Insect Olfactory Exploitation Of Plant Stress Indicators

M. Rosa Paiva*

Synopsis

Among plants, herbivores and their natural enemies, relationships co-evolved which were, to a large extent, based on the exploitation of an olfactory language. Olfactory signals are often produced when the organisms find themselves under stress. A possible definition is proposed, that could contribute to clarify the meaning of the word stress, based on the concept of ecological niche. Due to strong selective pressures, plants aimed at excluding herbivores by synthesising toxic secondary metabolites. Since these substances are in part volatiles, olfactory communication developed. However, some phytophagous insects managed to revert plant defense mechanisms to their advantage. Taking bark beetles and wood borers as an exemple, insect primary attraction is analysed, in relation to stress factors affecting their hosts. Secondary attraction is also considered for some scolytids. By sequestring volatiles from their hosts, with whom they established obligatory associations, specific pheromones are produced. Furthermore, bark beetles' predators evolved specific olfactory strategies, sometimes based on kairomonal cues, which are described. Man makes use of different types of semiochemicals, mainly applied to the management of insect populations. Among them, plant and insect stress indicators can become some of his best allies.

Olfactory communication, plant stress,
phytophagous insects.

1 Herbivory and Plant Stress

Stress is an almost intuitive concept, which eludes a precise definition. Similarly to other ecological terms, like bionomic strategies or adaptation, a tendency is implied to which boundaries are difficult to set. GRIME (1977) defined stress as any factor that restricts growth. Frequently biotic descriptors of the community are used to quantify stress effects. Among them, scope for growth (WARREN AND DAVIS, 1967) has been widely used.

An alternative attempt to define stress could be based on the inherent characteristics of the species, using the concept of ecological niche (sensum HUTCHINSON 1957). A stress response then occurs when one, or more, of the parameters required to shape the "hipervolume within which the organisms' fitness is positive“, approach, or even momentary exceed, the limits of their scales of tolerance.

It is generally believed that plant secondary metabolites primarily evolved as defence mechanisms against herbivory (e.g. MACKEY, 1979). This trait can be envisaged as a long-term response to the stress posed by high population densities of herbivores, particularly phytophagous insects.

In the course of their successful evolutionary trend, insects often managed to reverse the process to their advantage, adopting strategies which led even to the establishment of obligatory associations with their hosts. A classical example is the association between butterflies of the Sub-Family Danainae, and host plants containing pyrrolizidine alkaloids (e.g. BOPPRÉ, 1984), which are toxic to most animal groups. The males need to feed on plants containing the alkaloids, like *Heliotropium* spp., in order to produce the nitrogenous keton "danaidone“, an aphrodisiac pheromone indispensable to render them accepted by the females (PLISKE & EISNER, 1969).

In plants, the production of chemicals originally intended for defensive purposes, may sometimes be induced, or stimulated, by stress factors, including previous attacks by herbivores (e.g. HARRISON & CARBAN, 1986). It is further believed that in slow growing species the investment allocated to the synthesis of secondary metabolites remains fairly constant, throughout the plant's life cycle. On the contrary, in fast growers, large fluctuations can be observed, with the metabolite production rising under stress conditions (e.g. JONES & COLEMAN, 1993).

Olfactory communication plays a key role as mediator of both intraspecific and interspecific interactions in arthropods. Particularly relevant became the exploitation, by insects, of their hosts' volatile cues, emitted as a physiological response to stress conditions.

2 Olfactory Interactions: Types and Costs

Olfactory communication is vehiculated by pheromones among organisms of the same species, and by allelochemicals between emitters and receivers belonging to different species (KARLSON & LÜSCHER, 1959).

In general, two types of costs are associated with message transmission: direct and indirect ones. The

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Tab. 1
Types of olfactory messages convened by insects, example and adaptive value for the emitter and receiver.

SEMIOCHEMICALS' ADAPTIVE ADVANTAGE		
EMITTER	**RECEIVER**	**TYPE EXAMPLE**
PHEROMONES [Intraspecific messages]		
+	+	Aggregation: scolytids
+	–	Epideitic or dispersive: scolytids
–	+	Alarm: aphids
ALLELOCHEMICALS [Interspecific messages]		
+	+	Synomones: pollinators' recruitment
+	–	Allomones: carnivorous plant volatiles
–	+	Kairomones: scolytids' predators

former consist of the investments made for the production, transport, storage and emission of the volatiles. Such costs are almost impossible to quantify, although some attempts have been made (e.g. CHEW & RODMAN,1979). Perhaps more important are the indirect costs, mainly the so called espionage risks (e.g. DICKE & SABELIS 1989), arising from the interception of the messages by non-targeted receivers. Table 1 presents a summary of the types of messages convened by insects and of the resulting selective advantage.

