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Review

Developments in aspects of ecological phytochemistry: The role of *cis*-jasmone in inducible defence systems in plants

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Abstract

The challenges and opportunities for protecting agricultural production of food and other materials will be met through exploiting the induction of defence pathways in plants to control pests, diseases and weeds. These approaches will involve processes that can be activated by application of natural products, patented in terms of this use, to "switch on" defence pathways. Already, a number of secondary metabolite defence compounds are known for which the pathways are conveniently clustered genomically, e.g. the benzoxazinoids (hydroxamic acids) and the avenacins. For the former, it is shown that the small molecular weight lipophilic activator *cis*-jasmone can induce production of these compounds and certain genes within the pathway. Numerous groups around the world work on inducible defence systems. The science is rapidly expanding and involves studying the interacting components of defence pathways and the switching mechanisms activated by small molecular weight lipophilic compounds. Examples are described of how plant breeding can exploit these systems and how heterologous gene expression will eventually give rise to a new range of GM crops for food and energy, without the need for external application of synthetic pesticides.

Keywords: Secondary plant metabolites; Activators; Induction; Defence; Pest control; Benzoxazinoid; *cis*-Jasmone; Semiochemical

Contents

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1. Introduction

Developments in ecological phytochemistry will be driven by new pressures to exploit this area of science for food production and for bioenergy and liquid biofuels. There are undoubted costs for plants in producing secondary metabolites, but new work is questioning whether these costs would be a serious impediment to achieving high yields of nutritionally or energetically valuable primary metabolites, and also storage polysaccharides, lipids and proteins (Foyer et al., 2007). However, it is certain that, where secondary metabolites are to be exploited further in protection of crops against pests, diseases and weeds, then constitutive expression would be disadvantageous from considerations of adaptation and resistance. With the USA as one of the few countries capable of producing food above the levels required for self-sufficiency (FAO, 2006), and with its immediate plans for bioenergy and liquid biofuels, the world's rise in population will place demands on agriculture that must seriously impact on global food security. Simultaneously, there will be demands to reduce the carbon footprint for food production and transport, and to consider other aspects of environmental protection, maintenance or enhancement of species diversity and considerations of animal welfare and human health. This will mean that reliance on broad-spectrum eradicant synthetic pesticides will need to shift towards greater exploitation of naturally-occurring processes by which plants can resist damage by pests, pathogens and competition from other plants. Equally, the use of genetically modified (GM) organisms will inevitably extend to Europe. However, for the present, new molecular biological techniques must be developed for more dynamic and effective plant breeding programmes. These, combined with the kinds of phytochemical research described in this Special Issue, will give rise to new generations of GM crops with far more sophisticated approaches than are currently being exploited. Indeed, the virtual embargo on use of first generation GM crops in the EU could act as a stimulus for the development of new intellectual property for local exploitation, and also for commercial exploitation around the world.

2. Defence phytochemistry

2.1. Induction of semiochemical production

There are many types of compounds, both primary and secondary metabolites, that could be enhanced by breeding or by heterologous gene expression in crop plants to improve defence against pests, diseases and weeds. However, to satisfy concerns amongst the public and the food industry, it would be preferable to focus on regulatory processes that use expression of genes already found in the plant taxa involved, or at least in closely related species. To this end, many groups around the world have concentrated on signal chemicals (semiochemicals) (Pickett and Poppy, 2001) and the enhancement of biosynthetic pathways relative to those already present in crop plants. The main objective should be to use the plants themselves, or the application of plant activators, to cause expression of the defence genes based on warnings from sophisticated natural monitoring systems using long range detection of pest population build-up, for example, pheromone-based monitoring.

Knowledge of plant interactions with attacking organisms has advanced considerably in the last decade and, with this, it has been realised that plant natural defences are even more sophisticated and intricate than previously thought. Not only do plants adjust the jasmonic acid dependant and salicylic acid pathways in ways that are tailored to particular attackers, but they can also store information on the prior exposure to biotic stresses so that they are more resistant in the future, a phenomenon known as priming (Conrath et al., 2006; Kessler et al., 2006). In nature, plants have to defend themselves against multiple attackers and adjust defence responses so that these are appropriate to the particular suite of attacking organisms (Bruce and Pickett, 2007). Knowledge of the semiochemicals that insect pests employ to locate host plants has also advanced and it has become established that use of blends of host plant volatiles in specific ratios is the most widespread mechanism by which these insects detect host plants (Bruce et al., 2005).

Whether stress signalling occurs naturally between plants is still under debate. Certainly, when plants are damaged, small volatile lipophilic molecules, e.g. phytopheromones, can be released and if certain of these compounds are applied to plants via the air around them, they can cause those plants to repel pests, impede pathogen development or interfere with competing weeds. They can also attract antagonistic organisms such as the parasitic wasps attacking herbivorous pests. It is notoriously difficult to identify the phytopheromones that affect plants naturally, but insect olfaction is being used to try to identify compounds that might act on plants to induce defence. These compounds can be isolated from plants by various techniques. If they are volatile, they can be collected very simply by enveloping the plant in a positive pressure of air and drawing samples from that air through a porous polymer, which absorbs the compounds for elution and analysis by gas chromatography (GC). As well as analysing the effluent from GC by conventional chemical detectors, this can be linked to electrophysiological recordings from insect antennae, the main sensory organs of these organisms. Either by using the whole antenna (the electroantennogram, EAG) or recording from individual olfactory neurons (single cell recording, SCR), it can be determined which peaks eluting from the GC are of significance to the insect. Plants that are colonised by herbivores will produce additional electrophysiologically active peaks compared with intact plants. These are candidate repellents for herbivores and foraging stimulants for beneficial insects such as parasitic wasps, but are also potential signals as plant activators for switching on defence.

