Behavioural dynamics in the biological control of insects: Role of infochemicals

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Infochemicals tend to serve as messengers mediating interactions among host plants, insects and their natural enemies, parasites and predators having exploited the release of plant-produced chemicals as cues to locate their hosts and prey. Volatiles from such host plant complexes may emanate from the plant, the host insects and host by-products such as faeces. Plants therefore are vital sources of information for natural enemies. In many cases kairomones emanating from the herbivores act alongside the host plant components and are successfully utilized by the natural enemies in their host-finding process. The behaviour and success of natural enemies undergo considerable variation when the insects colonize different host plants and modify the behavioural sequence of natural enemies. Host habitat selection, host selection and acceptance are modified by a number of chemical stimuli resulting in a continuum of behavioural exercises linking biological control with the allelochemical web. Some of these aspects are discussed with emphasis on cotton boll worm – natural enemy interactions.

AWARENESS of the involvement of the host plant, insect and natural enemies in effective and sustainable pest management strategies has revolutionized the concept of biological control of phytophagous insects. Tritrophic interactions, as these are known, essentially focus on the abilities of natural enemies to use plant traits to locate insects, besides emphasizing on the ecological and evolutionary implications of the food chain[1,2]. In long or short-range locations of their insect hosts natural enemies use the host plant traits which influence their ability to detect and utilize insect hosts, so that phytochemicals enhance attack by natural enemies. Insect damage-induced chemical and physical responses of plants influence the biology of parasites so that a phytochemical connection becomes established at different trophic levels. The release rates of infochemicals tend to differ altering the quality of the host insects to the parasitoids. Chemical, tactile or visual cues enable the natural enemies to distinguish between infested and non-infested plants. The question as to whether plants release chemicals to attract parasites or whether parasites have evolved to detect these cues is a relevant one, involving coevolutionary implications.

Plant odourants dominate the atmospheric chemical environment forming 'aerial bouquets' and insects including parasites select a few critical signals that stimulate their behavioural patterns. Plants respond to insect feeding by releasing volatiles that attract natural enemies which in turn attack insect herbivores. Many parasitoids occur in specific habitats within which their hosts occur, habitat location forming an important aspect in their host selection process. Plant phenotypic variation plays a role in structure of parasitoid communities, often determining their composition[3]. Numerous ecological and physiological factors tend to influence this process of host location directed by signals originating from the microhabitat, plant, host insect or microorganisms. In this exercise they respond and use specific cues from host plants to locate them, including those from damaged plant leaves and odours from host insect faeces[4–7], so that natural enemies base their foraging strategies on chemical information from the first and second trophic levels[8–10]. While three trophic levels are common, the existence of a fourth is not uncommon involving the host plant, insect, predator and its parasitoid, as in the case of the soyabean looper, *Pseudoplusia includens*. Since antibiosis can have an effect on organisms through four trophic levels, the specific relationship between organisms of various trophic levels is important in determining host resistance. The predator *Podisus maculiventris* is at the third trophic level with the parasite *Telenomus podisi* at the fourth trophic level[11].

Natural enemies have exploited plant volatiles to locate their hosts and volatiles emitted by faeces of larvae may also be involved in orientation. Larval faecal volatiles may be related to the breakdown process of plant material after digestion by larvae. The presence of other volatiles may be the end product of the process related to microorganisms inhabiting the faeces[12].

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Induced defenses as signals to natural enemies

Volatiles released by damaged plants after insect feeding tend to increase the efficiency of natural enemies and plants producing such alarm responses attract more parasitoids and predators[13]. Being detectable these natural enemies learn to associate the volatiles with the prey. Induced defences increase emission of plant volatiles greatly and being diverse in chemical composition, the nature of their blends tends to be complex, changing with increasing induction. A whole suite of chemicals are released by damaged *Brassica oleracea* such as isothiocyanates, which are hydrolysis products of glucosinolates, undamaged plants emitting them in smaller amounts as also several terpenoids[14].

Intraspecific host plant variation that influences parasitoid success has been evident in both agricultural and natural systems and varietal differences in crop plants are known to influence parasitoid preference due to change in the nature of volatiles so that the role of plant phenotypic variation becomes important in the behavioural diversity of parasitoids. It is this intricate interaction between plants and natural enemies such as parasitoids that acts as a driving force leading to the production of adequate signals affecting the behaviour of natural enemies in a positive way. The parasitoids make use of these volatiles to identify the vicinity of host-infested plants, in particular the orientation of the larval parasitoids to the frass of host larvae, since they are in a position to identify the damaged plants from a distance[15–17]. Foraging parasitoids like *Microplitis croceipes* would be exposed to a wide range of volatile blends both from host plant and insect complexes in its environment. Learning by parasitoids enables behavioural variability, recognizing the odour of hosts as well as their exact site and environment. On the basis of information acquired immediately upon emergence from host puparium and during the first oviposition, they learn more in accordance with odours acquired by the host[18].

