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Third Trophic Level Influences of Plant Allelochemicals

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I. INTRODUCTION

Since the stimulating review of Price *et al.* (1980), it has been widely recognized that many plant characteristics can have a profound impact on the enemies of herbivores, and, consequently, that any theory of the evolution of plant–herbivore interactions should also consider the third trophic level.

The influences of plants on the third trophic level are diverse and, at first glance, paradoxical. Plant characteristics can be used as cues (e.g., plant volatiles) by the natural enemies of herbivores to find their prey or host or to provide those enemies with either shelter or complementary or alternative foods (e.g., floral or extrafloral nectaries and pollen). Thus, plants can have positive influences on the third trophic level. It has even been suggested that plants, when attacked by hervibores, may actively call for "bodyguards" as part of their defensive strategy (Dicke and Sabelis, 1988). Some plants, however, offer the herbivore an "enemy-free space" (Price, 1981), directly or indirectly impairing the activities of the third trophic level. Finally, emergent properties appear in plant communities, since the properties of neighboring plants can be beneficial or detrimental to the enemies of the herbivores of a given individual plant (Price *et al.*, 1980; Nordlund *et al.*, 1988).

Despite the conceptual difficulties arising from the diversity of these interactions, some unifying theories have been elaborated that suggest trends in the evolution of the total plant–herbivore–predator and parasitoid system. According to Feeny (1976) and Price *et al.* (1980), herbivores feeding on late successional (apparent) plants in temperate regions should be more vulnerable to natural enemies than those feeding on early successional plants that are difficult to find. First, being polyphagous on more apparent and predictable plants, they should themselves be more apparent and predictable; second, as they are feeding on plants characterized by compounds classified as digestibility reducers (e.g., tannins and resins), they have prolonged developmental times, resulting in longer exposure to their enemies; third, they cannot utilize plant chemical defenses for their own defense because the characteristic secondary compounds of their food plants (i.e., digestibility reducers) are not suitable for sequestration.

More recently, Bernays (1988) suggested that selective pressure exerted by generalist predators could be instrumental for the evolution of food-plant specialization in herbivorous insects: specialization might afford better protection from generalist predators through, for example, host-specific crypsis or host-derived chemical defense (Bernays and Graham, 1988).

This present chapter reviews those beneficial and detrimental effects of plants on the third trophic level, with an emphasis on the role of allelochemicals. Additionally, we shall test the theories described above and try to answer the following questions:

- Do some types of plants provide a better potential enemy-free space than others?
- Is there evidence for a selective pressure leading plants to call for bodyguards, and can we expect to find this strategy more developed in some plants or habitats than in others?

II. PROTECTION OFFERED TO HERBIVORES BY PLANTS

Specialist herbivores can benefit from host plants that impair the activity of natural enemies. For example, the parasitoid *Encarsia formosa* is far less efficient in reaching its host, *Trialeuroides vaporariorum*, on hairy varieties of cucumber than on hairless cucumber (van Lenteren *et al.*, 1977). This apparently self-defeating influence of plants on the third trophic level is best demonstrated by the utilization of plant toxins by herbivores for their own defense. The plant toxins can be utilized to deter or intoxicate natural enemies (Brower, 1970).

The simple act of feeding on plants containing toxins implies that the herbivores are contaminated by these toxins (Brower, 1984). Toxins used defensively are not necessarily concentrated in special tissues or organs and can even be simply present in the digestive tracts and released by regurgitation and defecation (e.g., Eisner *et al.*, 1990). It is worth noting that the amount of plant material in a caterpillar gut can account for half of its weight. Sequestration occurs when the insect herbivore, instead of detoxifying and/or excreting plant secondary compounds, accumulates them in its body, either by storing the noxious compounds in the body in nonsecretory structures or by storing them in secretory structures. The mode of storage influences the way the compounds are subsequently released and come into contact with the natural enemies. The mode of release includes reflex bleeding, enteric discharge, release from exocrine glands, and release due to wounding of the herbivore. The mode of release will in turn influence the protective efficiency of a given chemical class of compounds. For example, volatile irritants are most effectively released by glands that allow them to act at a distance and repel the enemies before contact with the prey. On the other hand, toxins that act as gustatory deterrents or affect physiological processes of the predator can be effective when liberated by the wounding of the herbivore.

A. Occurrence of Sequestration

Sequestration occurs in most orders of phytophagous insects, including Homoptera, Diptera, Coleoptera, Orthoptera, Hemiptera, Lepidoptera and Hymenoptera (Blum, 1981), and a brief overview is given in Table 1. Table 1 is far from exhaustive and aims only at stressing the broad distribution of sequestration by insect herbivores. Marine organisms of different taxa, which will not be considered here, have also been reported to sequester toxins from their food plants or other toxic foods

Table 1. Phytophagous insect orders in which sequestration of plant toxins occurs[a]

Order	Family	References
Orthoptera	Pyrgomorphidae	von Euw *et al.* (1967); Rothschild (1973); Bernays *et al.* (1977)
	Romaleidae	Eisner *et al.* (1971); Jones *et al.* (1988 and 1989); Blum (1981); Blum *et al.* (1990)
Homoptera	Aphididae	Rothschild *et al.* (1970); Malcolm (1990); Wink and Römer (1986); Witte *et al.* (1990)
Hemiptera	Lygaeidae	Duffey and Scudder (1972); Scudder and Duffey (1972); Duffey *et al.* (1978); Vaughan (1979); McLain and Shure (1985); Scudder *et al.* (1986)
	Rhopalidae	Braekman *et al.* (1982); Daloze *et al.* (1982); Aldrich *et al.* (1990)
Lepidoptera	Papilionidae	Brower (1984); Bowers (1988a); Brown and Francini (1990)
	Pieridae	Aplin *et al.* (1975)
	Danaidae	Reichstein (1967); Rothschild and Edgar (1978); Brower (1970, 1984); Brower *et al.* (1988a); Boppré (1990); Brown and Francini (1990)
	Nymphalidae	Bowers and Puttick (1986); Stermitz *et al.* (1986); Bowers (1988a,b)
	Lycaenidae	Rothschild *et al.* (1988); Bowers and Larin (1989)
	Arctiidae	Aplin and Rothschild (1972); Rothschild *et al.* (1977); Schneider *et al.* (1982); Boppré (1984, 1990); van der Meijden (1984); Dussourd *et al.* (1988); Wink and Schneider (1988); Ehmke *et al.* (1990); Hartmann *et al.* (1990)
	Noctuidae	Rothschild (1973)
	Ctenuchidae	Rothschild *et al.* (1973)
	Pyralidae	Montllor *et al.* (1990, 1991)
	Zygaenidae	Nahrstedt and Davis (1986)
Diptera	Tephritidae	Nishida and Fukami (1990)
Coleoptera	Chrysomelidae	Ferguson and Metcalf (1985); Pasteels *et al.* (1986, 1988a, 1988b); Rowell-Rahier and Pasteels (1986); Ehmke *et al.* (1991); Rowell-Rahier *et al.* (1991)
	Cerambycidae	Duffey and Scudder (1972); Sman *et al.* (1977a)
Hymenoptera	Tentredinidae	Eisner *et al.* (1974); Morrow *et al.* (1976); Nishida and Fukami (1990)

[a] The list of references is illustrative but not exhaustive.

(such as sponges) (Hay and Fenical, 1988; Hay and Steinberg, Chapter 10 of this volume).

The large number of known examples of sequestration in a very diverse array of herbivores could suggest that it is a general feature of insects feeding on toxic plants. However, there are well-known counterexamples of insects feeding on toxic plants that do not sequester plant allelochemicals (list in Rothschild, 1973), although some of them rely on autogenous chemical defense for protection (e.g., various chrysomelids, see discussion in Pasteels *et al.*, 1989; Pasteels and Rowell-Rahier, 1991; and butterflies, see Brown and Francini, 1990), suggesting that sequestration is not necessarily easily evolved. Interestingly, in several cases sequestration has replaced autogenous defense, or occurs simultaneous with it (see below), suggesting that in those cases, sequestration is an evolutionarily advantageous and derived condition compared to autogenous synthesis of defensive secretion, or a reinforcement of preexisting defense.

B. Overview

Table 1 illustrates the diversity of the mechanism globally designated by *sequestration of plant toxins*. In this section we compare and contrast the various modes of sequestration.