Many insects respond to methyl salicylate, which is related to the plant hormone salicylic acid (Lucas, 1999). Methyl salicylate is often produced during plant damage and this compound has been shown to control aphids on cereals in the field (Pettersson et al., 1994). It has also been used by other groups to increase defence against pathogens (Shulaev et al., 1997; Ryu et al., 2004). Another set of compounds produced on damage are sesquiterpene hydrocarbons such as (−)-germacrene D (Agelopoulos et al., 1999). Although the genes for this and its optical isomer, (+)-germacrene D, are available (Prosser et al., 2002), heterologous expression in the model plant *Arabidopsis thaliana* has not yet proved possible. However, recently, Beale et al. (2006) were successful in expressing, in *Arabidopsis*, the synthase gene for (*E*)-β-farnesene, which, in addition to being a plant stress-related compound, is also the aphid alarm pheromone. The (*E*)-β-farnesene thereby produced caused repulsion of the peach–potato aphid, *Myzus persicae*, and also increased foraging by the specialist parasitoid of aphids in cruciferous systems, *Diaeretiella rapae* (Beale et al., 2006).

Farmer and Ryan (1990) showed that another methyl ester of a plant hormone signal, jasmonic acid, was able to activate plant defence. This was not useful in agriculture, because methyl jasmonate affects so many genes that it can cause deleterious effects, as well as defence, in crop plants. However, whilst working on host-alternating behaviour of the blackcurrant-lettuce aphid, *Nasonovia ribis-nigri*, which colonises plants in the Asteraceae, e.g. lettuce (*Lactuca sativa*), as the summer host, but members of the Saxifragaceae, e.g. blackcurrant (*Ribes nigrum*), as the winter host, it was hypothesised that the winter host would act as a non-host plant in the spring when the aphids were migrating to find their summer host. *cis*-Jasmone was identified as one of the volatile semiochemicals released by *R. nigrum* contributing to such behaviour, but it was then realised that this compound was also a volatile component of the jasmonate pathway. However, it had been proposed (Koch et al., 1997) that *cis*-jasmone was a sink for this pathway because, although *cis*-jasmone was regularly encountered as a stress-related compound, no related behavioural effects had been associated with it. Thus, on finding that the compound did, in fact, repel spring migrants of *N. ribis-nigri*, its more general activity was considered. It was quickly shown to be attractive to predatory ladybirds and parasitic wasps (Birkett et al., 2000), so was then tested as an activator for the bean plants (*Vicia faba*) which were the subject of the work at that time. In the wind tunnel, bean plants that had been treated with *cis*-jasmone, but tested after a period when the *cis*-jasmone itself could no longer be detected, were highly attractive to the aphid parasitoid *Aphidius ervi* (Birkett et al., 2000).

One of the compounds found to be responsible for increased attraction and foraging by parasitoids was the monoterpene (*E*)-ocimene, and, although it could seen that its biosynthesis was induced by *cis*-jasmone, the effect remained for 8 days, whereas with methyl jasmonate, induction subsided after 48 h. Using differential display, genes whose expression was upregulated by *cis*-jasmone were investigated (Birkett et al., 2000). However, it was not possible to identify any particular genes in *V. faba* likely to be significant in the process of parasitoid recruitment, or to detect expression of any genes similar to the (*E*)-ocimene synthase known in *Arabidopsis* (Aharoni et al., 2003), so it was decided to move the work to the latter. To do this, it was necessary to establish that similar biological effects took place with *Arabidopsis*, and it was indeed shown that aphids were repelled and that parasitic wasps were attracted to plants that had been treated with *cis*-jasmone. Coupled GC-EAG of the volatiles from *Arabidopsis* was also used to find regions in the chromatogram where there were peaks of activity for insects. Unfortunately, the levels of volatiles were so low that they could not be identified by GC–mass spectrometry, so identification had to rely on retention times and biological activity to deduce the nature of the active compounds. Microarray data were initially obtained on a comparison between no treatment, *cis*-jasmone and methyl jasmonate. This gave rise to identification of a number of genes that were specifically upregulated with *cis*-jasmone, including *OPR1/2*, cell wall biosynthesis genes, and genes for a specific cytochrome P450 and an F-Box protein (Matthes et al., 2003; Pickett et al., 2003). Genes that were not induced by *cis*-jasmone, but which were induced by methyl jasmonate, included PR protein genes, stress genes such as those for heatshock proteins and genes such as *OPR3* and *LOX*. *OPR3*, which is upregulated by methyl jasmonate, is essential in the biosynthesis of jasmonic acid, as it is the oxophytodienoic acid reductase that captures the 9*S*,13*S* stereochemistry in the oxophytodienoic acids which, after reduction, passes on by oxidative decarboxylation to jasmonic acid (i.e. initially with the *epi*-jasmonic acid stereochemistry) and then to methyl jasmonate (Schaller et al., 2000; Schaller, 2001).

