THREE-TROPHIC-LEVEL INTERACTIONS AFFECTING THE SUCCESS OF BIOLOGICAL CONTROL PROJECTS

PETER W. PRICE[1]

ABSTRACT - The thesis is developed that the detection of pattern in three-trophic-level systems of plants, insect herbivores, and natural enemies, is a necessary step towards the development of theory on natural systems and applied biological control. When patterns are discovered the underlying mechanisms can be revealed, and will contribute to synthesis and general theory. The strongest patterns are those imposed by vegetation passing through ecological succession over landscapes, providing a template on which insect herbivores and their natural enemies must function. Plants provide food and habitat for insect herbivores and therefore their distribution and abundance dictate distribution of organisms up the trophic system and a carrying capacity on herbivore populations. As plant vigor decreases through a successional gradient and biomass of food increases herbivore populations shift from specialists on vigorous plants with latent population dynamics to generalists on mature plants, many of which show eruptive population dynamics. A combination of many factors indicates that natural enemies are relatively ineffective in earlier stages of plant succession and their impact increases as habitats become more stable and extensive and herbivores become more generalized in host exploitation. The implications for applied biological control are principally that ephemeral habitats, such as in agricultural systems, are unfavorable for applied biological control and sophisticated husbandry of natural enemies will be essential before successes in such habitats outnumber failures.

Index terms: biological control, predators, parasitoids, insect herbivores.

INTERAÇÕES EM CADEIAS ALIMENTARES DE TRÊS NÍVEIS QUE AFETAM O ÊXITO EM PROJETOS DE CONTROLE BIOLÓGICO

RESUMO - É desenvolvida a tese de que o conhecimento de padrões num sistema de três níveis tróficos entre plantas, insetos herbívoros e inimigos naturais, é um passo necessário para o desenvolvimento de uma teoria sobre sistemas naturais e controle biológico aplicado. Uma vez descobertos os padrões, torna-se possível revelar os mecanismos subjacentes, o que contribuirá para a síntese e a teoria geral. Os padrões mais fortes são aqueles que surgem em conseqüência da passagem da vegetação por uma seqüência ecológica de paisagens, assim fornecendo uma base de sustentação sobre a qual os insetos herbívoros e seus inimigos naturais devem operar. As plantas oferecem a alimentação e o hábitat para os insetos herbívoros. Conseqüentemente, a sua distribuição e abundância impõem a distribuição dos organismos sobre o sistema de sustentação alimentar e capacidade de sustentação para as populações herbívoras. Na medida em que diminui o vigor das plantas através de uma redução sucessiva e a biomassa alimentícia aumenta, as populaçõs herbívoras mudam de especialistas sobre plantas vigorosas com dinâmicas populacionais latentes, para populações não-especializadas sobre plantas maduras, muitas das quais desenvolvem dinâmicas populacionais eruptivas. Uma conjugação de vários fatores indica que os inimigos naturais são relativamente ineficazes nas fases iniciais da sucessão das plantas e que o seu impacto aumenta na medida em que os hábitats se tornam mais estáveis e extensivos, e os herbívoros se tornam mais generalizados no aproveitamento do hospedeiro. As inferências para o controle biológico aplicado são principalmente que os hábitats transitórios, tais como sistemas agrícolas, não são favoráveis para o controle biológico aplicado. O manejo sofisticado das populações de inimigos naturais será essencial para que os êxitos superem os fracassos nesses hábitats.

Termos para indexação: controle biológico, predadores, parasitóides, insetos herbívoros.

[1] Entomologist, PhD, Prof. Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011-5640, USA.

INTRODUCTION

The science of ecology seeks to find pattern in nature and to understand the mechanisms resulting in pattern. When general patterns and their mechanistic bases are adequately described, understood, and confirmed, they provide the foundations for true ecological theory. As with the theory of evolution developed by Darwin (1859), theory in ecology should start with empirical observation and build toward a functional explanation of patterns in nature. This ensures that hypotheses are developed based on facts of nature and not on imaginary scenarios.