1. *Site of Storage*

Plant toxins or their metabolites are often stored in the cuticle and/or in the blood. This is the case in most sequestering Lepidoptera, and also in the pyrgomorphid grasshoppers, rhopalid bugs, and diabroticine leafbeetles. Toxins in the integument are readily accessible to predators, and reflex bleeding is observed in rhopalids, leaf beetles, and arctiid moths.

In the lygaeids, cardenolides are stored in a modified epidermis. This is the only known case of *de novo* morphological specialization for storage. The integument of the bug *oncopeltus fasciatus* is morphologically characterized by a double-layered epidermis. The inner layer of the epidermis is heavily vacuolized, and these vacuoles are the sites of cardenolide storage. This overexpanded inner layer is supported by a basal lamina thicker than that lining the single-layered epidermis of other arthropods, presumably to prevent release of the cardenolides into the hemocoel (Scudder *et al.*, 1986). Additionally, the cuticle has special weak areas to allow the release of the cardenolide.

Sequestration of plant toxins in exocrine glands is less frequent than storage in other tissues. It is found in the larvae of some chrysomelids, in the adults of other chrysomelids, and in grasshoppers.

At least in the chrysomeline leaf beetles, sequestration is a derived condition, and autogenous biosynthesis is the primitive condition of the secretion. The larvae of most *Chrysomelina* and *Phratorina* produce iridoid monoterpenes that are absent in their host plant, and only some species feeding on Salicaceae derive salicylaldehyde from the host plant salicin. In the adults, most *Chrysolina* produce *de novo* cardenolides, but only the few species of *Oreina* feeding on the Asteraceae rich in pyrrolizidine alklaloids (PAs) sequester those alkaloids. Using cladistic rationale, if *Chrysolina* is taken as an outgroup for *Oreina,* the production of cardenolides must be considered as a plesiomorphic condition (Pasteels and Rowell-Rahier, 1991). In the larvae of several *Chrysomela* spp. and *P. vitellinae,* the utilization of plant phenolglucosides may have been facilitated by enzymatic preadaptation in the primitive larva biosynthesizing its autogenous iridoids (see the following for details). In the adults of those *Oreina* sequestering PAs rather than synthesizing cardenolides, the factors enabling the shift from endogenous biosynthesis to sequestration are not known. In both adults and larvae, sequestration is associated with the colonization of new host plants (Salicaceae in the larvae and Asteraceae in the adults) and radiation on these plant families.

In danaids, arctiids, and some ithomiines, plant PA metabolites are stored in androconial organs and used as aphrodisiacs. Glands producing aphrodisiacs are known in many Lepidoptera and generally synthesize compounds *de novo.* It is thus doubtful that these glands evolved for the storage of plant metabolites.

There is a similarity between some insect and plant chemical defenses (review in Nahrstedt, 1982). For example, many chrysomelids produce cardenolides, as do some plant families. However, since these leaf-beetles feed on plants devoid of cardenolides and biosynthesize their cardenolides from plant cholesterol (Van Oycke *et al.*, 1987), we must admit that this biosynthetic ability evolved in plants and insects by convergence. Bufadienolides and cardenolides are also produced by toads (Hoeriger *et al.*, 1970).

2. *Behavioral Effects of Sequestered Toxins*

It is usually assumed that insects sequestering toxins from plants are narrow feeding specialists. However, sequestering herbivores are usually not strictly monophagous. They can be specialists on one group of plants containing highly variable amounts of the classes of compounds that are sequestered, e.g., danaids feeding on asclepiads containing variable amounts of cardenolides, leaf-beetle larvae feeding on salicaceous plants with variable amounts of phenolglucosides, adult *Oreina* leaf-beetles feeding on PA-containing Asteraceae, or diabroticines feeding on cucurbits with different levels of cucurbitacins. As a consequence, natural populations of these insects usually show a broad spectrum in the level of sequestration or utilization of plant compounds (Malcolm and Brower, 1989, for the monarch; Smiley *et al.*, 1985, for *Chrysomela* larvae; Metcalf and Lampman, 1989, for diabroticines).

Lygaeinae feed on seeds of toxic Apocynales characterized by cardenolides (Aldrich, 1988). To our knowledge, variation in cardenolide content of bugs in natural populations has not been measured, although it is clear that such variation is observed in the laboratory with insects fed on various seed species, or seeds of the same species containing various amounts of cardenolides (Isman *et al.*, 1977b; Vaughan, 1979).

Other herbivores are specialized on various plant families characterized by the same class of toxins, e.g., *Junonia coenia* on iridoid-containing plants (Bowers, 1988b). Here also, large variation in chemical defense due to sequestration is to be expected, considering the interspecific variation in iridoid content between plants.

Finally, other insects are polyphagous and opportunistically sequester extremely different plant toxins with variable efficiency, e.g., romaleid and pygomorphid grasshoppers and *Arctia caja*.

Another feature of sequestration is that the sequestered compounds are usually not involved in simple relationships with feeding or oviposition behavior. In greenhouse experiments, ovipositing females of *Danaus plexippus* selected the plant with the lowest concentration of cardiac glycosides and the one with the least emetic action on birds (Dixon *et al.*, 1978). However, in the field, oviposition takes place only on plants with intermediate concentrations [200–500 μg/0.1g dry weight (dw) plant material] and those with low or high concentrations are rejected (Zalucki *et al.*, 1990). *Tyria jacobea* does not select *Senecio jacobea* plants with high PA concentration (van der Meijden *et al.*, 1984). Leaf trichomes seem more important than salicin content in influencing feeding behavior in *P. vitellinae* larvae (Rowell-Rahier and Pasteels, 1982). *Oncopeltus fasciatus* readily feeds on seeds devoid of cardenolides (Scudder *et al.*, 1986). On the other hand, the sequestered compounds can be phagostimulants: examples include the preference for high concentrations of the mustard oil glucosides by *Pieris* caterpillars (Schoonhoven, 1973), of cucurbitacins by Luperini leaf beetles (Chrysomelidae, Galerucinae) (Metcalf and Lampman, 1989), of iridoids by the nymphalid *Euphydryas chalcedona* and *J. coenia* (Bowers, 1983, 1984), as well as of quinolizidine alkaloids by the pyralid *Uresiphita reversalis* (Montllor *et al.*, 1990).

The PAs seem to stimulate ingestion in many insects that sequester them. This is interpreted as pharmacophagy, i.e., ingestion for another purpose than nutrition (Boppré, 1984). Of course, pharmacophagy and feeding can be linked when PAs are present in the food plant, e.g., *Zonocerus variegatus* feeding on *Crotalaria* (Bernays *et al.*, 1977; Boppré *et al.*, 1984). *Zonocerus*, however, is a polyphagous species and an opportunistic storer of various toxins (Bernays *et al.*, 1977).

Sinigrin and other glucosinolates are oviposition cues for *Pieris rapae* and *P. brassicae* butterflies and feeding stimulants for their caterpillars (Schoonhoven, 1973). Sinigrin and/or allylisothiocyanate are stored in their pupae and at least in the adults of *P. brassicae* (Aplin *et al.*, 1975).

According to Metcalf and Lampman (1989), the Luperini leaf beetles have developed receptors for cucurbitacin detection as well as detoxification pathways following the evolution of cucurbitacins in the Cucurbitacae. Almost identical phagostimulant effects were observed when a mixture of cucurbitacins was tested against the polyphagous *Diabrotica undecimpunctata howardi* (feeding on Cucurbitacae, Fabaceae, Convolvulaceae, and Poaceae), the oligophagous *Acalymma vittatum* (whose hosts include Cucurbitaceae and Fabaceae), and the specialists *D. virgifera* on corn and *D. cristata* on prairie grasses. Thus, the cucurbitacins are fairly broad feeding stimulants in beetles that have evolved different ways of handling the plant toxins or even have changed hosts in favor of plants devoid of cucurbitacins. Although the cucurbitacins are involved in feeding, there is no specialized relationship whereby the compounds necessary for defense are also necessary for feeding. Some cucurbitacins acting as phagostimulants are not sequestered, and at least some beetles are able to feed and develop on plants lacking cucurbitacins.

