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INTERACTIONS AMONG THREE TROPHIC LEVELS: Influence of Plants on Interactions Between Insect Herbivores and Natural Enemies

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INTRODUCTION

In his recent review of the developing theory of insect-plant interactions, Gilbert (52) identified four major thrusts in research: insect-plant coevolution, host plants as islands, plant apparency and chemical defense, and resource predictability versus evolutionary strategies of insects. From his review it is evident that, with a few exceptions (23, 45, 53, 64), developing theory is addressing primarily a two trophic level system. In reality, of course, all terrestrial communities based on living plants are composed of at least three interacting trophic levels: plants, herbivores, and natural enemies of herbivores.

We argue that theory on insect-plant interactions cannot progress realistically without consideration of the third trophic level. A closer look at the mechanisms of interactions reveals a paradox, and plants have many effects, direct and indirect, positive and negative, not only on herbivores but also on the enemies of herbivores. The third trophic level must be considered as part of a plant's battery of defenses against herbivores.

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We focus on insect herbivores and their enemies, particularly insect predators and parasitic wasps and flies (parasitoids). Much is relevant to other herbivores and their enemies, and the literature is richer than we can indicate in a review of this size (see 93 for another view). To clarify and abbreviate discussion, the term “enemy” will be employed only for enemies of herbivores: predators, parasitoids, and parasites.

THEORY OF INTERACTIONS

The interrelationships among plants, herbivores, and enemies of herbivores are encompassed by several areas of theoretical ecology that have not usually been viewed in the same context: theory of plant chemical defense, general dynamical population models of insect herbivores, and food web theory. Predictions from this body of theory are overlapping and reinforcing but they have barely begun to be tested in the context of the third trophic level.

The theory of plant chemical defense as developed by Feeny (44, 45) and Rhoades & Cates (99) permits certain predictions about the efficacy of the herbivores’ enemies as ultimately influenced by the life history of the plant. Plant species in the early stages of succession are short-lived and patchily distributed and so are very “unpredictable” (99) and “unapparent” (45). This ephemeral life means for herbivores that early colonization is important. The earliest herbivores to discover a plant (or patch of plants) can be expected, by chance alone, to arrive from nearby plants, but in patchy distributions such source plants are usually of different species. Therefore, as the defensive chemistry of a given plant species evolves, individuals will be favored that produce chemicals [the “toxins” of Rhoades & Cates (99) and “qualitative defenses” of Feeny (44, 45)] increasingly different from those of associated plants. Probably at least some herbivores will evolve the capacity to detoxify such compounds, but a high interspecific chemical diversity should pose a formidable barrier to the evolution of extreme herbivore polyphagy (see also 49). Therefore, a plant with a unique chemistry will be chemically defended from most insects; it will often escape even insects that can detoxify its compounds (and therefore tend to specialize on it) because it will often occur at some distance from its nearest conspecifics. However, should specialists find and oviposit on these plants, their offspring will develop rapidly—regardless of the concentration of the specific toxins (45)—and may be able to mature before enemies can find them. In addition, they will contain the chemicals of the host plant (at least in their guts), which are likely to have direct toxic effects on enemies (see also 23, 52).

Feeny (44, 45) and Rhoades & Cates (99) argue that the opposite situation prevails in the defensive strategy of plants (at least the dominant

species) in late-successional, temperate systems. These plants are long-lived and tend to grow in stands of low diversity; they are thus very “predictable” (99) and “apparent” (45) resources. Most plants in such a system would not be able to escape the average herbivore species for more than a small fraction of their lifespan. Therefore, plants that produce only toxins would be extremely vulnerable to at least a small group of specialists, and chemically distinct toxins would seem to confer little advantage (but see 36). In accordance with these factors, natural selection has apparently favored defensive mechanisms that, although potentially less lethal, cannot be circumvented without substantial cost to the herbivore. The common defensive strategy seems to involve a reduction of the availability to herbivores of essential nutrients. This has been achieved by a heavy investment in certain compounds—the “digestibility reducers” of Rhoades & Cates (99) or the “quantitative defenses” of Feeny (44, 45)—including tannins (42, 43), resins (44, 99), proteolytic enzyme inhibitors (107), and silica (25). These compounds can interfere with digestive efficiency and prolong the herbivores’ development. The apparently lower chemical diversity of such systems, when coupled with the fact that several digestibility reducing mechanisms have a similar mode of action (they interact with proteins within the gut), should result in greater herbivore polyphagy in late successional habitats. Futuyma (49) has shown such increased polyphagy for Lepidoptera. All of these effects on the herbivores can serve to enhance the effectiveness of enemies in comparison to early successional systems: (a) Greater herbivore polyphagy on plants that are already more apparent and predictable should result in herbivores that are also apparent and predictable. (b) Prolonged development time results in longer exposure of the more vulnerable, immature stages to enemies (45). (c) Herbivores that feed on nontoxic food cannot sequester chemicals for defense (45).

