CIS-JASMONE SWITCHES ON PLANT DEFENCE AGAINST INSECTS

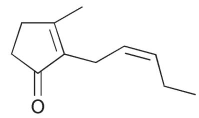
Toby Bruce, John Pickett and Lesley Smart from Rothamsted Research at Harpenden in the UK describe a volatile plant activator which could have an important part to play in plant defence mechanisms

Introduction

Plants have evolved a variety of mechanisms to withstand the damage and stresses caused by pathogens and herbivorous animals, as well as by many abiotic factors. One such mechanism involves the emission of volatile compounds, either constitutively or as a result of biotic infestation or physical damage, which can affect pathogen development and the behaviour of insect herbivores searching for a food source. A recent review by Agrawal and Karban (1999) compares the benefits to the plant of constitutive gene expression and induced defence strategies. Constitutively produced plant volatiles play a role in attracting pollinators and seed-dispersing animals; in addition, they can repel a wide range of potential herbivores and attract a smaller number of pest species that have evolved to take advantage of these chemicals in finding food. Plant volatiles that are induced on damage to repel insect attack also can act as an indirect plant defence mechanism by attracting other insects that prey on or parasitise the herbivores (Turlings *et al.,* 1990). Such compounds may also act as signals between plants, whereby defence mechanisms are induced in undamaged plants in response to volatiles produced by neighbouring infested plants, and specific volatiles, methyl salicylate and methyl jasmonate, have been implicated. Compounds containing six carbon atoms, *e.g.*, (*E*)-2-hexenal, which are rapidly emitted from damaged or wounded plant tissue, also have recently been shown to induce the expression of defence-related genes in intact plants (Bate and Rothstein, 1998).

The investigation of insect interactions with plant volatiles is now greatly facilitated by using sophisticated electrophysiological techniques, in particular gas chromatography (GC) coupled directly to neuronal or single-cell recording (SCR) from the olfactory organs of insects. Methyl salicylate, which was found to repel aphids such as the black bean aphid, *Aphis fabae*, and cereal aphids including the grain aphid, *Sitobion avenae*, and also to inhibit attraction to their host plants (Hardie *et al.,* 1994; Pettersson *et al.*, 1994), originally was discovered to be an aphid signal by SCR on the antenna of the bird-cherry-oat aphid, *Rhopalosiphum padi* (Pettersson *et al.,* 1994). More than 30 species of insects, both plant feeders and their natural enemies, from five orders subsequently have been found, by SCR and by recording from the whole antenna (electroantennography, or EAG), to possess olfactory receptors for this compound. Although it was originally investigated as a component of winter host volatiles that repelled the summer morph of *R. padi*, it has since been discovered to cause changes in the metabolism of treated plants such as production of chitinase (Forslund *et al.,* 2000). There are other volatiles that can induce plant defence mechanisms, for example, application of jasmonic acid to tomatoes in the field increased their resistance to a number of phytophagous insects (Thaler *et al.*, 1996). It appears that volatile plant activators could provide a means of switching on natural plant defence metabolism prior to pest attack.

cis-Jasmone



One such volatile plant activator involved with plant resistance to insects is *cis*-jasmone, or (*Z*)-jasmone. Its activity was first discovered at Rothamsted when components of blackcurrant volatiles that repelled the summer form of lettuce aphid, *Nasonovia ribis-nigri*, were being identified. Since then *cis*-jasmone has been found to have more intricate effects on interactions between pest insects and crop plants. *cis*-Jasmone occurs naturally as a component of flower volatiles, but can also be produced by damaged plant vegetative tissues (Loughrin *et al.*, 1995). It is a catabolite of the stress produced jasmonic acid, but had previously been considered as only a biological sink for the jasmonate pathway (Koch *et al.*, 1997). However, there is now evidence that *cis*-jasmone has a role in plant defence (Birkett *et al.*, 2000). It is also possible that *cis*-jasmone acts as an external signal, alerting recipient plants when their neighbours are being damaged by phytophagous insects and thereby enabling them to prepare their own defences prior to insect attack (Chamberlain *et al.*, 2000, Pickett & Poppy 2001). The practical use of *cis*-jasmone has initially focussed on the interaction between the grain aphid *S. avenae* and wheat, *Triticum aestivum*. Wheat plants sprayed with low levels of *cis*-jasmone as an aqueous emulsion are less attractive to aphids but more attractive to their parasitoids in laboratory bioassays. In the field, similarly treated plants have lower aphid infestations.