Iridoid glycosides act as oviposition stimulant in *J. coenia*, indicating its narrow specialization to plants producing this toxin (Pereyra and Bowers, 1988). Larvae of *E. phaeton* and *J. coenia* both sequester iridoids from their food plants. *J. coenia* does not, however, contain these toxins as adults. In this species the larvae are cryptic and of unknown palatability. The iridoid catalposide (found in *Catalpa*, but not in the host plant of the larvae of *J. coenia*) increases the feeding rate of larvae grown on artificial diet. However, larvae of both laboratory and wild strains of *J. coenia* can be reared on artificial diets that do not contain any iridoid (Bowers, 1984). Here again, feeding is not dependent on the presence of the sequestered compounds in the diet, although the larvae are able to modify feeding quantitatively. We could not find any data on the precise effect of iridoids on the feeding behavior of *E. phaeton*, but the latter is able to develop on several plants belonging to different families with different iridoid patterns, and the resulting larvae have very variable toxic and emetic properties. An interesting question is why *E. phae-*

ton takes full advantage of the use of plant allelochemicals for its own defense (e.g., retention of toxins in the adult stage, gregariousness of the larvae) whereas *J. coenia* does not. The storage by the larvae of *J. coenia* might be an example of specialized excretion of plant toxins. Why it has not yet evolved into full-fledged defensive sequestration, and whether it ever will do so is probably a question of the relative costs and benefits of sequestration as a defensive strategy.

Hypericin is a phagostimulant for *Chrysolina brunsviscensis*, and, according to Rees (1969), it is sequestered by this chrysomelid. However, such sequestration has been recently challenged (Pasteels *et al.*, 1990).

3. *Chemical Specificity*

Most sequestering insects have specialized not only in one class of compounds, but also within each class of toxin; some compounds are sequestered selectively (e.g., high-polarity cardenolides, aucubin and catalpol, senecionine *N*-oxide and seneciphylline *N*-oxide). The same compounds frequently are preferentially sequestered, even across different taxa of sequesterer. This may reflect the ubiquity of those compounds in host plants. If each herbivore were closely adapted to the chemical structures characteristic of one particular plant species, it might not be able to handle those present in closely related potential hosts. Additionally, the high level of intraspecific variation in toxin content in one particular plant species may also prevent a hypothetically more specialized sequesterer from adapting fully to that plant.

One might expect that insects would preferentially store the compounds most effective for defense. Catalpol is preferentially sequestered over aucubin by various nymphalids (Stermitz *et al.*, 1986; Bowers *et al.*, 1988b) and is also more emetic. However, there may be a trade-off for the insect between the storage of compounds that are toxic and therefore good for defense and the storage of compounds that are nontoxic for the insect itself. Comparative data on the toxicity of sequestered compounds and those not sequestered, for both the sequesterer and its natural enemies, are not available.

Alternatively, some basic chemical and physical properties of these compounds might make them relatively easier to sequester. Indeed, it would seem easier to evolve the ability to transport and store compounds with a narrow range of polarity than in the whole spectrum of polarity.

Even in those insects that sequester a large diversity of plant compounds, there is selectivity. Indeed, in the romaleids, the sequestration of allelochemicals characteristic of catnip seems easier than sequestration of those of the wild onion. The former are sequestered even when catnip is given in a mixed diet, but those of onion in detectable amounts only on a restricted diet of wild onion (Jones *et al.*, 1988; Blum *et al.*, 1990).

In a comparative study, Malcolm (1990) showed that the oleander aphid, *Aphis nerii*, sequesters significantly smaller quantities of cardenolides (269 µg/0.1 g dw) than the monarch butterfly (528 µg/0.1g dw) when reared on the same host plant, *Asclepias curassavica*. Large quantities of cardenolides are excreted by the aphid and found in the honeydew. Another difference relative to the monarch is that the uptake of cardenolides is far less specific; most of the cardenolides found in the host plant were also found in the aphid body and in its honeydew. Nothing is known about the turnover rate of the cardenolides in the aphids. The author suggests that the selection pressure for efficient sequestration might not be so high for these hemimetabolous aphids as for the holometabolous monarch. First, the aphid has access to the plant toxins during its entire lifetime, whereas the monarch has access only during the limited period of larval feeding. Second, aposematism is likely to have evolved by kin selection in the soft-bodied aphid feeding in dense aggregations of apomictic individuals, whereas it is likely that is has evolved by individual selection in the tough-bodied monarch, since the individual butterfly can survive predator attack (Brower, 1984; Malcolm, 1990). An effective defense, including bitter-tasting, low-polarity cardenolides easy to discriminate and remember by predators, is important for the aphids, allowing the sacrifice of only a few individuals of an aggregated clone. The monarch, on the other hand, stores large quantities of cardenolides of intermediate polarity and toxicity that can be used during its entire lifetime. Additionally, the monarch converts or eliminates low-polarity compounds because they are difficult to store. Unfortunately, data comparing the actual cardenolide contents of the phloem, on which the aphids feed, and of the leaves, that the monarch larvae chew, are lacking.

4. *Cost of Sequestration*

The cost of sequestration is a challenge to assess because it can be influenced by several parameters difficult to quantify. These include, for example, the transport of the toxins, the avoidance of autotoxicity, and the eventual transformation of the plant allelochemicals to stored compounds. Obviously, all these components are difficult to quantify in the same units. Bowers (in press) suggests that cost can be shown by a negative correlation of both amount and concentration of plant allelochemicals in the insect with performance parameters such as growth rate, biomass, or fecundity.

Few studies have estimated costs of sequestration. For example, Cohen (1985) showed that in the monarch there is a negative correlation between the concentration of cardenolides stored in the tissues and both body size and weight. There is no such correlation in the related queen butterfly, *Danaus gilippus.* The negative correlation in the monarch might represent metabolic cost (Brower and Glazier, 1975), but there is no necessary causal relationship between the cardenolides and body size or weight. The correlation could not be replicated experimentally by adding digitoxin, a cardenolide, to a control diet. According to Seiber *et al.* (1980), digitoxigenin is completely metabolized by the larvae of *D. plexippus* to a more polar product, which is converted back to digitoxigenin in the adults. This is thought to prevent intoxification of the larval tissue. In the same study, some indication of a physiological consequence of sequestration is present when the larvae are fed uzarigenin at concentrations at least four times higher than those encountered in their host plant. The larvae then become melanic. Additionally, Zalucki *et al.* (1990) observed a significant negative correlation between survival in the field of first instar *D. plexippus* larvae and the levels of cardenolides in plants.

In leaf-beetle larvae that biosynthesize their autogenous iridoid monoterpene defenses, the adults produced are lighter when secretions are constantly removed from the larvae, which have to renew it, than when secretions are not removed. In contrast, in *Phratora vitellinae,* which uses host-plant-derived salicin to produce salicylaldehyde, the adults are heavier when the secretion is removed daily than those in the control group. This is probably because glucose is liberated when salicin is transformed into salicylaldehyde, and thus the sequestered toxins acquire a nutritive value (Rowell-Rahier and Pasteels, 1986).

In adult leaf beetles of the genus *Oreina,* both *O. cacaliae* and *O. speciosissima* are capable of sequestering PAs from their host plants. *O. cacaliae* relies only on sequestration for defense; and its larvae are heavier when reared on the PA-rich *Adenostyles alliariae* than on the PA-poor *Petasites paradoxus. O. speciosissima,* although capable of sequestering these compounds, does not usually do so in the field, but rather relies on autogenous biosynthesis of cardenolides. The larvae of this species are heavier when reared on the PA-poor *P. paradoxus* than on the PA-rich *A. alliariae,* suggesting for this species a metabolic cost of sequestering the PAs present in *Adenostyles,* the total nitrogen content being similar in both plant species. However, just as in the case of the monarch described above, no causal relationship between PAs and growth of the larvae is known (unpublished results, 1990).

Bowers (1988b) could find no evidence of cost of sequestering iridoid glycosides in *Euphydryas anicia.* Larvae of *Junonia coenia* grow better at high concentrations of the iridoid glycoside catalposide. This is not owing to glucose recovery, because added glucose does not affect the growth, but is probably owing to increased feeding rate (Bowers and Puttick, 1989). Aucubin, catalpol, and their mixture (as well as dried leaves of *Plantago lanceolata*, added to artificial diet) increase the growth of the wild strain of *J. coenia*. However, when reared on those same artificial diets, laboratory strains of *J. coenia* grow significantly better than the wild strain (Bowers, 1988b). The laboratory strain was reared for 30 to 40 generations on a diet containing only 4% *P. lanceolata* powder and thus has not been exposed to the same large quantity of iridoid glycosides as the wild strain. Whether this reflects a long-term cost (depression of weight) for the population that has to handle large quantities of iridoid, or whether this reflects differences in other selective pressures is not currently known.

