Thus, when the cultivar Hulda was exposed to volatiles from another cultivar, Frida, the number of aphids settling was reduced by over 50%. Field trials showed a reduction of aphids on barley plants when intercropped with the appropriate ‘inducing’ cultivar. For example, there was a significant reduction of aphids on the cultivar Kara when it was grown in admixture in the field with the cultivars Frida and Alva (Ninkovic et al. 2002).

THE STIMULO-DETERRENT DIVERSIONARY STRATEGY, OR ‘PUSH-PULL’ STRATEGY

Although delivery of semiochemicals by plants, whether induced or not, provides a means of economically viable delivery, particularly for unstable or highly volatile compounds, the effects may not be sufficient to reduce the pest problem below the economic threshold (Chamberlain et al. 2001; Pickett et al. 2003). In an attempt to avoid rapid development of resistance to semiochemical control strategies, we and other groups put together a number of semiochemically based control methods into a stimulo-deterrent diversionary or ‘push-pull’ strategy (Miller and Cowles 1990; Smart et al. 1994; Pickett et al. 1997). This involves creating a ‘push’ effect from the main crop, using less attractive crop cultivars, repellents such as non-host volatiles, oviposition deterrent pheromones, or plant-derived antifeedants (see Figure 2).

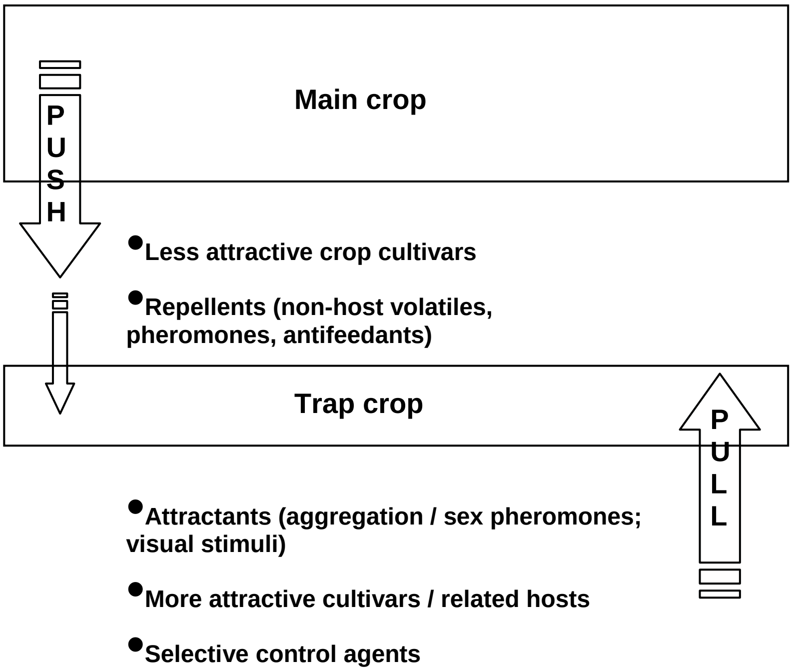


Figure 2. *The general principles of a ‘push-pull’ crop protection system*

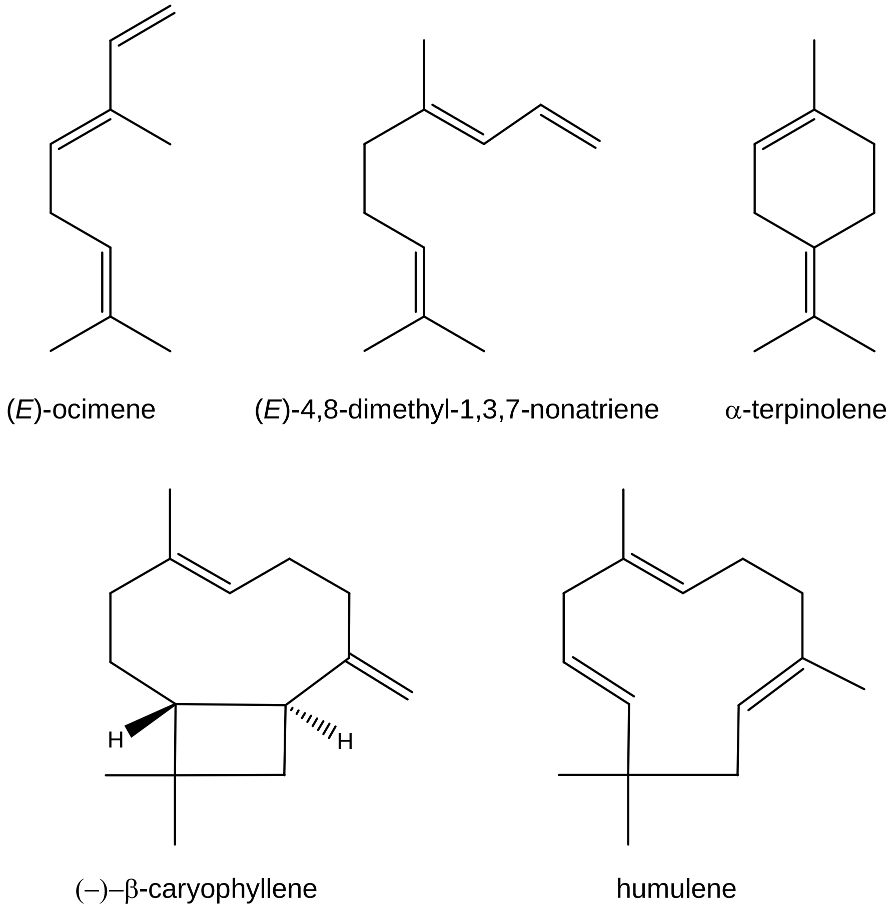
This system also requires a trap crop (‘pull’) to which the pests are attracted by aggregation or sex pheromones, visual stimuli, or more attractive cultivars/related hosts. On the trap crop can also be deployed a highly selective control agent. Economics do not usually allow the use of biological control agents in broad-acre crops, but application to a limited area of trap crop, particularly one in which the best conditions for infectivity with the biological agent can be established, will make the process economically feasible. Into this system also comes the potential to exploit beneficial organisms such as predators and parasitoids of the pests and so, as part of the ‘push’ strategy, there is also an involvement of foraging cues to ensure that the main crop is visited by predators and parasitoids before the pest population builds up. We have attempted to do this in the U.K. on oilseed rape, initially using a trap crop comprising turnip rape, which produces both visual cues and volatile semiochemical attractants (Cook et al. 2004). Eventually, we hope to ‘switch on’ the effects of ‘push’ and ‘pull’ by means of plant activators such as *cis*-jasmone, described above.