The theory based on general population models of herbivores and their enemies develops similar conclusions. Southwood (119) devised a synoptic model of population dynamics incorporating population growth, population density, and habitat stability. Elaborated by Southwood & Comins (121) and Southwood (120), the model predicted that enemies are less important as a controlling influence on the population at low levels of habitat stability (their “*r*-selected” habitat stability) than at higher levels of habitat stability. Organisms at the low end of the habitat-stability axis are likely to escape from enemies in space and time (121). Supportive evidence for the population-level predictions of this model comes from the literature on biological control. Many authors (e.g. 120, 140) have analyzed the relative success of biological control attempts in agroecosystems versus orchard and forest settings. The trend is for more successful introduction and establishment of enemies in orchard-forest habitats than in agroecosys-

tems. Agricultural systems are similar in many respects to an early-successional habitat: Disturbances create conditions unsuitable for the continued coexistence of plant, herbivore, and enemy (140), and colonization is an important aspect of the system. Orchard-forest systems represent conditions closer to a late-successional habitat. Long-term interactions among the three trophic levels are more likely to occur simply because the role of disturbance and recolonization is minimized.

Food web stability as a function of food chain length and the degree of specialization of organisms has been theoretically investigated by May (76, 77), Maynard Smith (78), Beddington & Hammond (7), and Pimm & Lawton (88, 89). These authors predict that, in general, stability should decrease as the number of connecting links in the food web increases. Specialized herbivores and their enemies, such as may be found on toxic plants in early succession, produce food webs of low connectance. More generalized herbivores and their enemies, as may occur on late-successional plants, show a decreased stability as a result of the greater number of interconnecting links. These predicted trends may, however, be counterbalanced by the relative instability of early-successional resources. Any realistic prediction of degree of stability depends on the relative balance of specialization at each trophic level and on the stability of the environment in which the food web exists.

PROPERTIES OF INDIVIDUAL PLANTS

Traits of individual plants may modify interactions between herbivores and their enemies by operating directly on the herbivore, the enemy, or both. These traits may be either chemical (such as toxins, digestibility-reducers, and nutrient balance) or physical (such as pubescence and tissue toughness).

Effects That Operate Directly on Herbivores

The opportunity to influence interactions between herbivores and enemies would not be great if plant defensive traits resulted in rapid death of the herbivore. Enemies would have no role to play. In addition, the herbivores themselves would probably soon evolve either an effective detoxification ability [so that the trait would have a negligible effect (45)] or an avoidance response. For these reasons, the less potent digestibility-reducers probably have far more significant direct effects on herbivores than do toxins. Digestibility-reducers can exert sublethal effects in three major ways: by impairing growth, lowering resistance to disease, and reducing fecundity.

Impairment of herbivore growth can result in a prolonged development time. This may have important consequences for interaction between the second and third trophic levels. That digestibility-reducers can prolong

development time is suggested by the fact that lepidopteran larvae feeding on mature, high-tannin (up to 5.5% of leaf dry weight) oak leaves grow much more slowly than those on young, low-tannin leaves (43). Some cannot even reach adulthood in a single season. More precise evidence comes from artificial diet studies by Chan et al (27) with the lepidopteran *Heliothis virescens*, a pest of cotton. They found that the presence of only 0.3% (dry weight) of condensed tannin (extracted from cotton) in the diet increased development time by 21%, even though the insects were switched to a normal diet before half of their larval life had been completed. Texas 254, a cotton variety resistant to this insect, contains 0.7% condensed tannin. Prolonged development time should increase the herbivore's risk of attack by enemies during its vulnerable immature stages (45). This prediction is supported by a review of the literature on parasitoids on Lepidoptera in early versus late-successional habitats (B. A. McPherson and P. Gross, unpublished), which indicates that in general significantly more parasitoid species colonized the latter: a mean of 2.8 parasitoid species on early-successional Lepidoptera and 6.4 species on those in late succession. Especially important may be the improved probability of temporal coincidence of insect herbivores with specialized parasitoids, which usually attack only particular instars of their host. Host populations that are developmentally well-synchronized may only include individuals of these suitable instars for short periods (56) unless development is prolonged.

Digestibility-reducers can also decrease herbivores' resistance to pathogens. Chan et al (27) found that only 63% of *Heliothis virescens* larvae survived to pupation on a high-tannin diet compared to 81% on one that was tannin-free. The role of pathogens was not investigated but, since tannins are probably not directly toxic (99), the decreased survival may well be due to stress that weakens herbivore resistance to such organisms (124). Stubblebine & Langenheim (127) reared the armyworm, *Spodoptera exigua*, on artificial diets with and without a leaf resin extracted from the legume, *Hymenaea courbaril*. One experiment was performed with larvae from a single egg mass that had been infected (inadvertantly) with virus. Viral mortality ranged from 0% among larvae on the resin-free diet to over 50% among those on the diet containing 1.6% resin (dry weight).

Digestibility-reducers may also affect herbivore-enemy interactions by causing decreased herbivore body size and hence fecundity [see (24) for correlations between body size and fecundity]. For example, when Feeny (42) reared larvae of the winter moth, *Operophtera brumata*, on artificial diets containing tannin concentrations equivalent to that of September oak leaves, the resultant pupae were significantly smaller than the control insects (22.4 mg vs. 30.8 mg). If smaller size results in lower fecundity, this will lower the rate of population increase. This greatly influences the ability

of enemies to control a local herbivore population [(139, 152) and see below].

Influence on enemy effectiveness through direct influence on herbivores is not limited to digestibility-reducing compounds; any plant character that can affect growth, resistance to disease, or fecundity can have such an influence (e.g. 137). Variation in plant nutrient content is probably important in this regard. While such variation probably seldom involves complete presence or absence of essential nutrients (48), changes in their proportions appear to be commonplace (62). Effects that are less than lethal should, therefore, also be commonplace. Negative effects of imbalanced diets on insect survivorship, growth, and development have, not surprisingly, been demonstrated in controlled artificial diets for a number of insects and nutrients (31).