Since *cis*-jasmone was acting differently to methyl jasmonate, the possibility was considered that it was formed by a different pathway, and not directly from jasmonic acid as had been proposed (Koch et al., 1997). Indeed, if OPR1/2 are, rather than reductases, isomerases converting the other three stereochemistries (i.e. not 9*S*,13*S*) that cannot yield jasmonic acid to the isomerised product, then this could undergo conversion to *cis*-jasmone without the necessary reduction and subsequent oxidation within the cyclopentane ring. Thus, the proposed isomerization would give the product with the 9,13-double bond from the 10,11-unsaturation of the oxophytodienoic acids. Support for this has now been provided by the Boland group (Schulze et al., 2007), who found an isomerase in the gut of a lepidopterous insect that converts (9*S*,13*S*)-oxophytodienoic acid into *iso*-oxophytodienoic acid (tetrahydodicranenone B) (Fig. 1). When *iso*-oxophytodienoic acid is placed onto plants, it does not yield jasmonic acid, but instead is

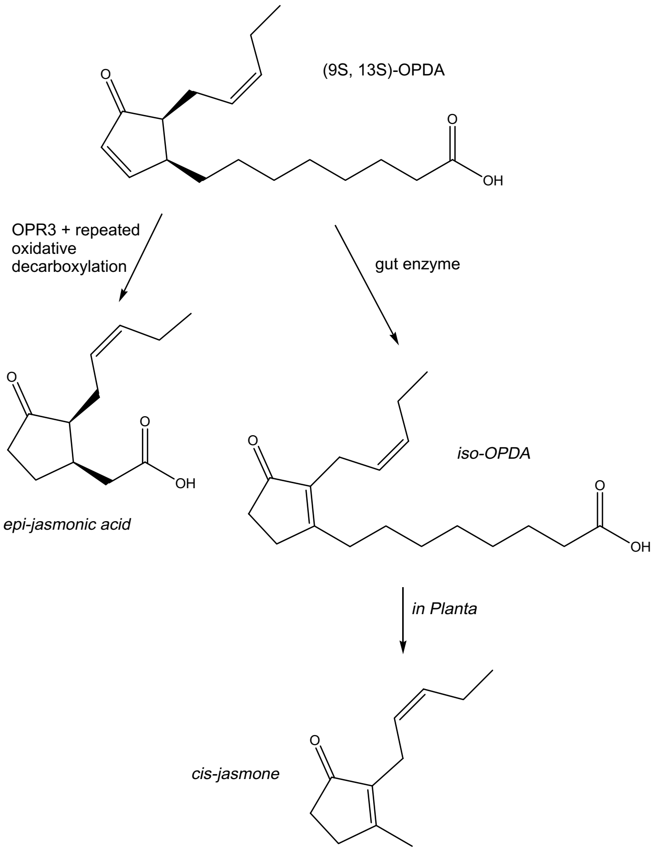

Fig. 1. Biosynthesis of *epi*-jasmonic acid from (9*S*, 13*S*)-oxophytodienoic acid (OPDA) via OPR3 and the activity of a newly isolated gut enzyme that isomerises OPDAs into *iso*-OPDA, which when placed on plants converts to *cis*-jasmone (Schulze et al., 2007).

immediately converted to *cis*-jasmone. This supports the proposed "isomerising" role for OPRI/2. According to Stelmach et al. (2001), there is a pool of oxophytodienoic acids, localised in plastids as glycolipid esters, and if these could be isomerised by OPR1 and OPR2, then the upregulation of the *OPR1* and *OPR2* by *cis*-jasmone could account for the fact that, once *cis*-jasmone has activated the plant, then the activation remains, as is the case with the upregulation of (*E*)-ocimene from beans (Birkett et al., 2000).

The temporal upregulation of transcripts by *cis*-jasmone is by no means uniform and this may imply a hierarchical response which will need to be investigated further. It has been possible to follow biologically, although not yet chemically, the upregulation of some of the genes that are upregulated by *cis*-jasmone. For example, a specific cytochrome P450 in the Cyp81 series upregulated by *cis*-jasmone, when overexpressed constitutively in transgenic *Arabidopsis*, causes repulsion of *M. persicae* and attraction of *A. ervi*. The wild-type *Arabidopsis*, by comparison, is attractive to *M. persicae* but of no interest to *A. ervi*, since it does not emit any cues for the presence of a herbivore. In a different approach, a promoter fusion between the F-Box protein sequence and the reporter luciferase demonstrates the tight regulation of *cis*-jasmone responsive genes. When *cis*-jasmone is introduced into the air around *Arabidopsis* expressing this construct, luciferase activity is produced which is confirmed by the addition of luciferin and detection of emitted light. This opens up the prospect of using reporters from the *cis*-jasmone system to construct the so-called "sentinel plants". Thus, when the potato aphid, *Macrosiphum euphorbiae*, and certain pathogens attack potatoes, *cis*-jasmone is produced. If this were detected by a plant having a suitable visual marker, although not necessarily luciferase, within a field of potatoes, then early warning of pest and disease would result. Also, it might be possible to use the *cis*-jasmone promoters in cereal plants linked to (*E*)-β-farnesene synthase (Beale et al., 2006) to switch on the defence pathway by a treatment with *cis*-jasmone and thus make the crop repellent to aphids and attractive to parasitoids.

In addition to the hierarchical structure implied in the *cis*-jasmone upregulation of genes, there is ecotypic variation in their response to *cis*-jasmone, specifically in connection with the expression of the cytochrome P450 and that of a glycosyltransferase-like sequence which also varies in certain ecotypes (Matthes, Verrier, Pickett, Napier, unpublished data). This does not appear to be the case with the F-Box protein gene, which seems to be consistently upregulated in the various ecotypes. Such observations are consistent with the cytochrome P450 playing an adaptive role in different niches. It can also be seen that certain other aspects of jasmonate signalling are not involved. For example, *cis*-jasmone does not signal through the F-Box protein COI1, since the methyl jasmonate- and coronatin-insensitive *coi1* mutant is unaffected in terms of *cis*-jasmone upregulation of the specific cytochrome P450 gene (Matthes, Verrier, Pickett, Napier, unpublished data).