PRACTICAL DEVELOPMENT OF A ‘PUSH-PULL’ AGAINST STEM-BORER MOTHS IN AFRICA

Working in collaboration with the International Centre of Insect Physiology and Ecology in Nairobi and its field station at Mbita Point, and with other agencies in Africa, including the Kenyan Agricultural Research Institute, we have helped to develop a system for controlling stem-borer moths, particularly in maize (Khan et al. 2000). Initially, alternative grass hosts were investigated by establishing a triplicated plot nursery at the field station at Mbita Point. The African colleagues made close observations of which grasses were favoured by the stem borers for oviposition and those which were not chosen. The main target pests were an indigenous noctuid, *Busseola fusca*, the maize stalk borer, and an introduced crambid, *Chilo partellus*, the spotted stalk borer. It was found that two forage grasses, Napier grass, *Pennisetum purpureum*, and Sudan grass, *Sorghum sudanensis*, were preferred to maize for oviposition by stem borers, and these plants were subsequently used as trap crops (the ‘pull’ effect) in field trials. Highly significant reductions of stem-borer numbers in maize were found when 50 m plots were surrounded by two or three rows of these trap crops and, in on-farm trials, yield increases of 1 to 1.5 tonnes per hectare were obtained (Khan et al. 2000). There was also a highly significant increase in oviposition in the trap crop as compared to the maize. In addition, Napier grass showed a low survival of the ensuing larvae, and it was found that a sticky secretion, produced within the stems by the presence of late larval instars, inundated the larvae and prevented their further development. Since the trap crop might be competitive with the maize, a gap was created between the trap crop and the main crop and, overall, there was a reduced area of the amount of maize produced. Therefore, any increase in yield as a consequence of stem-borer control needed to be set against control plots in which maize occupied the whole site.

