

Plant Chemicals Influencing Insect Behaviour

O. R. W. SUTHERLAND

Entomology Division, DSIR, Auckland

The relationship between insects and plants is a dynamic one, which may favour either the insect or the plant. The plant may discourage the insect's attention by various defence strategies or it may encourage visitations by insects. Plant chemicals are deeply implicated in this relationship and influence 2 main areas of insect behaviour. These are 1, feeding behaviour and 2, sexual and reproductive behaviour, and we will look at them in turn in this review.

1. Plant chemicals and feeding behaviour

The ultimate consumption of plant material by phytophagous insects is preceded by a complicated series of behavioural interactions between the food plant and the insect. If the insect is not already on the plant, it must get there. It must then decide whether or not the plant is suitable as food, and if it is, must finally chew, lick, or suck up nutrients from it. The behavioural elements which make up this intricate sequence depend upon the insect receiving various sensory stimuli from the plant. These may have a positive or a negative effect on the behavioural sequence.

Apart from visual cues such as shape and colour, and touch which is involved in some cases, much of the information the insect receives from the plant is chemical in nature. It is perceived by specialised sensory receptors scattered over the insect's body but concentrated on the mouth parts and the tarsi. These receptors are classified according to their primary function as either smell or taste receptors.

Plant chemicals which affect behaviour have also been classified into 2 main groups. There are those which the insect can utilise as nutrients as well as behavioural cues, and then there are those which have no apparent nutrient value but which serve only as sign stimuli, enabling the insect to select the appropriate food or host-plant. These are known as secondary plant chemicals. The relative roles of these 2 groups of chemicals was debated for years, some claiming, for example, that secondary plant substances exist solely to attract or repel animals or insects (Fraenkel 1959, 1969). The current view is that both are important and that insect species differ in their reliance on the 2 groups (Kennedy and Booth 1951).

So far I have implied that the insect is hunting for the plant – either to feed on, to gain shelter from, or to lay its eggs upon – and that it locates the plant by recognising its characteristic odour and taste. But this is not always the case. Plants have also evolved mechanisms for attracting insects to them, from which they, the plants that is, are the principal beneficiaries rather than the insects, and we shall look at these too.

Plant odours can attract or repel insects. In either case the volatile plant constituent affects the *orientation* of the insect with respect to the plant (Dethier *et al.* 1960). It may influence larval or adult orientation or both. We have found that 3rd instar grass grubs are strongly attracted by the odour of fresh ryegrass root and that the odour of some legumes is even more attractive but we have not, as yet, been able to identify the root volatiles involved (Sutherland 1972, Sutherland and Hillier 1974a). On the other hand, in the case of the attraction of young codling

moth larvae to apple we have been able to identify the attractant. The active material proved to be an obscure sesquiterpene called α -farnesene present in the cuticular coating of apples. Larvae moved rapidly to small filter paper rectangles treated with a few nanograms of the substance (Sutherland and Hutchins 1972). Young silkworm larvae which feed exclusively on mulberry are also attracted by the odour of their host plant. In this case the active compounds occurred in the mulberry leaves and were found to be the terpenoids citral, linalyl acetate, linalool, terpinyl acetate, and hexenol (Watanabe 1958, Hamamura 1970). In all these cases the insect's locomotory behaviour is influenced by the plant odour in such a way that the insect moves toward the plant in a directed fashion.

Some situations are more complex. During their tunneling in conifers, scolytid bark beetles cause the release of volatile oleoresins from the tree. These volatiles, together with the beetle pheromones which are released at the same time, attract flying dipterous predators to beetle-infested trees. But because the beetles tunnel beneath the bark the predator, having located the tree, still has to locate its prey. Females of one such predator, the dolichopodid fly *Medetera aldrichii* are guided in selecting their oviposition sites on the bark by volatiles emanating from the prey bark beetle galleries. Of these compounds D- α -pinene is particularly important. And the newly hatched fly larvae, which actually attack the immature scolytids, are strongly attracted by the same chemical (Fitzgerald and Nagel 1972). They move towards and then down the tunnel made by the adult beetles.