Behavioural studies

A number of laboratory bioassays showed the effects of *cis*-jasmone on the behaviour of *S. avenae* (Bruce *et al.*, 2003). Using an olfactometer, an arena in which movement of

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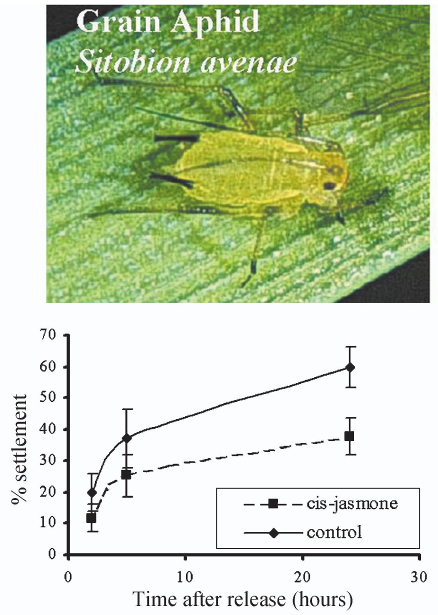

Figure 1 **Settlement of *S. avenae* in simulator bioassay**

insects can be recorded, with a gentle airstream directed towards the centre from each of 4 side arms, *cis*-jasmone was directly repellent to walking *S. avenae*. Aphids spent significantly shorter periods of time in the olfactometer arm with the cis-jasmone and made fewer entries into it.

Interestingly, the aphid's behavioural response to wheat was altered if the plant itself was treated with *cis*-jasmone. In laboratory and field trials wheat plants were sprayed using a hydraulic nozzle (Lurmark 015-F110) at 1 ms^{-1}. The *cis*-jasmone was formulated in a 0.1% aqueous solution of a non-ionic surfactant Ethylan BV (EBV) (Akcros Chemicals, Manchester, U.K.) and applied at a rate equivalent to 50 g ha^{-1} in 200 l ha^{-1}. Wheat seedlings treated with *cis*-jasmone and control seedlings sprayed with 0.1% aqueous EBV were tested under no-choice conditions on alternate days in a

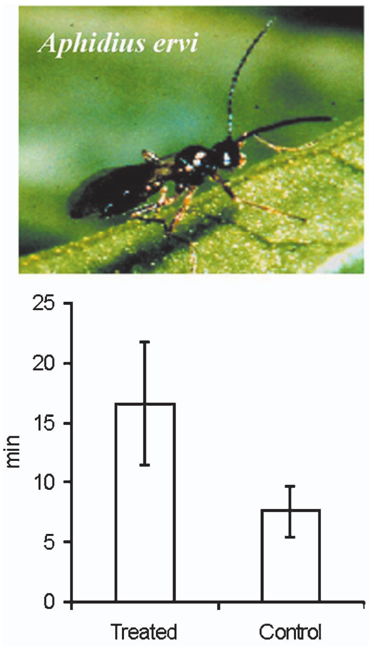

Figure 2 **Time spent foraging by *Aphidius ervi* on *cis*-jasmone and control wheat seedlings.**

Figure 3 **Field application of *cis*-jasmone**

Perspex simulator (90 × 30 × 30 cm, wind speed 0.8 ms^{-1}, 22°C, 40% R.H.). A tray of 50 wheat seedlings was positioned at the upwind end and 250 alate *S. avenae* were released at the downwind end. Numbers of aphids settled on *cis*-jasmone treated and control plants were compared. As shown in Figure 1 significantly fewer grain aphids were on the *cis*-jasmone treated plants 24h after release.

The mean intrinsic rate of population increase (r_m) of *S. avenae*, as determined from the number of nymphs produced over a time period equivalent to the time taken from birth to the production of the first nymph (Wyatt and White, 1977), was significantly reduced on *cis*-jasmone treated wheat seedlings. This was observed both under glasshouse conditions at variable temperature and under constant temperature in a controlled environment room.

Furthermore effects on the behaviour of the aphid parasitoid, *Aphidius ervi*, were also evident in a foraging bioassay, which recorded the length of time spent performing various behaviours by individual parasitoids when released on a standard 3 × 3 array of either treated or untreated wheat seedlings. It was found that total time spent by *A. ervi* was significantly greater on *cis*-jasmone induced wheat seedlings (Figure 2).

Field trials

Field plots of wheat were sprayed hydraulically with *cis*-jasmone (Figure 3), at a rate equivalent to 50 g ha^{-1} in 200 l ha^{-1}, in mid May and early June in four consecutive seasons, and aphid counts were made at weekly intervals. It was consistently found that aphid infestations were reduced in *cis*-jasmone treated plots (Bruce *et al.*, 2003). Using ANOVA with contrasts to compare total aphid numbers in *cis*-jasmone and control plots there was a significant difference in 3 out of 4 years (Figure 4).

