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Facets of chemical ecology in insect-plant interactions: An overview

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Abstract. An overall analysis of the complex interrelationships involved in insect-plant interaction has been attempted with particular reference to the mechanisms of host plant searching and acceptance, nutritional and non-nutritional factors, defense systems in plants and insects and recognition systems in plants to invasion by foreign organisms.

Keywords. Chemical ecology; insect-plant interaction; host selection; plant defence capability; wounding in plants; chemical defenses.

1. Introduction

The ability of phytophagous insects to utilize plant tissues for energy, growth and reproduction has made them targets for the serious economic losses sustained, and the resultant reduction in agricultural productivity. The diversity of their feeding habits on leaves, buds, stems, roots and seeds, combined with their ability to act as vectors of bacterial, fungal and viral diseases have been basically responsible for the losses sustained. The basic question involved is: Are plants passive to such depredations? if not, how do they react to insect attacks? What are the mechanisms of defense and if the plants tend to be resistant or tolerant, how do insects overcome the defenses? These are some of the fundamental questions that have cropped up over the years and the subject of 'chemical ecology' has come to the forefront in providing a convincing answer to problems concerning insect-plant interactions, an understanding of which is undoubtedly the basis for solving problems of applied ecology. In an attempt to analyse the complex relationships involved, this overview envisages to identify in a very brief and general way such aspects as mechanisms of host plant searching and acceptance, nutritional and non-nutritional factors, defense systems in plants and insects and finally recognition systems in plants to invasion by foreign organisms. Incidentally mention may be made of the involvement of coevolutionary factors in these interactions, so that as the plants tend to diversify and develop morphological and physiological defense systems, insects also tend to develop detoxifying mechanisms (Labeyerie *et al* 1987). Co-evolutionary mechanisms are very evident in gall-forming insects where the tendency towards specialization increases with increased intimacy between the insect and host plant (Ananthakrishnan 1983, 1984). The gall formers are generally specific to a single host and they modify plant growth, live within plant tissues for most part of their lives. Gall formation has been known to be a genetic commitment towards adaptation of exploitation of plant species. It is only through the unravelling of the diverse defense mechanisms that suitable techniques could be developed to control insects. Both plants and insects being dynamic systems, the complexity of age-correlated biochemical processes has made the study of insect-plant interactions a really challenging subject.

2. Basis of host selection

Host plant selection behaviour involving habitat selection and discrimination mechanisms between host species is known to play a significant role in insect-plant interactions. With plant species and individuals tending to vary in quality or suitability for insect growth, reproduction and survival, insects in turn tend to avoid plants of low quality, preferring to feed on those of high quality. This has led to aspects pertaining to the behavioural responses of insects to their food plant quality variation. Behavioural mechanisms tend to restrict their searching to habitats containing host plants. Insects are endowed with an array of sensory capabilities, chemosensory, mechanosensory, visual etc. By visual and chemical cues they seek a suitable habitat and are attracted to the host plant by chemical stimuli, and the olfactory and gustatory sensilla enable detection of these stimuli resulting in the acceptance or rejection of the host plant. The sensilla concerned with chemoreception are variously distributed, but are more abundant on the antenna mouthparts and legs and involve different types such as sensilla trichodea, chaetica, campaniformia etc., whose receptor cells enable transfer of information for the external environment to the central nervous system, for necessary behavioural action. Recognition and preference of host plants involve the integration of a complex of neural and metabolic events such as nutritional factors as well as the role of feeding deterrents and attractants and other behavioural factors (Ananthakrishnan *et al* 1985; Ananthakrishnan 1986; Bell and Carde 1986).

Choosing hosts involves considerable selection pressure which varies with species which may be mono-, oligo or polyphagous, and wherever strict monophagy is ensured, selection may cause specificity to increase. Reduction in the suitability of less preferred species as compared to most preferred ones may also lead to increased host specificity. Alternatively a decrease in specificity would be favoured when it threatens larval survival, and by decreasing specificity females would tend to lay more eggs to decrease the risk of larval death, due to such factors as plant senescence (Rausher 1983). It is only after they choose to settle down on a substratum aided by these chemical cues that they commence feeding, deriving such substances as water, nitrogen, carbohydrates, lipids, proteins, amino acids and certain minerals, which are vital for growth, development and reproduction. Nutritional rewards may vary with plant tissues and insects discriminate between young, maturing and senescent tissues (Ananthakrishnan and Raman 1986).