I have mentioned a number of terpenoids so far, but besides these volatile sulphur compounds have long been known to attract insects and in 2 cases the same compounds attract both adults and larvae. Although the vegetable weevil *Listroderes obliquus* is considered to be polyphagous, it inflicts particularly severe damage on plants in the families Cruciferae and Umbelliferae. The principal odours of these plants are characterised by volatile mustard oils and of these, allyl isothiocyanate and phenyl isothiocyanate are strong attractants for *Listroderes* larvae. The same compounds also attract walking adult weevils and are found in mustard, cauliflower, cress, turnips, and nasturtium (Matsumoto 1970).

Other sulphur-containing compounds characteristic of the odour of onions are used by the female onion maggot *Hylemya antiqua* to locate the plant and are attractive to her larvae. In particular, allyl sulphide ($\text{CH}_2:\text{CHCH}_2)_2\text{S}$, n-propyl sulphide ($\text{C}_3\text{H}_7)_2\text{S}$, methyl disulphide (CH_3S)₂, and propyl and iso-propyl mercaptan ($\text{C}_3\text{H}_7\text{SH}$) and ($\text{CH}_3)_2\text{CHSH}$ (Matsumoto 1970).

Fewer examples are known of plant-produced volatile repellents. But the catnip plant, *Nepea cataria* is very potent in this regard. It produces a cyclopentanoid monoterpene called nepetalactone which, although very attractive to cats, repels at least 17 species of phytophagous Homoptera and Coleoptera (Eisner 1964). Even polyphagous insects can be affected in this way. For example, the locust *Schistocerca gregaria* does not feed on lavender because the odour of the plant contains a volatile repellent, which causes hungry locusts to move away without actually coming into physical contact with the leaf at all (Goodhue 1962).

In the feeding sequence, once the insect has located the food plant an "arrestant" may prevent further searching behaviour. Arrestants are defined as chemicals which cause insects to aggregate in contact with them. They may be perceived as odours or tastes, and although they are thought to be widely implicated in insect feeding and egg-laying behaviour, few have been isolated and identified. One example is coumarin. This chemical is produced by *Melilotus* or sweetclover, and arrests flight by the sweet clover weevil *Sitona cylindricolis* (Heidweg and Thorsteinson 1961). The ultimate effect of such a chemical is aggregation of the insects on the host plant.

The next stage in the feeding sequence is ingestion. This process involves biting and swallowing and the chemicals which control these activities are perceived

as tastes by gustatory receptors. They are known as biting stimulants and feeding or phago-stimulants respectively, and have been studied very extensively. The biting behaviour of larvae of the silk moth *Bombyx mori* is stimulated by 3 components of mulberry leaves: β -sitosterol, which is contained in the waxy substance covering the upper surface of the leaves is 1, and 2 water soluble flavones isoquercitrin and morin are the others (Ito 1961, Hamamura 1970). These 3 chemicals are found together in only a very few plants, of which mulberry is one. In the case of grass grub, *Costelytra zealandica*, which is polyphagous, the reverse is true because 1 of its major biting stimulants, ascorbic acid, is found throughout the plant kingdom (Sutherland and Hillier 1974b). But obviously, being attracted to the right host plant, pausing on it, and taking a test bite is not enough. If the food is appropriate it must be ingested. This process is controlled by chemicals contained in the plant material and liberated during the test bite. Both feeding stimulants and feeding deterrents are perceived by the gustatory receptors located around and in the mouth and continued feeding depends on the relative stimulation from these. There will be a balance between stimulants and deterrents and this will determine host plant selection and the extent of feeding.

Phagostimulants fall into 2 broad categories: nutrient chemicals and secondary chemicals. In general it is true to say that phagostimulants for polyphagous insects tend, as one might expect, to be ubiquitous nutrient chemicals and those for oligo- and monophagous insects both nutrient and secondary chemicals. Sugars are widely effective as feeding stimulants, especially sucrose, as are some amino acids and lipids. Grass grubs respond strongly to sucrose, glucose, aspartic acid, and glutamic acid all of which are common to most plants (Sutherland 1971, Sutherland and Hillier 1974b). But a close relative, black beetle (*Heteronychus arator*), shows an unusual and strong response to maltose, as well as to sucrose (Sutherland 1976).