Divergent views exist regarding the role of induced defenses on herbivores, providing reliable signals to natural enemies indicating the presence of host insects. The view that plant volatiles have evolved to serve tritrophic communication is supported by evidence that release of green leaf volatiles increased after insect herbivore attack with many parasitoids and predators being attracted to the damaged host. Localized induction tends to increase the activity of phytophagous insects within the plant[19] enabling easy detection by natural enemies. Induction of allelochemicals may prolong development of host insect larvae making them more susceptible to the natural enemies or as in many cases allelochemicals may simultaneously reduce growth and attract more natural enemies[20]. Indirect effects of induced chemicals relate to their ability to prolong development of insect larvae, enhancing the possibility of natural enemy attraction[20]. Constitutive variation in phytochemistry as well as induced responses in plants after insect attack form the basis for phytochemical involvement with the third trophic level[21–25].

Behavioural diversity

The behaviour and success of natural enemies undergo considerable variation when insects colonize various plant species including crop systems in response to different volatile compounds, modifying the behavioural sequence. With regard to the specificity of an insect herbivore to a plant species and that of the parasitoid to the insect, genetically evolved responses to insect hosts and plant odours tend to aid in host-finding. Instances are known wherein innate responses are replaced by associative learning[26] as evident in the case of more generalized insect hosts and parasitoids, where the use of specific kairomones and synomones play a role so that the informational value of the stimuli depends on two factors insofar as parasitoids are concerned, viz. their reliability indicating available and suitable hosts and detectability of the stimulus with ease, both the factors tending to increase searching efficiency[27]. Reliability of plant cues depend on the periodicity of plant infestation over space and time and natural enemies combine the advantageous aspects of information from both trophic levels. When a parasitoid population is generally associated with a particular host species and its host plants, the parasitoid is expected to show high innate responses to these cues which act as reliable indicators of host presence. Host-derived stimuli are most reliable in indicating host presence, accessibility and suitability[28]. Species-specific chemical cues that reliably identify plant species are not always available to parasitoids, so that learning tends to become an important aspect in enabling the parasites to find their hosts. Noldus *et al.*[29] have shown that the sex pheromone of *Mamestia brassicae* females were adsorbed on to the leaf surface of Brussel sprouts to such an extent that it was capable of eliciting behavioural responses from *Trichogramma evanescens*. This illustrates the involvement of host habitat cues to close range host acceptance cues. In many instances kairomones emanating from the herbivores act alongside with host plant components and are successfully utilized by the parasitoids in their host-finding process[30–32]. Therefore, a close understanding of the intricacies of behavioural diversity of parasitoids appear essential in generating increased success in biological control programmes.

Natural enemies use substrate features of the host plant, in long- and short-range location of their resources, prey or host[33]. At short distances host-finding is readily accomplished, egg parasitoids being strongly influenced by host kairomones. As long-range cues, chemical features are used by parasites in locating their hosts[34–36]. Pheromones from their adult hosts have been shown to be important signals in locating eggs, related strains of a given host plant species have different volatile profiles so that females of successful parasitoids are capable of responding to more than one or a combination of cues. The specificity of the components of the plant–herbivore complex providing species-specific information is an aspect deserving increased scrutiny. There are instar-specific blends of chemicals emitted by faeces of second or fourth instar larvae and this is due to different digestive processes of the larvae and the different microorganisms inhabiting the faeces. In some cases as in *Pieris brassicae* volatiles from the host–plant complex do not mediate discriminations of parasitoids between sites infested by young or old larvae; but after landing on an infested leaf, the duration of searching is differently affected by cues such as those of silk or frass related to the presence of the first or fifth instar larvae[37]. Response to 7 or 8 carbon compounds by parasites is equally high and a 1-carbon shift in the peak responses from 6 to 7 carbon compounds occurs in frass so that the herbivore frass is a major source of 7-carbon compounds and of increased parasite behaviour[38]. Such frass volatiles as linalool, guiacol and 3-octanone mediating plant–herbivore–natural enemy interactions in relation to the soyabean looper *Pseudoplusia includens* were found to be the useful source of information for the parasitoid *Microplitis demolitor*[39].

