Novartis Foundation Symposium 223

INSECT–PLANT INTERACTIONS AND INDUCED PLANT DEFENCE

1999

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Symposium on Insect–plant interactions and induced plant defence, held at the Novartis Foundation, London, 13–15 October 1998

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This symposium is based on a proposal made by John A. Pickett

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Chairman's introduction

John A. Pickett

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We in the 'developed' countries are probably naïve in believing that we will continue to have a surplus of agricultural products for eternity. For the developing countries, the reality is one of food shortages. Although famines are fairly uncommon, there exist tremendously deprived areas in terms of the kind of food that people want to eat. With the world population set to rise to 8.5 billion by 2020, we are going to have to put a lot more technology into food production: there simply isn't a large enough area of land available for cultivation. If we don't use technology to improve agricultural production, we will stress even more the unexploited natural habitats that remain.

In introducing this subject, I'd like briefly to mention, by way of an example, some work we have been doing in Kenya. Here, as in many other parts of Africa, there can be tremendous crop losses through damage by lepidopterous larvae, particularly stem-borers, and the aggravated wind lodging of maize and sorghum crops. The farmers can't address pest problems by using pesticides simply because they can't afford them: even though Kenya's economy is quite a thriving one, it doesn't spend a lot of hard currency buying in basic agricultural materials such as fertilizers and pesticides: if it did, it would start to find itself in debt or without essential pharmaceuticals. However, there are alternatives. In collaboration with ICIPE in Kenya, we are developing an intercropping system which exploits signals sent out from plants to insects, telling them whether or not the plant from which the chemicals come is a suitable host (Pickett et al 1997, Hick et al 1997). By creating such a 'push–pull' situation within the maize crop, it is possible to control these stem-borers. There's also some evidence in this work of plants actually signalling between themselves. This is an aspect which has attracted media attention, and it's something that we would be able to capitalize on if we were able to characterize the kind of signals that are induced during plant stress. This is an exciting area, and one of which I feel we are only at the beginning. We all have to obtain resources and speak to the media: in doing this, we obviously put the best complexion on what we're doing. However, at this symposium, we need to take an objective appraisal of exactly where we are, and where we perhaps should be going in the future.

When I was asked to put together this meeting, I felt I needed some advice from a distinguished biologist. I would like to thank Marcel Dicke, who fulfilled this role very ably. With these thoughts in mind, I would like to start the meeting.

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Evolutionary aspects of plant–carnivore interactions

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Abstract. Plants can respond actively to damage by herbivores. In addition to a mode of defence that is directly aimed at the herbivore itself, plants can emit volatiles that attract carnivores, i.e. the enemies of their enemies. Knowledge of the mechanisms underlying the induction of these herbivore-induced plant volatiles and of the responses of the carnivores is progressing rapidly. Inferences on the initial causes of evolution of herbivore-induced plant volatiles remain conjectural. However, once plant–carnivore interactions have evolved to the net benefit of both participants this mutualism is expected to have evolutionary and ecological consequences for the three trophic levels involved. When plant selection and foraging behaviour of natural enemies is linked to plant fitness this can influence different aspects of the plant defence strategy. The way carnivores perceive and process plant information may influence the evolution of the plant signal (i.e. quantitative and qualitative composition of the odour blend in response to herbivore damage). Vice versa, the signal-to-noise ratio of the information may influence the way carnivores respond to plant cues (innately or through learning). Selection will act on herbivores to disconnect the plant–carnivore link, for example by boycotting the informational value of herbivore-induced synomones. Through plant selection and feeding behaviour herbivores can influence their chance of being found by carnivores. Hence, responses of carnivores to plant cues can influence the evolution of food-plant use by herbivores. The conspiracy between plants and carnivores is at the heart of evolutionary ecology, and wide open for experimental and theoretical investigations.

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In spite of the fact that half of the insect world munches plants, the world is still green. Why that is so has been a matter of debate between ecologists, some favouring that it is mainly the defensive ability of plants (bottom-up effect), others emphasizing the suppressive power of carnivores that attack the herbivorous arthropods (top-down effect) (Strong et al 1984). As often, the truth is probably somewhere in the middle, whereby both bottom-up and top-down effects reduce the impact of herbivores on plants, acting in concert but varying in their degree of importance (Hunter & Price 1992).