That such mechanisms operate in nature is strongly suggested by numerous observed correlations between insect performance and levels of various nutrients in plants. Most thoroughly studied is the role of nitrogen, recently reviewed by McNeill & Southwood (79). Most studies involve temporal fluctuations of nitrogenous compounds within single plants. Such studies no doubt reveal important ecological influences upon interactions between herbivores and enemies, but they provide only limited insight into the potential evolutionary importance for plants of a genetically controlled variation of nitrogenous compounds. One exception is the resistance of rice to the rice planthopper and the rice leafhopper. Resistant varieties had low levels of amino acids, especially asparagine (22), which resulted in significant reductions in leafhopper rate of weight gain and fecundity (28). Survivorship was also significantly reduced, probably owing to increased susceptibility to pathogens. Slansky & Feeny (115) also investigated a system involving variation in levels of nitrogenous compounds between different species of crucifers. In this case, however, the lepidopteran *Pieris rapae* grew just as fast on low- as on high-nitrogen plants because it consumed more of the former and utilized the nitrogen within that food more efficiently. Nevertheless, as Slansky & Feeny (115) point out, low nitrogen levels may still increase herbivore vulnerability to enemies. *P. rapae* actively feeds for only a small fraction of every day and spends the remainder of the time resting and digesting food in a more cryptic position. In order to increase consumption of low-nitrogen plants, larvae must spend longer periods more exposed to enemies.

Other variable factors may produce relevant sublethal effects in herbivorous insects. The importance of leaf water content has been demonstrated for growth of the cecropia moth, *Hyalophora cecropia*, (108), and for other moths and butterflies (109). Physical factors, such as pubescence, can also be important. Wellso (149) found that cereal leaf beetles, *Oulema melano-*

pus, exhibited increased development time, lower adult weight, and lower survivorship when reared on small grain cultivars with greater trichome densities. Small larvae had to bite individual trichomes repeatedly before gaining access to the nutritious adaxial cells. Later instars consume trichomes whole, but they are siliceous and therefore indigestible and capable of lacerating the midgut. This permits entry into the hemocoel of “potential pathogens”—bacteria that are nonpathogenic under the relatively anaerobic conditions of the gut but lethal in the body cavity (19). Finally, even the so-called toxins (99) can have these sorts of sublethal effects. Erickson & Feeny (40) found reduced growth rates of the black swallowtail, *Papilio polyxenes*, on diets to which sinigrin had been added. Also, Stubblebine & Langenheim (127) found that legume resins, which increased susceptibility of the armyworm, *S. exigua*, to viral infection, may actually better fit the definition of toxins—small, lipid-soluble molecules (99). Resins had no effect on survivorship among virus-free insects, so their direct effects are truly sublethal.

The three major categories of sublethal effects have thus far been portrayed as though they could influence interactions between herbivores and enemies either by mechanisms that operate within the generation time of the herbivore (the categories of impaired growth and increased susceptibility to disease) or else by mechanisms acting across generations (the reduced fecundity category). However, impaired growth and increased susceptibility can also operate across generations. For example, an impaired growth rate can prolong generation time, which dramatically reduces a population's intrinsic rate of increase (29). And, since rate of increase is also a function of age-specific survivorship, mortality due to an increased susceptibility to disease agents will, of course, also reduce the rate of increase. A rate of increase that is specific to an individual plant (or small patch of plants) may be especially pertinent to small, relatively sessile herbivores like mites, aphids, and whiteflies, which spend more than a single generation on a single plant.

The reduction of rates of increase by plant factors can be of central importance in determining the ability of enemies to control herbivore populations. For example, Van Emden (139) demonstrated the potential importance of variable rates of herbivore increase on different plants, in the context of predation, using a difference equation model. A particular fixed predation rate was unable to control a phytophagous insect that had the potential in the absence of predators of multiplying 1.2-fold each day on a given host plant. However, control was achieved when the rate of increase was only slightly less: 1.15. Of course, this is a gross oversimplification since a fixed predation rate ignores functional and numerical responses. Nevertheless, it does illustrate the potential for at least temporary numerical

escape before a predator's own numerical response is manifested (assuming the predator has a long generation time).

Van Emden's model has been tested with experimental systems involving resistant cultivars on which particular herbivorous insects realized reduced rates of increase. Starks et al (122) tested the effect of a parasitoid, *Lysiphlebus testaceipes*, on population growth of the aphid, *Schizaphis graminum*, on resistant and susceptible varieties of barley. Absolute mortality attributable to parasitoids was similar on the two varieties. However, since there were fewer total insects on the resistant variety, the rates of parasitism on it were much higher. These higher rates enabled the parasitoids to check aphid population growth on the resistant variety at all initial levels of aphid infestation, whereas they were only able to do so on the susceptible variety at the lowest inoculum level (three). With inoculums of six or twelve aphids per susceptible plant, aphids were still increasing at an exponential rate at the end of four weeks. These results are consistent with those of Wyatt (155, 156), who studied population growth of the aphid, *Myzus persicae*, on four chrysanthemum cultivars with and without the parasitoid, *Aphidius matricariae*. Finally, Dodd (33) studied the interaction between predation and plant resistance in the cabbage aphid, *Brevicoryne brassicae*, on different varieties of brussels sprouts. The potential growth rate of aphids was only slightly less on the variety "Early Half Tall" than on "Winter Harvest." However, when aphid populations declined during inclement conditions, the residual mortality attributed to predation was much greater on "Early Half Tall." Since predator densities were not controlled, however, it is impossible to determine whether each predator was more effective on "Early Half Tall" or whether this plant type was simply more attractive to certain predators.