Communication between plants and herbivores is primarily detrimental for the emitter. Nevertheless, the same volatiles released by the plants, can act as synomones, in synergism with pheromones produced by the phytophagous respondents. As a result, natural enemies of the insects are recruited, in this case to the plant's advantage.

A plant-to-plant chemical language, based on volatile emission, has also evolved in some species, but is still insufficiently studied. One of the scarce well documented examples demonstrated that cotton plants, infested with a pathogen, will produce a pheromone to alert neighbours, towards this potential danger. As a result, the receivers increase their production levels of phenols, which hinder the pathogen's development (ZERINGUE,1987).

3 Volatiles Denouncing Host's Stress: Insect Primary Attraction

The production of secondary metabolites that convey information on the health/vigour condition of the plants, obviously acts in detriment of the emitter. Contrary to the production of synomones, this can be envisaged as an unavoidable consequence of the metabolic pathways unfolding under stress conditions.

Efficient exploiters of this type of communication can be found among the scolytids and cerambycids. Several species of bark and ambrosia beetles, and some wood borers, are thus able of obtaining information about their host's physiological condition by olfactory perception. Although visual cues are also involved, the beetles respond to volatiles produced by plants weakened by pathogen attack, or other stress factors, to single out the appropriate hosts for colonisation.

Host selection by primary attraction (e.g. WOOD, 1972, 1982) is thus exhibited by several forest insects, like ambrosia beetles. These scolytids bore into the xylem of recently cut timber and constitute serious pests, due to an obligatory association with wood staining fungi of the genus *Monillia*. Among them, the genus *Trypodendron* and particularly the striped ambrosia beetle, *T. lineatum* (Oliv.), has been closely investigated. Pioneer females, which are the first to emerge in the early Spring, respond to ethanol (MOECK, 1970), a product originating from the anaerobic decomposition of vegetable material.

Tomicus piniperda L., the pine shoot beetle, which normally reproduces in tree stumps and logs, can be considered as an unusual bark beetle, since pheromone production is absent. However, the mechanisms of host colonisation are guided by attraction to a specific terpene, terpinolene, which acts in synergism with ethanol (BYERS et al., 1985; VITÉ et al., 1986).

Although considered as secondary insects, that is adapted to explore dead plant material, both *Trypo-*

dendron lineatum and *Tomicus piniperda* can attack living trees, under conditions of high population density. Regarding the ambrosia beetle, trees submitted to some form of stress will be selected, specially if damaged, ethanol emitting host material is available (PAIVA et al. 1983). In northern Portugal, an area which is located on the boundary of the beetles' ecological range, the pine shoot beetle is sometimes observed attacking stressed *Pinus pinaster* Ait., *P. nigra* L. and *P. pinea* L. (PAIVA & MASSALSKI, 1990).

Forest fires constitute a major stress factor affecting coniferous plantations in Mediterranean habitats. Scorched trees undergo physiological alterations reflected in the resin, and thus in the chemistry of terpene production (e.g. KRAWIELITZKI et al. 1983). Resulting from the occurrence of wild fires, or from the incorrect application of cultural practices, namely prescribed burning (e.g. FERREIRA, 1988), standing trees thus become preferred targets for colonisation by several species of bark beetles. Additionally to the pine shoot beetle, the Mediterranean engraver beetle, *Orthotomicus erosus* (Woll.) and the six toothed bark beetle, *Ips sexdentatus* Boern, can also cause important losses (PAIVA & MASSALSKI, 1990).