5. *Physiological Exaptation and Adaptation*

The cost of sequestration is difficult to assess in that very little is known of the physiological and biochemical mechanisms needed for the transport and storage of toxic plant allelochemicals (review in Duffey, 1980). Although it is tempting to consider sequestration as an obvious potential defensive strategy for insects feeding on toxic plants, it is not always adopted by herbivores.

Plant allelochemicals, irrespective of whether they are stored in defensive glands or in other herbivore tissue, have to be transported from the gut to the point of storage. This transport can be passive or active depending on the polarity of the compound. In the case of the PA *N*-oxides stored by the moth *Creatonotus*, Wink and Schneider (1988) showed that uptake across the midgut was selective and not owing to simple diffusion; rather, it was carrier mediated. This process is rather specific for PAs, since other alkaloids (nicotine, lupanine, 13-hydroxylupanine, colchicine) were not so transported. Addition of another PA (heliotrine) to the experimental gut preparation causes competitive inhibition of the uptake of senecionine *N*-oxide. Moreover, PA uptake is inhibited by KCN, which inhibits electron transport, and thus is energy dependent. von Nickisch-Rosenegk *et al.* (1990) showed that the uptake of digoxin by larvae of the cardenolide-sequestering moth, *Syntomeida epilais*, was also carrier mediated. The gut of *Oncopeltus fasciatus* is permeable to cardenolides, which are probably taken up passively, whereas the guts of cockroaches and the locust are impermeable (Duffey *et al.*, 1978; Scudder and Meredith, 1982).

From a physiological point of view, the tissues that are in contact with the toxins must be protected from autotoxicity. For example, cardenolides act by specifically inhibiting the Na^+-K^+ ATPase. In both the monarch and the milkweed bug, which sequester cardenolides, this enzyme is not inhibited by the cardenolide ouabain (Vaughan and Jungreis, 1977; Moore and Scudder, 1985).

The cyanogenic glucosides linamarin and lotaustralin are produced autogenously by many Zygaenidae (Davis and Nahrstedt, 1982), including some feeding on noncyanogenic plants. Interestingly, at least one species, *Zygaena trifolii,* also is able to incorporate some linamarin and lotaustralin from its diet, as shown by rearing larvae on cyanogenic plants with added labeled (aglycone ^{14}C) glucoside. Only a small part (20 to 40%) of the ingested glucoside is incorporated. The rest is metabolized, since it is not found in the feces (Nahrstedt and Davis, 1986). Autogenous synthesis is widely distributed in the Zygaenidae and is probably a useful taxonomic character. Since these moths can synthesize cyanogenic glycosides, they may be preadapted for storage of the host-plant compounds. Thus *Zygaena* species feeding on cyanogenic *Lotus* sequester very high concentrations of cyanogenic glycosides. Resistance to cyanide is well known in the zygaenids and was already recognized as a character of the subfamily Zygaeninae in 1907 (Jones *et al.,* 1962).

Enzymatic preadaptation might be responsible for the switch to sequestration in species primitively biosynthesizing their own defense. For example, the phenolglucoside salicin can be used as the precursor of salicylaldehyde (present in the defensive secretion of the larvae of *P. vitellinae* and *Chrysomela* species) with minimal changes in the biochemical mechanisms involved in the biosynthesis of iridoid monoterpenes in related species. Indeed, two enzymes seem necessary for the last steps of the biosynthesis of iridoid monoterpenes, a beta-glucosidase and an oxidase. The same are also necessary to transform salicin into salicylaldehyde. Additionally, the beta-glucosidase activity found in the secretion of species synthesizing defensive compounds *de novo* and in the secretion of species transforming salicin is not very specific. The oxidase, on the contrary, seems highly specific. Thus, Pasteels *et al.* (1990) proposed that a single change in the specificity of the oxidase is very likely the only prerequisite for the utilization of plant precursors by the larvae. Preexisting glands and enzymes, only slightly modified in their specificity, are used to derive toxins from plants, and thus no additional cost is required for the metabolism of plant precursor by the larvae than that for the autogenous biosynthesis of defense. Additionally, there is an economy in toxin biosynthesis and possibly in active excretion of the plant toxin. Moreover, the plant glucoside acquires a nutritive value owing to the glucose released during its metabolism. This host-plant influence on the larval secretion is possible only because the plant precursor is a glucoside.

C. Effect of Plant Toxins on Predators and Parasitoids

1. *Protection of the Herbivores*

Both vertebrate and invertebrate natural enemies exert strong selective pressure on herbivore populations. Several reviews emphasize the effect of insect chemical defense on predator and parasitoid behavior (e.g., Eisner, 1970; Blum, 1981; Pasteels *et al.*, 1983a; Brower, 1984; Whitman *et al.*, 1990). To our knowledge, there is no evidence suggesting that sequestered plant allelochemicals act differently from autogenous defensive compounds. In general, herbivores sequestering their defensive compounds from their hosts are probably a lot more variable in toxin content, both at the population and individual levels, than those biosynthesizing autogenous compounds, since plants are notable for variation in their allelochemicals at all levels (organ, individual, population, and temporal). The nutritional quality of the host plant can act indirectly on the efficiency of sequestered chemical defense, since a trade-off between fast growth and better predator avoidance exists (Damman, 1987). Predators can also affect the feeding behavior of the herbivores and therefore their intake of plant allelochemicals. For example, the gregarious caterpillar *Hemileuca lucina* (Saturnidae) feeds in suboptimal microhabitats of the plant when it is harassed by predatory wasps (Stamp and Bowers, 1988).

a. Against Vertebrate Predators. Studies involving birds as predators of chemically defended herbivorous insects, especially adult butterflies, are by far the commonest in the literature. For example, the sequestration of cardenolides by the monarch has been documented in detail. In feeding trials these butterflies are avoided by several species of birds, including the blue jay *(Cyanocitta cristata bromia)* which is commonly used in laboratory trials (Brower and Van Zandt Brower, 1964). The emetic potential of adult *Danaus plexippus* is influenced by the food plants on which the caterpillars were reared (Brower *et al.*, 1968). Blue jays are able to develop both conditioned visual aversion as well as conditioned taste discrimination of cardenolides. Dose–response experiments with purified plant cardenolides confirm that cardenolides are responsible for the emetic properties of the monarch (Brower and Fink, 1985). These data, however, do not necessarily mean that butterflies are always protected from bird predation in the field. In Mexican overwintering sites, the monarchs are eaten by black-headed grosbeaks *(Pheucticus melanocephalus),* which are relatively insensitive to the emetic effect of the cardenolides. The overwintering monarchs are also eaten by black-backed orioles *(Icterus galbula abeillei),* which utilize a modification of their fruit-eating behavior to open the bodies of the butterflies and thus avoid epidermal tissue with high cardenolide content (Brower *et al.*, 1988a). In contrast, not much predation occurs in the Californian overwintering site, although occasionally chickadees (probably *Parus rufescens barlowi*) peck at a butterfly (Tuskes and Brower, 1978). The difference between these two sites might be associated with differences in the butterflies' cardenolide content. The Mexican populations have a much lower content than those in California. In the case of the eastern Mexican population, the butterflies lose their cardenolides during migration but are able to track their milkweed host in space and time (Malcolm and Brower, 1989). Indeed, the host plants encountered during migration have low contents of cardenolides.

Many tests of unpalatability for birds involve both chemical and visual components simultaneously, and their effects are often difficult to separate. Warning, or aposematic, coloration contributes to the survival of prey defended by plant toxins against birds. Wiklund and Sillén-Tullberg (1985) showed that aposematic larvae and adults of *Danaus plexippus* and *Papilio machaon* survived attack by quail *(Coturnix coturnix)* better than their pupae, which, at least in the case of the monarch, are equally unpalatable but not aposematic. Additionally, Sillén-Tullberg (1985), using normal red *Lygaeus equestris* (Hemiptera) and mutant grey cryptic ones, showed that great tits *(Parus major)* learned to avoid the prey without killing any individual only when they were brightly colored, although both cryptic and aposematic *L. equestris* were equally toxic. Indeed, with domestic chicks, Roper and Redston (1987) showed that conspicuousness can directly affect the strength of initial learning and the duration of memory of a noxious stimulus. The implications of aposematism, mimicry, and gregariousness for predator behavior are clearly linked to the defensive strategies of herbivores, especially against "visual" predators (for review, see Guilford, 1990; Bowers, in press).