Nonetheless, a great deal more needs to be done and there are a number of outstanding questions regarding *cis*-jasmone as a modulator of plant gene expression:

- What are the biochemical activities encoded by *cis*-jasmone-induced genes?
- How are these biochemical processes linked to *cis*-jasmone-induced modulation of plant/insect interactions?
- What is the *in planta* signalling route for *cis*-jasmone?
- What is the basis by which the plant discriminates between *cis*-jasmone and methyl jasmonate?
- What is the biosynthetic pathway for *cis*-jasmone?
- What is the significance of ecotype variation in *Arabidopsis* responses to *cis*-jasmone?

2.2. Practical developments

Potentially useful effects have already been found in wheat and demonstrated in the field. When wheat is attacked by aphids such as the bird–cherry–oat aphid, *Rhopalosiphum padi*, it produces a suite of compounds (Pettersson et al., 1994; Quiroz et al., 1997), including the isoprenoid oxidation product 6-methyl-5-hepten-2-one.

This compound is also produced by plants on which aphids are feeding and attracts the parasitic wasp *A. ervi* (Du et al., 1998). When *cis*-jasmone is used to activate defence in wheat, this is one of the compounds for which production is upregulated and a reduction in attack by the grain aphid, *Sitobion avenae*, is seen as a consequence (Bruce et al., 2003a). Field studies on winter wheat have also been done, in which *cis*-jasmone was sprayed as an emulsifiable concentrate in May and showed significant protection against aphids through to June (Bruce et al., 2003a, 2003b). It was not possible to do this in the field for the parasitic wasp due to erratic climatic conditions, but using polythene tunnels and wheat seedlings, increased parasitoid foraging was demonstrated with a similar *cis*-jasmone treatment (Bruce et al., 2003b).

2.3. Induced antibiotic response

Although when wheat is treated with *cis*-jasmone, aphid numbers are reduced through repellency caused partly by the increased production of 6-methyl-5-hepten-2-one, an antibiotic effect is seen, expressed in the vegetative parts of the plant and causing a reduction in population increase by aphids. This effect was traced to the benzoxazinoids (hydroxamic acids), particularly 2,4-dihydroxy-7-methoxy-1,4-benzoxazin-3-one (DIMBOA) and phenolic acids (Moraes et al., 2008). The benzoxazinoids have been studied extensively, particularly by Hermann Niemeyer (1988). They can cause a reduction in numbers of insects and airborne pathogens, show activity within the rhizosphere against fungi, bacteria and nematodes, and there is also an allelopathic effect on weeds (Zasada et al., 2007; Belz, 2007). The compounds can be extracted and fed back to plants that do not produce them, and these, as a consequence, become resistant to aphids (Argandona et al., 1980). They are also active against aphids when applied in artificial diets (Corcuera et al., 1982). These compounds can be measured qualitatively by GC–coupled mass spectrometry on derivatised samples, with unequivocal identification by tandem mass spectrometry.

The biosynthetic pathway for the production of the benzoxazinoids has now been established for both maize and wheat (Frey et al., 1997; Nomura et al., 2002, 2003). The main part of the pathway is initiated by a new route to indole, catalysed by Bx1, which is homologous to tryptophan alpha synthase. This reaction takes place in the chloroplast and is followed by a series of oxidation steps through to DIMBOA, catalysed by cytochrome P450 enzymes in the CYP71C group localised in the endoplasmic reticulum. The benzoxazinones are readily glycosylated and the glucosides are stored in the vacuole, but are released as active compounds, such as DIMBOA, by glucosidases (Sue et al., 2006). In maize, eight genes associated with this pathway have been mapped to the same cluster on chromosome 4 (Frey et al., 1997, 2003). In hexaploid wheat, multiplication of the genes during polyploidation has taken place, but there is a similar clustering of the genes onto chromosome groups 4 and 5 of each of the three genomes (A, B, and D) (Nomura et al., 2003). Each homoeolog of the first five genes in the benzoxazinoid pathway has been sequenced and their locations within the three genomes determined (Nomura et al., 2005).

The studies by Pettersson et al. (1999) on the induction of defence by antagonistic weeds showed that, using a convection driven wind tunnel, barley plants of certain cultivars could induce defence in other barley plants. This can also be done in the field: the barley variety Kara, grown with various other varieties, showed significant defence against aphids, particularly when grown with the varieties Frida and Alva (Ninkovic et al., 2002; Glinwood et al., 2003).

2.4. Effects within the rhizosphere

Working with Pennacchio et al. (Chamberlain et al., 2001), it was shown that stress-related signals associated with aphid feeding could pass from plant to plant through the rhizosphere. This was investigated using a hydroponic system in which damaged and undamaged plants could be maintained in the same solution: when a damaged plant was taken out of the solution and replaced by an intact plant, the latter would subsequently become more attractive to the parasitoid *A. ervi*. So far, attempts to identify the compounds involved have not proved successful. However, returning to aggressive weeds such as the couch grass, *Elytrigia repens*, it was shown that the molluscicidal 6-hydroxy-1,2,3,4-tetrahydro-β-carboline-3-carboxylic acid was also able to stimulate defence in intact barley plants (Glinwood et al., 2003).