Plants can certainly defend themselves very effectively. Well known is the strategy of *direct* defence that is aimed at the herbivore directly. Direct defence can be mediated by plant chemicals such as toxins, repellents or digestibility reducers, or by plant structures such as thorns and spines. But even when herbivores can break through this first line of defence, plants are not left helpless victims. Plants can additionally defend themselves by enhancing the effectiveness of natural enemies of herbivores, so-called *indirect* defence (Price et al 1980). Indirect defence can involve the provision of shelter for carnivores (e.g. domatia) or the provision of alternative food such as floral and extrafloral nectar. With a few exceptions, these strategies are forms of constitutive indirect defence, acting before herbivore attack and aimed at preventing this occurring. When herbivores do attack, plants have a strategy of inducible indirect defence: they can emit volatiles that attract and arrest carnivores. This intriguing and seemingly mutualistic conspiracy between plants and carnivores has aroused the interest of many ecologists and the subject of plant–carnivore chemical communication is presently a fast growing research area in chemical ecology.

Plants can provide the enemies of their enemies with chemical information about the presence, identity and densities of herbivores. The benefit for carnivores in responding to these plant cues is high, since the possibility of using herbivore-derived information is limited because of strong selection on herbivores not to reveal themselves (Vet et al 1991, Vet & Dicke 1992).

A wealth of empirical data has been produced on this mode of indirect defence of plants. (For reviews I refer to Vet & Dicke 1992, Tumlinson et al 1993, Turlings et al 1993, Dicke 1994, Dicke & Vet 1999). Different approaches, often successfully combined, are being applied to unravel the mysteries of plant–carnivore interactions. First the *mechanistic approach*, focusing on the 'how' of the interactions. Studies include the identification of the plant chemicals involved (e.g. Turlings et al 1990), the biosynthetic pathways that underlie volatile production (e.g. Hopke et al 1994), and the identification of the herbivore factors that initiate the induction process (e.g. Mattiacci et al 1995, Alborn et al 1997). On the side of the responding carnivore, research is aimed at identifying exactly which cues carnivores respond to behaviourally and which behaviours are evoked by each of the cues (e.g. Geervliet et al 1996, Powell et al 1998). In the present contribution I will focus on a second approach, the *functional approach*, where we study the 'why' (i.e. the evolutionary aspects) of plant–carnivore interactions. Here the sorts of questions that are being asked include the following. How did plant–carnivore mutualism evolve and under which conditions is signalling an 'evolutionarily stable strategy' (ESS, after Maynard Smith 1982, e.g. Godfray 1995, Sabelis & De Jong 1988)? Why do carnivores need plants (e.g. Vet et al 1991, Vet & Dicke

1992) and how do carnivores deal behaviourally with variation in plant information (e.g. Geervliet et al 1998a)? How do plant–carnivore interactions affect the fitness and dynamics of all tritrophic participants?

Until recently both these approaches have been limited to single species plant–carnivore interactions, ignoring food web complexity (e.g. non-linear trophic interactions such as intra-guild-predation) and neglecting the impact plant–carnivore interactions can have on other species in the community. Recently, however, there has been increased attention on a more holistic community level approach to plant–carnivore interactions. Chemically mediated interactions between all members of plant-inhabiting arthropods are being investigated as a basis for studying the importance of indirect food web interactions at the community level (e.g. Pallini et al 1997). It is realized that inferences on the evolution of this indirect mode of defence are tenuous when the emission of these volatiles is not viewed in a broader ecological context of species interactions. After all, the emitted herbivore-induced plant volatiles are 'free information' that can also be exploited by organisms other than the beneficial carnivores. Responses of herbivores, other plants, competitors or predators of the carnivores, may also determine the ecological costs and benefits of these plant signals (for a discussion on this see Dicke & Vet 1999).

Evolution of plant–carnivore interactions

Although evolutionary models may predict the conditions under which plants would benefit from emitting signals to carnivores, and whether this trait is evolutionarily stable (e.g. Sabelis & De Jong 1988), this tells us little about the evolutionary history of plant–carnivore interactions. It is most likely that the induction and release of plant volatiles after herbivory have been tailored to serve other functions than to attract 'bodyguards'. Turlings et al (1995), for example, suggest that the production and emission of terpenoids, produced by the plant in response to herbivore damage, may have evolved because terpenoids are deleterious to the feeding herbivores, hence serving the initial function of direct, not indirect, defence.

When volatile cues, produced by feeding damage, reliably accompany the presence of suitable herbivores, possibilities arise for carnivores to exploit this information. The well developed ability of associative learning, as shown for many insect parasitoids, has probably played an important role in the evolution of the initial responses of these carnivores to plant signals. Once the signal response has developed to the net benefit of both plant and carnivore, the stage is set for co-evolution. When plant fitness is linked to plant selection and foraging behaviour of the carnivores, plants will be selected to produce clear, detectable and reliable signals. In their turn, carnivores are selected to optimize their response to the plant signals.

Hence the fact that plants conspire with carnivores can have considerable evolutionary and ecological consequences for both partners, but also for the herbivore that is caught between the devil and the deep blue sea. Below I will consider some of these consequences in more detail.

