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# Chemodynamics of insect-plant interactions

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Instances of coevolutionary adaptations in insect-plant interactions are discussed and an overall analysis of the chemical ecological basis of host plant suitability and resistance has been attempted including the implications of the impact of volatiles in tritrophic interactions.

**Key-words**—Insect-plant interactions, Coevolution, Chemical ecology, Chemical defences.

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## सारांश

### कीट-पादप अन्तर-साहचर्य की रासायनिक-गतिविधियाँ

टी० एन० अनन्थकृष्णन

कीट-पादप अन्तर-साहचर्य में सहविकासीय अनुकूलता के उदाहरणों की विवेचना की गई है तथा पोषी पादप अनुकूलता एवं प्रतिरोध के रासायनिक-पारिस्थितिक आधार को विश्लेषित करने का प्रयास किया गया है।

INSECTS and plants have been coevolving organisms essentially engaged in overcoming each other's defence arsenals, plants producing newer deterrents through adopting novel metabolic pathways and insects overcoming them by diverse detoxifying mechanisms. Consistent biochemical interactions have had considerable influence on the evolution of insects. Plants have had greater effect on insect evolutionary changes or strategies at least from the chemical viewpoint, since chemical arsenals like hormones, pheromones and the like essentially determine the success of an insect. It is the selection pressure exerted by insect feeding on plants that has led to a wider range of biochemical reactions, the intensity of which is yet to be fully explored. While it is well known that all organisms, from bacteria to the most advanced plant or animal, synthesize the same range of sugars, amino acids, fatty acids and so on, the essential difference between the chemistry of primitive and advanced groups lies in the diversity of secondary metabolites or allelochemicals. Since plants are able to synthesize a variety of substances such as non-protein amino acids, terpenoids, alkaloids and flavonoids their structural diversity has increased greatly during the course of evolution concomitant with periodic changes in the intensity

of herbivore stress (Swain, 1974). With over 5,00,000 species of insects and 2,50,000 species of plants and over 300 million years of evolutionary history the stage has been set for intensive researches on insect-plant interactions, more particularly on the biochemical coevolution of these groups which naturally calls for diverse adaptive strategies from their origin to recent times.

It is well known that the first land plants appeared in the late Silurian or early Devonian, their success being due in part to proanthocyanadins or condensed tannins which are antibacterial, antifungal and antiviral. The origin of insects in the Carboniferous was preceded by the pteridophytes in the upper Devonian containing the sesquiterpene compounds, while in the Permian, with the arrival of tree-like ferns, further diversification as mono-, di- and sesquiterpenes were produced which had juvenile hormone effects on the early orthopteroids, as suggested by the aborted wings in some fossil elements. With the radiation of angiosperms in the Mesozoic, the condensed tannins became converted into hydrolysable tannins and by Middle-Cretaceous

the angiosperms became predominant and became the major part of the world flora by the early Tertiary. Diverse groups of insects made their appearances, the plants serving as platforms for their radiation, producing such chemicals such as alkaloids, glycosides, terpenoids and so on. The occurrence of hydrolysable tannins in larger proportions of genera in more ancient angiosperms than in recent taxa was also evidenced. Therefore the effects of this biochemical coevolution appears to have been principally on increasing the heterogeneity of secondary compounds. Though much work has been done on Lepidoptera and their hosts, the diversification of angiosperms with subsequent colonisation of butterflies represents only 'just one episode in a large-scale coevolutionary association of land plants' (Mitter & Brooks, 1983).

Insect pollination offers a very good example for coevolution between the plant and the pollinator. Though primitive angiosperms like Magnoliaceae and Nymphaeaceae which appeared in the Mesozoic are still pollinated today by insects, Asteraceae which evolved by Early Palaeocene developed the inflorescence structure to provide a landing platform for large insects like the Lepidoptera. Available fossil data suggest roughly contemporaneous radiation of Lepidoptera and angiosperms (Swain, 1978). The best modern example concerns the heliconiine nymphalid butterflies, which feed on Passifloraceae. It is also known that the evolution of *Heliconius* occurred after the diversification of the Passifloraceae. Bees appeared about the same time as the plant families Scrophulariaceae and Lamiaceae, and have been evolving for around 35 million years. Papilionaceae and Orchidaceae are the families best adapted for pollination by bees (Price, 1984).