In the literature of biological control and three-trophic-level interactions we have a rich array of empirical observations made over the course of a century of intensive study. The many case histories illustrate the diversity of interactions seen in nature, the details of interactions, the complexity of relationships, and the idiosyncratic nature of many systems. We have a literature of special cases showing a bewildering diversity of mechanisms involved with three-trophic-level relationships. However, the identification of pattern in the nature of interactions, or the predictability of results, is still in an elementary state. Lagging even further behind is the understanding of mechanisms that drive pattern in these complex interacting groups of species on three trophic levels. Therefore, in the further development of the science of biological control, I think that some emphasis should be placed on the discovery of general patterns of interactions in nature and the driving forces resulting in pattern. From these initiatives hypotheses can be erected and tested, and ultimately a theory of three trophic levels may emerge.

No matter what form of biological control is undertaken three trophic levels are inevitably involved: plants, the herbivores, and the natural enemies of herbivores. Even though practitioners in the biological control of weedy plants would like to forget about the third trophic level, they are forced repeatedly into the realization that the efficacy of herbivores in regulating plant populations is severely compromised by natural enemies of herbivores (Goeden & Louda 1976). And whereas biological control of insect pests may seem to focus on natural enemies of herbivores, the linkages among plants and predators and parasitoids are so strong in many cases that a two-trophic-level view of interactions is simply unrealistic and perhaps misleading (Bergman & Tingey 1979; Lawton & McNeill 1979; Price et al. 1980; Nordlund et al. 1981; Barbosa & Letourneau 1988). We are faced with a complex arena of interactions, with each case demanding detailed study. But given the rich diversity of empirical studies, the challenge to detect pattern and generality is pressing, because predictability in nature makes us more effective husbanders of nature.

This chapter is devoted to the search for pattern in three-trophic-level interactions, and the underlying mechanisms. I offer one view of how pattern can be identified, a perspective that must be regarded as a working hypothesis in need of considerable further development and testing. Since biological control commonly involves the reconstruction of three-trophic-level systems after their disruption, any generality, pattern or mechanistic understanding should be directly applicable.

My approach in the detection of pattern is to view nature as a series of building blocks. The first block is the primary producers, photosynthesizing plants. Built up on this block are the feeders on plants, the herbivores, and on these the parasites and predators of herbivores. This simple view captures both the history of terrestrial life as it evolved, and the flow of energy in present-day ecosystems. But the ramifications of this perspective are extensive and will be examined trophic level by trophic level in the following sections. The thesis is that plants impose pattern on herbivores and natural enemies, and these bottom-up effects are very strong in terrestrial three-trophic-level systems.

THE FIRST TROPHIC LEVEL

Plants as food

Vascular plants are the major primary producers in terrestrial systems. They provide food for the second trophic level of herbivores, and ultimately the whole food web. One hundred percent of a herbivore population depends for 100 percent of the time on plants as food. Hence, these elementary facts dictate the expectation that plants should play an overwhelming role in the ecology of herbivores, in their distribution, abundance and population dynamics.

That food availability is fundamental to herbivore ecology should come as no surprise, even though this factor frequently did not appear in population dynamics models for insect herbivores (Morris 1963, 1969, Price et al. 1990). The larger the primary productivity of a locality or a plant population, the higher is the carrying capacity likely to be for herbivores. High and damaging populations of herbivores can only be sustained by high primary productivity. Therefore patterns of productivity and standing biomass in vegetation must play an important role in herbivore ecology and the capacity of a herbivore species to become a nuisance to humans.

A graphic case of bottom-up effects in terrestrial trophic systems concerns the human population explosion coincident with the industrial revolution. Industry demanded human aggregation into urban areas, more efficient agricultural practice, and an agrarian revolution. Food became plentiful, human nutrition improved, resistance to diseases increased, and the population increased rapidly, decades before human hygiene, immunization or drug therapy became effective (McKeown 1976). Primary production was the key to dramatic population increase. Of course diseases have always had strong impact on human populations (McKeown 1976; McNeill 1976, 1980), but the immune system, strong selection for resistant genotypes, and cultural evolution typically equilibriate epidemics rapidly. This leaves primary production as the long-term driving force in human population dynamics. A similar situation must surely generally prevail in terrestrial insect herbivore populations.