The plant

Selection for good signalling ability can potentially affect all components of a plant's defence strategy: the composition of the odour blend, signal transduction and biosynthetic pathways, systemic responses to herbivore damage, or the relative investments into direct and indirect defence. Selection will act on existing genetic and phenotypic variation in these traits within and between species. The possibilities for change are obviously limited by certain phylogenetic and physiological constraints.

The existence of variation in the composition of odour blends is increasingly being shown for different plant systems. Plant volatiles may differ due to different abiotic factors, but also among plant species, plant genotypes, plant parts and according to different biotic factors such as infestation by different herbivore species, stages and densities (see Dicke 1998, Dicke & Vet 1999, Dicke 1999, this volume). Hence, there are, and were, possibilities for selection to alter the qualitative and quantitative composition of the plant odours produced after damage to meet the receiver's need for clarity. We see a great variety of plant responses to mechanical and herbivore damage (Fig. 1). Some plants (on the left of the figure) produce the same odour blend after mechanical or herbivore damage, i.e. there are no qualitative differences in odour composition (e.g. cabbage plants, Mattiacci et al 1994, Geervliet et al 1997). Plants at the other extreme (on the right) show a different strategy since here novel information dominates the volatile blend. The major components of the odour blend produced after damage by herbivores consists of compounds that are not emitted when plants are mechanically damaged (or undamaged) and different herbivore species induce specific volatile compounds (e.g. broad bean, Powell et al 1998).

Seen in the light of co-evolution between plants and carnivores there will be selection on the qualitative and quantitative composition of the odour blend to optimize signal clarity. Hence, the way carnivores perceive and process qualitative and quantitative differences in odour blends may direct the evolution of the plant signal in response to herbivore damage (see below).

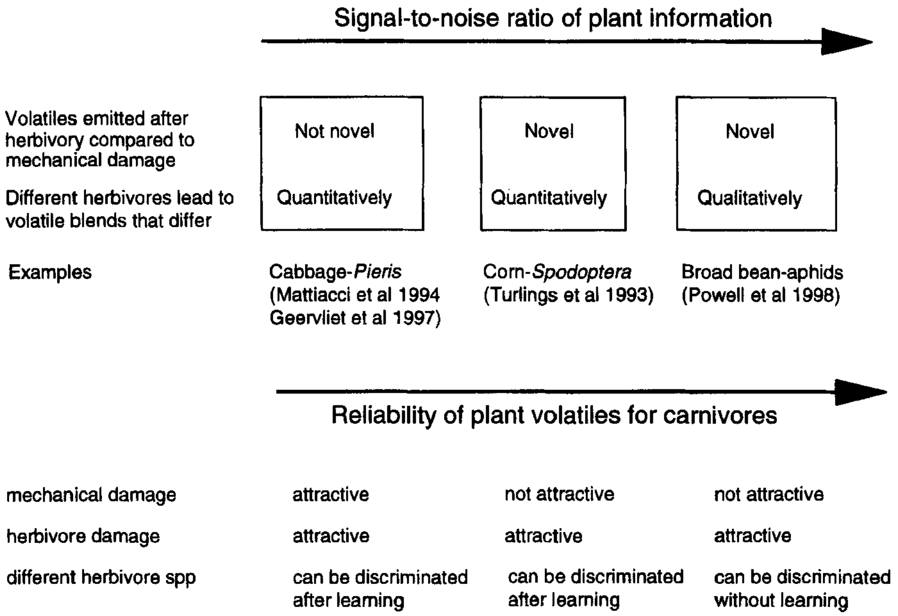

FIG. 1. The relationship between signal-to-noise ratio of chemical plant information that is produced after damage and the response of carnivores.

The carnivore

In the evolutionary setting of real plant–carnivore mutualism, carnivores, in turn, are selected to optimize their response to those plant signals that indicate the presence of suitable herbivores. They can do this by increasing their sensory and behavioural ability to perceive the signal, by efficient information processing and decision making, by enhanced discrimination between signal and noise, and by other behavioural adaptations. I expect carnivores to show some degree of adaptation to the most prevailing and suitable plant–herbivore complexes. Hence, carnivore populations are expected to vary in their responses to plant volatiles and other major foraging cues. Kester & Barbosa (1991) compared different populations of the parasitoid *Cotesia congregata* that were associated with *Manduca sexta* on tomato and tobacco. The populations not only differed in survivorship responses to nicotine concentrations in their host's diet, but also in ovipositional preferences for hosts on tobacco or tomato in the field and in searching responses to these host plants. Unfortunately, there is still very little knowledge of such population differences and of genetic variation in the use of plant volatiles, or infochemicals in general, by predators and parasitoids. In contrast, at least for parasitoids, there is more insight (and more studies) into phenotypic plasticity in the use of infochemicals. Perhaps this is not surprising with respect to plant cues. The variable nature of plant cues may hamper the evolution of genetically fixed responses, especially in longer-living carnivores. Selection for flexibility in response to plant cues can be expected. Indeed we do find much phenotypic plasticity, due to learning processes, in the responses of parasitoids to plants (Turlings et al 1993, Vet et al 1995).

