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CHEMICAL ECOLOGY OF INSECTS AND TRITROPHIC INTERACTIONS

Faheem Ahmad, Muhammad Aslam and Muhammad Razaq
University College of Agriculture, Bahauddin Zakariya University, Multan.
email: aslamuca@yahoomail.com

Abstract: This paper reviews the chemical ecology of insects to explain the role of semiochemicals in plant-herbivore, herbivore-carnivore and plant-carnivore interactions. The semiochemicals, mediating tritrophic interactions may be produced by plants, herbivores or their natural enemies (carnivores). Some semiochemicals attract the herbivores and carnivores and mediate interaction among them, while on the other hand some repel them. The semiochemicals are used by herbivores, parasites and predators as cues to locate food, host or prey. The same chemicals are also used for defensive purpose by some herbivores against their natural enemies as they are sequestered through their bodies.

Keywords: Chemical ecology, herbivores, semiochemicals, trophic interactions.

INTRODUCTION

All the organisms in an ecosystem are linked biochemicaly and their relationship is obvious in food chains and food webs. If simplest or linear food chains in a generalized food web is considered, it contains at least three trophic levels having feeding links with each other. In this tritrophic interaction the member of lower trophic level is forced to evolve, to reduce feeding by higher trophic level; whereas the members of higher trophic levels evolve to increase consumption [Price *et al.* 1980]. Another important feature of tritrophic interaction is that the alternate trophic levels in food chain usually have symbiotic relationship. The natural enemies of herbivores favour plant by reducing the herbivore and plants favour the natural enemies by making herbivores more vulnerable to them. To understand such tritrophic interactions, it is necessary to study different factors, i.e. bio-chemicals (semiochemicals) that mediate interaction in addition to integrating the trophic levels. Semiochemicals elicit behavioral and physiological responses in the receiver, which results in the interaction between them [Nordlund 1981]. In tritrophic interaction the semiochemicals produce different responses such as attraction, repulsion, arrest, detteration and stimulation. These chemicals are studied in chemical ecology, the main objective of which is to identify the semiochemically-mediated interactions between organisms [Ruther *et al.* 2002].

In this paper, chemical ecology in relation to tritrophic interactions is reviewed to understand how biocommunication is useful in the study of plant to plant, plant to insect and insect to insect interactions in the ecosystem.

TYPES OF SEMIOCHEMICALS USED IN TRITROPHIC INTERACTION

Semiochemicals are basically of two types, i.e. pheromones and allelochemicals. Pheromones are intraspecific semiochemicals, which mainly mediate the insect-to-insect interaction. These are further classified in to different types, depending upon their functions, such as sex pheromones, alarm pheromones, trail marking pheromones, territory marking pheromones, egg marking pheromones and aggregation pheromones [Nordlund 1981]. The main importance in tritrophic interaction studies is given to allelochemicals, which are interspecific semiochemicals. Allelochemicals are of different types. If some allelochemical pertinent to the biology of one organism evokes a response in the receiver in the favour of the emitter, it is known as allomone. Synomones are the allelochemicals which produce the response favorable for both the emitter and the receiver, whereas the kairomones produce favourable response only for the receiver and apneumones are the allelochemicals which are released by non-living substance, resulting in the response in the favour of one and against another organism in the same habitat [Ruther *et al.* 2002].

All the terms discussed above can be used alternately [Nordlund 1981, Pasteel 1982], because the semiochemicals produced by organisms may act in any of the above discussed way depending upon its effects on different organisms. For example, the pine tree terpenoids, which act as allomone for herbivores [Smith 1963] but specialized bark beetle find its food by using the same chemical cue, hence it may be considered as kairomone and the same chemical cue also attract the predators of bark beetle, acting as synomone [Wood 1982].

PLANT-PRODUCED SEMIOCHEMICALS AND TRITROPHIC INTERACTION

Plants produce semiochemicals as intrinsic defense against herbivores. But these chemicals may also affect the third trophic level resulting in the tritrophic interaction. The similar effect is contributed by plants' extrinsic defense [Price *et al.* 1980]. These chemicals mediate plant-natural enemy interaction. The floral scent, plant volatiles and food bodies serve as synomone for pollinators [Pellmyr and Thien 1986]. Also plants provide food to the predators in the form of pollens, nectar and extra floral nectar [Leius 1967]. The predators with the help of these cues find their potential host (herbivore) feeding on the same plant. Some parasites [Smiley 1978] and predatory ants are attracted towards plants due to nectar [Bentely 1977]. Plant odours are also important in tritrophic interaction [Read *et al.* 1970, Vinson 1984]. Kesten [1969] reported that *Anatis ocellata,* the coccinellid predator of pine aphid is attracted towards its prey by the odour of pine needles. *Chrysopa carnea* is also reported to be attracted towards Caryophyllene, a terpenoid released by damaged cotton leaves [Flint *et al.* 1979].

