Molecular messengers in insect biocommunication: Modality and relevance in biological control

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Increasing relevance of molecular communication in insects involving the dynamics of receptor mechanisms, especially relating to tritrophic systems, has increased the prospects of better utilization of biological control practices. The need for intensive studies of receptor systems in insects, to be able to appreciate the involvement of such molecular messengers as kairomones and pheromones in biocommunication is highlighted in this article.

VOLATILE phytochemicals restricted to alcohols, ketones, aldehydes (C_{16}), esters (C_{14}), aromatics ($< C_{12}$), terpenes ($< C_{15}$) play an important role in insect communication systems and prospects for manipulating natural enemies as well as pest populations have led to the increased recognition of such systems. Advances in microanalytical chemistry, ability to manipulate chemicals for insect control as well as electroantennogram responses of insects, reflecting the adaptive significance of differential olfactory sensitivity to both insect hosts and parasites, have enabled a better understanding of the responses to chemical systems. Biocommunication, in which one insect produces a signal, which, when responded to by another, confers some advantage to the signaller, has become an essential component of behavioural studies[1]. It is the primary mode of information transfer used in such functions as host location by herbivores and natural enemies, avoidance of predation and signalling of opposite sexes for mating. Analysis of the air surrounding plants for head space volatile yields mixtures of a dozen or even a hundred compounds. Smaller molecular weight compounds tend to be more volatile and are of importance in attracting the host from a distance.

Molecular messengers

Infochemicals, as these are called, involve the pheromones, kairomones, allomones, and synomones, and may include locomotor stimulant, arrestant, attractant, repellent, or deterrent behaviour. Of all communications systems, chemical communication is the slowest, since on release, they linger in the air and are no more under the control of the emitter. AMCE or amplitude modulated chemical emission is known in a few instances that have communication value beyond that of the chemical blend. A mixture of chemicals or a single chemical released into the environment by a female, triggers an immediate response of sexual behaviour by forming signals disclosing the presence of conspecific females to the males, which by positive anemotaxis locate the females upwind. Pheromones are 10–18 carbon compounds, and blends or mixtures are more effective and even at low molecular levels the females evoke sexual responses in males. A hierarchy of behavioural patterns occurs with increasing stimulation by sex pheromones, culminating in mating. Significantly enough, males of some danaid butterflies have eversible extrusible abdominal hair pencils which produce the pheromone danaidone directly on the female antennae and act as aphrodisiacs. While the components of the pheromones vary with insects, what is more relevant is the nature and diversity of olfactory responses of these chemicals. For example, in the silkworm *Bombyx mori* the chemical composition of the pheromone is (E,Z)-10,12-hexadecadienol, in the pink bollworm *Pectinophora gossypiella*, it is a blend of Z,Z-7,11-hexadecadienyl acetate and E,Z-7,11-hexadecadienyl acetate and in the honey bee queen, *Apis mellifera*, it is (E)-9-*oxo*-2-decenoic acid and (E)-9-hydroxy-2-decenoic acid. Behavioural responses depend on the frequency of interaction of the pheromonal components with the receptor cells. While the electro-antennogram (EAG) represents the summated receptor potentials of the antenna, single cell recordings are more specific allowing us to make comparisons on structure–activity relationships. For example, a sensillum trichoderm from the antenna of the male silkworm responding to bombykol and bombykal, as is evident from the difference in the spike amplitude (Figure 1).

Insect molecular bioelectronics

More than 2000 sensory neurons, largely olfactory, are associated with a large number of sensillae in the antennae, which efficiently filter the chemical molecules from the airstream (Figure 2). The sensillae are filled

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with a fluid and pheromone molecules that impinge on the sensory hairs reach the acceptor sites of receptor cells by surface diffusion. The acceptor molecules are activated and induce conductance charges across cell membranes of dendrites which produce electrical impulses that pass down the antennal hairs to the insect brain[2,3]. The receptors of the sensillae vary in number and distribution and in terms of receptivity the complements of each sensillum is different. The abundance of olfactory and mechanosensory sensilla on the terminal segment of the antenna of an egg parasite such as *Anastatus ramakrishnae* enables it to detect the parasitized from a non-parasitized host egg (Figure 3). Chemistry of signal transduction is vital for the overall communication system and the frequency interactions of pheromonal components with the receptor cells is important[4]. Adsorption of molecules on antennal hair surfaces increases the efficiency of the 'molecular catch'[5].