Eliminating visual cues, Nishida and Fukami (1990) showed that some commonly sequestered bitter compounds, such as clerodendrin and cucurbitacin, are deterrent against sparrows in feeding tests with treated rice grains. Interestingly, the cucurbitacins are deterrent against both vertebrate and invertebrate predators (e.g., praying mantids; Ferguson and Metcalf, 1985) but not all of them (e.g., not toads and mice, Gould and Massey, 1985). This example illustrates that defense can be aimed against a broad spectrum of predators, but no defense is perfect.

Lizards are probably understudied predators of insect herbivores, particularly in tropical habitats. Small local populations of the lizard *Ameiva ameiva* can be conditioned to avoid unpalatable butterflies *(Heliconius)* in the wild (Boyden, 1976). Although in this case the unpalatability is not linked to plant allelochemicals, these experiments suggest that insectivorous lizards could act as a selective force in the evolution of chemical defense. Indeed, the lygaeid *N. bicrucis* is distasteful to green anoles when fed on pyrrolizidine-rich *Senecio* but not when reared on sunflower seeds that do not contain PAs (McLain and Shure, 1985). The bugs survive lizard attack without apparent harm. The same bugs are palatable to toads, but toads do not chew before swallowing and have poor gustatory discrimination.

Feeding trials as well as analysis of stomach contents showed that the mouse *Peromyscus melanotis* preys naturally on monarch butterflies in the Mexican overwintering colonies (Brower *et al.*, 1985, 1988b). These mice are not influenced negatively by cardenolides; rather, female mice in monarch colonies are larger, heavier, and more active reproductively. Moreover, they actually immigrate to the overwintering monarch colonies (Glendinning *et al.*, 1988). However, at least three other mice species present in the same area are deterred to variable extents by the cardenolides in monarch (Glendinning, in press; Glendinning and Brower, 1990).

b. Against Invertebrate Predators. Ants, wasps, coccinellid larvae, and carabids have been utilized in predation studies with chemically defended herbivores. To our knowledge, surprisingly little attention has been given to the role of spiders as predators, an exception being the report of the defensive role of PAs in ithomiine butterflies (Brown, 1984). The prey tested against invertebrate predators are often but not always soft-bodied larval stages. Among the invertebrates, ants are the laboratory test predator par excellence, but it is not always clear that they are ecologically the most important in the context studied. Depending on the studies, very different parameters are measured. The prey can be used whole; for example, Morrow *et al.* (1976) offered live sawfly larvae *(Perga affinis)*, which regurgitate oils from *Eucalyptus* leaves, to ants and observed their behavior. In other, more quantitative studies, sucrose solutions were offered to ants, and either the number of ants drinking or the quantity consumed was estimated. For example, the defensive secretion of the grasshopper *Romalea guttata* was more deterrent (as determined by the number of ants visiting the baits) when the grasshoppers were allowed to sequester either wild onion or catnip allelochemicals than when they were feeding on their normal polyphagous diet and not sequestering allelochemicals (Jones *et al.*, 1989; Blum *et al.*, 1990). The azoxyglycoside cycasin sequestered by the lycaenid butterfly *Eumaeus* stops feeding by ants after 15 min when it is added to sucrose solution (Bowers and Larin, 1989). The delay suggests a toxic rather than a repellent effect. Interestingly, both cycasin and the regurgitate of the sawfly were also tested against birds and are active against them as well (Morrow *et al.*, 1976; Bowers and Larin, 1989). This was also true for the bitter cucurbitacins (as described) and once more demonstrates the nonspecificity of chemical defense.

The deterrency or repellency of volatile compounds, such as salicylaldehyde (which is derived from the host-plant glucoside salicin), has been shown against several invertebrate predators (for example, predaceous coccinellid larvae). Females of *Phratora vitellinae* apparently avoid (as an oviposition host) the willow *Salix viminalis,* which does not contain salicin, not because their larvae performed poorly, but because larvae were defenseless against some predators on this host (Denno *et al.*, 1990). Foraging ants avoid paper disks impregnated with salicylaldehyde (Matsuda and Sugawara, 1980) or sucrose solutions containing salicylaldehyde in low concentration (Pasteels *et al.*, 1983b). The glucoside salicin, which is stored in the eggs of some Chrysomelinae, is deterrent and toxic to ants (Pasteels *et al.*, 1986). Adult female sawflies *(Tenthredo olivacea)* preferred to feed on chrysomelid larvae of the species they had previously encountered, independent of whether they secreted salicylaldehyde or autogenous iridoid monoterpenes (Pasteels and Grégoire, 1984). The response of predators to plant-derived defenses in the chrysomelids has been reviewed by Pasteels *et al.* (1988a).

Predatory wasps can be important enemies of soft-bodied herbivores. Like birds, they are visual predators and masticate their prey. Examples of their ecological impact are described by Damman (1987), Stamp and Bowers (1988), and Bernays (1988). Bernays (1988) showed that a generalist wasp avoids more oligophagous caterpillars when an alternative and less oligophagous caterpillar is available as prey. In these experiments, deterrence upon contact or after biting the prey was observed for several specialized caterpillars that are also able to sequester plant toxins (e.g., *Battus philenor, Euphydryas editha, Danaus plexippus*). Some more specialized wasps, such as *Symmorphus cristatus,* are not influenced negatively by the salicylaldehyde produced by *Chrysomela aenicollis* (Smiley and Rank, 1986). Before bringing them to the nest, the wasps wipe the dorsal surfaces of the larvae, where the glands are located, on dead logs (Rank, personal communication, 1990). At least one other wasp, *Odynerus nidulator,* specializes in *Chrysomela populi* larvae, which also produce salicylaldehyde (Fabre, 1891). Montllor *et al.* (1990, 1991) demonstrated that quinolizidine alkaloids, when sequestered in small amounts by *Uresiphita reversalis* but concentrated in its cuticle, are deterrent to predatory ants and wasps.

2. *Toxicity of Plant Allelochemicals to Natural Enemies*

In the examples listed in the previous section, the plant toxins exert mostly deterrent and/or repulsive effects on predators. However, the activity of the plant toxins on natural enemies of the herbivores can be more insidious: the plant allelochemicals sequestered by herbivores can have a toxic effect on the predator without first influencing its behavior. For example, *Aphis nerii* fed on the asclepiad *Cionura erecta* can serve as prey for the coccinellid, *Adonia variegata.* When this aphid is the sole food of the larvae, the resulting adult coccinellids are deformed (brachypterous or apterous) and have reduced fecundity and life expectancy. When fed on *A. nerii* from *Nerium oleander* or *Cynanchum acutum* host plants, the ladybird larvae developed normally. The cause of the toxic effect remains unknown; toxicity is not caused by cardenolides since *C. erecta* does not contain any (Pasteels, 1978). Wink and Römer (1986) showed that carabids feeding on aphids that accumulate alkaloids from lupins can be paralyzed for as long as 48 hr, but subsequently recover.

Parasitoids, too, can be influenced negatively by plant toxins. For example, the ichneumonid parasitoid *Hyposoter exiguae* is poisoned by alpha-tomatine, an alkaloid found in tomato plants and acquired from its less sensitive herbivorous host *Heliothis zea* when it feeds on tomatoes (Campbell and Duffey, 1979). The detrimental effects of nicotine and the flavonoid rutin on several larval parasitoids of herbivores are reviewed by Barbosa (1988). The consequences of sequestration of plant allelochemicals in plant–insect–parasitoid interactions are developed by Duffey *et al.* (1986).

There are few reports of sequestration of plant toxins in predators via the herbivores (e.g., cardenolides sequestered in aphids and retained in ladybirds or lacewings feeding on those aphids, Rothschild *et al.* 1973). The parasitoid *Nyctemera annulata,* feeding on the moth *Tyria jacobeae,* can acquire PAs from its herbivorous host, which has itself acquired them from its host plant (Benn *et al.*, 1979). Reichstein *et al.* (1968) provide evidence suggesting that the tachinid fly *Zenilla adamsoni* acquires cardenolides sequestered by its host *Danaus plexippus.* These examples suggest that specialized natural enemies are able to withstand plant toxins and possibly use them for their own defense.

D. Evolution of Sequestration

Undoubtedly, insects relying on sequestration for defense usually need elaborate physiological and biochemical mechanisms specific to the class of compounds sequestered. As plant toxins are chemically very diverse, independent evolution of sequestration is expected to occur even in closely related insect taxa. Few insects seem able to sequester a wide variety of toxins (with the exception, however, of the pyrgomorphid and romaleid grasshoppers and the moth *Arctia caja*), and most herbivorous insects are extremely specialized in their sequestration capacities.