Returning to Fig, 1, selection will act on the carnivore's ability to discriminate between signal and noise, i.e. between relevant and irrelevant variation in plant information. Plant species differ in the specificity of information they provide to carnivores after being damaged in different ways: mechanical damage, damage by non-suitable herbivores and damage by suitable herbivores. The more specific the information on the presence and identity of suitable herbivores, the easier it will be for carnivores to fine-tune their sensory and behavioural responses to these cues, either by genetic adaptation or by phenotypic plasticity.

Signal-to-noise ratio of plant information and responses of carnivores

We can hypothesise that qualitative differences are more important in odour recognition and discrimination learning than quantitative differences. Support for this hypothesis comes from experiments by Vet et al (1998). *Leptopilina heterotoma*, a parasitoid of *Drosophila* larvae that feed on different substrates, learned qualitative differences in odour cues more easily (i.e. with a simpler learning paradigm) than quantitative differences. On the left of Fig. 1 the signal-to-noise ratio of the plant information is low. No qualitatively different compounds are being emitted when plants are damaged mechanically or by different herbivore species. Hence, any type of damage in the field will create a considerable amount of noise, i.e. plant volatiles not related to the presence of suitable herbivores. An example of such a plant is cabbage (Mattiacci et al 1994, Geervliet et al 1997). Both mechanically damaged plants and plants damaged by non-host herbivore species are attractive to the parasitoid *Cotesia glomerata* (Steinberg et al 1993, Geervliet et al 1998b) and the lack of specificity in chemical plant information is a likely constraint on the optimization of foraging by this parasitoid species.

The signal-to-noise ratio increases when shifting to the right in Fig. 1. Plants emit novel compounds after being damaged by herbivores and (total right) even produce different compounds after being damaged by different herbivores.

We expect that the signal-to-noise ratio of the information influences the way carnivores respond. When signal-to-noise ratio is low, learning of small but consistent quantitative differences in odour blends or the use of other sensory modalities will be required to discriminate between signal and noise. Empirical data for *C. glomerata* show that during foraging this parasitoid does acquire the ability to distinguish even between plants infested by one of two *Pieris* host species that differ in suitability (Geervliet et al 1998b). It remains unknown whether this acquired ability is based on the use of minor quantitative differences in odour blends or on the use of visual cues. *C. glomerata* may use visual cues, such as the differences in size of the feeding holes, to distinguish between host plants infested with *P. brassicae* or *P. rapae.* In behavioural experiments using cabbage plants with artificial holes of different sizes, the parasitoids were shown to readily associate the size of the holes with the presence of hosts (J. M. Verdegaal, F. L. Wäckers & L. E. M. Vet, unpublished data).

When signal-to-noise ratio is higher (Fig. 1, middle), discrimination between plants damaged mechanically or by herbivores is more readily achieved. The parasitoid *Cotesia marginiventris* is not attracted to mechanically damaged maize. Parasitoids are attracted to host-infested maize plants on the basis of herbivore-induced terpenoids that are not produced after mechanical damage. Plants infested by different herbivores do not differ in these induced terpenoids, but consistent quantitative differences exist in green leaf volatiles emitted as a result of mechanical damage. These differences appear to be sufficient for the parasitoids to associatively learn to distinguish between plants infested by one of two host species (Turlings et al 1993). On the right in Fig. 1 the signal-to-noise ratio is highest and learning may not be necessary for discrimination between plants infested with suitable and non-suitable herbivores. Empirical data show that the aphid parasitoid (*Aphidius ervi*) readily discriminates between broad bean plants infested with a suitable and a non-suitable aphid host and that experience is not needed for this discrimination. Plants infested with the non-host aphid are not even preferred over undamaged plants (Du et al 1996, Powell et al 1998). Similar evidence is given by Takabayashi et al (1995) for discrimination among plants infested by herbivores of different larval instars. Without prior oviposition experience, the parasitoid *Cotesia kariyai* is attracted to maize plants infested by 1st–4th instar caterpillars (suitable host instars), while plants infested by 5th–6th instar larvae (non-suitable host instars) are not attractive. The same results are obtained when plants are treated with regurgitant of 3rd instar larvae (attraction) or 6th instar larvae (no attraction). I refer to Dicke & Vet (1999) for further examples.

Is specificity of plant information synonymous with qualitative differences?