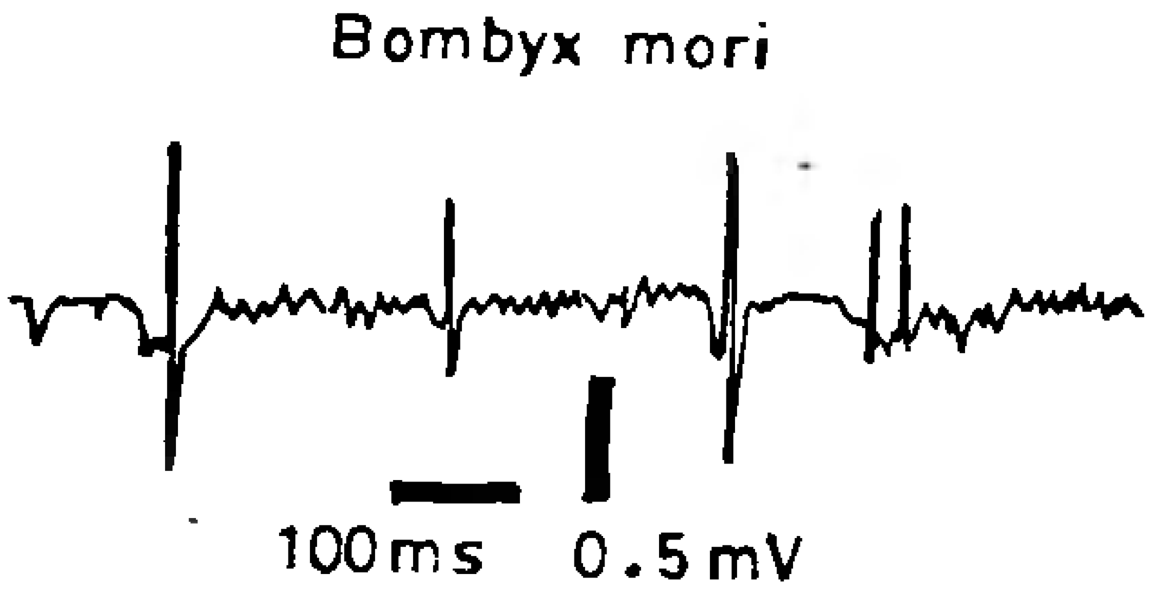

Figure 1. Single cell recordings from a sensillum trichodeum of *Bombyx mori*. Spikes with a large amplitude represent responses to bombykol and those with a smaller amplitude represent responses to bombykal.

Single cell recordings from sensilla basiconica of *Leptinotarsa decemlineata* have shown five types of responses to different volatiles showing well-developed capacity of odour discrimination to *cis* and *trans* (E and Z) isomers of 2-hexen-1-ol, 3-hexen-1-ol, *trans* C6 alcohols and C6 aldehydes, *cis*-3-hexen-1-ol and methyl