It is presently believed that behavioural specialisation sets the stage for evolution of physiological adaptations including detoxification that are specific to secondary compounds of the particular host (Bernays & Graham, 1988). The various pathways that produce chemicals of modern plant/insect interactions find their origin in the shikimic acid pathway. These compounds include the phenylpropanes (Tannins, phenols, lignins, quinones). The shikimic acid pathway also leads to the synthesis of phenylalanine and other amino acids, as well as the acetate pathway which produces the isoprenoid or C<sub>5</sub> compounds from which a host of terpenoids result and which play an important role in the attractance/deterrence of phytophagous insects. Today it is well known that plants are capable of chemical communication, producing

intercellular chemical signals as a reaction to insect injury (Edwards & Wratten, 1987; Ananthakrishnan, 1990). Some of these chemical signals are oligosaccharides, chitinases, glycine-rich glycosides, arachidonic acid, eicosapentanoic acid, and proteinase inhibitor inducing factors. P11F mobilise enzymes responsible for the disruption of chymotrypsin and trypsin activity in insects (Schoonhoven, 1972). Elevated activity of such enzymes as phenylalanine ammonia lyase, tyrosine ammonia lyase, peroxidase and polyphenol oxidase are equally evident (Suresh & Ananthakrishnan, 1988).

The consumer role of insects is a complex one involving an integration of nutritional and related reproductive behaviour (Frazier, 1986; Price, 1986; Haukioja, 1980, 1990). It is the behavioural aspect of insects that contributes to the degree of host specificity. External information is passed on by the olfactory, visual, gustatory and chemosensory receptors to the internal environment, and with the integration of this information into the physiological state of the insect, necessary responses are evoked. It is here that chemosensory systems play an important role. Varied number of sensillae occur at different sites such as labial palps, antennae, tarsi and so on, each with several receptor cells which play a role in the recognition of attractant and deterrent factors (Ananthakrishnan *et al.*, 1985). While at one concentration, the receptor evokes an attraction response, at a different concentration the same receptor promotes a deterrence effect. Host plant switching by insects is essentially based on this principle. The electroantennogram (EAG) technique is used in studies relating to the behavioural diversity of insects in relation to different concentrations of chemical substances.

As a result of selection pressure exerted by insect feeding, host plants tend to diversify their biochemical pathways and production of newer compounds enables the plants to overcome feeding pressures. In this way, distinct chemotypes in plant populations tend to evolve (Ananthakrishnan, 1990). Likewise, in response insects may overcome plant defences by means of detoxification mechanisms such as the induction of Mixed Function Oxidases (MFOs). Favourable chance mutations may also lead to the development of distinct insect biotypes (van Emden, 1991). A good example of biotype evolution relates to the brown plant hopper (BPH) *Nilaparvata lugens* (Homoptera) which has four biotypes, each inflicting a particular type of damage to the rice crop. In this connection it would be proper to indicate the recent changes taking place in the infestation diversity of *Retithrips syriacus*