Future outlook

Worldwide, more than 40% of potential crop yield is lost directly or indirectly because of insect pests, but more than 540 of the world's most notorious insects are rapidly acquiring resistance to standard pesticides available. To compound the hazard, there are fewer effective pesticides

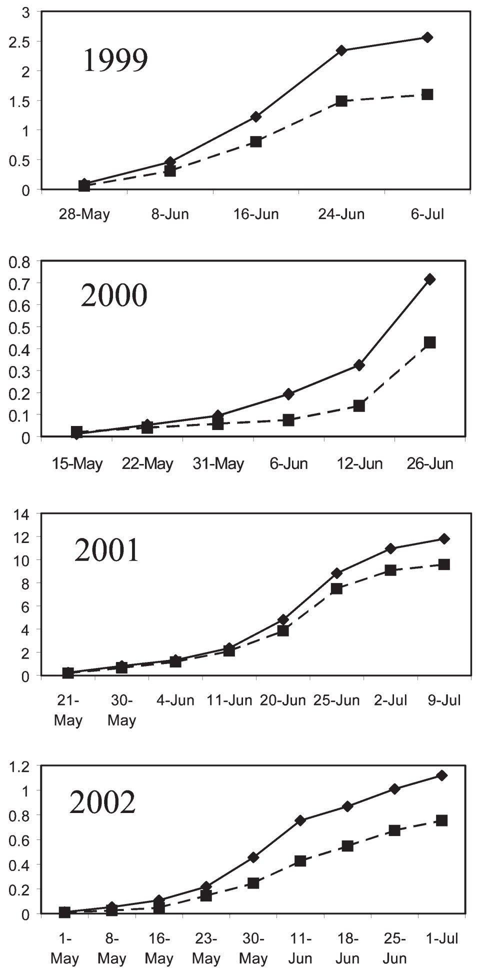

Figure 4 **Cumulative Cereal Aphid Counts in Field Plot Trials with *cis*-jasmone treatment 1999–2002 (control: ——: *cis*-jasmone: - - -)**

available. Twenty years ago, growers could choose from a range of 800 products. By 2003, because of recent EU regulations, there could be only 225 available. Just as human health is under threat from antibiotic resistance, so crop health is under threat from insecticide resistance. The pests are gaining ground and our defences are increasingly fragile. Many old pesticides, now disappearing from the armoury, are not vanishing because they are dangerous, but because manufacturers are required under EU legislation to re-register them. This means they have to spend 3 or 4 years assembling a 50,000 page safety dossier on a chemical already out of patent – with little promise of economic return. Of 190 compounds under review, 94 have been withdrawn, mostly for economic reasons. Meanwhile, insects are evolving strains resistant to an increasing range of pesticides.

These issues have led to the recent interest in the defensive systems developed by plants themselves. *cis*-Jasmone is being actively studied in this regard. It is a semiochemical that switches on the defences of completely undamaged wheat plants, inducing changes that make the plants less attractive to cereal aphids and able to slow the development and reduce the fertility of colonising populations. Treated plants are also more attractive to natural enemies of aphids. Thus, *cis*-jasmone has been shown to have a mode of action on plants, which involves alterations in crop metabolic pathways switching on traits making the plant less favourable to phytophagous insects, but more attractive to their predators and parasitoids. This opens up possibilities both to learn more about plant defence metabolism and to use *cis*-jasmone-based products as crop protection agents. The precise nature of the changes in plants induced by *cis*-jasmone is still under investigation and is likely to be multi-factorial. Preliminary tests have shown that some varieties of wheat are more responsive to *cis*-jasmone treatment than others and it is probable that these varieties are the ones that have more inducible resistance to insects. New formulations of *cis*-jasmone need to be tested as the twice per season hydraulic spray may not be the most efficacious treatment. Slow release formulations are being developed and it is hoped that even greater reductions in field aphid infestation levels can be obtained.

Further identification studies on plant activators are in progress and the molecular genetic mechanisms underpinning these effects are being studied by other colleagues at Rothamsted Research in programmes funded by both DEFRA and BBSRC.

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Professor John Pickett, FRS, is Head of the Biological Chemistry Division and has an international reputation in all aspects of Chemical Ecology, including the identification of semiochemicals for development of new methods of pest control. His team includes Drs *Toby Bruce* and *Lesley Smart*, entomologists with 7 and 17 years experience, respectively, in Chemical Ecology, and having expertise in laboratory behavioural assays, field simulation and field techniques to determine the effects of insect and plant-derived semiochemicals on pest and beneficial insects.