Initially, the ‘push’ effect was created by one of the plants that was found not to be used for oviposition by stem borers, the molasses grass, *Melinis minutiflora*, also grown as a forage crop for cattle. This, planted between each row of maize, caused a dramatic reduction in stem borers (Khan et al. 2000), with a decrease in numbers of over 80%. Indeed, there was a highly significant reduction in stem borers at the more practically useful ratio of one row of *M. minutiflora* to three or four of maize. A statistically significant effect could still be seen at a ratio of one row in twenty rows of maize.

Using GC-EAG, we found key physiologically active compounds from the trap crops that were responsible for their high attractiveness to gravid stem-borer moths (Khan et al. 2000). We then turned to *M. minutiflora*, our hypothesis being that, as a non-host for these insects, there would be additional physiologically active compounds acting as repellents. This was indeed the case, and subsequent behavioural studies showed that the active compounds found specifically in *M. minutiflora*, but not in the trap-crop plants, comprised (*E*)-ocimene, (*E*)-4,8-dimethyl-1,3,7-nonatriene, (-)-β-caryophyllene, humulene and α-terpinolene (Figure 3). On noting the presence of the first two compounds, we realized that *M. minutiflora* is treated as a non-host because it produces chemicals that would be emitted by a highly infested maize plant. We subsequently showed that this phenomenon was responsible for the increased foraging by parasitoids of the stem borers (Khan et al. 1997). For example, in the Y-tube olfactometer, the parasitoid *Cotesia sesamiae* responded to the nonatriene at a similar level to that found in the live plant and in an extract of the plant. Indeed, in two of the trial areas, one near Mbita Point in Nyanza Province, Suba District, and the other in the high maize-yielding area near Kitale in Trans Nzoia, use of one row of *M. minutiflora* to three rows of maize gave highly significant increases in foraging by stem-borer parasitoids.



(*E*)-ocimene (*E*)-4,8-dimethyl-1,3,7-nonatriene α-terpinolene

(−)–β-caryophyllene humulene

Figure 3. *Electrophysiologically active compounds identified in Melinis minutiflora volatiles*

AFRICAN STEM BORER 'PUSH-PULL' CONTROL – THE WAY FORWARD

We would like to review the prospect of using biotechnological approaches to maximizing and exploiting these effects on stem borers. We could contemplate transferring the systemic release of the nonatriene from *M. minutiflora* to maize itself. However, it must be remembered that maize under insect attack, as referred to above, already produces the nonatriene. What we really require is a maize plant that produces the nonatriene by induction more effectively. Often, the laying of eggs can induce defence (Blaakmeer et al. 1994; Hilker et al. 2002; Hilker and Meiners 2002), so if we could, even by conventional plant breeding, enhance the response of the plant to egg-laying in terms of nonatriene production, then this would give an early defence against colonization of maize by stem borers and may remove the need for the laborious intercropping approach. Nonetheless, it must be pointed out that, once the intercrop has been established, then the farmer only has to keep the plot free of extraneous and aggressive plant material and the system will largely look after itself. It will produce not only a higher maize yield, even taking into account the smaller area through the loss of land to the trap crop, but will also have added value in terms of the cattle forage provided by both the trap crop and the intercrop (Khan and Pickett 2004). Indeed, involvement with farmers, particularly at Farmers' Days (barazas), has introduced a number of ideas and an alternative for the term 'push-pull', which in Kiswahili is reversed to 'pull-push', or 'vuta sukuma'.

We have had requests that we should use, as an intercrop, a legume rather than a grass. The farmers would very much like to grow edible legumes. We have, as yet, been unable to find an edible legume that has the effect of attracting stem-borer parasitoids. Nonetheless, a series of forage legumes in the *Desmodium* genus such as silverleaf desmodium, *D. uncinatum*, do repel stem borers when used in the intercropping system. However, during these trials, we noticed, with great surprise, that the desmodium was also controlling another extremely important pest in sub-Saharan subsistence agriculture, the African witchweed, *Striga hermonthica* (Scrophulariaceae) (Matúšová and Bouwmeester in press). The pernicious striga weed develops underground as a parasite on the maize roots and then appears above the surface, where it begins to photosynthesize and produces beautiful purple flowers, setting seed which will remain viable in the soil for up to 20 years.