Allelochemical influence on parasitoid fitness

The fitness of natural enemies is related to the quality of hosts, which in turn is affected by plant nutrition and allelochemicals so that the diversity and abundance of the hosts influence the diversity and abundance of natural enemies[40]. Host plant nutritional characters indirectly alter the fitness of parasitoids through change of herbivore quality[41] and plants with digestibility reducing substances support herbivory. Besides the influence of host physiology on the fitness of parasitoids and the effects of plant physiology on the biology of natural enemies, the effects of plant allelochemicals on parasitoid success and fitness are essential aspects, since some of them may prevent normal nutrient use or cause inhibition of enzyme systems[42,43].

Some insects sequester toxic plant products and actively metabolize and store the allelochemicals as defences against their natural enemies, which in turn also separates them from their host insects. The transfer of a plant toxin, say an alkaloid through a herbivore to a carnivore is also known. In parasitoid–host relationship the future development of the host is important to the parasitoid. While plant odours or floral scents attract or arrest natural enemies, some relatively odourless crucifers produce enzymes in response to attacking insects that quickly convert inactive mustard oils to volatile parasite-attracting derivatives[44]. In such a situation a shift to a different plant may enable a phytophagous insect to escape from parasitoids that use plant compounds as host-finding cues.

The stem borer *Chilo partellus* produces volatiles attracting the parasite *Cotesia flavipes* and an exogenous elicitor of this plant response has been identified in the regurgitate of the larva[45]. β-galactosidase, as this elicitor is known, affects the production of attractants to the natural enemies[46]. Of particular interest is the presence of anthraquinones and anthrones in some chrysomelids. They not only act as feeding deterrents against predators, but also influence a parasitoid to gain an evolutionary advantage by specialization on such protected eggs, there being no transfer of these chemicals from the second to the third trophic levels[47]. Although several plant-derived volatile compounds of host plant origin play a significant role in natural enemy activity, several plant-derived volatile compounds from trichomes also inhibit the activity of natural enemies, in particular, 2-tridecanone and 2-undecanone which significantly alter cocoon spinning behaviour[48], aspects which may interfere with efficient biological control.

A comparison of volatiles of the frass of *Helicoverpa armigera* indicates that larvae fed on artificial diet had no significant kairomonal compounds like docosane and hexatriacontane, while the frass of *H. armigera* fed on *Abutilon* and *Gossypium* plants indicated the presence of several host-seeking kairomonal compounds that considerably influenced parasitoid behaviour. Therefore the behaviour and success of natural enemies undergo considerable variations when the herbivores colonize different host plant species in response to different volatile compounds which modify the behavioural sequence of natural enemies[49,50].

Cotton–Heliothis–natural enemy interactions

Extrafloral nectaries in cotton appear to be an important source for parasitoids such as braconids, ichneumonids and trichogrammatids involved in the control of bud worms and boll worms of cotton. These parasites are twice as abundant in cotton cultivars with extrafloral nectaries which act as an energy source, with sugars and varying types of aminoacids, increasing the longevity three to four times of parasitoids like *Trichogramma*[51]. *Trichogramma chilonis* showed increased parasitization of *H. armigera* eggs deposited on flowers and young squares in view of the nectary source. *Campoletis sonorensis* and *Microplitis croceipes* lived longer, exhibited higher fecundity and showed increased vigour in nectaried cotton varieties, besides altering the physiological response of parasitoids[52]. Several parasitoids show differential preference for various cotton cultivars due to the availability of adequate kairomonal resource.

Volatile chemicals in cotton affect the behaviour of parasitoids associated with the plant, a given chemical tending to act both as a plant orientation compound or feeding stimulant or toxin for the herbivore. Members of other trophic levels may be affected by chemicals through association with the plants and of the chemicals and associated metabolites found in the body of their prey. Analysis of volatiles of cotton cultivars in flowers, and squares revealed that in addition to their nutritional quality, kairomonal compounds like tricosane and pentacosane act as attractant resources for many of the parasitoids. Cotton gland chemicals also tend to influence parasite biology[53].