In general, the chemical ecology of wood borers is not yet as thoroughly understood as that of bark beetles. The eucalyptus borer *Phoracantha semipunctata* Fab. an Australasian species, became a serious pest in most eucalyptus growing regions located outside its' area of origin. Host tree selection is accomplished by females searching for ovipositing sites. Field observations showed that stressed trees in a stand, like the ones suffering from drought, or water logged, were preferentially selected. A comparative analysis of the bouquet of odours emitted by healthy trees, and by the ones either already attacked by the borer, or diseased, was conducted. Significant differences were detected in the relative amounts of several monoterpenes emitted (MATEUS et al., 1995) – Figure 1. Furthermore, it was established that logs previously attacked by the borer proved significantly more attractive for oviposition, than not attacked ones (PAIVA et al., 1993).

4 Host Volatiles' Sequestration : Secondary Attraction

Most scolytids sequester plant volatiles to produce aggregation pheromones (eg. WHITE et al. 1980). In general these substances are secondary alcohols, derived by allylic oxidation, or hydration, from their hosts' monoterpenes (e.g. VANDERWEL & OEHLSCHLAGER, 1987). A detoxification mechanism is

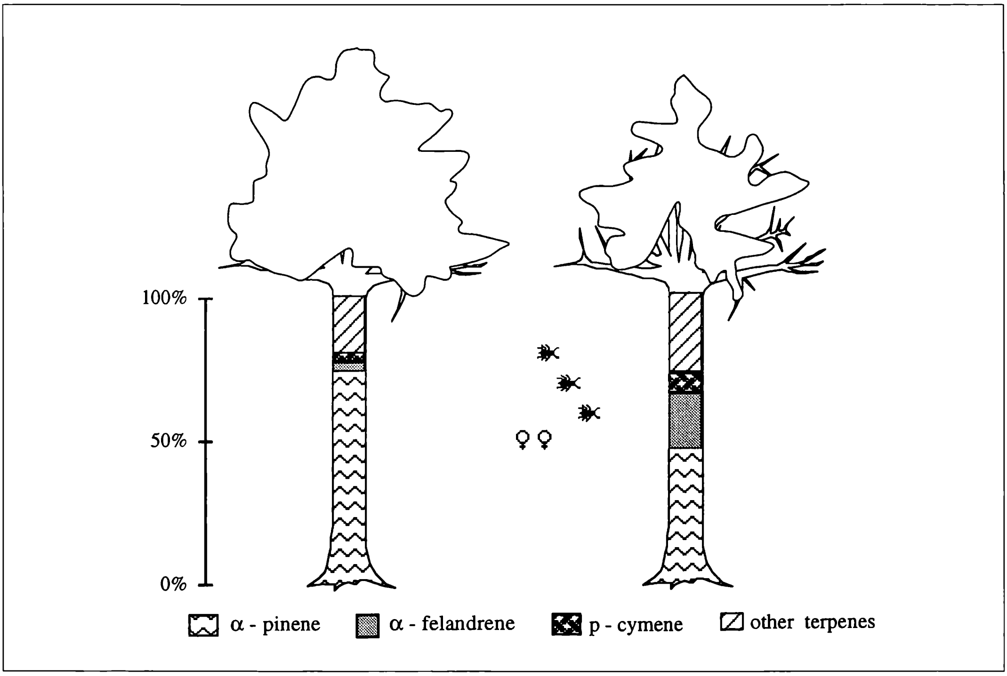

Fig. 1

Comparison of the relative percentages of the main monoterpenes emitted by vigorous and stressed *Eucalyptus globulus*, resulting in a differential attractiveness to the eucalyptus borer *Phoracantha semipunctata*. Based on PAIVA et al. (1993).

certainly involved, since the terpenes are toxic to the scolytids, when exposed to them (e.g. FRANCKE & VITÉ, 1983). Additionally to the alcohols, cyclic ketals are also emitted, as components of the pheromone bouquet, but their biosynthetic origin is not clear.

The spruce engraver beetle *Ips typographus* L. is a forest pest of major economic impact in central and northern Europe. In this polygamic species males are the pioneer insects, selecting the new hosts to be colonised. The beetles sequester a-pinene, to produce two components of their aggregation pheromone bouquet. Both enantiomers of the terpene, (–)-a-pinene and (+)-a-pinene, are oxidised and released, respectively as *cis-* and *trans-*verbenol. However, only *cis-*verbenol, acting in synergism with 2 other substances, attracts females and other males. A mass attack is thus triggered (BAKKE et al. 1977), which is indispensable to overcome the hosts' resistance.