3. Plant defense capabilities

Morphological and physiological traits such as leaf toughness, hairiness or trichomes, surface waxes, cell silicates and proliferation of wounded tissues, interfere with locomotion, feeding and oviposition. Colour may be a remote factor as they act at meaningful distances and prevent an insect from landing on a plant. Alongside colour, size, plant shape and density are other remote factors. Yellowish green leaves are mostly preferred i.e. that reflect light with wavelengths within 500–600 nm range. Due to deposition of additional lignin and cellulose, the plant tissues become more resistant to feeding action. Leaves of greater toughness cause increased larval mortality. Thick hypodermal layers have been considered a factor of resistance. Sometimes thick cell walls inhibit digestion and this is very well seen in the feeding of several grasshoppers. The recognition of C_4 plants with high photosynthetic capacity, and C_3 plants with low photosynthetic capacity reflects the differences in the nutritive value of plants and C_4 plants tend to be a poorer food source for insects. Again solid stems are resistant to borer insects and hard, woody stems with closely packed, tough vascular bundles are the main resistant factors and in some cases the cortex also tends to be thick. Trichomes which are hair-like, cellular outgrowths of the epidermis of plants are among the more important morphological defenses of plants against insects. Some trichomes possess glands which exude chemicals which may be of the nature of a sticky film to trap insects. Their shape, size, density and erectness contribute to the degree of morphological resistance. The basic constituents of trichomes are cellulose and lignin and where they are very dense, biting insects have to consume them to reach the epidermis and in so doing death ensues due to an inadequate diet. Trichomes act as mechanical barriers to insect activity and insects are trapped or impaled by glandular, or non-glandular trichomes and more particularly by hooked trichomes (Juniper and Southwood 1986). Wounding results in the proliferation of cells and other plant products which act as defensive mechanisms. This takes us to the question of the nature of chemical defenses and implications of wounding in plants.

4. Implications of wounding in plants

Wounding disrupts the normal patterns of synthesis of chemical substances giving rise to quantitative and qualitative changes in terpenoids, some of which, after wounding, tend to inhibit the development of bacteria and fungi and are included in a class of phenolic antibiotic compounds termed phytoalexins of which benzoic acid, flavonoids and isoflavonoids are important. It must be recognized that steroids, alkaloids and phenylpropane compounds viz. lignins, tannins, phenols and quinones play an important role in the life of the plant. The rapid turnover rate of alkaloids, the involvement of steroids in plant hormone function, of the large array of polyphenols, flavonoids in wound reactions, point to the dynamic role of these substances. Phenylpropanes are formed through the shikimic acid pathway which serves for biosynthesis of phenylalanine and include also volatile aromatic compounds. Also involved are the isoperene units or C_5 compounds which in turn are constituents of a large number of terpenoids, mono, di- and serquiterpenes discussed subsequently. Shikimic acid plays a fundamental role in the metabolism of aromatic amino acids and these are mobilized into the primary metabolism serving as storage chemicals or as regulation of biochemical process (Kogan 1977).

Wounding also results in increased synthesis of cinnamic acid derivatives, the most important being the accumulation of chlorogenic and caffeic acids. Chlorogenic acid is the mobile resource for the synthesis of other phenylpropane derivatives. The enzyme acting on phenylalanine is phenylammonialyase (PAL) and the production of chlorogenic acid in response to wounding is due to rise in PAL activity. Response to wounding in plants is also the formation of a large protective covering over the cut surface which may form a barrier against water loss and to various micro-organisms, and this is suberin or lignin. Lignin is a polyphenolic polymer, while suberin is a polymer of long chain fatty acids in which cinnamic or coumaric acids are associated. Free coumarin is released only upon cell disruption through the action of endogenous β-glucosidase. Wounding of plants through insect feeding also results in ethylene production which can influence a wide range of plant responses and alteration of plant growth, chlorophyll and foliar senescence. Feeding also promotes abscissic acid (ABA) levels which act as defenses for diverse plant stresses (Visscher 1983, 1987).