On the other hand, *Pieris brassicae*, the oligophagous cabbage white butterfly, relies largely on secondary plant chemicals for food plant selection. Sucrose certainly plays a role, but the presence of mustard oil glucosides is essential for continued feeding. In particular, sinigrin, glucocapparin, glucotropaeolin, and glucosinabin (Schoonhoven 1967). In this regard, the feeding behaviour of the cabbage white butterfly agrees well with the dual discrimination theory of Kennedy and Booth (1951) which stresses the phagostimulant character of both secondary plant chemicals and nutritious substances.

Turning again to the silk moth, *Bombyx mori*, which is monophagous, you will recall that β -sitosterol and isoquercetin were powerful biting stimulants, and one might have expected some highly specific "mulberry factor" to be required for ingestion. In fact this is not the case. The phagostimulants for *Bombyx* larvae are principally sucrose, inositol, and cellulose which, together with silica and phosphate, promote continuous feeding. All these compounds are commonly found in green leaves. Apparently the monophagy of this insect is determined mainly by feeding deterrents present in virtually every other plant. This situation underlines the importance of feeding deterrents, and in recent years many instances have been reported of plant constituents which deter feeding by insects (Chapman 1974). These are usually regarded as being a part of the plant's overall defence strategy against insect attack. Other elements of the plant defence may include physical factors such as prickles, hairs, oils or waxes, repellent odours, and toxins. Some or all of these may combine to confer "resistance" on a plant.

Feeding deterrents include many different chemicals and some are amongst the normal constituents of plants. Larvae of the tropical army worm *Spodoptera litura* are polyphagous but there are some plants which they do not eat, and if extracts from the leaves of these plants are painted on to otherwise acceptable leaves, these are then rejected by the *Spodoptera* larvae. Three such unacceptable

plants are *Cocculus trilobus*, *Clerodendron trichotomum*, and *Parabenzoin trilobum*. Research has shown that each of these has a separate and chemically distinct feeding inhibitor. In *Cocculus* it is an alkaloid isoboldine (Wada and Munakata 1968); it consists of 2 diterpenes in the case of *Clerodendron* (Kato *et al.* 1973); and 2 sesquiterpenoids in *Parabenzoin* (Wada, Enomoto *et al.* 1968; Wada, Matsui *et al.* 1970).

The same seems to be true of pasture plant resistance to grass grubs. The feeding deterrents present in resistant lucerne (*Medicago sativa*) and *Lotus pedunculatus* are quite different chemically and each species contains more than 1 deterrent (Sutherland *et al.* 1975a, b).

One of the very few cases where resistance has been positively linked to an identified feeding deterrent is that of sweet clover resistance to the blister beetle, *Epicauta*. Varieties of sweet clover (*Melilotus*) containing high concentrations of coumarin are resistant, whereas those with low concentrations are susceptible (Gorz *et al.* 1972).

But where nature fails to impart resistance to a plant, man may succeed and the artificial creation of resistance holds great potential. Let us look at an example. Azadirachtin is a potent feeding deterrent derived from the neem tree *Azadirachta indica*. If the chemical is applied to the soil in which young bean plants are growing, it is absorbed by the bean roots, translocated to the growing points and protects treated beans from attack by hungry locusts (*Schistocerca gregaria*) (Gill and Lewis 1971). Such a systematic action by an applied resistance factor is a very exciting development and offers considerable promise.

2. Plant chemicals and sexual and reproductive behaviour

Plant chemicals are also involved in the egg-laying behaviour of many phytophagous insects but here their role is less predominant and they take their place beside other factors such as texture, surface configuration, and colour. Nor is the plant odour always essential for expression of the behaviour pattern, although maximal egg-lay does depend upon the presence of all factors at appropriate levels. In the case of the codling moth, gravid females will lay some eggs in the absence of any olfactory stimulant at all, but the presence of the apple volatile α -farnesene stimulates a much heavier egg-lay (Wearing and Hutchins 1973).

Females of another lepidopterous species, the spruce budworm *Choristoneura fumiferana*, are very selective during oviposition. They prefer white spruce to balsam fir or red or black spruce. Several factors including needle spacing, light, and gravity have been implicated in this selectivity but the odour of the needles is especially important. A crude mixture of natural pinenes induces a strong ovipositional response, and of these D- α -pinene and L- α -pinene are each highly active (Städler 1974). It seems that the blend of terpenes in the volatiles of the various spruces determines the final selection of oviposition site by the female moth.