(Thysanoptera). Of the many host plants, *Ricinus communis* was found to be most favoured, in which the brownish red-stem variety was preferentially infested. Recently (Ananthakrishnan *et al.*, 1992) it was observed that this species has established itself even on the green-stem variety which was hitherto avoided. The expanding trophic diversity has enabled its colonisation even on the leaves of *Eucalyptus globulus* and *Manihot utilissima*, so very diverse in their biochemical profiles. While the terpenoid pathway constitutes the major static defence in the former, cyanogenic glycosides are characteristic of the latter host. *Retithrips syriacus* has accordingly adapted itself to the diverse biochemical profiles, enabling successful colonisation of these hosts. Gas chromatographic analyses of the volatiles of uninfested *Ricinus communis* revealed 9,12—octadecadienal, dimethyl acetal and naphthalene, while anal exudates of the thrips were found to contain a host of compounds including 2-thiophene carboxylic acid, naphthalene and cyclopentane butanoic acid. Similarly, phytol, cyclohexane and undecane were detected from uninfested *Eucalyptus globulus*; the anal droplets contained cyclohexane, undecane, phosphothioic acid, naphthalene and 2-furan carboxaldehyde. The major volatile detected in *Manihot utilissima* was cyclohexanone, while the thrips released dodecenoic acid and naphthalinone. This indicates, the uptake and transformation of plant natural products and volatiles constitute an important array of substances governing the sensitivity of the herbivore in host selection. The physiological status of the hosts was also found to be significantly altered, particularly in relation to enhanced defences and was manifest as increased activity of phenolic enzymes. These include the phenylalanine ammonia lyase, tyrosine ammonia lyase, peroxidase and polyphenol oxidase which are mobilised proportionate to the degree of infestation. However, age-correlated changes in *Terminalia catappa* irrespective of feeding stress of *Rhipiphorothrips cruentatus* also influenced alterations in the physiological status and hence the degree of susceptibility to thrips (Suresh & Ananthakrishnan, 1987). The number of isoenzymes was found to be a function of phenological changes (Suresh & Ananthakrishnan, 1988) which under herbivore stress has however been maintained high. Manifestations of induced defences indicate host responses subsequent to which, prolonged colonisation only indicates the adaptive ability of thrips to successfully overcome host defense. Regarding cyanogenic glycosides, the presence of one such compound called dhurrin in young

sorghum leaves attracts attention. There is a compartmentalisation of the cyanogenic glycoside which is shielded from the enzymes in the plant, enabling tolerance of the compound. On being ingested by an insect, the enzymes and the glycoside combine to release HCN, which, while being toxic to the insect, gets released into the amino acid pool in the plants (Harborne, 1988).

In considering the cotton-*Heliothis* system emphasis may be laid on the impact of different cultivars on *Heliothis armigera*, and especially the effect of antibiosis on the insect and the degree of host plant resistance in terms of phenolics offered by the different cultivars (Ananthakrishnan *et al.*, 1990; Annadurai *et al.*, 1990). In this connection, mention may be made of tritrophic interactions involving host plant, insect and natural enemies, as against the earlier bitrophic proposition involving only the insect and its natural enemies. Tritrophic interactions are exemplified by the fact that different growing stages of the cultivars release volatiles into the air, which not only influence the behaviour of the host insect, but also exert considerable influence on other natural enemies of the insect. In addition, the frass of *Heliothis* and *Spodoptera* also contain volatiles sufficient enough to attract natural enemies of these insects. It was also observed that the different developmental stages of cotton are characterized by shifts in the levels of metabolites. Highest levels of phenols as detected in MCU7 conferred increased resistance to *H. armigera*. The other cultivars namely Suvin, LRA 5166, MCU11, TCHB were relatively less resistant. Of the phenolic acids which impart resistance, gallic acid forms the central theme for which any number of transformations can result not only in the diverse tissues of a host plants, but manifests in various molecular forms all through the Plant Kingdom. The parent compound of gallic acid and plant polyphenols in general is B-penta-o-galloyl (Harborne, 1989). Qualitative differences in flavonoids were specific to plant parts with the flowers containing higher number of fractions. Early flowering stages are characterized by apigenin, aureusidin-6-glucoside, luteolin and gossypetin, while chrysoeriol and myricetin replace luteolin and the glucoside in the later stages of development. Young leaves contain hesperitin. Mature and senescent leaves are characterized by gentisic acid and luteolin along with chrysoeriol respectively. Such changes in the profiles of phenolic acids and flavonoids indicate age-specific alterations which also determine the degree of susceptibility to herbivores. Of all the host plant tissues, the mature bolls of *Gossypium hirsutum* are most attractive to

*Heliothis armigera*. Differential attraction was evident on analysis of the feeding preferences of another coexisting pest, *Spodoptera litura*, which mainly chose to feed on mature leaves. Age-specific consumption rates and related changes in developmental durations appear directly correlated to the nutritional status of the cultivars. Mention must be made of the major groups of secondary compounds, viz., the condensed tannins, terpenes, cyclopropenoid fatty acids and flavonoids that comprise the fractions in the cultivars. Bioassays for toxicity of the phenolic acids (Ananthakrishnan *et al.*, 1990), including tannic acid and pyrogallol, confirmed their defensive role against herbivory by drastically disrupting the nutritional and growth parameters of noctuids. Phenolics incorporated in the diet were detected in the frass. The rate of egestion was linearly related to the ability to withstand phenolic toxicity.