Striga has received a considerable amount of attention, but most of the really effective solutions involve more expensive technology than is normally available to subsistence farmers in these circumstances. However, with the *Desmodium* intercrop, there is a tremendous impact on striga development. We have subsequently shown that this is through a suicidal germination mechanism in which allelopathic chemicals are produced by the desmodium roots, some causing a dramatic germination of striga seeds, but others preventing the development of the subterranean phase of the parasite and thereby inhibiting colonization of the maize plant (Khan et al. 2002; Tsanuo et al. 2003). There has been a rapid take-up of this approach by farmers, and we have used various media instruments for promoting this, including pamphlets and a regular radio programme. The farmers themselves have transferred the technology at Farmers' Days and also, in one district, Vihiga, by putting on an extremely innovative show about the whole 'push-pull' system. There are now 15 regions using the 'push-pull' approach, involving over 4,000 farmers in many of the regions around the Victoria Lake basin, originally starting in Kenya but now including Uganda and Tanzania (Khan and Pickett 2004). When tested in comparative trials, this approach has proved to be more effective than use of pesticides, and substantially cheaper (Parrott 2005).

CONCLUSIONS

Thus, it can be seen that understanding the interactions of plants with insects can yield new ways of exploiting, at the practical level, plant defence. This may be delivered by application of natural plant activators or intercropping regimes and a 'push-pull' system. Basic science, and particularly understanding the chemical ecology of pest–plant interaction by combined analytical-chemical, neurophysiological and behavioural studies, can lead through to real practical developments.

ACKNOWLEDGEMENTS

Rothamsted Research receives grant-aided support from the Biotechnology and Biological Sciences Research Council (BBSRC), UK, with additional funding provided under the Biological Interactions in the Root Environment (BIRE) initiative. Field studies in Africa are funded by the Gatsby Charitable Foundation and the Rockefeller Foundation. This work was in part supported by the Department for Environment, Food and Rural Affairs (Defra), UK.

REFERENCES

Aharoni, A., Giri, A.P., Deuerlein, S., et al., 2003. Terpenoid metabolism in wild-type and transgenic *Arabidopsis* plants. *Plant Cell,* 15 (12), 2866-2884.

Beale, M.H., Birkett, M.A., Bruce, T.J.A., et al., in prep. Aphid alarm pheromone from transgenic plants affects aphids and their parasitoids.

Birkett, M.A., Campbell, C.A.M., Chamberlain, K., et al., 2000. New roles for *cis*-jasmone as an insect semiochemical and in plant defense. *Proceedings of the National Academy of Sciences of the United States of America,* 97 (16), 9329-9334.

Blaakmeer, A., Hagenbeek, D., Van Beek, T.A., et al., 1994. Plant response to eggs vs. host marking pheromone as factors inhibiting oviposition by *Pieris brassicae*. *Journal of Chemical Ecology,* 20 (7), 1657-1665.

Bruce, T.J., Pickett, J.A. and Smart, L.E., 2003a. *cis*-Jasmone switches on plant defence against insects. *Pesticide Outlook,* 14 (3), 96-98.

Bruce, T.J.A., Martin, J.L., Pickett, J.A., et al., 2003b. *cis*-Jasmone treatment induces resistance in wheat plants against the grain aphid, *Sitobion avenae* (Fabricius) (Homoptera: Aphididae). *Pest Management Science,* 59 (9), 1031-1036.

Bruce, T.J.A., Wadhams, L.J. and Woodcock, C.M., 2005. Insect host location: a volatile situation. *Trends in Plant Science,* 10 (6), 269-274.

Chamberlain, K., Guerrieri, E., Pennacchio, F., et al., 2001. Can aphid-induced plant signals be transmitted aerially and through the rhizosphere? *Biochemical Systematics and Ecology,* 29 (10), 1063-1074.

Cook, S.M., Watts, N.P., Hunter, F., et al., 2004. Effects of a turnip rape trap crop on the spatial distribution of *Meligethes aeneus* and *Ceutorhynchus assimilis* in oilseed rape. *IOBC/WPRS Bulletin,* 27 (10), 199-206.