In all these examples, the plant-produced chemicals have directly influenced insect behaviour. But the case of the polyphemus moth *Antheraea polyphemus* is somewhat different. Like many other lepidopterous species, female moths release a pheromone which attracts males and stimulates copulation. But the moth will not mate in the laboratory unless leaves of the host plant red oak are present. Once a sexually mature female perceives the odour of the leaves she adopts a calling posture, releases the pheromone and mating ensues (Riddiford and Williams 1967). The leaf volatile which triggers this behaviour has been identified as trans-2-hexenal, but the chemical is not specific to red oak. In fact, it is commonly found in green leaves and certainly has been found in maple, birch, beech, and elm leaves in roughly the same quantity as in oak. The reason that these other leaves fail to stimulate sexual activity is that they contain masking odours which block the action of the hexenal (Riddiford 1967).

Plant chemicals can also indirectly affect the sexual behaviour of male Lepidoptera. Various plants containing pyrrolizidine alkaloids are visited by Lepidoptera – *Heliotropium* and *Crotalaria* are 2 such plants. Amongst the visiting Lepidoptera are males of the subfamily Danainae. These insects are attracted to the plants by olfactory cues and spend considerable periods licking at the leaf surface. The significance of this behaviour is now becoming clear. Males of this family possess hairpencil pheromone glands which disseminate an aphrodisiac pheromone making females receptive to mating. In the case, for example, of *Danaus chrysippus* the aphrodisiac is a dihydropyrrolizine and chemical evidence has now been obtained that the precursors for the biosynthesis of the dihydropyrrolizines in danaine hairpencils are acquired during males' visits to those plants which contain the pyrrolizidine alkaloids (Pliske 1975). In the case of *Danaus chrysippus* the pheromone precursor is obtained by licking *Heliotropium* plants (Schneider 1975). So here the link between the plant chemicals and insect behaviour, although indirect, is very intimate indeed.

The insect does not, however, always modify the plant chemical before utilising it. Take the example of larvae of the sawfly *Neodiprion sertifer* (Hymenoptera: Diprionidae) which feed on Scotch pine (*Pinus sylvestris*). The insects extract from the ingested plant tissue a terpenoid resin and store it unaltered in 2 compressible diverticular pouches of the foregut. When the larvae are disturbed or attacked, they discharge the resin through the mouth and it is an effective deterrent to predators such as birds, spiders, and ants. The material contains at least 9 compounds, all of which are found in host tissues and which actually comprise the chemical defence of the pine. The insect has simply appropriated the intact resin and utilised it for its own defence (Eisner *et al.* 1973).

In the examples we've been discussing the main beneficiary of the plant-insect relationship is the insect, which derives food and shelter from the plant. But there are cases where the plant appears to derive all the benefit and our last example is one of those. As you know, many insects are attracted to flowers and feed on the nectar. In so doing, they transfer pollen from one flower to another. Some species of orchids, however, produce no nectar and have evolved a special mechanism for ensuring pollination. The flowers of *Ophrys* spp. produce chemicals which are identical with the chemicals used as a sex attractant by females of some wasp species (Scoliidae, Sphecidae). Males of these species are attracted to the flowers by the odour and attempt to copulate with them. The flowers themselves are constructed in such a way as to encourage copulatory activity and in so doing the male wasps cover their head with pollen, which is then carried on to the next flower (Kullenberg 1961). Several species of orchid and several species of solitary bees and scoliid wasps are involved in this extraordinary relationship. And, perhaps not surprisingly, since sex attractants are characteristically specific, the orchid scents are specific for species groups of the hymenopterous males (Kullenberg 1973). So far, little is known of the chemicals involved but again terpenes, particularly γ -cardinene, play an important role (Priesner 1973).

It should be clear by now that the relationship between the plant and the behaviour of the insects associated with it may be relatively simple as perhaps in the case of grass grubs or highly complex as in the case of the pyrrolizidine-seeking male danaine butterflies. But whatever the complexity, the value in unravelling the threads of the relationship is undoubted. Understanding the mechanisms of insect behaviour gives us the power to manipulate the behaviour and therein lies a major hope for pest control in the future.