Effects That Operate Directly on Enemies

The activities of natural enemies can be influenced directly in either positive or negative ways by a variety of properties of their hosts' food plants. These characteristics have far-reaching effects on resource utilization patterns in herbivores.

ATTRACTANTS The availability of secreted nutrients, particularly nectar, greatly influences the presence and abundance of not only mutualists with the plant—particularly ants (9), but also other predators and parasitoids (51, 53, 116). The adaptive finesse of the plant in manipulating the protective third trophic level is illustrated by Tilman's (135) demonstration that black cherry maintains maximum secretion from extrafloral nectaries at the time when ants are most able to prey upon the major herbivore, *Malacosoma americanum*. Bentley's (9) review covers much of the litera-

ture on plant-ant mutualism, although she omits mention of extrafloral nectaries on galls. The existence of such nectaries was noticed by Theophrastus (133). Bequaert (10) lists 16 European species of cynipid wasps producing secreting galls; many others exist in North America (146–148). The copious nectar produced by these galls attracts a host of insects, including, no doubt, the gall-makers' parasitoids. Bequaert's review (10) suggests, however, that ants may often exclude other nectar feeders (e.g. parasitoids), thereby protecting the gall-maker.

The production of floral nutrients allows a loose mutualism to form between plants and enemies. The tarnished plant bug, *Lygus lineolaris*, was hardly attacked by the braconid *Leiophron pallipes* on weedy species of *Oenothera*, *Daucus*, *Amaranthus*, and *Solidago*, but parasitism commonly reached 30–40% on *Erigeron* species (125). This difference was later explained when Shahjahan (111) showed that gravid parasitoids were more attracted to *Erigeron* flowers where higher-quality nectar increased their life span. This would increase the probability that *Lygus* bugs on *Erigeron* will be encountered by a parasitoid.

How parasitoids use plant chemicals as searching cues has been reviewed by Vinson (141). These phytochemicals may act either directly as they volatilize from the plant, or after they pass through the herbivore's gut and are excreted [see (93) for examples].

HERBIVORE POSITION AND ENEMY SEARCH PATTERNS Herbivore species experience different attack rates on different plant species [e.g. (11, 60) and reviewed in (151)] or on different parts of the same plant (150, 151). Where the mechanisms behind these differential attack rates have been examined, it has usually been found that herbivore individuals may escape attack by occupying stations that are (a) seldom or never searched by enemies; (b) inaccessible to enemies; or (c) located on a plant part that offers resistance to enemy searching movement. Due to the small size and highly stereotyped behavior of many parasitic and predaceous insects, small amounts of plant variation between species, within species, and within individuals can have a large impact on enemy foraging efficiency.

The specialized searching patterns of many small enemies often restrict them to certain plant species or to particular parts of a single plant species. Since the foliage of different plant species is not equally attractive to parasitoids, herbivores run different risks of attack depending on which plant species they occupy (e.g. 80, 82). Some parasitoids specialize their search to specific plant organs. Spruce budworm larvae feeding in staminate cones suffer higher parasitism than those in vegetative buds (35), and the gall-maker, *Neuroterus quercus-baccarum*, is attacked by fewer parasitoid species when its galls occur on oak catkins than when on leaves, the usual

location (2). On an even finer scale, position on a leaf can influence risk of attack. The predatory bug, *Anthocoris confusus*, follows a searching path along leaf margins and midribs, and aphids feeding in these locations are more vulnerable to attack (41). The gall-maker, *Massalongia betulifolia*, is less often attacked by parasitoids when located on the leaf midrib (25%) than when on the leaf lamina (44%) (3).

It is difficult to determine why enemies have not evolved to search in these accessible locations. A contribution was made by Monteith (82) when he found a positive correlation between the searching preferences of two tachinid parasitoids and their survivorship on red-headed pine sawflies feeding on different plant species. Microclimatic differences between plants and between plant parts may also be important (151). Enemies may be adapted to neglect certain accessible locations simply because they are not profitable. Finally, the host may recently have expanded its resource utilization and the parasitoids may not yet have adapted to this range extension.