Signals are released from attacked sites or transported to uninfected or unwounded cells where they trigger almost immediately biochemical processes that produce chemicals which have primary roles in plant defenses. In some cases chemicals are produced at or near the sites of wounding to arrest the attacking pests. These chemicals are of the nature of insect-induced proteinase inhibitors and phytoalexin producers. An important role for plant cell wall fragments released at the wounding sites is envisaged. The majority of inhibitors from plants are specific for the serine class of proteins and protein inhibitors are widely distributed. Resistant varieties have doubled the level of trypsin inhibitors. Specificity and concentration are important aspects in proteinase inhibitors as plant defenses (Ryan 1983).

The large diversity of chemical substances results from plant metabolism and these phytochemicals involved in host plant resistance (HPR) are alkaloids, flavanoids, glycosides, terpenoids, tannins and lignins, which act as feeding deterrents, growth inhibitors, toxicants and oviposition deterrents. Recent researches also show that oviposition deterrents can offer the first line of defense against insects and active plant constituents cause the avoidance of egg-laying; besides chemical markers are left behind which prevent others from laying eggs at or near the site of already laid eggs. For many phytophagous insects selection of an oviposition site is a critical stage in host choice (Singer 1986). This is because newly hatched insects are incapable of selecting hosts till they have fed on the hosts selected by their mother.

Host plant selection is not merely an insect recognizing a particular chemical or avoiding it, but it is rather a process resulting from the integration of numerous chemical and nonchemical factors involving a subtle interplay of orientational, ovipositional and feeding factors as well as visual, tactile and environmental factors (Renwick 1989). Many of these non-nutritional factors which have no part to play in the metabolism of plants are termed secondary plant substances or allelochemics.

5. Chemical defenses

Plants have provided thousands of compounds and with every passing day hundreds of them are being isolated and identified. Terpenoids, phenolics, proteinase inhibitors, nitrogen compounds, alkaloids and growth regulators including hormonomimetic compounds are known, which defend against insect attack (Kogan 1977). Terpenoids are biologically the most important class of natural plant products, acting as attractants for pollinators as well as feeding deterrents and toxicants. They are non-nitrogenous and use a 5-carbon-branched chain as a building unit. Pyrethrum from dried chrysanthemum is a toxic monoterpene, while gossypol of cotton, a serquiterpene is a major defense chemical against cotton insects. Cucurbitacins are triterpenoids imparting a bitter taste and are feeding deterrents (only attractant to cucurbitaceous beetles). Azadirachtin from neem (*Azadirachta indica*) is a very effective monoterpene acting as a feeding deterrent at very low concentrations. Alkaloids are the best known among the toxins against insect attack, solanaceous hosts providing a host of examples like solanine, nicotine, tomatine, leptadine, strychnine, atropine and many of them are known to inhibit sugar receptors and hence block sugar responses. Phenolic compounds are non-nitrogenous compounds containing one or more hydroxyl groups attached to a benzene ring. Tannins are polymeric phenolic compounds with strong protein adsorbing properties. Proanthocyanadins or condensed tannins elicit variable responses according to the concentration involved. Protein-complexing capacity of various biosynthetically limited polyphenols is the principal means by which polyphenols like tannins exert their defensive role in plants. This is particularly true of gallic acid which undergoes a wide range of modification, often oxidative, leading to a host of secondary metabolites (Brattsten and Sami Ahmed 1986). Proteinase inhibitors are polypeptides that bind to enzymes and are found in large quantities in seeds and foliage. Some plant species produce a variety of proteinase inhibitors, each with a different specificity. Although specific enzyme inhibitors and animal hormone analogues provide protection at lower concentrations, this is not the case in adapted insects even at higher concentrations. It is in this situation that plants produce novel substances, not present in attacked plants. In short, phenolic compounds which provide mechanical support for plants, also provide pre- and postinfestation factors involving polymeric phenols and phytoalexins which are allelopathic and allelochemic agents in insect-plant interactions. Secondary plant chemicals or allelochemics, defined as the most ecologically active plant compounds, play a vital role in insect behaviour and are non-nutritional compounds which interfere with insect feeding and reproduction (Schoonhoven 1972). The array of allelochemical substances produced during shikimic acid metabolic pathway, serve as attractants, feeding deterrents, repellents and stimulants are implicated in host plant selection process involving host finding for feeding and oviposition by the adult female as well as host feeding for feeding, growth and development of the larva. Some of these are termed allomones favouring the producing organisms and others as kairomones, favouring the receiving organism (Feeny 1976; Rhoades and Cates 1976). Antibiotic effects of allomones relate to disruption of normal growth and development of larvae and reduced longevity and fecundity. Some allomones have antixenotic effects which disrupt normal host selection behaviour through acting as repellents, locomotory excitants and deterrents. Phenolic compounds are universally present in higher plants and possess one or more phenolic hydroxyl groups and as indicated earlier the phenylpropanes are important and formed in part via the shikimic acid pathway. They exist as monomers such as cinnamic acid, flavonoids, isoflavonoids and as polymers such as tannins and lignins. What is puzzling and complex is that it is not possible to describe insect and plant relationships based on phenolics alone, since different classes of secondary compounds may be involved at a number of different levels of interaction (Harborne 1978). Attractants more particularly to pollinating insects are mono and sesquiterpenes and volatile aromatic substances include simple aliphatic alcohols, ketones and esters. Some of the major plant volatiles attractive to insects are limonene, geraniol (mono), bisabolol (sesqui), vanillin, methyleugenol which are aromatic (Hedin *et al* 1971). Insects recognize odours from individual flowers limiting their attention to specific flowers. Having been attracted to flowers they depend on nectar for nutrition, especially the butterflies and it is noteworthy that increased amounts of nitrogen in nectar of flowers reflect the nutritional needs of the specific pollinators.