REFERENCES

- CHAPMAN, R. F. 1974: The chemical inhibition of feeding by phytophagous insects: a review. *Bulletin of Entomological Research* 64: 339-63.
DETHIER, V. G.; BARTON BROWN, L.; SMITH, C. N. 1960: The designation of chemicals in terms of responses they elicit from insects. *Journal of Economic Entomology* 53: 134-6.

- EISNER, T. 1964: Catnip: Its raison d'être. *Science, Washington* 146: 1318-20.
- ; JOHNESSEE, J. S.; CARRELL, J.; HENDRY, L. B.; MEINWALD, J. 1973: Defensive uses by an insect of a plant resin. *Science, Washington* 184: 996-9.
- FITZGERALD, T. D.; NAGEL, W. P. 1972: Oviposition and larval bark surface orientation of *Medetera aldrichii* (Diptera: Dolichopodidae): response to a prey-liberated plant terpene. *Annals of the Entomological Society of America* 65: 328-30.
- FRAENKEL, G. 1959: The raison d'être of secondary plant substances. *Science, Washington* 129: 1466-70.
- ; 1969: Evaluation of our thoughts on secondary plant substances. *Entomologia experimentalis et applicata* 12: 473-86.
- GILL, J. S.; LEWIS, C. T. 1971: Systemic action of an insect feeding deterrent. *Nature, London* 232: 402-3.
- GOODHUE, R. D. 1962: The effects of stomach poisons on the Desert Locust. Ph.D. Thesis, University of London.
- GORZ, H. J.; HOSKINS, F. A.; MANGLITZ, S. R. 1972: Effect of coumarin and related compounds on Blister Beetle feeding in Sweetclover. *Journal of Economic Entomology* 65: 1632-5.
- HAMAMURA, Y. 1970: The substances that control the feeding behaviour and the growth of the silkworm *Bombyx mori*. In Wood, D. L.; Silverstein, R. M.; Nakajima, M. (eds.) *Control of insect behaviour by natural products*. Academic Press, New York.
- HEIDWEG, H.; THORSTEINSON, A. J. 1961: The influence of physical factors and host plant odour on the induction and termination of dispersal flights in *Sitona cylindricollis* Fabr. *Entomologia experimentalis et applicata* 4: 165-77.
- HILLYER, R. J.; THORSTEINSON, A. J. 1969: The influence of the host plant or males on ovarian development or oviposition in the diamond back moth *Plutella maculipennis* (Curt.). *Canadian Journal of Zoology* 47: 805-16.
- ITO, T. 1961: Sterol requirements of the silkworm, *Bombyx mori*. *Nature, London* 191: 882-3.
- KATO, N.; MUNAKATA, K.; KATAYAMA, C. 1973: Crystal and molecular structure of the p-bromobenzoate chlorohydrin of clerodendrin A. *Journal of the Chemical Society Perkin II*: 69-73.
- KENNEDY, J. S.; BOOTH, C. O. 1951: Host alternation in *Aphis fabae* Scop. I. Feeding preferences and fecundity in relation to the age and kind of leaves. *Annals of Applied Biology* 38: 25-64.
- KULLENBERG, B. 1961: Studies in *Ophrys* pollination. *Zoologiska Bidrag fran Uppsala* 31.
- 1973: Field experiments with chemical sexual attractants on Aculeate Hymenoptera males. I. *Zoon Supplement* 1: 31-42.
- MATSUMOTO, Y. 1970: Volatile organic sulphur compounds as insect attractants with special reference to host selection. In Wood, D. L.; Silverstein, R. M.; Nakajima, M. (eds.) *Control of insect behaviour by natural products*. Academic Press, New York.
- PLISKE, T. E. 1975: Attraction of Lepidoptera to plants containing pyrrolizidine alkaloids. *Environmental Entomology* 4: 455-73.
- PRIESNER, E. 1973: Reaktionen von Riechrezeptoren männlicher Solitärbielen (Hymenoptera, Apoidea) auf Inhaltsstoffe von *Ophrys*-Blüten. *Zoon Supplement* 1: 43-54.
- RIDDIFORD, L. M. 1967: Trans-2-hexenal: Mating stimulant for Polyphemus moths. *Science, Washington* 158: 139-41.
- ; WILLIAMS, C. M. 1967: Volatile principle from oak leaves: Role in sex life of the Polyphemus moth. *Science, Washington* 155: 589-90.
- SCHNEIDER, D. 1975: Pheromone communication in moths and butterflies. In Salun, R.; Hillman, P.; Parnas, I.; Werman, R. (eds.) *Sensory physiology and behaviour*. Plenum, New York.
- SCHOONHOVEN, L. M. 1976: Chemoreception of mustard oil glucosides in larvae of *Pieris brassicae*. *Koninklijke Nederlandse Akademie Wetenschappen, Proceedings Series C*. 70: 556-68.
- SUTHERLAND, O. R. W. 1971: Feeding behaviour of the Grass Grub *Costelytra zealandica* (White) (Coleoptera: Melolonthinae) - I. The influence of carbohydrates. *N.Z. Journal of Science* 14: 18-24.
- 1972: Olfactory responses of *Costelytra zealandica* (Coleoptera: Melolonthinae) larvae to grass root odours. *N.Z. Journal of Science* 15: 165-72.
- 1976: The influence of maltose and other carbohydrates on the feeding behaviour of *Heteronychus arator* (Scarabaeidae: Coleoptera). *Experimentia* 32: 701-20.
- ; HILLIER, J. R. 1974a: Olfactory response of *Costelytra zealandica* (Coleoptera: Melolonthinae) to the roots of several pasture plants. *N.Z. Journal of Zoology* 1: 365-9.
- ; — 1974b: Feeding behaviour of the Grass Grub *Costelytra zealandica* (White) (Coleoptera: Melolonthinae). 3. The influence of amino acids, ascorbic acid and inorganic salts. *N.Z. Journal of Zoology* 1: 211-6.
- ; HUTCHINS, R. F. N. 1972: α -farnesene, a natural attractant for codling moth larvae. *Nature, London* 239: 170.
- ; HOOD, N. D.; HILLIER, J. R. 1975a: Lucerne root saponins a feeding deterrent for the Grass Grub *Costelytra zealandica* (Coleoptera: Scarabaeidae). *N.Z. Journal of Zoology* 2: 93-100.