Demyttenaere, J.C.R. and De Pooter, H.L., 1996. Biotransformation of geraniol and nerol by spores of *Penicillium italicum*. *Phytochemistry Oxford,* 41 (4), 1079-1082.

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

Doughty, K.J., Kiddle, G.A., Pye, B.J., et al., 1995. Selective induction of glucosinolates in oilseed rape leaves by methyl jasmonate. *Phytochemistry,* 38 (2), 347-350.

Du, Y.J., Poppy, G.M., Powell, W., et al., 1998. Identification of semiochemicals released during aphid feeding that attract parasitoid *Aphidius ervi*. *Journal of Chemical Ecology,* 24 (8), 1355-1368.

Farmer, E.E. and Ryan, C.A., 1990. Interplant communication airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves. *Proceedings of the National Academy of Sciences of the United States of America,* 87 (19), 7713-7716.

Glinwood, R., Ninkovic, V., Pettersson, J., et al., 2004. Barley exposed to aerial allelopathy from thistles (*Cirsium* spp.) becomes less acceptable to aphids. *Ecological Entomology,* 29 (2), 188-195.

Hardie, J., Isaacs, R., Pickett, J.A., et al., 1994. Methyl salicylate and (-)-(1*R*,5*S*)-myrtenal are plant-derived repellents for black bean aphid, *Aphis fabae* Scop. (Homoptera: Aphididae). *Journal of Chemical Ecology,* 20 (11), 2847-2855.

Hilker, M. and Meiners, T., 2002. Induction of plant responses to oviposition and feeding by herbivorous arthropods: a comparison. *Entomologia Experimentalis et Applicata,* 104 (1), 181-192.

Hilker, M., Rohfritsch, O. and Meiners, T., 2002. The plant´s response towards insect egg depostion. *In:* Hilker, M. and Meiners, T. eds. *Chemoecology of insect eggs and egg deposition*. Blackwell Publishers, Berlin, 205-233.

Karban, R., Baldwin, I.T., Baxter, K.J., et al., 2000. Communication between plants: induced resistance in wild tobacco plants following clipping of neighboring sagebrush. *Oecologia,* 125 (1), 66-71.

Khan, Z.R., Ampong-Nyarko, K., Chiliswa, P., et al., 1997. Intercropping increases parasitism of pests. *Nature,* 388 (6643), 631-632.

Khan, Z.R., Hassanali, A., Overholt, W., et al., 2002. Control of witchweed *Striga hermonthica* by intercropping with *Desmodium* spp., and the mechanism defined as allelopathic. *Journal of Chemical Ecology,* 28 (9), 1871-1885.

Khan, Z.R. and Pickett, J.A., 2004. The 'push-pull' strategy for stemborer management: a case study in exploiting biodiversity and chemical ecology. *In:* Gurr, G.M., Wratten, S.D. and Altieri, M.A. eds. *Ecological engineering for pest management: advances in habitat manipulation for arthropods*. CSIRO, Collingwood, 155-164.

Khan, Z.R., Pickett, J.A., Van den Berg, J., et al., 2000. Exploiting chemical ecology and species diversity: stem borer and striga control for maize and sorghum in Africa. *Pest Management Science,* 56 (11), 957-962.

Koch, T., Bandemer, K. and Boland, W., 1997. Biosynthesis of *cis*-jasmone: a pathway for the inactivation and the disposal of the plant stress hormone jasmonic acid to the gas phase? *Helvetica Chimica Acta,* 80 (3), 838-850.

Lucas, J.A., 1999. Plant immunisation: from myth to SAR. *Pesticide Science,* 55 (2), 193-196.

Matthes, M., Napier, J.A., Pickett, J.A., et al., 2003. New chemical signals in plant protection against herbivores and weeds. *In: The BCPC international congress Crop science & technology, Glasgow, 10-12 November 2003*. British Crop Protection Council, Alton, 1227-1236.