Plants as food and habitat

A complicating feature of terrestrial plants as food for small herbivores like insects is that plants are relatively large, and provide both a place to live as well as a place to feed for insects. The three-dimensional arenas provided by plants become complex environments in which enemies must search for herbivores. In addition endophytic lifestyles commonly make attack difficult and reduce efficacy of natural enemy responses (Price et al. 1980, Price 1988).

For these reasons food webs based on terrestrial plants may well have a stronger bottom-up component than in pelagic lake environments. In water columns primary productivity is by small algae and trophic systems build from small organisms to larger and larger fishes. The habitat is simple, without sanctuary from predation. While nutrients in the water, light and water flow are critical abiotic features in these systems the probability of a strong effect from top predators is high. The trophic cascades down food webs imposed by predators, recognized by Carpenter et al. (1985) in pelagic lake systems, probably will not be recognized as easily in terrestrial systems because of the habitat complexity provided by the plants. Indeed there is a higher probability that plants will have strong effects up the trophic system that impinge upon the third trophic level, as discussed later in this chapter.

If plants play an important role as habitats for insect herbivores, then larger more complex plants should provide more habitats than smaller simpler forms. As a result, more insect herbivore species should colonize large plants than small plants. This is, indeed, a pattern observed repeatedly in the literature

(Price 1977, 1980, Moran 1980, Lawton 1983, Strong et al. 1984). This provides another pattern-producing effect that plants have on upper trophic levels.

Vegetation as a template in space and time

If one accepts this very general argument, the logical development is that as primary productivity changes over a landscape, so the nature of food supply will change herbivore distribution and population dynamics. That is, ecological succession of vegetation provides a template on which the adaptive syndromes of herbivores are superimposed. Early successional stages will be patchy due to disturbance and all herbivores adapted to exploiting these open and ephemeral sites must be effective dispersers and colonizers. Bright light, high nutrients and rapid growth will be characteristic in such disturbances (Coley 1983, Coley & Aide 1990, Coley et al. 1985), and weedy plant species probably impose "weedy" adaptive syndromes on the insects that exploit such early successional sites (Feeny 1975, 1976). Carrying capacities provided by plant biomass will be low relative to late succession so the potential for high densities of herbivores is low.

As woody plants colonize patches of disturbed ground, vegetation will change and young, rapidly growing woody plants will dominate. Many species of herbivore concentrate on vigorous woody growth, and will colonize this stage in succession. Woody plants will eventually mature, growth will slow, and ultimately senescence and death will result in the opening of new patches in the forest (Shugart 1987; Shugart & West 1981). Biomass production becomes very high in late succession, providing for potentially high populations of generalist herbivores. In north temperate regions forests are extensive and durable, providing long-lasting stable environments for herbivores. Herbivores are likely to adapt with syndromes including sedentary behavior, poor colonizing ability,

and a capacity to utilize the high biomass available as potential food.

Thus vegetation over a landscape provides a kaleidoscope of vegetation types in space and through time and each herbivore species must adapt to exploit effectively one feature of the vegetation in this dynamic pattern.

THE SECOND TROPHIC LEVEL

Food for herbivores

It is worth reiterating the obvious fact that 100 percent of insect hervibores in a population depend 100 percent on plants as food. The selective forces on effective exploitation of plant food must be always very strong. This self-evident observation appears to be lost in many efforts to model insect population dynamics, when plant food quantity and quality is ignored, either because food supplies are not evaluated, or because they are totally ignored as in predator-prey equations.

However, taking the building-block approach, we must recognize that herbivores need plants for food, and therefore plant species dictate the distribution of herbivores, and the potential abundance of herbivores. Plants have their own nutritional and physiological needs and so the abiotic environment dictates part of plant distribution and abundance.