Sillén-Tullberg (1988) showed in a phylogenetic study that butterfly larvae warning coloration has evolved independently at least 12 times. Warning coloration was used as the criterion of unpalatability; this number is therefore probably an underestimate, since some cryptic larvae are known to be unpalatable (see Bowers, in press). Many of these cases of unpalatability can be traced to sequestration of host-plant allelochemicals. In addition to the examples cited by Sillén-Tullberg, the larvae of the lycaenid *Eumaeus atala* sequester cycasin from their host plants (Cycadacae) (Rothschild *et al.*, 1986; Bowers and Larin, 1989; Bowers, in press).

In the other extensively studied group, the Chrysomelidae, sequestration has evolved at least six times independently: in the larvae of *Gastrolina* (1 sp.), in the eggs and larvae of some *Chrysomela* (6 spp.), and in those of one species of *Phratora*, in the adults of some *Oreina* species and of *Dibolia* species, as well as in all stages of several Luperini (Pasteels and Rowell-Rahier, 1991; Pasteels *et al.*, 1988a).

If sequestration requires sophisticated biochemical processes, one should expect its evolution to be rather difficult and more the exception than the rule. Although negative results are less frequently reported than positive ones, Rothschild (1973) published an impressive list of nonsequestration of plant toxins by specialist herbivores. In the Chrysomelinae, all of which are oligo- or monophagous herbivores, most species are defended by chemicals synthesized *de novo*, and sequestration is the exception (Pasteels *et al.*, 1989, 1990; Pasteels and Rowell-Rahier, 1991). All Heteroptera secrete chemicals *de novo* in their defensive metapleural glands (Staddon, 1979; Aldrich, 1988). Many are specialized herbivores, but only some lygaeids and rhopalids sequester plant toxins. In the Lepidoptera, sequestration could be more frequent than *de novo* synthesis. We do not know if this pattern reflects a true lepidopteran ability (or their inability to synthesize toxins *de novo*) or results from investigatory bias stimulated by the celebrated monarch story. However, even in the Lepidoptera, *de novo* synthesis occurs in specialists feeding on toxic plants, e.g., in the osmeterial glands of papilionid caterpillars, or in the defensive glands of notodontids, or in the cyanogenic glycosides synthesized by zygaenids and heliconids (Nahrstedt and Davis, 1983).

The fact that *de novo* chemical defense is as common or even more common than sequestration in specialists does not support the hypothesis that oligophagy evolved in herbivores for better protection. It is, however, compatible with the view that specialized herbivores should be strongly defended in some way, given that they are predictably exposed to heavy predation.

In some chrysomelids and true bugs, sequestration has replaced *de novo* synthesis in the course of evolution, indicating that the use of plant toxins can offer clear advantages over *de novo* synthesis. As discussed above, in the Chrysomelidae, the use of plant glycosides is more economical than *de novo* synthesis, owing to enzymatic exaptations. In the Lygaeidae, sequestration could be less costly, since it appears to be a passive process. In this case, the sequestered cardenolides may be more efficient in deterring vertebrate predators, whereas the original volatiles produced by the metapleural glands are probably aimed at keeping small invertebrate predators at a distance (Pasteels *et al.*, 1983a; Aldrich, 1988).

Whereas in the Chrysomelinae and Heteroptera, sequestration is a secondary event, Brown and Francini (1990) (see also Brown *et al.*, 1991) suggest an opposite pattern in butterflies. They argue that, within the neotropical butterflies, storage of the toxins (e.g., alkaloids, aristolochic acid, glucosinolates, glycosides) of the larval host plants is mostly encountered in the more primitive families (e.g., Troidini, Pierini, and Eumaeini, respectively, in the Papilionidae, Pieridae, and Lycaenidae). A second evolutionary step would be the accumulation of the toxins by the adults (e.g., in Danainae and Ithominae, which collect pyrrolizidine alkaloids from the nectar of Eupatoriae or from decomposing Boraginaceae). The third evolutionary step would be the autogenous (endogenous) biosynthesis of defensive toxins at all stages (e.g., cyanogenesis in the Acraeinae and Heliconiini). In this stage, plant toxins (e.g., PAs and HCN) are ingested and tolerated, but not stored.

In this evolutionary scenario, *de novo* synthesis is advantageous compared to sequestration. Autogenous compounds could offer a more reliable defense, since plant toxins are quite variable in amounts, not only between taxa, but also within a plant species. Also, *de novo* synthesis would liberate the insect from obligatory oligophagy. For the butterflies, the suggestion of Brown and Francini (1990) supposes that sequestration of aristolochic acids, glucosinolates, pseudocyanogens, cardenolides, PAs, or iridoid glycosides has a common origin and should share some basic cellular mechanism. No available data support this hypothesis. In any case, this evolutionary scenario does not support the idea that oligophagy evolved for better chemical defense, unless the herbivores were originally totally devoid of such defenses. Many insect herbivores, however, apart from the taxa already discussed, are chemically defended by *de novo* synthesis (e.g., sawfly larvae, Boevé and Pasteels, 1985; cerambycids, Vidari *et al.*, 1973; thrips, Howard *et al.*, 1983; aphids, Edwards, 1966; phasmid, Meinwald *et al.*, 1966).

As stressed by Brown and Francini (1990), leaf beetles, bugs, and butterflies have very different life histories, and the evolution, either primary or secondary, of sequestration might be strongly associated with some yet unidentified life-style patterns.

III. BENEFICIAL INFLUENCES OF PLANTS ON THE THIRD TROPHIC LEVEL

Plants offer the predators and parasitoids of herbivores shelter and/or food (e.g., floral or extrafloral nectaries, pollen, food bodies). Since plants benefit from these predators and parasitoids, a mutualistic relationship has evolved, exemplified by ant–plant symbioses (review in Hölldobler and Wilson, 1990). The third trophic level can also benefit from plants in a less spectacular, but probably more widespread way, by using plants as cues to find their herbivorous prey (Dicke and Sabelis, 1988; Dicke *et al.*, 1990c; Nordlund *et al.*, 1988; Vinson, 1976, 1981, 1984a, b; Vinson *et al.*, 1975; Williams *et al.*, 1988; Whitman, 1988).

A. Chemical Cues from Plants

Predators and parasitoids do not encounter their prey or hosts randomly; rather, they have developed searching strategies in which they use cues originating not only from these prey or hosts but also from the habitat (including the plants housing their prey or hosts). It is convenient to distinguish successive steps in this searching behavior, e.g., host-habitat location, host location, and host acceptance, although there can be some overlap between phases (Vinson, 1976). Cues from plants are expected to be more important in the early phases of this searching behavior. The host specificity of a parasitoid is sometimes at least as dependent on the plant on which the herbivore feeds as on the species of herbivore involved (Nordlund *et al.*, 1988). Many parasitoids attack an herbivore species feeding on one plant but not on others, whereas other parasitoids attack systematically almost all the herbivore species suitably located on a given plant species (examples and references in Vinson, 1981). Of course, cues from the herbivores themselves are the deciding factors in the final steps of host location and acceptance. Additionally, cues resulting from the interactions between the plants and their herbivores seem particularly relevant for host location. Plants may provide visual and/or chemical cues, but the latter seem most important for parasitoids and arthropod predators.

At first glance, plant cues may be expected to play a major role when the interactions between the three trophic levels are strongly specific, i.e., a predator or a parasitoid specialized on a specialist herbivore, since the specificity of the interactions implies that reliable cues are available. Indeed *Phaeogenes cynarae,* a monophagous internal parasitoid of prepupae and pupae of the plume moth *(Platyptilia carduidactyla),* a specialist on thistles, uses a chemical cue from wounded globe artichokes *(Cynara scolymus)* to initiate searching behavior (Bragg, 1974). However, olfactory cues of plant origin are also used by less specialized parasitoids feeding on oligo- or polyphagous hosts. Host location by the braconid *Microplitis croceipes* is directed by olfactory signals, including plant components, although its host, *Heliothis zea,* is polyphagous (Drost *et al.*, 1986; Eller *et al.*, 1988a, b). A similar influence of odors resulting from the interaction between plants and herbivores in the attraction of parasitoids was reported for the related species *M. demolitor,* which attacks a variety of noctuid species feeding on plants as diverse as cotton, tobacco, or soybean (Hérard *et al.*, 1988a, b; Turlings *et al.*, 1990). Olfactory plant cues are used by *Campoletis sonorensis,* a parasitoid of various noctuids (Williams *et al.*, 1988), and odors from the plant–host complex act as cues for the generalist caterpillar parasitoid, *Cotesia marginiventris* (Turlings *et al.*, 1989). Both cultivated and presumably also wild herbs (e.g., cotton, Elzen *et al.*, 1984a; artichoke, Bragg, 1974; cowpea, Drost *et al.*, 1986; collard cabbage, Read *et al.*, 1970) and trees (e.g., oak, Hassel, 1968; pine, Camors and Payne, 1972) are reported to emit olfactory cues used by parasitoids.