Parasitoids such as *Campoletis sonorensis* antennate and probe cotton to a higher degree than other plants and cotton buds were more extensively antennated and probed than leaves and stems and hence the importance of cotton volatiles in providing host habitat location. Related species or strains of a given plant would differ in attraction if the volatile profiles were altered. *Gossypium barbadense* lacks myrcine, γ-bisabolene, and β-bisabolol which are major components of *G. hirsutum*. Typical gas chromatograms of volatiles of glanded cotton *G. hirsutum* showed the presence of α-pinene, myrcene, ocimene, β-caryophyllene, α-humulene, γ-bisabolene and β-bisabolol. Individual compounds produced varying degrees of long-range attraction and antennation upon contact. Caryophyllene oxide, a fragrant cotton sesquiterpene attractant to *C. sonorensis* was also capable of reducing *H. virescens* growth rate when added to the artificial diet gut in higher concentrations[54].

Results of behavioural studies in response to five cotton cultivars TCHB, Suvin, LRA, MCU 5 and MCU 7, indicated that the parasitoid *Trichogramma chilonis* showed increased antennation and probing behaviour towards volatiles of the cultivar Suvin compared to others. Gas chromatographic studies revealed the presence of several volatile compounds such as docosane, caryophyllene, hexacosane and nonacosane which significantly induced the behaviour of parasitoids. While caryophyllene has been detected in the squares of Suvin, TCHB, MCU 7 and MCU 11, octodecane, undecane and dodecane were identified in LRA. Tetradecenoic and hexadecenoic acids were typical of MCU 11. In many instances kairomones emanating from herbivores act alongside with host-finding process. Volatile compounds emanating from the scales of *Helicoverpa armigera* and *Corcyra cephalonica* moths were identified as hexatriacontane, docosane and nonacosane which increased the activity of *T. chilonis*[55,56]. Similarly kairomones from *Helicoverpa* eggs influenced the behaviour of *T. chilonis* and the egg predator *Chrysopa scelestes*. The abdominal tip exudates of *Spodoptera litura* females were identified as complex compounds containing dodecane, heptadecane, octadecane and pentadecenoic acids which influenced the activity of the egg parasitoid *Telenomus remus*[57].

In response to herbivory, some plants release volatile chemicals particularly attractive to parasites and one of the best documented examples pertain to the spider mite *Tetranychus urticae*, its predator *Phytoseiulus persimilis* and the host plant, which form a good example of tritrophic interactions[58,59]. Cucumber plants infested by the spider mite release β-ocimene, and 4,8-dimethyl, 1,3,7-nonatriene, while lima beans releases a mixture of linalool, β-ocimene, the nonatriene and methyl salicylate which are highly attractive. The volatiles released alert uninfested neighbouring plants so that they become better protected from spider mite attack. Cotton seedlings when infested by these mites release volatile cues which both attract predatory mites and alert neighbouring plants to withstand herbivore attack. Linalool released at the rate of 1 ng/hour before damage increased to 110 ng/hour six hours after the attack. In several other cases like the tritrophic system in soyabean plant, involving *Pseudoplusia* and *Microplitis molitor* and its parasites, besides linalool, other attractants like guiacol, 3-octanone from frass have been noticed[60].

Conclusion

The searching behaviour of parasites and predators of herbivorous insects or phytophages, particularly information from plants in their searching process indicates the importance of tritrophy. Plant volatiles mediate searching behaviour at longer distances, not to mention of host insect volatiles or herbivore-derived chemicals calling for a need to exploit the foraging strategies of natural enemies for efficient biological control. The degree of insect infestation is related to the value of plant information and induced defences greatly increase emission of plant volatiles. The use of semiochemicals to enhance the behaviour of biocontrol agents in agroecosystems holds great promise in future pest control measures. Volatile chemicals promoting the behaviour of natural enemies as well as the fact that the same chemicals affect the growth and survival of herbivores indicate that manipulation of volatile profiles contribute significantly in biocontrol strategies. For instance, compounds such as caryophyllene act as feeding deterrents and growth inhibitor in *Heliothis*, while the same compound influences the searching efficiency of natural enemies. Natural enemies have evolved the capacity to learn to use induced responses to locate their hosts. Plants in turn use the third trophic level as another line of defence against herbivores. Plants are therefore to be considered as a dynamic component of insect–plant–natural enemy interactions. The possibility of using naturally occurring compounds from plants to reduce herbivore damage and increase the effectiveness of biocontrol agents is a potential area for future research. In-depth studies of semiochemicals of plants and their role in natural enemy activity would nable screening and developing hybrid varieties that roduce significant source of such chemicals for enhan- ing natural enemy activity.

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