Although many studies have shown that parasitoids learn plant odours (reviewed in Turlings et al 1993, Vet et al 1995) it remains to be elucidated *how* parasitoids deal behaviourally with natural variation in plant odour cues. We know that *Cotesia glomerata* learns to discriminate between odours of different cabbage cultivars (Geervliet et al 1998b). The question remains *what* these parasitoids learn and on what basis they discriminate between these cabbage plants. Do they learn complete odour bouquets, or do they learn on the basis of qualitative differences in one (or a few) key components between plants? The latter is perhaps suggested by studies with *L. heterotoma* where parasitoids easily learned to distinguish between yeast patches that differed in the presence of one volatile compound only (Vet et al 1998). Note that we go beyond the more traditional question of how insects (mostly herbivores) recognize and select plants on the basis of chemical information (Bernays & Chapman 1994). Here we focus on how insects deal sensorily and behaviourally with *variation* in plant volatiles.

If it is indeed easier for carnivores to perceive, process and learn qualitative differences, and if qualitative differences are interpreted as synonymous with specificity, this may direct the evolution of the plant signal in response to herbivore damage towards greater qualitative differentiation of the odour blend.

The herbivore

The very fact that plants guide the searching of carnivores has evolutionary and ecological consequences for the herbivore. The conspiracy between plant and carnivore is based on the feeding activity of the herbivore itself and selection will act on the herbivore's diet choice and feeding behaviour to reduce the conveyance of information that reveals its presence. The elicitor of plant volatiles has been identified as a component of herbivore oral secretions (Mattiacci et al 1995, Alborn et al 1997). Selection may act on variation in the quality and quantity of oral secretions to minimize the induction of volatile production. Another strategy to sabotage the effect of induced defence is to desert locations emitting volatiles (such as feeding holes), to continue feeding on a different part of the leaf (Mauricio & Bowers 1990), or to chew the leaf petiole before consuming the detached leaf (Weinstein 1990).

Herbivores can select food plants that constitute a relatively enemy-free space. Escape from carnivores can be a driving force in the evolution of plant selection by herbivores (e.g. Bernays & Graham 1988). Plant selection may involve e.g. the choice of plant species, plant genotypes, plants under different abiotic conditions, and plant parts. The butterfly *Pieris napi japonica*, for example, prefers to oviposit on *Arabis spp.* while these plants are of lower quality for larval development than alternative food plants. However, it was demonstrated that the *Arabis* plants were representing an enemy-free space since they were searched less readily by the herbivore's major parasitoid, *C. glomerata* (Ohsaki & Sato 1994).

The chances of a herbivore successfully escaping from carnivores through plant selection are best when there is a relative focus of the carnivores on plant stimuli over herbivore stimuli, i.e. for carnivores specialized at the plant level (Vet & Dicke 1992). A successful shift will then depend on the chemical relatedness of the induced odours of the two plant species and the way carnivores use the odours. Chemical relatedness of plant volatile profiles is determined by the specifics of sensory perception. Insects such as bees are known to generalize between different classes of odours which apparently are interpreted as chemically related (e.g. Getz & Smith 1990). However, as mentioned above, little is known about how carnivorous arthropods perceive and interpret plant odour composition and its variation.

Herbivore density affects the amount of induced volatiles and thus the degree of carnivore attraction. If plants do not respond to a low herbivore load or if carnivores ignore the response of plants to a low herbivore density, such a density also reflects an enemy-free space. Hence, even the evolution of clutch size decisions of herbivores may be influenced by plant–carnivore interactions.

Epilogue

The conspiracy between plants and carnivores is in the heart of evolutionary ecology, and is wide open for rigorous experimental and theoretical investigations. It is, for example, important to study whether the laboratory-measured mechanisms of induced defence really act as protecting systems under realistic field conditions. There is promising progress towards the manipulation of plant traits by means of the plant's signal transduction pathway (Karban & Baldwin 1997), providing exciting experimental possibilities to study the costs of plant volatile production, measured in terms of plant fitness. The elegant field experiments of Baldwin (1998) have shown the power of using this experimental approach to study the ecology of direct defence.

As mentioned above, the way carnivores deal with variation in plant odours in nature remains a striking gap in our knowledge. Experimental behavioural analyses with natural and modified odour blends can help us assess whether quantitative or qualitative differences in compounds matter to foraging carnivores.

To finish, it goes without saying that studies on defence in plants are of great value to the applied field of insect pest management. After all, plant defence is central to plant resistance (direct defence) and biological control (indirect defence), two major pillars of the promising practice of integrated pest management.