Matúšová, R. and Bouwmeester, H.J., in press. The effect of host-root-derived chemical signals on the germination of parasitic plants. *In:* Dicke, M. and Takken, W. eds. *Chemical ecology: from gene to ecosystem.* Springer, Dordrecht. Wageningen UR Frontis Series no. 16. [http://library.wur.nl/frontis/chemical_ecology/04_matusova.pdf]

Miller, J.R. and Cowles, R.S., 1990. Stimulo-deterrent diversion: a concept and its possible application to onion maggot control. *Journal of Chemical Ecology,* 16 (11), 3197-3212.

Ninkovic, V., Olsson, U. and Pettersson, J., 2002. Mixing barley cultivars affects aphid host plant acceptance in field experiments. *Entomologia Experimentalis et Applicata,* 102 (2), 177-182.

Nordlund, D.A. and Lewis, W.J., 1976. Terminology of chemical releasing stimuli in intraspecific and interspecific interactions. *Journal of Chemical Ecology,* 2 (2), 211-220.

Parrott, S., 2005. *The quiet revolution: push-pull technology and the African farmer*. Gatsby Charitable Foundation, London. Gatsby Occasional Paper.

Pettersson, J., Ninkovic, V. and Ahmed, E., 1999. Volatiles from different barley cultivars affect aphid acceptance of neighbouring plants. *Acta Agriculturae Scandinavica. Section B. Soil and Plant Science,* 49 (3), 152-157.

Pettersson, J., Pickett, J.A., Pye, B.J., et al., 1994. Winter host component reduces colonization by bird-cherry-oat aphid, *Rhopalosiphum padi* (L.) (Homoptera, Aphididae), an other aphids in cereal fields. *Journal of Chemical Ecology,* 20 (10), 2565-2574.

Pickett, J.A. and Poppy, G.M., 2001. Switching on plant genes by external chemical signals. *Trends in Plant Science,* 6 (4), 137-139.

Pickett, J.A., Rasmussen, H.B., Woodcock, C.M., et al., 2003. Plant stress signalling: understanding and exploiting plant-plant interactions. *Biochemical Society Transactions,* 31 (1), 123-127.

Pickett, J.A., Wadhams, L.J. and Woodcock, C.M., 1997. Developing sustainable pest control from chemical ecology. *Agriculture, Ecosystems and Environment,* 64 (2), 149-156.

Pickett, J.A., Wadhams, L.J., Woodcock, C.M., et al., 1992. The chemical ecology of aphids. *Annual Review of Entomology,* 37, 67-90.

Preston, C.A., Betts, H. and Baldwin, I.T., 2002. Methyl jasmonate as an allelopathic agent: sagebrush inhibits germination of a neighboring tobacco, *Nicotiana attenuata*. *Journal of Chemical Ecology,* 28 (11), 2343-2369.

Quiroz, A., Pettersson, J., Pickett, J.A., et al., 1997. Semiochemicals mediating spacing behavior of bird cherry-oat aphid, *Rhopalosiphum padi* feeding on cereals. *Journal of Chemical Ecology,* 23 (11), 2599-2607.

Schaller, F., 2001. Enzymes of the biosynthesis of octadecanoid-derived signalling molecules. *Journal of Experimental Botany,* 52 (354), 11-23.

Schaller, F., Biesgen, C., Müssig, C., et al., 2000. 12-Oxophytodienoate reductase 3 (OPR3) is the isoenzyme involved in jasmonate biosynthesis. *Planta,* 210 (6), 979-984.

Shulaev, V., Silverman, P. and Raskin, I., 1997. Airborne signalling by methyl salicylate in plant pathogen resistance. *Nature,* 385 (6618), 718-721.

Smart, L.E., Blight, M.M., Pickett, J.A., et al., 1994. Development of field strategies incorporating semiochemicals for the control of the pea and bean weevil, *Sitona lineatus* L. *Crop Protection,* 13 (2), 127-135.

Tsanuo, M.K., Hassanali, A., Hooper, A.M., et al., 2003. Isoflavanones from the allelopathic aqueous root exudate of *Desmodium uncinatum*. *Phytochemistry,* 64 (1), 265-273.

Vander Horn, P.B., Backstrom, A.D., Stewart, V., et al., 1993. Structural genes for thiamine biosynthetic enzymes (thiCEFGH) in *Escherichia coli* K-12. *Journal of Bacteriology,* 175 (4), 982-992.