Recent attempts have shown the importance of tritrophic relationships on insect-plant interactions, which involve the host plant, the insect and the parasite or predator (Campbell and Duffey 1979; Barbosa *et al* 1982; Barbosa and Letournean 1988). The discovery of tricosane and heptanoic acid as attractants of *Trichogramma* and Potato tuber moth (Harborne 1978) has paved the way for further studies in this direction. There are also indications available of the role of volatiles emanating from the larval frass, larval cuticle and moth scales attracting the parasites towards the host organisms (Donald *et al* 1986). Interesting information is available of the secretions of dorsal and ventral abdominal glands of some corieds and pentatomids attracting parasites. The response of trichogrammatids and larval parasites to chemicals of the frass of *Heliothis armigera* and *Spodoptera litura* and antibiotic properties of such phenolic substances as resorcinol, phloroglucinol, gallic acid, pyrogallol to mention a few, are now being studied by the author and associates and appear to be of interest (Ananthakrishnan *et al* 1990).

That plants could change their chemical compounds to render their tissues less suitable for insect growth and reproduction as a direct result of the damage inflicted by insects has been well documented. At the same time the detoxification mechanisms of insects are equally well known, the major objective being the solubilization of a generally lipophilic compound into a water soluble one to be excreted, through the action of mono-oxygenases which are capable of oxidising a wide variety of oxidative reactions and referred to as MFOs are mixed function oxidases. Reduction of hydrolyses may also occur in the detoxification process. It must also be emphasized that while these processes are operative to counteract the defenses of plants and insects, phytophagous insects are equally capable of sequestering natural products regularly. Further, gall-forming species and plant-sucking insects tend to inject substances into the plant tissues that increase the nutritional quality, their saliva containing polyphenolic oxidative enzymes which tend to neutralize plant defense phenolic compounds and/or which could be involved in the production of auxins or auxin-like compounds (Miles 1972). In this connection the role of leaf miners appears to be of interest in that they retard senescence of leaves in which they feed to produce 'green islands' containing higher levels of cytokinins.

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