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DISCUSSION

Poppy: I'm interested in the question of qualitative versus quantitative change. Louise Vet, like myself, you view a qualitative change as a new compound coming into the picture. But I think some of the people in the audience here can view qualitative change as a dramatic change in the ratio of existing compounds. What is the general consensus about this? And if one is talking about changes in the ratio, how dramatic do these changes need to be to separate them from the inherent variability in chemical profiles from undamaged and damaged plants?

Pickett: As a chemist, I have always regarded qualitative differences as involving the generation of new compounds. But, as you say, as far as the insect or any other recipient of semiochemical messages is concerned, a change in ratio could give a quality signal.

Firn: How many compounds are involved in detection? When you are talking about a ratio, are you talking about just two compounds? How many bits of information from individual compounds does an insect need to be able to make a choice?

Vet: That is a critical question. When an insect learns to respond to a novel plant, we have no idea precisely what it actually learns. For instance, does it learn the whole composition of plant odours, consisting of many compounds in different ratios? I would like to hear what plant physiologists or insect physiologists have to say about this.

Firn: Do insects respond to a loss of information as well as a gain? If you remove a volatile, does this put the insect off?

Vet: Yes. In bioassays if you try to make a mixture of compounds that will give a similar response as the actual plant, then although there may be a response it is frequently not as strong as to the genuine volatile composition.

Tumlinson: The number of compounds involved in this sort of interaction depends on the plant: in some you get fewer compounds and others, such as cotton, there is an enormous number involved. In the early work that Ted Turlings did with me in which we were trying to duplicate the volatiles produced by corn (Turlings et al 1991), we could make a synthetic blend that attracted the parasitoids, but it didn't compete with the natural blend — they could tell the difference, even though all the same compounds were present, simply because it's very difficult to reproduce and dispense exactly the same proportions of compounds in a multi-component blend. I therefore think that small differences in proportions of compounds are going to be detected and learned by these insects. When we start talking about qualitative differences, these can be very subtle.

Turlings: The differences that we observe in the volatile blends by chromatography are not that important: instead, what is critical is whether or not the insects can smell the difference. If you look at two closely related species feeding on corn plants, there are hardly any differences in the chromatograms except for one compound that's produced a lot more by one than the other. But I can easily smell the difference and, after some experience, just like the parasitic wasp, tell you which species it is. The same thing is true with the synthetic blend: this looks almost identical to the natural blend, but it smelt quite different to me as well to the insect. But if you give the insect the appropriate experience, it is very much attracted to it.

Vet: You are putting an important qualifier in here: 'if you give the insect the appropriate experience'. It needs that experience, but then what does it learn? In the case where there are two odour blends that are practically identical, but only differ a little in one component, your conclusion must be that they find out about that. But do they find out about the one component only and the rest has to be exactly the same, or is it that the rest doesn't really have to be exactly the same — it could be variable — but it's not noticed as being an important variable?

Städler: There is a technical problem here, also. We always think that the GC chromatogram is representing what the insect is smelling. We have had quite a few examples where the chromatogram doesn't show what is really essential, because the critical components are present in such tiny amounts or because the column did not let these compounds go through.

Tumlinson: There's no doubt that the gas chromatograph is not nearly as sensitive as the insect at detecting compounds and differences.

Dicke: Our appreciation of what the plant does has steadily been growing each year. For instance, with the lima bean system with spider mites, 10 years ago we had some 17 compounds. Subsequently our equipment has improved and now we can detect four times as many compounds. We are getting more knowledgeable about the minor components of the volatile blend. Thus our appreciation of the complexity that the insect is confronted with has increased with technological advances.

Firn: Presumably in 10 years' time you will be seeing hundreds of volatiles in the GC traces as detection sensitivity increases. The question is, which of these components are the important ones? Has anyone done any work with mutants which lack particular volatiles, to see whether that actually modifies the insect responses?

Dicke: I am not aware of work with mutants, but research here in Britain at the John Innes Centre has made two selected lines of *Brassica oleracea* that differ in glucosinolate composition and thus in volatiles derived thereof. They have shown effects on the behaviour of the parasitoid *Diaretiella rapae* (Bradburne & Mithen 1998).

Tumlinson: Insects are learning, and with just a few exceptions I don't think that there's any one compound that's vital: it is the whole blend the response is addressed to. Therefore, if you remove one compound, the insects will learn the blend that's remaining.

Vet: Thinking in evolutionary terms, what then is a better signal? If there is selection pressure on the plants for reliable signals, if there can be selection on the qualitative/quantitative differences in the plant, is it going to be a qualitative difference, or is it just as good to be quantitatively different?

Haukioja: If the evolutionary role of the production of signals by the plant is to reduce herbivory, and the parasitoids need learning to be able to connect their behaviour to this signal, isn't it a surprisingly complicated mechanism? I mean that the first time the parasitoid chooses the herbivore it does it by random and then it learns, and only after learning will the signal really be of benefit to the plant.