A very nice example of this dependency is provided in studies of ithomiine butterflies by Vasconcellos Neto (1990). In Brazil, the distribution, phenology, and abundance of ithomiine butterflies is determined to a large extent by the distribution of host plants in the family Solonaceae. In four of the five species of ithomiine studied in detail, distribution, phenology and `abundance was dominated by the cycle of "dry and rainy seasons and with the phenologies and dynamics of their host plants (Vasconcellos Neto 1980). Predators and parasitoids act on their population sizes, but they are not the main factors molding the

reproductive cycles" (Vasconcellos Neto 1990), p. 294). In only one species, *Mcclungia salonina*, were egg and larval parasitoids of major importance, for this herbivore was confined to a host plant that was restricted to permanently favorable sites for host plant growth and herbivore growth and therefore a dependable resource for natural enemies. Plant distribution and abundance are also of critical importance to *Heliconius* butterfly population dynamics in Costa Rica (Gilbert 1990).

Plant succession and herbivore population dynamics

We should anticipate that the adaptive syndromes of herbivores will differ widely depending on the nature of the plant resources they exploit. Early successional herbivores will differ in many attributes when compared with late successional herbivores. The blend of plant distribution over the landscape and consequent adaptive syndromes of herbivores is likely to generate major large-scale patterns in insect herbivore population dynamics.

A continuum in herbivore dynamical types probably exists from those characteristics of early succession and those in late succession. I will use two extremes to illustrate the radical differences in population dynamics that may be expected.

After disturbance rapid colonization by plants usually follows, and rapid plant growth is evident in these open and sunny locations. Herbivores associated with such colonizing plants will encounter frequently plants in a vigorous condition, and must adapt to this condition. In fact vigorous plants will favor herbivore survival in many such cases (Craig et al. 1986, 1989; Price 1989; Price et al. 1987a,b, Price et al. 1990). One example is a willow shoot-galling sawfly, *Euura lasiolepis*. It preferentially attacks young, vigorously growing plants, and its larvae survive best in such resources (Price & Clancy 1986a, Craig et al. 1986, 1989, Preszler & Price 1988, Price et al. 1990). However, the most vigorous shoots which are most favorable

are a limited resource, and prevent sawflies from reaching very high and damaging densities in most localities (Sacchi et al. 1988). The production of vigorous shoots in any one willow patch is moderately stable over a decade or more, and so herbivore populations remain moderately stable. The main variable during sawfly population dynamics is winter precipitation, for soil moisture in June (in the Northern Hemisphere) dictates the vigor of willow shoot growth, and hence the number and quality of vigorous shoots required for survival of the sawfly (Price & Clancy 1986a; Preszler & Price 1988, Price et al. 1990). The relative stability of these populations warrants their classification as species with **latent or noneruptive population dynamics.**

Important aspects of the adaptive syndrome of this species are that the ovipositing female sawfly locates the optimal sites for larval survival, the larva is endophytic, and it must survive or die at the exact location in the plant that its mother selected. Thus, there is a very tight link between female oviposition preference and larval performance (Craig et al. 1989), much more strongly developed than in many systems studied focusing on exophytic feeders (Thompson 1988; Futuyma 1990). Because of this linkage, plant quality plays a central role in this herbivore's population dynamics, and abiotic effects on plant growth, especially water availability, feed up through the trophic system from below. Many other herbivores relate to plants in a similar way and are similarly constrained in their population dynamics to be latent species: gallers, shoot borers and cone borers in particular (Price et al. 1990). Other specialists on vigorous new growth include many *Heliconius* butterflies (Gilbert 1990), many aphids (Service 1984a,b, Service and Lenski 1982), and many leaf beetles (Kearsley & Whitham 1989; Bach 1990; Landsberg 1990, Landsberg & Wylie 1983, 1988) and other herbivores on *Eucalyptus* (Landsberg 1987). All insect herbivores in natural environments that specialize on vigorous plant growth are likely

to remain relatively stable in their population dynamics because vigorous plant parts are very limiting most of the time under primaeval conditions. Many will be constrained to be rare species (Gilbert 1990).