Both genetic predisposition and learning *(sensu lato)* are involved in the use of plant olfactory cues by parasitoids. Innate responses to plant cues are expected in specific tritrophic interactions, whereas learning is expected to occur in more polyphagous relationships. Learning was reported to be stronger (i.e., longer memory of the learned cue) in the polyphagous parasitoid *Itoplectis conquisitor* than in the oligophagous *Nemeritis canescens* (Arthur, 1971), although *I. conquisitor* was conditioned to color (Arthur, 1966) and *N. canescens* to odor, so that the comparison may not be valid. Genetic predisposition to plant odors, however, has been reported for oligophagous parasitoids attacking polyphagous herbivores. *Campoletis sonorensis* is more attracted by cotton than by other plants (Elzen *et al.*, 1983) and is genetically predisposed to be attracted by various cotton volatile sesquiterpenes (Elzen *et al.*, 1984a,b, 1986). On the other hand, learning of olfactory cues has been reported for the much more specialized parasitoid *Nemeritis canescens* (Arthur, 1971; Taylor, 1974). Innate preferences, learning of cues in habitat, and host location by parasitoids are reviewed by Vet *et al.* (1990), who give a model describing their interplay. The consequences of the use of olfactory cues on the population dynamics of herbivores and the resulting aggregative search behavior of natural enemies unfortunately remain a neglected subject (for review see Roland, 1990). Roland (1990) suggested that parasitoid search could be more efficient when the herbivores are aggregated in patches of host abundance, since cues are not ubiquitous; this behavior could explain partly why mixed tree stands support higher parasitoid numbers (Simmons *et al.*, 1975) and why herbivore abundance is lower in polycultures than in monocultures (Risch *et al.*, 1983).

Learning (i.e., modification of behavior following experience) of plant cues involves different processes. Associative learning after a brief contact with host or host feces seems widespread (Drost *et al.*, 1986; Hérard *et al.*, 1988a). Several parasitoid wasps have been conditioned in this way to recognize and subsequently fly to novel, otherwise unattractive odors [e.g., *Nemeritis canescens* to geraniol (Arthur, 1971) and *Microplitis croceipes* to vanilla (Lewis and Tumlinson, 1988)]. Imprinting of the adults at the time of emergence from the cocoon is strongly suspected in the wasp *Microplitis demolitor* (Hérard *et al.*, 1988b). Finally, in *Cotesia marginiventris*, both associative learning and sensitization occur, since experience increases not only the response toward the conditioned stimulus but also to a lesser extent to the odor of an alternative plant–host complex (Turlings *et al.*, 1989).

The orientation of predators toward their prey is less studied than the orientation of parasitoids toward their hosts. However, some predators are also known to use plant cues. Olfactory plant cues, and/or cues resulting from the interaction between the plants and the herbivores, are used not only by the strictly monophagous beetle, *Rhizophagus grandis*, preying exclusively on the bark beetle *(Dendroctonus micans)*, itself highly specialized on spruce (Grégoire, personal communication, 1990; Baisier *et al.*, 1988). Cues from plants are also used by oligophagous predators of bark beetles (Rice, 1969; Williamson, 1971; Fitzgerald and Nagel, 1972). Other examples of such use include specialist predators of aphids feeding on cotton (e.g., the lacewing *Chrysopa carnea*, Flint *et al.*, 1979) or on pine trees (e.g., the coccinellid *Anatis ocellata*, Kesten, 1969), the specialist mite *Phytoseilus persimilis* predatory on the polyphagous spider mite *Tetranychus urticae* (Dicke and Sabelis, 1988), the more polyphagous predatory mite *Amblyseius potentillae* (Dicke *et al.*, 1990a), and possibly even the highly polyphagous yellow jacket wasp *Vespula maculifrons* (Aldrich *et al.*, 1985, 1986) or arboreal ants (Dejean and Djieto, 1990). All these examples clearly indicate that, as with the parasitoids, both herbs and trees can provide olfactory cues to predators in highly specialized or more generalized tritrophic interactions.

Not unexpectedly, predators, like parasitoids, show both genetic predisposition and learning abilities to plant odors or plant-derived cues. The predatory mite *Phytoseilus persimilis* is more attracted by volatile compounds emitted from lima bean leaves *(Phaesolus lunatus)* infested by two-spotted spider mites, *Tetranychus urticae*, than by compounds emitted from cucumber plants infested by the spider mites, when they have been reared on spider mites on lima bean leaves. The reverse is true when the predatory mites are reared on spider mites on cucumber leaves. The underlying mechanism seems to be sensitization, and no evidence of associative learning has been obtained (Dicke *et al.*, 1990b). Recent studies have demonstrated that some arboreal ants, such as *Oecophylla longinoda* or *Tetramorium aculeatum*, are attracted by plant odors. The ants are extremely aggressive and protect the plants by preying on the folivorous insects. Both workers and gynes show an innate predisposition to the odor of some plants, but imprinting to the odor of the plants on which their nest was located determines their further attraction to the plants (Dejean and Djieto, 1990). Invasion of new plants is initiated by single gynes or by budding.

B. Evolution of Mutualisms between Plants and the Third Trophic Level

Plants and herbivore enemies share such obvious common interests that mutualistic relationships can be expected to have evolved frequently. If the ability to use plants chemicals as cues to find herbivores has evolved in many predators or parasitoids, it is far less evident that specific attractants for the third trophic level have evolved in plants.

It seems unlikely that plant odors attracting herbivore enemies are inherently present compounds unless they serve other functions, e.g., plant defense, since they could also be used by the herbivores themselves to find their host plants. Caryophyllene and β-caryophyllene attract the green lacewing to cotton (Flint *et al.*, 1979) but also attract the boll weevil, a common pest of cotton (Minyard *et al.*, 1969). Alpha-pinene and other coniferous monoterpenes are part of the attractive bouquet for predators and parasitoids, but they are also used as primary attractants by many bark beetles (Wood, 1982). The primary function of these sesqui- and monoterpenes is most probably defensive. The fragrant cotton sesquiterpene caryophyllene-oxide, attractive to the parasitoid *Campoletis sonorensis* (Elzen *et al.*, 1984b), reduces growth rate of *Heliothis virescens* (Stipanovic *et al.*, 1986). Alpha-pinene is toxic for many insects, but bark beetles and their specialized enemies are highly resistant to this toxin, which they use as an attractant (Everaert *et al.*, 1988). Allyl-isothiocyanate, which attracts the parasitoid *Diaretiella rapae,* is not present in this form in Cruciferae, but it is released from mustard oil glucosides after leaf damage by herbivores. However, mustard oil and mustard oil glucosides are deterrent for unspecialized herbivores and attractive in the broad sense to many specialized cruciferous herbivores (references in Read *et al.*, 1970). The terpenoids released by corn injured by herbivores are used as cue by *Cotesia marginiventris* but may be produced in defense against herbivores (Turlings *et al.*, 1990). In all these cases, it is very doubtful that the olfactory cues used by the third trophic level have evolved in plants for the special purpose of attracting predators and parasitoids. The fact that at least some parasitoids can be conditioned to novel odors (Arthur, 1971; Lewis and Tumlimson, 1988) demonstrates that herbivore enemies use available odors opportunistically in their habitat and host locations.