The implications of volatiles being released from different parts of the host plant can be far-reaching (Ananthakrishnan *et al.*, 1991). Majority of the volatiles detected in the cultivars significantly modulate the behaviour of the herbivores and their natural enemies. While caryophyllene was detected in the squares of such cotton cultivars as Suvin, TCHB, MCU7 and MCU11 octadecane, undecane and dodecane were identified in LRA 5166. Caryophyllene was detected even in the bolls, especially those of MCU7 and TCHB, while pentadecanol was present in TCHB. Tetradecanoic and hexadecanoic acids were characteristic of MCU 11. Behavioural response of *Trichogramma chilonis* varied in response to hexane extracts containing the volatiles and was specific, being characterized by high antennation and probing behaviour specially when exposed to extracts from the squares, flowers and bolls. This appears to be directly related to enhanced parasitism as site-specific events. Susceptibility was highest in association with the nutritionally most suitable cultivar, viz., Suvin. Parasitism rates also reduced in linear measures with inherent host plant resistance. Such observations were common to also the predatory potential of *Chrysopa scelestes*.

Mention must be made also of volatiles released as body odours which mediate the predatory and parasitic behaviour of natural enemies enabling host location and enhance their biocontrol potential. Compounds such as hexatriacontane, pentacosane, heptadecane, docosane and 2,6,10 dodecatrienal-3,7,11-trimethyl, identified from active moth scales influence the parasitic potential of *Trichogramma chilonis* can be employed in manipulating entomophagous activity in biocontrol programmes

(Ananthakrishnan *et al.*, 1991).

Equally interesting is the impact of glandular hairs and their secretions on insects such as aphids, leaf hoppers, and the like. The glandular hairs of solanaceous hosts release  $\beta$ -farnesene which acts as an alarm pheromone preventing the aphids from colonisation (Gregory *et al.*, 1986). Strangely enough the very same plant also produces caryophyllene that suppresses the action of  $\beta$ -farnesene and also attracts predators to a large degree. In the case of some *Solanum* species, two types of glandular hairs are observed, one of which secretes a phenolic substance that exudes on to the plant surface when disturbed by the landing of the aphid. Enzymatic reactions ensue, culminating in the formation of a sticky residue which immobilises the aphid and arrests its movements. Subsequent struggles aggravate the situation for the aphid due to enhanced output of peroxidases that mobilise the formation of the arrestants.

It is well known that insects are incapable of synthesizing cholesterol and therefore depend exclusively on phytosterols of host plants such as sitosterol, fucosterol, stigmasterol, campesterol and related substances (Svoboda *et al.*, 1978). Subsequent conversion of these compounds to cholesterol forms the basis for the production of insect growth hormones which are now understood as polypeptides (Karlson, 1983). It is interesting that plants are also known to synthesize compounds that disrupt normal development of the insects which feed on them. Examples of such compounds are phytoecdysones, juvabione, antijvenile hormones or precocenes, and juvocimenes that mimic the functions of insect hormones and are hence designated as hormonomimetic compounds (Menn & Borkovec, 1989). With advances in genetic engineering techniques it has been possible through structural elucidation of polypeptides, to not only identify the genes aiding in their synthesis, but also develop inhibitors of enzymes mobilising such synthesis. Incorporation of such genetic factors into host plants, employing baculoviruses as carriers, may modulate production of hormones which can disrupt the physiology of the insect invader. Genetically engineered transgenic plants with the ability to synthesize defensive proteins such as phytoagglutinins, lectins and proteinase inhibitors are considered as alternate means to avoid excessive use of biocides that also tend to disrupt the natural enemy complexes. Evidences also point to insects' ability to overcome resistance based on single gene expressions (van Emden, 1991), and therefore emphasis is currently laid on the need to evolve multigene resistance mechanisms.

Mechanisms of coevolution are dynamic phenomena with biochemical implications extending into the third trophic level also, an analysis of the chemical ecological basis of which is central to a proper understanding of the diversity prevalent in species specific instances of insect-plant interactions.

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