Poppy: But there are demonstrations of innate responses. We have shown with the aphid parasitoid, *Aphidius ervi*, that there are innate responses to some of these herbivore-induced synomones (Du et al 1996), and Professor van Emden (Reading University, UK) has suggested that Hopkins' Host Selection Principle may apply to aphid parasitoids, although he now believes that their results may be explained by early adult learning, when the parasitoids emerge from the mummy (Wickremasinge & van Emden 1992, van Emden et al 1997). You could say therefore that there is likely to be no such thing as a truly naïve parasitoid, because wherever it emerged from it has gained chemical information from the host and the host plant.

Tumlinson: But as soon as the host moves to another plant, it has to learn again. This may benefit it immediately, but if there are no other plants of that same type or those same odours around, the learning process has to start over again.

Vet: I think the function of the learning process is to cause a real reduction in spatiotemporal variation. The parasitoid enters a situation that is highly unpredictable beforehand, so by being able to focus on that plant type and the surrounding plant population, the parasitoid will get a benefit in its foraging efficiency. Whether or not the plant benefits from that is not as clear: there are many factors involved. It could be, of course, that by having encountered one caterpillar where there is an aggregated distribution of caterpillars, it will benefit because the parasitoid will remain in that area. Or if plants are related to other plants that are there, closely related plants will benefit because they are more related then the plants that are further away: that's where you can see a benefit of the learning for the plant.

Karban: What is the evidence that plants benefit from releasing this information?

Turlings: I'll try to answer this question in my paper (Turlings & Fritzsche 1999, this volume), but it's not the ultimate evidence. We found that parasitization by *Cotesia marginiventris* reduces feeding by its hosts tremendously: far less leaf material was eaten by parisitized than by unparasitzed caterpillars. In a preliminary laboratory test, this resulted in a higher survival rate of plants attacked by parasitized caterpillars. For other parasitoids this may be quite different. As Louise Vet mentioned, there are even parasitoids that cause their hosts to eat more.

Poppy: The aphid situation is an unusual one, because we are dealing with a clonal organism and a species which will reproduce parthenogenetically and has telescopic generations. Therefore, from an evolutionary point of view the benefit of the plant calling in a parasitoid to kill an aphid are clear: it can have a big impact in terms of that population of aphids on that plant in a very short time. However, with Lepidoptera this may not always be the case: after all, what is the benefit to a plant of bringing in a parasitoid that increases the duration of feeding? That individual plant hasn't benefited at all in the short term.

Vet: I tried to show with the data from my postdoc, Jeffrey Harvey, that this is not really the case. He showed that there was a relation between feeding rate of parasitized caterpillars and parasitoid clutch size, but then it depends whether or not this is more than the feeding rate of an unparasitized caterpillar: this is the crucial fact.

Haukioja: If production of these volatiles is an evolved defence, there should be (or should have been) genetic variance in volatile production due to insect damage. Is there any information on that?

Dicke: Genotypes of plants differ in what they emit. This is as far as we got. No one has shown that you can select for differences, apart from perhaps the research at the John Innes Centre I just mentioned, and the evidence from Jim Tumlinson's group that naturalized cotton produces more volatiles than agricultural varieties. This might indicate that in the absence of selection on this production you lose it. However, this is indirect evidence.

Tumlinson: One problem is that too many of us are working with agricultural varieties. As Marcel Dicke said, we examined about five different varieties of cotton that are grown in southeastern USA. There is slight variation, but not a whole lot. But cotton that is naturalized in the Everglades showed a huge difference: it releases probably eight times the quantity of volatiles.

Vet: Did you follow-up that with field experiments showing the effects of these differences on insects?

Tumlinson: No.

Dicke: With all the work on agricultural plants, it is perhaps surprising to see that in virtually all agricultural plants we have studied we find this phenomenon. One might expect that volatile release would not have been selected for because these crops have always been bred for other traits, such as yield or disease resistance. This selection might even have worked against volatile production.

Pickett: I'd like to say something about non-agricultural crops. In the example I gave in the introduction of the stem-borer control in Africa (p 1), we actually use non-food crops for the intercropping repellent crop plant and for the attractant trap crop. We are thereby capitalizing on the two extremes. We didn't think about it in these terms initially: we simply looked at a whole range of plants and found the ones, mostly wild or forage plants, that did what we required of them.

Schultz: This *segues* to another question that Louise Vet raised about early and late succession. As I look around the room I think there are only a couple of us who work late in succession, on trees for instance. I would prefer not to argue from absence of evidence about whether these phenomena are important late in succession. There are plenty of natural history hints to suggest that they probably are operating. For example, many tree-feeding insects sniff the leaves and move on a basis that suggests that they're trying to avoid being the target. I think we oversimplify our view of the chemistry of late successional plants: they are more complex than we give them credit for. Secondly, there just hasn't been enough work done to draw a conclusion about this. I'll bet we're going to find all of the same phenomena.