STRUCTURAL REFUGES A number of herbivorous insects are concealed from their enemies by plant structures offering barriers to parasitoid penetration. Variation in the size and complexity of these plant parts makes for variation in the accessibility of the herbivores using them. Such structural differences among the cultivars of *Brassica oleracea* affect the parasitism rates of the herbivore, *Pieris rapae*; attack rates are high on cauline leaves of open-growing varieties such as brussels sprouts, and low on the heading varieties such as cabbage, where this caterpillar escapes attack when it feeds in the folds of the leaves (87). More subtle differences in plant structure are responsible for different parasitism rates on different food plants for moths of the genus *Rhyacionia*, which mine pine buds. When *R. frustrana* var. *bushnelli* feeds on pines with large buds and robust stems it suffers less parasitism than when it feeds on small buds, probably because when it burrows deeply it is beyond the reach of small parasitoids (55). A similar mechanism explained why percent parasitism of the European pine shoot moth, *R. buoliana*, by *Itopectis conquisitor* was much higher (25 times higher between pure stands) in pupae collected from Scots pine than in those collected from red pine (1). The ovipositor of *I. conquisitor* is too short to penetrate to the center of many red pine buds. In addition, the percentage of buds protected by needles was higher in red than in Scots pine (where needles were splayed at a greater angle from the stem). Burrowing beyond the reach of parasitoids is also important in bark beetles, where parasitism rates have been negatively correlated with bark thickness (5), and in insects attacking inflated fruit (75). Porter (91) noted that when North American species of apple maggots fed in apples they were less often parasitized by *Opius melleus* than when they fed in smaller native fruits

such as hawthorn because the ovipositor of the parasitoid could not reach hosts in the larger exotic fruit.

Difficulty in reaching concealed hosts might be overcome through the evolution of longer ovipositors. Although this has undoubtedly occurred in the coevolutionary race, we are unaware of any cases that demonstrate this strategy. Parasitoids that attack bruchid weevils seem to have overcome the problem through behavioral and phenological adaptation: Bruchids feeding on maturing legume seeds are protected by thick, tough seed pods; parasitoids may thus be adapted to attack while the pod is still young, thin, and soft, or after it has fallen to the ground and begun to ferment (14, 15). Other parasitoids enter the pod through the hole bored by the ovipositing female bruchid (81). Similar problems face parasitoids attacking gall-forming insects, and similar phenological (144) and behavioral (143) adaptations have arisen.

INTERFERENCE WITH ENEMY SEARCH MOVEMENT Certain plants bear structures and produce secretions that impede the movements of small predators and parasitoids in search of prey. By increasing searching time such plant structures weaken the functional responses of enemies. Various plant galls, for instance, produce glutinous substances (10, 32) that can immobilize small insects and can presumably hinder parasitoids just when the gall is young and actively growing—i.e. when the gall-maker is most vulnerable to attack.

The role of plant trichomes as a defense against herbivores is well known [for reviews see (74, 145)], but a dense mat of trichomes can also lower enemy foraging efficiency. *Encarsia formosa*, a normally effective parasitoid of the greenhouse whitefly, is greatly hindered by the hairs produced by cucumber. As a result, whitefly populations flourish on this plant (137, 153). In addition, honeydew produced by the whitefly accumulates on the hairs and then sticks to the parasitoid, forcing it to spend a significant amount of time grooming. The walking speed of *E. formosa* is three times greater on glabrous than on hairy cucumber varieties (64); this fact makes biological control feasible on the former (39). Tobacco hairs produce a viscous exudate that impedes the tiny parasitoids, *Trichogramma minutum* and *Telonomus sphingii*, resulting in reduced parasitism of *Manduca sexta* eggs (69, 95). Independent of any physiological function trichomes may serve, their length and density may evolve to a point where direct deterrence to herbivory may be held at a submaximal level by the counter-balancing force they exert on efficient foraging by the natural enemies of herbivores.

PLANT TOXINS Many toxic chemicals, more or less unaltered from plants, may render herbivorous insects toxic to predators and parasitoids

(e.g. 59, 106). Chemicals may be sequestered [e.g. cardenolides (102, 142)], hemolymph composition may change owing to unavoidable uptake of compounds from the midgut (110), compounds may simply be in transit through the gut (37), or plant chemicals may be used in defensive secretions [see (38) and review (104)].

Variation in the food consumed, which very likely results in important differences in the chemical composition of the herbivore, can affect its susceptibility to predator attack. Jays will consume the grasshopper, *Poekilocerus bufonius*, fed on dandelions but not on *Asclepias* spp. that contain cardenolides (105). The defensive regurgitant of the grasshopper, *Romalea microptera*, effectively deterred ants when its foodplant was *Eupatorium capillifolium* or *Salix nigra*, but not when it had eaten lettuce (37). Brower et al (17, 18) showed that monarch butterflies, *Danaus plexippus*, exhibited a spectrum of palatability to jays when reared on different asclepiadaceous individuals (different either intra- or interspecifically); palatability correlated negatively with cardenolide content.

Toxins derived from plants can also affect larval parasitoids [see (47) for review], which select for adaptations to detoxify or sequester them. Jones (68) found that two parasitoids attacking cyanogenic *Zygaena* spp. produced rhodanese, an enzyme that detoxifies cyanogenic compounds. In addition, *Zenillia adamsonii*, a tachinid that attacks the monarch butterfly, sequesters cardenolides in its body (98), and a species of *Microplitis* (Braconidae) sequesters pyrrolizidine alkaloids originally produced by the herbivore's host plant (8).

Toxins derived from plants by herbivores can directly affect parasitoid survivorship. Smith (118) found unusually high larval mortality of two parasitoids of the California red scale, *Aonidiella aurantii*, when the scale fed on sago palm compared to when it fed on citrus hosts (100% compared to less than 5% for one species, and 44% compared to 12% or less for the other); no toxic principle was determined. Larval survivorship of *Apanteles congregatus* was drastically lowered when its host, the tobacco hornworm, was fed a high-nicotine diet compared to one with low nicotine content [see (134) and references therein]. Since nicotine occurs in the hemolymph of hornworms feeding on tobacco (110) it is probable that this was the causal agent. A more detailed example presented by Campbell & Duffy (23) demonstrated the effects on the ichneumonid, *Hyposoter exiguae*, of adding tomatine to the artificial diet of its host, *Heliothis zea*. Parasitoid larval development was slowed; percent pupal eclosion, adult weight, and longevity were reduced; and extracts of larvae contained tomatine.