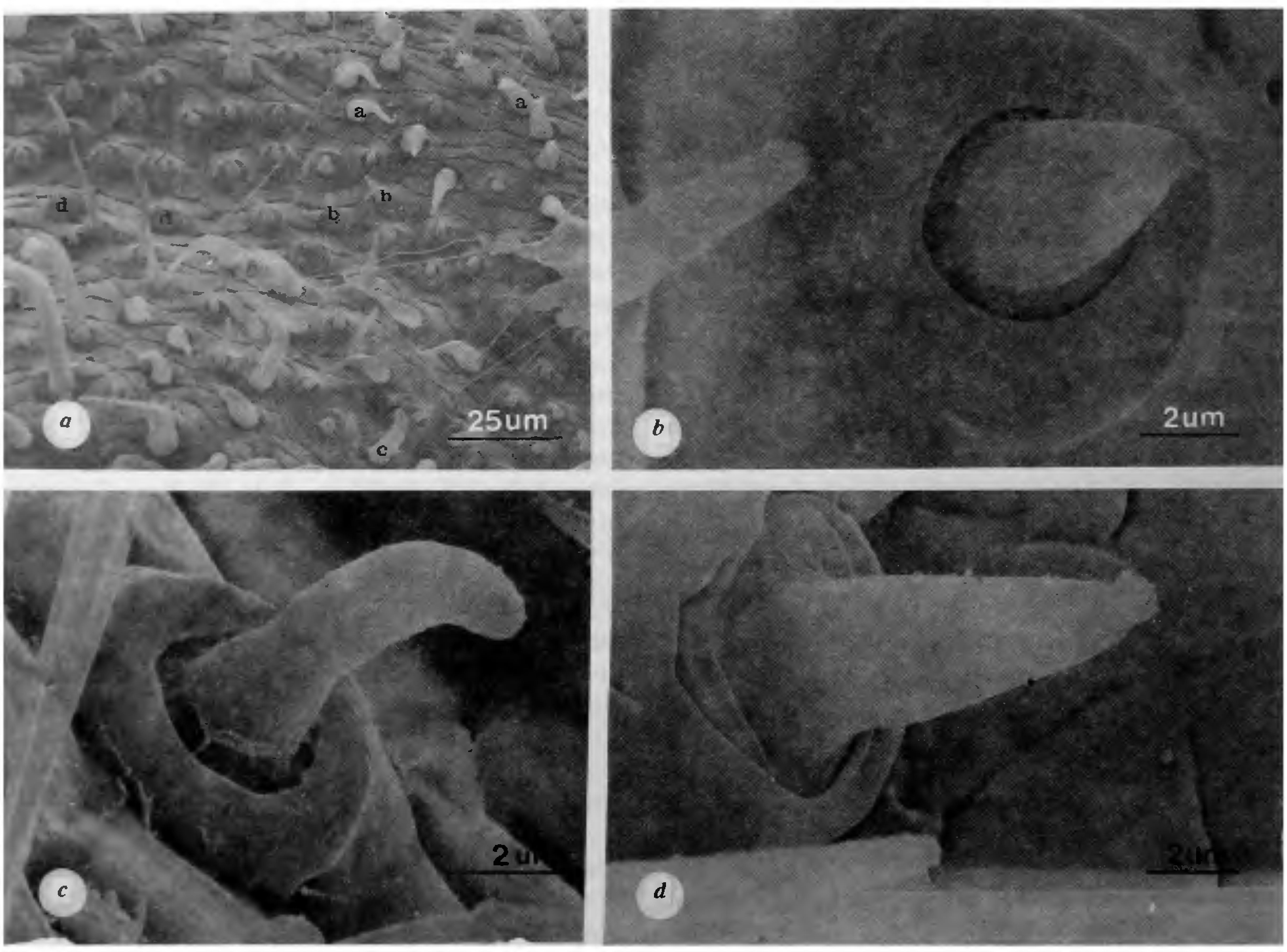

Figure 2 *a–d*. *a*, Sensillar diversity on the distal segment of an antenna. Numerous sensilla chaetica (a) with grooved shafts and pointed tips; sensilla basiconica (b); sensilla trichodea (c) with slightly grooved shafts and conical pegs (d). *b*, A putative sensilla basiconica. *c*, An enlarged SEM of sensilla basiconica. *d*, SEM of sensilla trichodea.

salicylate (Figure 4). Similarly in *Locusta migratoria*, individual sensilla coeloconica showed receptor responses to C5–C9 aliphatic acids, alcohols and aldehydes. In *Apis mellifera*, sensilla placodea and sensilla trichoidea occurring in large numbers on the 8th terminal segment of antenna, show ten distinct olfactory responses[6]. Olfactory responses offer the maximum efficiency, since the signals achieved through olfaction act at very minute concentrations, even at molecular levels such as 1–20 mol ml^{-3} air, though more efficient response occur at 100–200 mol ml^{-3} air as in the case of several lepidopterans.

To cite specific instances, moths being active after dark emit IR rays during wing vibrations and the fine structure of the antennae shows that parts of the antennae serve as infrared receptions, the pectinations of the antennae indicating the operative wavelength. IR radiation being a wavelength phenomenon can be 'tuned into' and the vibrating scent molecules given off by the female, enable the male to 'home-in' towards the molecules. As a result, the insect operates as a tiny electronic detector of infrared and microwave frequencies. The entire concept has come to be known as 'insect molecular bioelectronics'.