2.5. Priming or potentiation

A common theme underlying responses to a range of biotic and abiotic stresses is the phenomenon of priming, or potentiation, whereby previous exposure makes the plant more resistant to future exposure. Primed plants display faster and/or stronger activation of the various defence responses that are induced following attack by either pathogens or insects (Engelberth et al., 2004; Conrath et al., 2006; Kessler et al., 2006). As well as exposure to the stress cues themselves, priming can be elicited by chemical signals (Jakab et al., 2005; Nowak and Shulaev, 2003). There is evidence that such chemical priming occurs in nature, in interactions between herbivore-damaged and intact plants. A small lipophilic molecule from the damaged plant primes the intact plant, which only manifests its defence when it is subsequently attacked by the herbivore (Kessler et al., 2006). This plant then defends itself much more strongly against herbivore colonisation and development, and also becomes attractive to the parasitoids. An interesting aspect of priming is that there can be long-term changes in plant responses, suggesting that plants have the capacity for storing information (Bruce et al., in press). There is plenty of evidence that plants are adept at altering their physiology and metabolism in response to prior experience. However, much still remains to be learnt about the mechanism by which plants store information on previous exposure. The "memory" that occurs in plants is certainly different from the memory that occurs in animals and it appears to be more adaptive than intelligent.

3. Conclusions

The establishment of *cis*-jasmone as a potentially useful plant activator has allowed its patenting and we are seeking to develop this by a breeding programme involving the British Wheat Breeders (BBSRC Research Grant, 2007–2010, "The potential to control insects and other organisms antagonistic to wheat by upregulation of hydroxamic acids"). It is hoped that this practical development will be of value in the subsequent generation of new pest-resistant varieties, but also in exploiting heterologous gene expression for the long term, and that this will be a stimulus to other, more practically-oriented groups developing this type of technology, both in the state sector and in industry. We expect that the many groups working on the scientific understanding of this process, as well as our own molecular biological studies on *cis*-jasmone as a new signal, will yield new ways of exploiting phytochemistry in the interests of food, energy and other material production. With such novel use of plant activators will come new concepts of integrated pest management, with companion cropping as an integral feature (Cook et al., 2007; Hassanali et al., in press).

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References

Agelopoulos, N., Birkett, M.A., Hick, J., Hooper, A.M., Pickett, J.A., Pow, E.M., Smart, L.E., Smiley, D.W.M., Wadhams, L.J., Woodcock, C.M., 1999. Exploiting semiochemicals in insect control. Pestic. Sci. 55, 225–235.

Aharoni, A., Giri, A.P., Deuerlein, S., Griepink, F., de Kogel, W.-J., Verstappen, F.W.A., Verhoeven, H.A., Jongsma, M.A., Schwab, W., Bouwmeester, H.J., 2003. Terpenoid metabolism in wild-type and transgenic Arabidopsis plants. Plant Cell 15, 2866–2884.

Argandona, V.H., Luza, J.G., Niemeyer, H., Corcuera, L.J., 1980. Role of hydroxamic acids in the resistance of cereals to aphids. Phytochem. 19, 1665–1668.

Beale, M.H., Birkett, M.A., Bruce, T.J., Chamberlain, K., Field, L.M., Huttly, A.K., Martin, J.L., Parker, R., Phillips, A.L., Pickett, J.A., Prosser, I.M., Shewry, P.R., Smart, L.E., Wadhams, L.J., Woodcock, C.M., Zhang, Y., 2006. Aphid alarm pheromone produced by transgenic plants affects aphid and parasitoid behaviour. Proc. Natl. Acad. Sci. USA 103, 10509–10513.

Belz, R.G., 2007. Allelopathy in crop/weed interactions – an update. Pest Manage. Sci. 63, 308–326.

Birkett, M.A., Campbell, C.A.M., Chamberlain, K., Guerrieri, E., Hick, A.J., Martin, J.L., Matthes, M., Napier, J.A., Pettersson, J., Pickett, J.A., Poppy, G.M., Pow, E.M., Pye, B.J., Smart, L.E., Wadhams, G.H., Wadhams, L.J., Woodcock, C.M., 2000. New roles for *cis*-jasmone as an insect semiochemical and in plant defense. Proc. Natl. Acad. Sci. USA 97, 9329–9334.

Bruce, T.J.A., Martin, J.L., Pickett, J.A., Pye, B.J., Smart, L.E., Wadhams, L.J., 2003a. *cis*-Jasmone treatment induces resistance in wheat plants against the grain aphid, *Sitobion avenae* (Fabricius) (Homoptera: Aphididae). Pest Manage. Sci. 59, 1031–1036.

Bruce, T.J.A., Matthes, M.C., Napier, J.A., Pickett, J.A., in press. Stressful memories of plants: evidence and possible mechanisms. Plant Sci. 173 (6), 603–608.

Bruce, T.J., Pickett, J.A., 2007. Plant defence signalling induced by below- and above-ground attacks. Curr. Opin. Plant Biol. 10, 387–392.

Bruce, T.J., Pickett, J.A., Smart, L.E., 2003b. *cis*-Jasmone switches on plant defence against insects. Pestic. Outlook 14, 96–98.

Bruce, T.J., Wadhams, L.J., Woodcock, C.M., 2005. Insect host location: a volatile situation. Trends Plant Sci. 10, 269–274.

Chamberlain, K., Guerrieri, E., Pennachio, F., Pettersson, J., Pickett, J.A., Poppy, G.M., Powell, W., Wadhams, L.J., Woodcock, C.M., 2001. Can aphid-induced plant signals be transmitted aerially and through the rhizosphere? Biochem. Syst. Ecol. 29, 1063–1074.