If toxins are present in herbivore bodies, they present potentially formidable barriers to successful attack by generalist parasitoids and to colonization in evolutionary time, as indicated by the larger number of parasitoid species

on late-successional herbivores compared to early-successional species reported above.

EVOLUTIONARY CONSEQUENCES FOR HERBIVORES Plant influences on enemy effectiveness can have important evolutionary consequences for the herbivores involved. As we have documented above, these insects will frequently experience lower vulnerability to enemies when feeding on one plant species or structure than another. With regard to birds and cryptic prey, Brower (16) suggested that (except where prey species diversity is low) density-dependent selection will limit the similarity between prey species and restrict the diet breadth of any one species to those plants on which it is best protected. As an interesting example, desert grasshoppers that live on and mimic stems (stems exhibit low interspecific variation) are more polyphagous than those that resemble foliage (foliage varies more from one species to another) (84). Ricklefs & O'Rourke (101) regard the backgrounds and the morphological adaptations that match them (the "escape space") as a limiting resource for which species compete. The amount of escape space will partly determine herbivore species diversity in a community.

With some modifications, the same arguments apply when considering invertebrate enemies such as parasitoids that differ from birds in their use of more specific chemical and physical cues in host finding. Thus escape space can be described not only by mimetic appearances, but also by any of a wide variety of niche parameters important to host finding and oviposition behavior by enemies (e.g. position on leaf, gall shape, odors produced during feeding, food plant species, etc) (158). Competition for escape space or "enemy-free space" (71) resulting from density-dependent selection by such enemies is probably more important than competition for food in generating the tremendous niche diversity found in herbivorous insects, as illustrated by Askew's (2) studies on cynipid wasps.

All plant preferences by phytophagous insects are probably influenced to some extent by the effectiveness of enemies associated with the food items. For generalist herbivores, restriction in diet breadth or changes in the order of foodplant preferences can result at least as much from differential vulnerability to enemies as from differences in foodplant quality (52). Smiley (116) suggests that predation pressure by parasitoids and ants may explain why *Heliconius melpomene* is specific to *Passiflora oerstedii* despite its ability to grow "about equally well" on four other *Passiflora* species. (However, his data show that growth rates are significantly lower on at least three of these species; this might produce an important difference over evolutionary time.) On the other hand, host plant range extensions may be reinforced by enemy ineffectiveness on a novel plant species. An extreme case concerns two closely related leafminers of the genus *Tildenia* on hosts growing together

(P. Gross, unpublished). In one year 42% of the leafminers on *Solanum carolinense* were attacked by 25 species of parasitoids, while on adjacent *Physalis heterophylla* only one parasitoid species attacked 5% of the other leafminers. Such events have undoubtedly occurred when agricultural crops are imported. Native herbivores can expand their host ranges before enemies evolve the corresponding host-finding abilities, resulting in creation of new pest species. For example, cutworms (e.g. *Perosagrotis* spp.) prefer cultivated grains over the native grass, *Agropyron smithii*, but their parasite, the tachinid *Gonia capitata*, still lays its microtype eggs on *A. smithii* (126).

For specialized herbivores in the early stages of a speciation event via a host plant shift, serendipitous acquisition of enemy-free space may increase the viability of the founders (21, 91). On the other hand, host shift “attempts” may be throttled by enemy faunas already associated with the new plants. This is suggested by a review (54) indicating that enemies have interfered with as many as half the reported cases of herbivorous insects introduced for weed control.

PROPERTIES OF PLANT POPULATIONS

The properties of plant populations that influence the third trophic level have been poorly studied. Because much more research is needed in this area, it will not reward a thorough review at this time. Plant density and patch size influence herbivores and enemies alike [(85, 86); but cf (103)]. The most obvious effect of increased plant density and patch size is to increase resources for herbivores to which many species respond positively, with subsequent density-dependent responses by their enemies. Conversely, plants may occur at such a low density that specialized enemies find few specific herbivores, resulting in little or no parasitism (66). Plant density also influences microclimate, nutritional quality of foliage, and concentration of nectar and honeydew—all factors that effect members of higher trophic levels. One important effect of plant density is its impact on the diversity of associated plants that influence the upper trophic levels profoundly. This is discussed in the next section.

PROPERTIES OF PLANT COMMUNITIES

Emergent properties, which may well influence herbivore-enemy interactions, appear when plant species co-occur. The degree of association of a host plant with other plants [see (4) for the effect on the plant-herbivore relationship] affects three-trophic-level interactions in two major ways: (a) The herbivore-enemy interactions on one plant species can be influenced

by the presence of associated plant species; (b) the herbivore-enemy interactions on one plant species can be influenced by the presence of herbivores on associated plant species.

Plants with which the host plant is associated can be nectar and pollen sources for adult parasitoids and predators (e.g. 57, 113, 138, 154). Such nutrient sources frequently result in increased longevity and fecundity of enemies (72, 128, 130, 131), which may strengthen their functional and numerical responses [as suggested in (57)]. Quantitative studies are mostly on parasitoids (72, 73, 130, 131, 136), but effects on predators have also been noted (128).