- ; MANN, J.; HILLIER, J. R. 1975b: Feeding deterrents for the Grass Grub *Costelytra zealandica* (Coleoptera: Scarabaeidae) in the root of a resistant pasture plant *Lotus pedunculatus*. *N.Z. Journal of Zoology* 2: 509-12.
- STADLER, E. 1974: Host plant stimuli affecting oviposition behaviour of the Eastern Spruce Budworm. *Entomologia experimentalis et applicata* 17: 176-88.
- WADA, K.; ENOMOTO, Y.; MATSUI, K.; MUNAKATA, K. 1968: Insect antifeedants from *Parabenzoin trilobum* (1). Two new sesquiterpenes, shirimodiol-diacetate and -mono-acetate. *Tetrahedron Letters* No. 45: 4673-6.
- ; MUNAKATA, K. 1968: Naturally occurring insect control chemicals. Isoboldine, a feeding inhibitor, and cocculolidine, an insecticide, in the leaves of *Cocculus trilobus* D.C. *Journal of Agricultural and Food Chemistry* 16: 471-4.
- ; MATSUI, K.; ENOMOTO, Y.; OGISO, O.; MUNAKATA, K. 1970: Insect feeding inhibitors in plants. Part 1. Isolation of three new sesquiterpenoids in *Parabenzoin trilobum* Nakai. *Agricultural and Biological Chemistry* 34: 941-5.
- WATANABE, T. 1958: Substances in Mulberry leaves which attract silkworm larvae (*Bombyx mori*). *Nature, London* 182: 325-6.
- WEARING, C. H.; HUTCHINS, R. F. N. 1973: α -farnesene a naturally occurring oviposition stimulant for the codling moth, *Laspeyresia pomonella*. *Journal of Insect Physiology* 19: 1251-6.
-