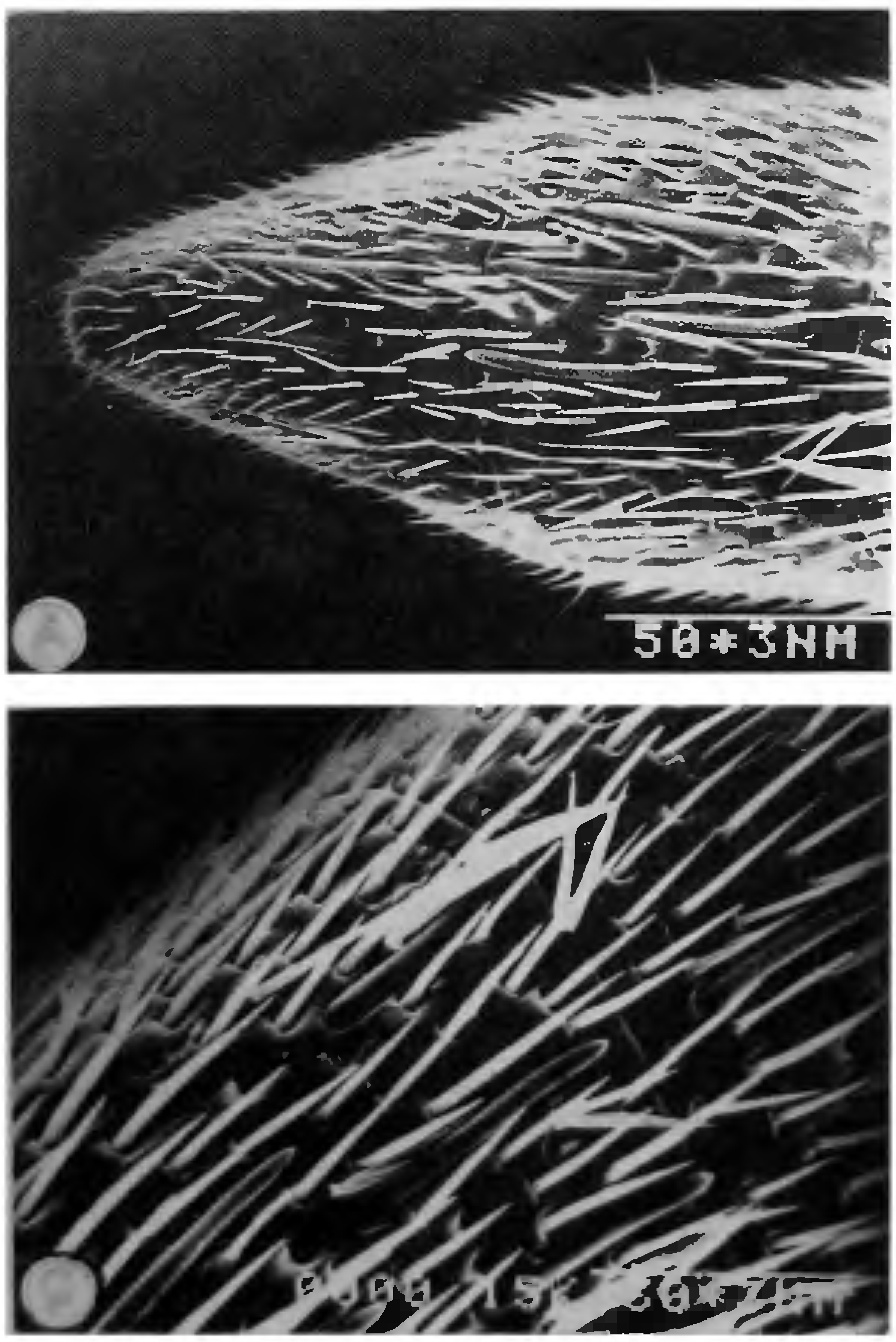

Figure 3. Chemosensory and olfactory sensillae on the terminal antennal segment of *Anastatus ramakrishnae*.

Volatile chemicals and parasite host-seeking behaviour

Parasitoids are faced with problems of nutritional specificity of hosts, a combination of nutritional and hormonal factors affecting host suitability. Plants communicate with members of the third trophic level, since plants under attack by insects emit chemical signals that guide natural enemies to the site of plant damage. Semiochemicals mediating host finding emanate from frass, mandibular, labial and other secretions, exuviae and moth scales and damage tissues associated with the plant host[7]. In egg parasites tuning to the long distance sex-attractant pheromones of their host, unrelated parasitoids using aggregation pheromones of their hosts, and location of specific larval hosts by frass odours, the role of chemical communication or signalling effects in the behaviour of insects, have struck roots. Such signals become valuable when host insects are concealed as in the case of bagworms, like *Eumeta crameri* which are established pests of some social forestry trees like *Acacia nilotica*. Chemical communication between its