Many predators and parasitoids are carnivores in their immature stages, while the adults feed on nectar [Hagen 1986]. These adults are attracted to nectaries of the plants where they lay eggs and the larvae feed on the herbivores providing benefit to the plants [Hespenheide 1985]. Plants also increase the fitness, lifespan and fecundity of natural enemies by providing the best quality food in the form of pollens and nectar, and in turn the natural enemy reduces the herbivores quickly [Sundby 1967, Foster and Ruesink 1984]. Some volatiles produced by the plants act as allomones to herbivores [Rosenthal and Janzen 1979]. These volatiles mediate tritrophic interaction as seen in case of mustard aphid, *Brevicoryne brassicae* L. and its parasitoid *Diaeretiella rapae* M'Intosh. *B. brassicae* is attracted to mustard plant due to sinigrin, but *D*. *rapae* uses the similar mustard oil to find mustard and ultimately the host (*B. brassicae*) [Read *et al.* 1970].

Plants also provide food to natural enemies of herbivores indirectly by sustaining the honeydew producing herbivores. The predators are attracted towards that sugar-rich honeydew and ultimately consume its prey. In Finland, the green trees sustain aphids on their foliage, hence attract the ants, which drive off the defoliating geometrid, *Oporina autumnata* larvae, a serious pest of green trees [Laine and Niemela 1980]. Moreover, plant volatiles when cycled through the body of herbivores act as kairomones between insect and natural enemies, especially the parasitoids [Pair *et al.* 1982, Obreycki *et al.* 1983, Vinson 1984]. Corn earworms, *Heliothis zea*, derive trichosane from corn, which is passed unchanged into its eggs. Its parasitoid, *Trichograma evanescens* uses this chemical as a kairomone and finds eggs of the host [Lewis *et al.* 1972]. Plant-produced biochemicals also indirectly affect the tritrophic interaction by altering the size, vigour, growth rate and survival rate of the herbivores. Size of the insects is reduced due to secondary plant metabolites resulting in increase or decrease in efficacy of predators [Royama and McKelvy 1970], because predators prefer a specific size of prey to consume. *Aphytis melinus*, a predator of Californian red scales, *Aonidiella aurantii*, can consume host of about 0.39 mm^2 and larger, while *Aphytis linginanenis* can utilize the prey of about 0.55 mm^2 size and larger [Luck and Podoler 1985]. Due to some digestibility reducers the herbivores spend more time in feeding on the plant and thus the time available for predators to find the prey is increased. This aspect was studied by Price *et al.* [1980] in Maxican bean beetle on plants rich in tannin and on plants poor in tannin. They found that the pentatomid predators were more effective for the herbivores feeding on plants rich in tannin as compared to those feeding on plants poor in tannins. Tritrophic interaction is also affected by the quality of host diet [Cheng 1970]. Growth and survival of the host is adversely affected by their diet, which ultimately affects the third trophic organisms. Adverse effect on herbivore survival results in greater damage to parasitoid population, if the host is parasitized.

In contrast to the role of chemical ecology in the favour of third trophic level, there are certain cases where the semiochemicals produced by plants may act against the third trophic organisms. Some times the associated plant volatiles may mask the attractants of the natural enemies. For example, the body odour of Larch and Larch sawfly, *Pristiphora erichsonii*, are attractant of the parasitoids leading to 86% parasitization in pure stand of Larch, but if other trees are grown in association, the parasitization is decreased to 12% due to masking effect of the volatiles produced by associated trees [Monteith 1960].

In other cases the allomonal defense may become harmful to plants, as they also repel the natural enemies, but some herbivores become more specialized to the same chemicals. Williams *et al.* [1980] and Dimock and Kennedy [1984] concluded that wild tomatoes release a contact poison, Methy Ketone, 2- tridecanone, to repel herbivores but it acts mainly against natural enemies. Similarly Coccinellid and Chrysopid larvae are deterred due to glandular trichomes [Gurney and Hussey 1970, Elsey 1974, Belcher and Thurston 1982].