However, recent studies by Dicke, Sabelis, and co-workers suggest that specific attractants might have evolved in some plants as part of their antiherbivore arsenal. Lima bean plants infested by the spider mite *Tetranychus urticae* release mono- and sesquiterpenes and methyl salicylate, which are attractive to the specialized acarine predator, *Phytoseilus persimilis* (Dicke *et al.*, 1990a). Plants located downwind also attract the spider mite predator (Dicke *et al.*, 1990c; Bruin *et al.*, personal communication). Since these compounds are probably induced specifically by spider mite attacks, it is difficult to imagine that they might have evolved as broad-spectrum herbivore deterrents, or that they later were exploited as herbivore attractants. On the contrary, they are used by spider mites as epideictic pheromones (Dicke *et al.*, 1990c). Those compounds (linalool, E-β-ocimene, dimethyl-nonatriene, methyl salicylate) are considered to be typical plant compounds, but it remains to be proven that a specific metabolic pathway is indeed triggered in plants attacked by spider mites and then in undamaged neighboring plants.

The attraction of generalized predators such as ants may be facilitated by offering shelter and/or food, since nesting and food requirements of predatory ants are expected to be rather different from those of folivorous herbivores. It might be the reason that clear symbiotic relationships between plants and ants have evolved many times independently. However, even in those cases, trade-offs and compromises are necessary (Hölldobler and Wilson, 1990). Arboreal ants, including those housed by highly specialized myrmecophytes, usually herd various honeydew-producing Homoptera, which can be very detrimental to plants. This habit could be the reason why, despite its diversity, myrmecophytism remains a relatively uncommon phenomenon adopted by a small fraction of the world's plant taxa.

Few attempts have been made to incorporate ant–plant mutualism into theories on the evolution of plant defenses. In his very stimulating study on mutualism between *Leonardoxa africana* (Caesalpiniaceae) and ants, McKey (1984) suggested that ant mutualism is expected in plants with short-lived leaves, and that patrolling ants are primarily restricted to young leaves in plants with long-lived mature leaves. Mutualistic ants provide a mobile defense (that can be reclaimed) limited to those tissues requiring ant protection (e.g., young leaves), if they lack chemicals such as tannins and lignins. Those compounds are present in long-lived mature leaves and considered a one-time investment. Investment in harboring ants is somewhat equivalent to producing toxins (*sensu* Rhoades and Cates, 1976) or qualitative chemical defense (*sensu* Feeny 1976), since many such defenses appear to represent investments that can be reclaimed (McKey, 1979). McKey (1988) further suggested that supporting ant mutualists could be advantageous over producing toxins, when ephemeral tissues lack phenological defense as a consequence of continuous or asynchronous growth.

IV. CONCLUSIONS

The effects of plant allelochemicals on third trophic level animals can be divided into two categories; first, those in which the plant allelochemicals benefit the herbivores (second trophic level) by offering them protection against natural enemies (third trophic level), and second, those in which the plant allelochemicals benefit the natural enemies. We propose that only direct influences of plant allelochemicals have a predictive value and require evolutionary specialization. In the case of protection against natural enemies of insects, plant allelochemicals have a direct influence on the herbivores that have to handle them, and the relationship between plants and herbivores should be chemically specialized. In the second category, the direct interaction is between the plant and the parasite or predator, so that we expect these to be chemically specialized; we cannot, however, on those grounds alone predict anything about the chemical relationship between the plant and the herbivore or that between the herbivore and its natural enemies.

One of the questions posed at the beginning of this chapter was whether some types of plants provide better potential enemy-free space, e.g., nonapparent plants with mobile toxins. Another parallel question was whether host-plant specialization by herbivores could have evolved as a consequence of the selective pressure of natural enemies. The two questions are related, since specialist herbivores are prevalent on plants that are rich in "mobile" toxins. To answer these questions, we must consider not only physical or chemical protection of the herbivores resulting from host-plant range, but also the risk of being encountered by their enemies because of their dietary specialization. We must also keep in mind that learning and sensitization can be major factors.

A. Negative Influence of Plant Allelochemicals on the Third Trophic Level

As pointed out by Price *et al.* (1980), Bernays (1988), and Bernays and Graham (1988), herbs appear to offer better protection to herbivores against the third trophic level since their mobile toxins can be sequestered, and specialized herbivores are able to acquire specific crypsis. We believe that the negative effect of plant allelochemicals on the third trophic level are mostly, though not always, found in connection with specialized interactions between host plants and herbivores. The chemicals utilized in plant-derived chemical defense of insect herbivores are deterrent and/or toxic compounds that require specific adaptations on the part of the insects handling them (avoidance of autotoxicity, ability to store and transport them), regardless of their trophic level. Seen from the third trophic level, there is little or no difference between autogenous and derived toxins in the prey animal.

However, though chemical defense is prominent in specialized herbivores feeding on herbs, many herbivores secrete autogenous compounds; plant-derived defense is probably less frequent than commonly believed and is often a secondary evolutionary event. The selective pressure exerted by natural enemies might have resulted in the evolution of strong defense in specialized herbivores and not necessarily in the evolution of a restricted diet for better defense. Chemical defense of herbivorous insects, plant derived or autogenous, is often associated with visual cues (e.g., aposematism, gregariousness), which suggests that in these instances it mainly protects the herbivores against the attack of visually hunting predators. Of course, other types of cues can also be associated with chemical defense; for example, auditory or olfactory aposematism. As for crypsis, specialist Lepidoptera can be more cryptic than polyphagous ones (Bernays and Graham, 1988).

The spatial distribution of the specialist herbivore necessarily reflects that of its host plants, and, relative to a polyphagous insect, the specialist is often more aggregated; it cannot, unlike the generalist, feed on a wide variety of host plants and so become more widely dispersed in space. Specialist herbivores can thus be considered as food patches of relatively high density for their natural enemies. Some predators are well known to have aggregative responses to food patches (e.g., great tits, Smith and Dawkins, 1971; or coccinellid larvae, Hassel and May, 1974) and an area-restricted search when prey distribution is patchy (Edmunds, 1990; Schuler, 1990). From this generalization, we can predict that specialist herbivores will be subjected to greater selective pressure by natural enemies of this sort than generalists living in the same environment. This scenario is effectively the reverse of that previously proposed by other authors (Bernays and Graham, 1988). Thus, whereas specialization may perhaps offer refuge from some generalist predators, it will tend to increase danger from specialist natural enemies, or by generalists with learning ability. The development of search images has been reported for several predators (review in Curio, 1976), but the precise mechanism that leads to the selection of a specific prey could be more diverse than just the learning of a specific image (Allen, 1989; Edmunds, 1990; Guilford, 1990).

Additionally, the theory of apostatic (frequency-dependent) selection predicts that predators will concentrate on the more common morph of the palatable prey, thus favoring the development and maintenance of polymorphism. If one enlarges this concept to include chemical defense within a guild of herbivores feeding on one host-plant taxon, an analogous diversity of chemical defense should be favored. One consequence might be that, among the herbivores of the guild, only some will evolve plant-derived defense, while others are protected by autogenous chemicals, and yet others, by host-specific crypsis or mechanical devices. For example, some sympatric chrysomelid larvae feeding on Salicaceae derive salicylaldehyde from salicin (e.g., *Phratora vitellinae* and *Chrysomela* spp.), whereas others produce autogenous iridoid monoterpenes (e.g., *P. laticollis* and *Plagiodera versicolora*). At least one predator, the sawfly *Tenthredo olivacea*, feeds preferentially on the most common species (Pasteels and Grégoire, 1984).

Generally, parasitoid richness is considered to be larger on the herbivores living on trees than on herbs (Hawkins and Lawton, 1987). Additionally, parasitoids of externally feeding herbivores on trees include a larger proportion of specialists than those on herb-feeding herbivores (Hawkins *et al.*, 1990). Factors such as the more complex architecture of trees, allowing the existence of more niches, are invoked to explain these phenomena. It is not clear that they are in any way causally related to the differences in the principal allelochemicals between trees and herbs, or if the total number of parasitoids and the resulting risk is higher on trees than on herbs.

B. Positive Influence of Plant Allelochemicals on the Third Trophic Level

The positive effect of plant allelochemicals on the third trophic level is mostly mediated by attractant olfactory cues that are provided by both herbs and trees, and that act on both specialist and generalist parasitoids (or predators) feeding on specialist and generalist insect hosts. Presently, we cannot suggest a selective pressure that would have resulted in specialization of herbivorous insects on either herbs or trees to escape those recognition cues. It is doubtful whether the olfactory cues used by the third trophic level have ever evolved in plants for the primary special purpose of attracting predators and parasitoids. This type of interaction implies that the parasitoid has acquired recognition mechanisms and appropriate behavioral patterns, but the evolutionary process does not necessarily require specific adaptations of the herbivorous insect.

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