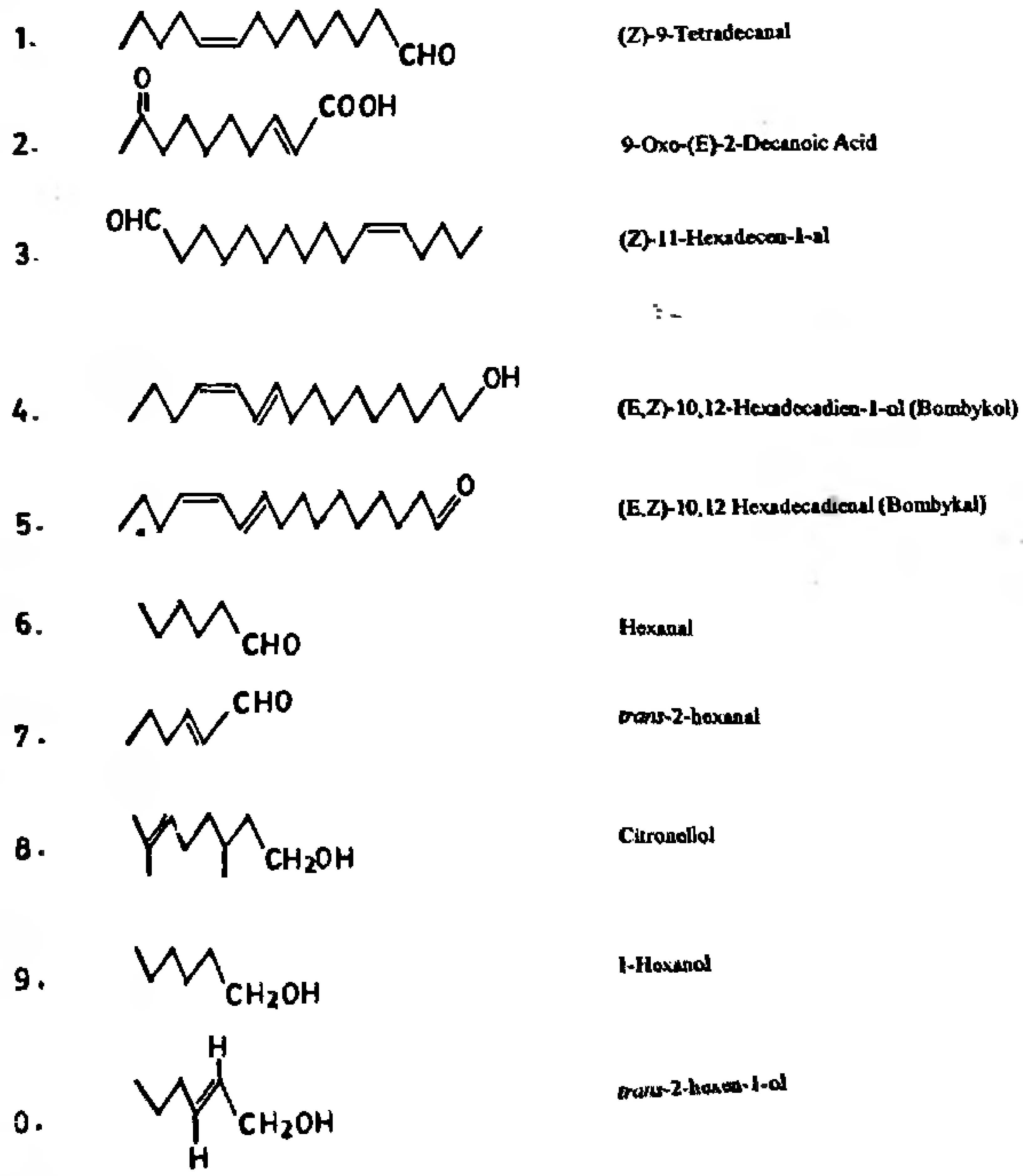

Figure 4. Representative structural profiles of some allelochemics.

ichneumonid parasite *Sinophorus psyscheae* has been established, wherein heptacosane, eicosane and octadienal in the larval and bag extract act as positive cues along with frass extracts which attract more parasites[8].

The long chain hydrocarbon tricosane in moth scales acts as a kairomone for *Trichogramma* eliciting and maintaining host-seeking behaviour. Volatile chemicals such as hexatriacontane, pentacosane, heptadecane, docosane and 2,6,10 dodecatrienal identified from scales of cotton fed *Helicoverpa armigera* have been known to influence the parasitic potential of *Trichogramma chilonis* and can be employed in manipulating entomophagous activity in biocontrol programmes[9,10]. Of equal interest are the volatile profiles of body washings and egg washings of *Helicoverpa armigera* reared on various cultivars of chickpea. While phytol, nonyl phenol, xylazine, cyclopentane, benzofuranal, octacosane, hexatriacontane, pentacosane, tricosane and docosane were common to both, body washings have in addition trimethyl butanol, nonanoic acid and eicosane. All the cultivars CO-1, CO-3, CO-2, SHOBA, H-28, ICCU-7 have in common the volatiles tricosane, octacosane, pentacosane and eicosane, which were reflected in the body and egg washings, enabling *Trichogramma* to efficiently parastize *Helicoverpa*[11].