In this example, the chirality of the monoterpenes present in the resin ultimately determines the capacity of *I. typographus* to produce its aggregation pheromone (KLIMETZEK & FRANCKE, 1980). Furthermore, it has been hypothesised that the relative proportion of both enantiomers, can be linked to the physiological condition of the tree: a vigorous host should contain a larger amount of (+)-a-pinene than a weakened, or stressed one (HACKSTEIN & VITÉ, 1978). The probability of a tree being preferred by *I. typographus* would thus be associated with its volatile emission (VITÉ, 1987).

After a mass attack has succeeded, several scolytid species produce pheromones indicating to conspecifics that the host has been fully colonised. These - dispersive, spacing or epideitic pheromones (e.g. JUTSUM & GORDON, 1989), shift the attack to other hosts, or parts of the host, thus preventing resource over-exploitation. In *Ips typographus* both sexes produce (–)-verbenone, which inhibits the response of attracted beetles to the aggregation blend (BAKKE, 1981).

Specific predators and parasites of phytophagous insects mainly locate their prey, or hosts, by means of kairomones. This is achieved by intercepting pheromonal messages, emitted by the herbivores, which were targeted to reach other individuals of the same species. Additionally, synomones emitted by the plants, are sometimes necessary to synergise the effect of the kairomone.

Among the natural enemies of bark beetle's, different olfactory strategies appear to have evolved, regarding prey location. Thus, some predators, like the clerid *Thanasimus formicarius* (L.), may be considered as generalists, preying upon more than 20 scolytid species (KOHNLE AND VITÉ,1985). This species is attracted to a wide range of pheromonal blends, as well as to the conifers' terpenes.

On the contrary, indications exist that a specialised olfactory strategy was adopted by other predators. Such is the case of the ostomid beetle *Nemosoma elongatum* (L.), that responds to chalcogran, 2-ethyl-1,6 dioxaspiro [4,4, nonane], the pheromone of its primary prey, which is made up by scolytids of the genus *Pityogenes,* namely *P. chalcographus* (L.), and *P. quadridens* Hartig (KOHNLE & VITÉ, 1985). Similarly, the mediterranean colydiid beetle *Aulonium ruficorne* Ol., is a predator which appears to respond preferentially to the pheromone mixture of the locally most abundant prey species, *Orthotomicus erosus* (Woll.) (PAIVA, 1995).

5 Anthropogenic Exploitation of Volatile Stress Indicators

Semiochemicals have been identified and commercialised for several decades, originating new techniques of integrated pest management (IPM). Among them, some indicators of plant and insect responses to stress are already in use. Clearly, strategies for their application will vary widely, according to the behavioural responses of the target organisms.

Aphids produce an alarm pheromone, which is released when the colony is attacked. The behavioural response consists in an increased mobility, resulting in a reduction of the efficiency of predators and parasites. For many species, (E)-b-farnesene is used as pheromone. The production of the same substance, from glandular thrichomes on the leaves of *Solanum berthaultii* was reported by GIBSON AND PICKETT (1983). This relative of the potato thus achieves a reduced colonisation by aphids, and aphid transmitted virus. In IPM programmes, the addition of an alarm pheromone to a pyrethroid (contact insecticide) increases aphid mobility, and thus insecticide efficiency (PICKETT et al. 1989).

Regarding bark beetles, primary and secondary attractants, have been widely used in forest protection schemes over the last decades. Probably the most important success so far recorded was the giant campaign launched against *Ips typographus,* in Scandinavia, which resulted in a significant reduction of the population effectives of the spruce engraver beetle (BAKKE, 1989; VITÉ, 1989). Field tests using repellents, or inhibitory semiochemicals, are in progress. A successful case reported was the drastic reduction in the colonisation rates of logs of pine and ash, respectively by *Tomicus piniperda* and by the ash bark beetle *Leperisinus varius,* achieved after spaying with verbenone and ipsdienone (KOHNLE et al., 1992).

Plant and insect volatiles indicators of stress, should thus be placed among the most promising semiochemicals for the development of future IPM strategies. On the other hand, Man's exploitation of plant-insect olfactory relationships is pushing the evolution of this type of communication one step further.

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Address

M. Rosa Paiva
Universidade Nova de Lisboa, FCT/DCEA
Q. da Torre
P-2825 Monte de Caparica
Portugal

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