Associated plants supporting honeydew-producing herbivores are another important nutrient source for many enemies (26, 30, 61, 157); longevity and fecundity of the enemies may be increased (58, 157). The quantitative effects vary according to plant species and herbivore producing the honeydew (157). Some parasitoid species, such as *Coccophagus scutellaris*, elicit honeydew secretion from homopterans as in ant trophobiosis (26). Gardener (50) found that *Tiphia vernalis* adults use honeydew produced by aphids and that Japanese beetle larvae were more heavily parasitized near plants infested with aphids than in areas free of aphids.

Associated plants may provide odors or other conditions attractive to enemies. Read et al (97) found that aphids on sugar beets adjacent to collard plants were more frequently parasitized by *Diaeretiella rapae* than those on sugar beets not near collards. The parasitoid normally attacks hosts on crucifers and apparently searched all plants in the vicinity of a collard plant. Smith (117) showed that some syrphid and anthocorid predators of aphids colonized brussels sprout plants among weeds more readily than plants on bare ground. This behavior is probably a function of the predators' tendency to move from plant to plant and the ameliorated conditions provided by the weedy vegetation.

Alternatively, associated plants may interfere with the attractiveness of a plant to herbivores and their enemies, either by masking attractive odors from the host plant or by a direct repellent effect of the volatile chemicals of the associated plant. Tahvanainen & Root (132) found that nonhost plants such as tomato and common ragweed, when associated with the crucifer *Brassica oleracea*, interfere with the searching and feeding behavior of the specialist herbivore *Phyllotreta cruciferae* on *Brassica*. They concluded that "the environmental capacity of diverse natural communities is lower than that of natural or man-made monocultures. The 'associational resistance' resulting from the higher taxonomic and microclimatic complexity of natural vegetation tends to reduce outbreaks of herbivores in diverse communities." It is likely that many specialist parasitoids are influenced by masking or repellent chemicals produced by associated plants.

An example of this associational resistance to parasitoids centers on studies of host location by the tachinid flies, *Bessa harveyi* and *Drino bohémica* (83). Many trees and forest understory plants apparently interfere with the host location abilities of the parasitoids by masking the odor of the true host plant (*Larix laricina*). Parasitism of the host sawfly, *Pristiphora erichsonii*, when *Larix* was associated with other plants, was lower (10–13%) than in pure stands of *Larix* (up to 86%). Although the herbivore responded to vegetation in a way similar to that of the parasitoids (avoiding *Larix* branches in contact with other plant species), those that did feed in these less apparent sites contributed disproportionately to the next generation because food was abundant and parasitism was low. Indeed, such unapparent sites for herbivores may act as important refugia from enemies. Similar patterns of parasitism have been observed on herbivores of herbaceous plants (100, 112).

Associated plants may also support herbivores that act as alternate hosts, as indicated in studies of biological control and insect population dynamics (e.g. 20, 46, 63, 90, 113, 123). On associated plants enemies may remain at high population levels when the primary herbivorous host is at low population levels or when enemies are not well-synchronized with herbivore phenology. A well-documented example is that of the egg parasitoid, *Anagrus epos* (34). Wild blackberries support the herbivore, *Dikrella cruentata* (a leafhopper), which is attacked by *Anagrus*. Wild grape, growing in the same habitat, is attacked by another leafhopper, *Erythroneura elegantula*. However, the leaf flush of wild grapes occurs just when the *Anagrus* adults are emerging after the first generation attack on *Dikrella*, so the parasitoid is present to colonize grape and attack the *Erythroneura* eggs as soon as they are laid. Atsatt & O'Dowd (4) suggest that selection may have favored those grape plants with a delayed leaf production that was synchronous with the availability of parasitoids.

THE PLANT'S PERSPECTIVE: A PARADOX

The causal relationships dealt with to this point have been those directed from the first trophic level towards the second and third. Superficially, at least, it would seem that the consequences of these for the plant would necessarily be in a direction opposite to their consequences for the herbivore (excluding, of course, herbivore mutualists such as pollinators). However, more careful examination reveals that mechanisms that produce negative effects on the herbivore do not automatically lead to positive effects on the plant. Such paradoxical situations are best understood from the perspective of individual plant fitness.

One such paradox arises upon consideration of the consequences of digestibility-reducers for plant-herbivore interactions. In general, insects reared on diets of low digestibility (for example, high cellulose content) have a strong tendency to compensate through increased consumption (6). Similar compensation can be expected in response to plant digestibility-reducers (43). This means that the per capita damage by those insects that complete maturation on digestibility-reducing plants is actually greater because of those compounds. Therefore, from a plant-fitness perspective, the fact that digestibility-reducers can increase enemy efficacy may be more important than originally conceived. Instead of being a supplement to the positive selective value of a digestibility-reducing trait, enhanced enemy efficacy may be essential to making the value positive in the first place.