Conrath, U., Beckers, G.J.M., Flors, V., García-Agustín, P., Jakab, G., Mauch, F., Newman, M.-A., Pieterse, C.M.J., Poinssot, B., Pozo, M.J., Pugin, A., Schaffrath, U., Ton, J., Wendehenne, D., Zimmerli, L., Mauch-Mani, B., 2006. Priming: getting ready for battle. Mol. Plant Microbe In. 19, 1062–1071.

Cook, S.M., Khan, Z.R., Pickett, J.A., 2007. The use of push–pull strategies in integrated pest management. Annu. Rev. Entomol. 52, 375–400.

Corcuera, L.J., Argandona, V.H., Niemeyer, H.M., 1982. Effect of cyclic hydroxamic acids from cereals on aphids. In: Kehl, H. (Ed.), Chemistry and Biology of Hydroxamic acids. Karger AG, Basel, pp. 111–118.

Du, Y., Poppy, G.M., Powell, W., Pickett, J.A., Wadhams, L.J., Woodcock, C.M., 1998. Identification of semiochemicals released during aphid feeding that attract parasitoid *Aphidius ervi*. J. Chem. Ecol. 24, 1355–1368.

Engelberth, J., Alborn, H.T., Schmelz, E.A., Tumlinson, J.H., 2004. Airborne signals prime plants against insect herbivore attack. Proc. Natl. Acad. Sci. USA 101, 1781–1785.

FAO, 2006. Statistical Yearbook 2005–2006, vol. 1. Food and Agriculture Organisation.

Farmer, E.E., Ryan, C.A., 1990. Interplant communication: airborne methyl jasmonate induces synthesis of proteinase inhibitors in plant leaves. Proc. Natl. Acad. Sci. USA 87, 7713–7716.

Foyer, C.H., Noctor, G., van Emden, H.F., 2007. An evaluation of the costs of making specific secondary metabolites; is the yield penalty incurred by host plant resistance to insects due to competition for resources? Int. J. Pest Manage. 53, 175–182.

Frey, M., Chomet, P., Glawischnig, E., Stettner, C., Grün, S., Winklmair, A., Eisenreich, W., Bacher, A., Meeley, R.B., Briggs, S.P., Simcox, K., Gierl, A., 1997. Analysis of a chemical plant defense mechanism in grasses. Science 277, 696–699.

Frey, M., Huber, K., Park, W.J., Sicker, D., Lindberg, P., Meeley, R.B., Simmons, C.R., Yalpani, N., Gierl, A., 2003. A 2-oxoglutarate-dependent dioxygenase is integrated in DIMBOA-biosynthesis. Phytochemistry 62, 371–376.

Glinwood, R., Pettersson, J., Ahmed, E., Ninkovic, V., Birkett, M., Pickett, J., 2003. Change in acceptability of barley plants to aphids after exposure to allelochemicals from couch-grass (*Elytrigia repens*). J. Chem. Ecol. 29, 261–274.

Hassanali, A., Herren, H., Khan, Z.R., Pickett, J.A., in press. In: Crute, I., Dalton, H., Leaver, C., Pretty, J. (Eds.), Integrated Pest Management. Philosophical Transactions of the Royal Society London B (Special Issue: Sustainable Agriculture), doi:10.1098/rstb.2007.2173.

Jakab, G., Ton, J., Flors, V., Zimmerli, L., Métraux, J.-P., Mauch-Mani, B., 2005. Enhancing Arabidopsis salt and drought stress tolerance by chemical priming for its abscisic acid responses. Plant Physiol. 139, 267–274.

Kessler, A., Halitschke, R., Diezel, C., Baldwin, I.T., 2006. Priming of plant defense responses in nature by airborne signaling between *Artemisia tridentata* and *Nicotiana attenuata*. Oecologia 148, 280–292.

Koch, T., Bandemer, K., Boland, W., 1997. Biosynthesis of *cis*-jasmone: pathway for the inactivation and the disposal of the plant stress hormone jasmonic acid to the gas phase? Helv. Chim. Acta 80, 838–850.

Lucas, J.A., 1999. Plant immunisation: from myth to SAR. Pestic. Sci. 55, 193–196.

Matthes, M., Napier, J.A., Pickett, J.A., Woodcock, C.M., 2003. New chemical signals in plant protection against herbivores and weeds. In: Proceedings of the BCPC International Congress – Crop Science and Technology, Glasgow, 10–12 November 2003, pp. 1227–1236.

Moraes, M.C.B., Birkett, M.A., Gordon-Weeks, R., Smart, L.E., Martin, J.L., Pye, B.J., Bromilow, R.H., Pickett, J.A., 2008. *cis*-Jasmone induces accumulation of defence compounds in wheat, Triticum aestivum. Phytochemistry 69, 9–17.

Niemeyer, H., 1988. Hydroxanic acids (4-hydroxy-1,4-benzoxazin-3-ones), defence chemicals in the Gramineae. Phytochemistry 27, 3349–3358.

Ninkovic, V., Olsson, U., Pettersson, J., 2002. Mixing barley cultivars affects aphid host plant acceptance in field experiments. Entomol. Exp. Appl. 102, 177–182.

Nomura, T., Ishihara, A., Imaishi, H., Endo, T., Ohkawa, H., Iwamura, H., 2002. Molecular characterization and chromosomal localization of cytochrome P450 genes involved in the biosynthesis of cyclic hydroxamic acids in hexaploid wheat. Mol. Gen. Genom. 267, 210–217.