Analysis and behaviour of such volatiles through EAG studies have shown increased response for 6 and 7 carbon aldelydes, alcohols, esters and ketones, while the parasites showed increased response to 7 and 8 carbon compounds, perhaps in view of host body scales containing cuticular hydrocarbons. That frass is a source of 7 carbon volatiles is supported by the presence of heptanoic acid in the frass. After herbivore damage there appears to be a shift from 6 to 7 carbon volatiles released by the plant[12,13]. Further studies on frass analysis of several herbivores are needed to further confirm not only the degree of attraction of parasites, but also behavioural manipulation of mass-released natural enemies.

Recent observations have shown that β-glucosidase[14] is an elicitor that affects production of attractants to natural enemies as evidenced by the analysis of regurgitants of caterpillars of *Pieris brassicae*. Overlapping of chemical signals with the interception of messages by natural enemies, results in 'chemical espionage'[15] enabling them to locate the target for the parasitoid. Only species of *Trichogramma* and *Telenomus remus*, which are egg parasites have been known to respond to lingering sex-pheromone scents. Abdominal tip exudates of *Spodoptera litura* comprising dodecane, heptadecane, octadecane and pentadecenoic acid sufficiently influenced the activity of the egg parasite *Telenomus remus* showing increased host egg tapping behaviour[9]. Since a factor that induces the systemic response seems to be present in the regurgitates of fed larvae, the need for their analysis in diverse lepidopteran larvae appears useful for a better perception of the attractants to natural enemies. Further, since plant species vary considerably in their green leaf volatiles composition, allowing for specialization of parasites on specific plant species[16], an understanding of the diversity of responses of parasites to these volatiles could enhance the efficacy of biological control of crop pests.

1. Lewis, T., *Insect Communication*, Royal Entomological Society, London, 1984, pp. 1–27.
2. Visser, J. H., *Entomol. Exp. Appl.*, 1977, **25**, 86–97.
3. Visser, J. H., *Annu. Rev. Entomol.*, 1986, **31**, 121–144.
4. Ramaswamy, S. B., in *Functional Dynamics of Phytophagous Insects* (ed. Ananthakrishnan, T. N.), Oxford & IBH, New Delhi, 1994, pp. 55–78.
5. Colbow, K., *Insect Olfaction*, Simon Fraser University, K. Burnaby, Canada, 1987, pp. 75.
6. Metcalf, R. L., *Crit. Rev. Plant Sci.*, 1986, 256–301.
7. Ananthakrishnan, T. N., *Curr. Sci.*, 1990, **59**, 1319–1322.
8. Ananthakrishnan, T. N., *Biological Control of Social Forest and Plantation Crops Insects*, Oxford & IBH, New Delhi, 1994, pp. 54–64.
9. Ananthakrishnan, T. N. and Senrayan, R., *Phytophaga*, 1992, **4**, 87–94.
10. Ananthakrishnan, T. N., Senrayan, T., Murugesan, S. and Annadurai, R. S., *J. Bisoci.*, 1991, **16**, 111–119.
11. Ananthakrishnan, T. N., Daniel Wesley, S., John Peter, A. and Marimuthu, S., *Int. J. Ecol. Environ. Sci.*, 1994, **20**, 317–331.
12. Ramachandran, V. and Norris, D. M., *J. Chem. Ecol.*, 1991, **17**, 1665–1690.
13. Ramachandran, R., Norris, D. M., Philips, J. K. and Philips, T. W., *J. Agric. Food Chem.*, 1991, **39**, 2310–2317.
14. Mattiacci, L., Dicke, M. and Posthumus, M. A., *Proc. Natl. Acad. Sci. USA*, 1995, **92**, 2036–2040.
15. Vinson, S. B., in *Chemical Ecology of Insects* (eds Bell, W. J. Q. and Carde, R. T.), Sinauer, Sunderland, 1984, pp. 111–124.
16. Whitman, D. W. and Eller, F. J., *Chemecology*, 1990, **1**, 69–75.

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