Bouton et al (12) tested the importance of relative enemy efficacy in the selection for digestibility-reducing traits. Identical numbers of larvae of the Mexican bean beetle, *Epilachna varivestis*, were introduced to cages containing plants of one of two soybean lines. Laboratory studies (70) had previously revealed differences in the performance of the beetles (including growth rate and the ability to convert plant biomass to beetle biomass) on the two lines; these differences closely paralleled those between winter moth larvae on diets with and without tannin (42). The cause of these differences is unknown. Survivorship to pupation on the variety PI 80837 (the "high-tannin analog") was only 0.88 of that on the Harosoy Normal variety. However, since each larva on PI 80837 destroyed 1.26 times as much leaf area, this line actually sustained an estimated 1.11 times as much damage ($1.26 \times .88$). The situation was reversed in cages where the predatory pentatomid, *Podisus maculiventris*, was introduced. Survivorship on PI 80837 was now only 0.23 of that on Harosoy Normal (predators were able to consume more of the slower growing larvae), so the overall damage was only 0.29 (i.e. $1.26 \times .23$) of that on Harosoy Normal. So the level of predation *can* determine the relative amounts of herbivore damage on plants with and without sublethal traits.

Plant traits that facilitate parasitoid attack constitute a second category of mechanisms that negatively affect herbivores without automatically increasing plant fitness. Such traits can be expected to benefit the plant population as a whole by contributing to lower herbivore densities. But in order to become fixed in the population they must somehow enhance individual plant fitness, presumably by reducing localized herbivore damage. This is by no means a universal feature in parasitoid attack.

The effect of parasitoid activity on localized herbivory strongly depends on the particular herbivore-parasitoid combination. Parasitism does not always affect host feeding; many internal parasitoids that attack larvae are relatively inert within the host until after it has completed feeding (e.g. 94).

Among parasitoids that do affect host feeding there is a spectrum of effects. Some hosts may quickly terminate feeding as a result of paralyzation by the ovipositing female or through rapid consumption by the immature parasitoid [e.g. some Banchini (Ichneumonidae) (92)]. In other cases, host feeding may continue in spite of internal parasitoid activity. This can result in reduced consumption (13, 129), but it can also result in an increase (65, 114); and in the case of *Pieris rapae*, consumption may either increase or decrease, depending upon whether they are attacked by gregarious or solitary parasitoids, respectively (96). The examples involving unchanged or increased herbivore feeding suggest that in some cases plants may only be able to benefit from higher parasitism by mechanisms involving parasitoid-host population dynamics. Whether such dynamic processes occur on a scale sufficiently localized to benefit individual plants requires careful investigation.

Thus plant traits have important consequences for herbivores and their enemies, but we need to investigate more closely the consequences for plant fitness. Plant fitness should be central to the study of the adaptive function of purported plant defenses; emphasis has traditionally been placed on the effects of defenses on herbivores.

CONCLUSIONS

We have argued for a holistic approach to plant-herbivore interactions. Consideration of the third trophic level is indispensable to an understanding of any part of the system. We cannot understand the plant-herbivore interaction without understanding the role of enemies. We cannot understand predator-prey relationships without understanding the role of plants. Enemies should be considered as mutualists with plants and part of plant defense. They can be manipulated by natural selection on plants with compromises made between intrinsic defense and traits that foster effective enemies. Thus good intrinsic plant defense frequently results in negative impact on enemies, and a lowering of these defenses may benefit enemies and plant fitness. Plant fitness must be recognized as a central theme. The costs and benefits must be measured and ultimately incorporated into a quantitative theory of plant-herbivore-enemy interactions.

Emphasis on the third trophic level extends the theory of plant-herbivore interactions and broadens its basis. Plant fitness is fundamental in considering plant-herbivore interactions. Acknowledgment that the plant is the basic level at which natural selection operates in the three-trophic-level system avoids paradoxical arguments such as those discussed in this review. Theories on population dynamics, biological control, and the actual num-

bers of parasitoid species on early- versus late-successional herbivores are all consistent with Feeny's prediction that enemies are favored by persistent plants with quantitative defenses. Further studies should proceed with a view to furthering theory on plant-herbivore-enemy interactions rather than on a two-trophic-level system.

Implications of the three-trophic-level theory for agriculture are extensive. Many crop plants cultivated in monocultures are actually derived from early-successional species: Unapparent plants have been made apparent (44, 45). Manipulation of this vulnerable system to reduce herbivore impact must be subtle and based on detailed knowledge. Increased diversity within a field, either genotypic or plant species diversity, would decrease plant apparency (45), but associated plants may mask cues used by enemies for searching and reduce their efficiency. Breeding programs to increase plant resistance to herbivores may well select for lines that confer increased resistance of herbivores to their enemies. Manipulations for the biological control of weeds should attempt to reduce efficacy of enemies to enable a strong numerical response of herbivores to their superabundant plant food. Again cost-benefit analysis will help to optimize management practices; such optimization cannot be achieved without considering the enemies of herbivores.

Many areas of research need more concentrated effort. Plants probably always influence the third trophic level, but we need to understand better what aids and hinders enemies. The role of enemy-free space needs more exploration. One common effect of plants will be through microorganisms in herbivores, particularly the gut microorganisms (e.g. 67) and mutualists elsewhere in the body. Digestibility of food, vulnerability to pathogens, and plant specificity may all be mediated by associated microorganisms. Isogenic lines of plant species are available to help unravel the impact of one plant trait at a time on herbivores and enemies, providing a potent tool for analyzing interactions. Tropical systems must be integrated into the theory developed largely on knowledge from temperate latitudes. The challenges are great for the development of a quantitative theory on plant-herbivore-enemy interactions, but the potential rewards are also considerable.

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