Vet: Interestingly, we have a lot of generalist parasitoids there and we know from one study in which we compared the behaviour of generalists and specialists, that the generalists in particular seem to do a lot of learning, because they can fill in the details as they go along.

Schultz: Of course, with trees we have the handicap that if we're going to answer Rick Karban's question about whether there is an advantage to the plant, we have a 50-year wait for them to reproduce.

Pickett: When the plant is damaged, it produces a rapid burst of a large number of compounds. As Ted Turlings says, the insect may not be responding to the major components. This then takes us back to the question that Richard Firn raised: what is the plant making all that material for? How has it evolved to do that? Is the volatile release a side issue to other more important defence chemistry associated with the oxidative bursts, or are the associated chemicals having some effect outside the particular system with which we are concerned, for example against pathogens rather than insects?

Firn: While a plant may benefit directly by making a few compounds to modify insect behaviour, it would be wrong to imagine that we must seek a role for every volatile compound produced. There are good reasons to expect considerable redundancy (Firn & Jones 1996). Because there is a low probability of any chemical possessing specific, potent biological activity, plants will have been selected which produce a great diversity of volatiles. There will probably be many compounds that are along for the ride. This is a reasonable explanation of why there may be 100 volatile compounds produced when many fewer could give the quality of information necessary.

Schultz: I think that we're still waiting for an explanation as to why oak trees emit many millions of metric tons of isoprene in the atmosphere. Perhaps some of these things are combinatorial chemistry advantages that arise secondarily.

Lamb: Is there a correlation between chemical complexity and length of life cycle?

Schultz: There's not enough work done on the long life cycle end to answer that question.

Firn: Please remember that considerable chemical complexity occurs in microbes, which have an incredibly short life cycle. It is also worth noting that although we tend to think of volatile production as being unique to plants, it is common to many organisms. I think we give off volatiles if we are damaged, don't we?

Pickett: Yes. You can smell blood very sensitively. If I cut my hand now, you would probably smell it.

Firn: I had the impression that parasites were fairly specific. Therefore, is there a danger that parasitic insects are attracted to volatiles that have been induced by a herbivore that the parasite cannot use as a host?

Vet: You are right that parasitoids can be extremely specific. What happens is that the more specific these parasitoids are, the more directed or guided their search is by cues that are directly derived from the host itself.

Schultz: At the other extreme, my student, Ahnya Redman, has been able to show that Gipsy moth wounding of aspen trees attracts generalized parasitoids that then parasitize all the other caterpillar species in the same place. Apparently, volatiles emitted by the wounded trees attract a wide range of parasitoid species with broad host preferences.

Pickett: Jon Gershenzon, would you say that the enzymology backs up the idea that Richard Firn has suggested, that there is a more general production capability of volatiles and that is in fact what we are discussing? The enzymology does not seem highly specific. Many of the genes that have been cloned and then expressed for depyrophosphorylases can give a wide range of products. This would suggest the evolution of product generation is the issue, rather than of the production of specific compounds.

Gershenzon: By and large we don't have the information yet to know how many enzymes are involved in the production of herbivore-induced volatiles. First, we must remind ourselves that this is a large group of compounds which keeps getting larger with the increasing sensitivity of detection techniques. The production of some volatiles is induced by herbivory, whereas in certain plants, such as cotton (as shown by the work of Jim Tumlinson), there is actually a stored reservoir of preformed isoprenoid volatiles that are simply released by herbivory. These stored compounds, which are largely cyclic terpenoids, are actually sequestered in the sub-epidermal pigment glands and are released immediately by feeding. The herbivore-induced terpenoid compounds which emerge later are typically acyclic compounds. To produce these many different volatiles, a large number of different enzymes is probably required.

It is also interesting to note that almost every plant that has been looked at seems to produce a rather similar set of herbivore-induced volatiles. In the systems that have been studied, we frequently see linalool, ocimene, β-farnesene, caryophyllene, the C_{11} and C_{16} homoterpenes, etc. For some reason, we keep going back to the same set of compounds. This is in contrast to the compounds sequestered prior to attack, which show much more diversity. Thus, for the herbivore-induced volatiles, we may be dealing with the same enzyme systems in taxonomically distant species. This can help focus the search for the biochemical machinery involved. I think it is striking that, when you consider the enormous universe of isoprenoids out there — 30 000 or so at last count — there is actually a rather restricted group that keep coming up again and again as herbivore-induced volatiles. In my mind, that makes the quest for the enzymology and function of these compounds much more interesting.

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