HERBIVORE-PRODUCED SEMIOCHEMICALS AND TRITROPHIC INTERACTION

Herbivores are the real link in tritrophic interaction, which on one hand interact with plants and on the other hand with its natural enemies. Thus, in both ways they have to cope with the plant's intrinsic defense and the natural enemies attack. So herbivores produce semiochemicals either to cope with the plant defense or to deter natural enemies. Such semiochemicals also play a vital role in the tritrophic interaction. An example of synomone mediated herbivore-predator interaction is that Lycaenid butterfly larvae and aphids produce synomone (sugar rich honeydew) which attracts ants for protection against natural enemies [Atsatt 1981, Pierce and Mead 1981]. A mutualistic association develops between ants and the aphids, ants protect aphids and butterfly larvae from other natural enemies [Way 1963] and in turn the aphids provide food to ants in the form of honeydew.

Herbivores also produce some kairomones, which are detected by their natural enemies. These kairomones may be attractive to parasitoids in the form of body odour [Loke and Ashley 1984, Noldus and van Lentern 1985], sex pheromones [Sternlicht 1973, Kennedy 1984], aggregation pheromones [Wood 1982], excretory products [Lewis and Jons 1971, Nordlund and Lewis 1985], body scales [Loke and Ashley 1984] and eggs [Jones *et al.* 1973] etc. For example bee wolf, *Philanthus triangulum*, a predatory wasp detect the bee only by using its body odour of the bee [Tinbergen 1972]. Predators usually use the prey's pheromones to detect them in termites and *Megaponera foeteus* [Longhurst and Howse 1978, Howse 1984]. Such kairomones, which are utilized by insects to find their food, are classified as foraging pheromones [Ruther *et al.* 2002]. Plants also respond to kairomones released by herbivores. Buds, fruits, flowers and leaves are often shed by plant on detection of herbivore [Coakley *et al.* 1969, Bultman and Faeth 1986]. Fruit abortion [Carter 1939] and increase in growth rate [Detling and Dyer 1981] are some other effects resulting due to insect-plant interaction. Herbivore produced allomones are also important in tritrophic interaction. Allomones may act against either plants or natural enemies, for example gall insects produce certain chemicals, which result in gall formation, providing favourable habitat for the herbivore. Herbivores derive many compounds from their host plants and use as allomone against natural enemies. A well-known illustration of this phenomenon is the cycling of cardiac glucosides from milkweed plant to milkweed butterfly [Brown 1969]. Feeding on such butterflies causes vomiting in avian predators.

Similarly tomatine, an alkaloid produced by tomato plant is acquired by corn earworm, *Helithis zea*. This alkaloid does not harm the earworm but produces adverse effects on parasitoids, *Hyposter exigua,* which results in reduced survival, longevity and delayed larval growth of parasitoid larvae inside the host body [Campbell and Duffey 1981]. The cycling of toxins to third trophic level is a prominent factor in determining the fitness of parasitoids [Price 1983]. Survival of parasitic wasps of *Drosophila melanogaster* mainly depends upon its ability to survive in high concentration of ethanol in the host's body. Similarly the high concentration of nicotine in hornworms affects the survival of *Appenteles spp.* [Gilmore 1938].

PREDATOR-RELEASED SEMIOCHEMICALS AND TRITROPHIC INTERACTIONS

In tritrophic interactions the semiochemicals released by natural enemies cannot be neglected because these also alter the behavior or physiology of plants or herbivores. Some predators release synomones which are acquired from plants, as many of the predators and parasitoids obtain food from plants. Plants respond to synomones produced by predators. For example the plant, *Piper cenocladum,* produces food bodies only when it detects the presence of a particular species of ants, i.e. *Pheidole bicorins* [Risch and Rickson 1981]. In contrast some kairomones are also produced by natural enemies, the enemy avoidance kairomones [Ruther 2002]. When herbivores detect these kairomones, they escape from the habitat to avoid the attack of predator [Dicke and Grostal 2001].

The production of kairomones is most common in marine ecosystem [Phillips 1977]. When *Daphnia spp.* is exposed to predator-born kairomone in water, the plankton moves in deep water [Von Elert and Loose 1996, De Meester *et al.* 1999]. In terrestrial ecosystem many ants, wasps and bees may respond to formicid kairomone of predatory ants [Spengler and Taber 1970, Chadab 1979].

In contrast to the situations discussed above, predators may also produce allomones to attract their prey, or to camouflage their own true identity. In such cases the predator may derive some chemicals from their prey and mimic its body odour to its prey's [Vander Meer and Wojcik 1982]. Some spiders produce allomones which are similar to sex pheromones and attract the male prey towards the web [Stowe *et al.* 1987]. In spite of being the predator, the third trophic level even have a forth-trophic level above it. So, it also produces some allomones to avoid the attack of its predators or hyperparasites. Some insects such as ladybird beetle, stink bug, ants and ground beetles synthesize defensive compounds [Blum 1981], while some predators derive toxins from their prey and use against their own predators [Eisner *et al.* 1980].

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