Nomura, T., Ishihara, A., Imaishi, H., Ohkawa, H., Endo, T.R., Iwamura, H., 2003. Rearrangement of the genes for the biosynthesis of benzooxazinones in the evolution of Triticeae species. Planta 217, 776–782.

Nomura, T., Ishihara, A., Yanagita, R.C., Endo, T.R., Iwamura, H., 2005. Three genomes differentially contribute to the biosynthesis of benzoxazinones in hexaploid wheat. Proc. Natl. Acad. Sci. USA 102, 16490–16495.

Nowak, J., Shulaev, V., 2003. Priming for transplant stress resistance in in vitro propagation. In Vitro Cell. Dev. Biol.-Plant 39, 107–124.

Pettersson, J., Ninkovic, V., Ahmed, E., 1999. Volatiles from different barley cultivars affect aphid acceptance of neighbouring plants. Acta Agric. Scand., Sect. B, Soil Plant Sci. 49, 152–157.

Pettersson, J., Pickett, J.A., Pye, B.J., Quiroz, A., Smart, L.E., Wadhams, L.J., Woodcock, C.M., 1994. Winter host component reduces colonization by bird–cherry–oat aphid, *Rhopalosiphum padi* (L.) (Homoptera, Aphididae), and other aphids in cereal fields. J. Chem. Ecol. 20, 2565–2574.

Pickett, J.A., Poppy, G.M., 2001. Switching on plant genes by external chemical signals. Trends Plant Sci. 6, 137–139.

Pickett, J.A., Rasmussen, H.B., Woodcock, C.M., Matthes, M., Napier, J.A., 2003. Plant stress signalling: understanding and exploiting plant–plant interactions. Biochem. Soc. T. 31, 123–127.

Prosser, I., Phillips, A.L., Gittings, S., Lewis, M.J., Hooper, A.M., Pickett, J.A., Beale, M.H., 2002. (+)-(10 *R*)-Germacrene A synthase from goldenrod, *Solidago canadensis;*. cDNA isolation, bacterial expression and functional analysis. Phytochemistry 60, 691–702.

Quiroz, A., Pettersson, J., Pickett, J.A., Wadhams, L.J., Niemeyer, H.M., 1997. Semiochemicals mediating spacing behavior of bird cherry–oat aphid, *Rhopalosiphum padi* feeding on cereals. J. Chem. Ecol. 23, 2599–2607.

Ryu, C.-M., Farag, M.A., Hu, C.-H., Reddy, M.S., Kloepper, J.W., Paré, P.W., 2004. Bacterial volatiles induce systemic resistance in Arabidopsis. Plant Physiol. 134, 1017–1026.

Schaller, F., 2001. Enzymes of the biosynthesis of octadecanoid-derived signalling molecules. J. Exp. Bot. 52, 11–23.

Schaller, F., Biesgen, C., Müssig, C., Altmann, T., Weiler, E.W., 2000. 12-Oxophytodienoate reductase 3 (*OPR3*) is the isoenzyme involved in jasmonate biosynthesis. Planta 210, 979–984.

Shulaev, V., Silverman, P., Raskin, I., 1997. Airborne signalling by methyl salicylate in plant pathogen resistance. Nature 385, 718–721.

Schulze, B., Dabrowska, P., Boland, W., 2007. ChemBioChem 8, 208–216.

Stelmach, B.A., Müller, A., Hennig, P., Gebhardt, S., Schubert-Zsilavecz, M., Weiler, E.W., 2001. J. Biol. Chem. 276, 12832–12838.

Sue, M., Yamazaki, K., Yajima, S., Nomura, T., Matsukawa, T., Iwamura, H., Miyamoto, T., 2006. Molecular and structural characterization of hexameric β-D-glucosidases in wheat and rye. Plant Physiol. 141, 1237–1247.

Zasada, I.A., Rice, C.P., Meyer, S.L.F., 2007. Improving the use of rye (*Secale cereale*) for nematode management: potential to select cultivars based on *Meloidogyne incognita* host status and benzoxazinoid content. Nematology 9, 53–60.

Prof. John A. Pickett CBE FRS FRSC FRSE Professor John A. Pickett, originally an organic chemist (BSc 1967, PhD 1971, DSc 1993), has gained worldwide recognition for his investigations into natural chemical products (semiochemicals) that affect the behaviour and development of animals and other organisms. In 1976, he moved to Rothamsted Experimental Station (now Rothamsted Research) to lead a team working on pheromones and other semiochemicals for new methods of pest control. He was appointed Head of the now Biological Chemistry Department in 1984, and to Science Director of the Centre for Sustainable Pests and Disease Management in 2007, but is still very much personally involved with day-to-day research activities in the UK and around the world.

His contribution to the field of chemical ecology has been acknowledged with the 1995 Rank Prize for Nutrition and Crop Husbandry, election to Fellowship of the Royal Society in 1996, the Institute Society of Chemical Ecology Medal in 2002 and appointment to CBE for services to Biological Chemistry in 2004, among many other international measures of esteem. He is a long-standing member of the PSE and presented a plenary lecture at the PSE50 meeting in Cambridge, April 2007.

Dr. Michael A. Birkett Michael is a Senior Research Scientist at Rothamsted Research with a background in Biochemistry, Biological Chemistry and Synthetic Organic Chemistry (BSc University of Nottingham, 1990, PhD University of Nottingham, 1994). At Rothamsted, he is the principal mass spectrometrist for the Chemical Ecology group, with responsibilities including the identification of (i) biologically active compounds located by electrophysiology, often involving investigations of minute (sub-nanogram) amounts of chemicals in extremely complex mixtures and (ii) plant defence signals that mediate plant/insect and plant/plant interactions. He also leads research on the role, identity and biosynthesis of semiochemicals affecting arthropod pests of medical and veterinary importance, and on the development of novel green chemistry approaches to commercial-scale semiochemical production.

Dr. Toby J.A. Bruce Toby gained an MSc in Applied Entomology from Imperial College London before embarking on his PhD at the University of Greenwich. He started at Rothamsted Research in 2000 and was promoted to Band 5 in 2007. His aim is to understand the underlying mechanisms of chemical communication between organisms. His research focuses in particular on the chemical ecology of host location in insects and on alarm and sex pheromone signals. He has devised strategies for utilising semiochemicals for insect pest management at the field level, ranging from plant activators that switch on plant defence to pheromone monitoring systems. As volatile semiochemicals are difficult to formulate, Toby has developed approaches utilising essential oils to protect unstable compounds and has contributed to the development of plants expressing semiochemicals. As a direct result of his research and development work, pheromone traps are commercially available to wheat growers in the UK.

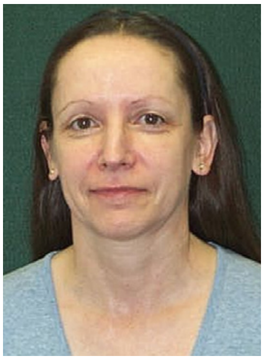
Dr. Keith Chamberlain Keith completed his PhD and spent his early career working with Prof. Louis Wain, FRS, at the Unit of Plant Growth Substances and Systemic Fungicides at Wye College, on structure–activity relationships in systemic fungicides. In 1978, he transferred to Rothamsted Research to work on the translocation of xenobiotics in plants and, in collaboration with Richard Bromilow, published many papers and several book chapters on the physicochemical requirements of compounds for translocation in the vascular system of plants. In 1998, he joined Prof. John Pickett's chemical ecology group, where he has studied the production and emission of plant volatiles, particularly in response to herbivore damage.

Dr. Ruth Gordon-Weeks Ruth has an honours degree in Zoology and Biological Chemistry from the University of Hull. After graduating, she spent a year at Sheffield University studying the neuroendocrine system of the cockroach before moving to the Max Planc Institute in Munich to work on genetic defects in the primary structure of collagen and their role in hereditary diseases of human connective tissue. She then returned to the UK to take up a PhD position working on the processing of pituitary peptide hormone precursors at the National Institute of Medical Research, Mill Hill. She joined the Biochemistry Department at Rothamsted in 1986 to work on plant signalling in response to tobacco mosaic virus infection and the regulation of plant nutrient transporters. In 2003, she transferred to the Biological Chemistry Department to join the Chemical Ecology Group, where she is currently studying the role of the hydroxamic acid pathway in resistance and its regulation by plant volatile signalling compounds.

Dr. Michaela C. Matthes Michaela Matthes studied Biology at the University of Ulm and finished her studies with a Diploma in Immunology in 1988. She was awarded a PhD in 1992 for work performed in the field of T-cell activation at INSERM, Centre d'Immunologie de Marseille-Luminy. From 1993 to 1997, she worked on an EU-funded project at ZENECA, Jealott's Hill Research Station, Bracknell, applying molecular marker technology to breeding programmes, characterising germplasm collections and investigating biodiversity. In 1997, she transferred to IACR-Long Ashton, initially working on somaclonal variation in oil palm (funded by PORIM), but then her research interests shifted to the field of signal perception and transduction, specifically during interactions of plants with insects, which is carried out at Rothamsted Research.

Prof. Johnathan A. Napier Johnathan studied Agricultural Sciences at the University of Nottingham (BSc 1984) and gained a PhD from King's College, London (1990) for studies on the role of plant hormones on reserve mobilisation in wheat grains. He then spent three exciting years in the department of Plant Sciences, University of Cambridge, working on protein targeting to the chloroplast before joining Long Ashton Research Station (Bristol). Here, he established his research programme on manipulating plant lipid metabolism, in particular the reverse-engineering of transgenic plants with the capacity to synthesise omega-3 long chain polyunsaturated fatty acids. His major contributions to this field were recognised by individual merit promotion (2003), the award of his DSc (2006) and the European Lipid Science Award (2006). Johnathan and his research group relocated to Rothamsted research in 2003 on the closure of the Long Ashton site, allowing closer collaborations with eminent and like-minded colleagues such as John Pickett.

Ms. Lesley E. Smart BSc Lesley Smart joined the Insecticides and Fungicides Department at Rothamsted, later to become the Biological Chemistry Department, in 1972, conducting laboratory and field experiments to evaluate the effects of pesticides on honeybees and other beneficial insects. In 1986, she joined Professor Pickett's Chemical Ecology Group, where she has designed and developed laboratory and field experiments to study the use of semiochemicals in pest management strategies, in particular the push–pull strategy.



Ms. Christine M. Woodcock Christine joined the Insecticides and Fungicides Department at Rothamsted, later to become the Biological Chemistry Department, in 1972, initially undertaking laboratory and field assessment of toxicants and semiochemicals influencing the behaviour of slugs, wheat bulb fly and aphids. In 1989, within John Pickett's Chemical Ecology Group and in collaboration with Dr. Lester Wadhams, she studied the technique of electrophysiological recording from insect antennae, coupled with high resolution gas chromatography, to identify behaviourally active compounds for pest and beneficial organisms in agricultural systems. These include crop pests and haematophagous pests of farm animals and human beings, as well as the parasitoids and predators of these pests. She has published over 120 papers in this field.