At the other end of the continuum are the species with **eruptive population dynamics**. These typically occur in mature forests in northern latitudes, with long-term environmental stability, high carrying capacity of foliage for leaf feeders, and extensive tracts of host species in a low diversity of dominant plant species.

In such environments a conspicuous adaptive syndrome of insect herbivores (even though it is probably not the most common one) is that females lay eggs away from places where larvae will feed, they oviposit months before eggs hatch, clutch sizes are large, many eggs are laid before female dispersal, and females may even be very weak flyers or flightless (Barbosa et al. 1989, Price et al. 1990). This syndrome is characteristic of the important insect herbivore defoliators of northern temperate forests: spruce budworm, fall webworm, fall cankerworm, spring cankerworm, winter moth, gypsy moth, forest tent caterpillar, western oak inch worm, and others (Price et al. 1990).

This syndrome evolved repeatedly in disparate phylogenetic lineages no doubt because of the stable environments provided by late successional vegetation. Long-term stability and predictability would greatly reduce selective pressures on dispersal and colonizing ability. High biomass of food in terms of leaves for exophytic, relatively mobile, leaf chewers, weakens the pressure for ovipositing females to be selective. A general trend will be for larvae to evolve with a capacity to be generalists capable of maturing on a wide variety of leaf qualities, minimizing the heterogeneity of leaf quality in the forest canopy. As a result, broadly adapted larvae will facilitate the acquisition and utilization of new host plant species, and generalized feeders, across several to many plant species, are likely to emerge (Wallner 1987; Barbosa et

al. 1989, Price et al. 1990). Once larvae are generally adapted to utilize and survive upon a broad spectrum of leaf qualities, in a forest with a high biomass of leaves, an eruption sooner or later to exploit all leaves in the forest canopy seems inevitable.

The key difference of these eruptive species from the latent species is that the link between female preference during oviposition is dislocated from the site of larval feeding, and hence larval performance. Females oviposit on bark, twigs, or moss, and even drop eggs from the forest canopy in the case of eruptive stick insects in Australia (Readshaw 1965). They oviposit commonly when host trees are leafless, many months before the spring, so females cannot evaluate food quality for larvae. If females cannot be selective, they lose little by producing large egg clutches, and gain considerably by allocating less to flight and more to eggs.

The focal driving force in the adaptive syndrome of eruptive lepidopterous insect herbivores is not yet clear. This is because phylogenies of the nonbutterflies in the Macrolepidoptera are poorly developed. Nevertheless, with some assurance we can deduce that the general syndrome of insect herbivores in mature forest has evolved many times because of the common denominator of the resource base, in the form of plant food. Eruptive population dynamics has emerged repeatedly as a result of evolution in late successional environments, among rather general feeders, when a separation of female oviposition and larval feeding site occurs. Examples include: macrolepidoptera in the families Geometridae and Lymantriidae; Microlepidoptera in the families Tortricidae and Psychidae; acridid grasshoppers in climax grasslands; stick insects in Australian *Eucalyptus* forests (Barbosa et al. 1989, Price et al. 1990).

Given the 'enormous capacity of the evolutionary process to break out of "the pattern of nature", we should expect that exceptions exist in the broad pattern of latent species in earlier stages of succession and

eruptive species in later stages of succession. This is indeed the case. There are eruptive species in earlier stages of succession, although the documented cases are few compared to those in mature forest. Chrysomelids in earlier stages of succession are examples: *Trirhabda* species on goldenrod (Messina 1981, 1982), *Disonycha pluriligata* on *Salix exigua,* and rootworms in the genus *Diabrotica* feeding on *Zea mays* and other crops (Metcalf et al. 1962; Kogan 1990). In all cases females lay eggs at the base of the plant in the soil, and therefore cannot forage effectively for high-quality larval feeding sites. This loss of linkage between female preference and larval performance appears to be fundamental in the evolution of eruptive insect herbivore species.

In general, it is apparent that the interaction between plants as providers of food, and insect herbivores as consumers of plants, dictate the major broad-scale features of population dynamics of the herbivores. I have not had to invoke the role of the third trophic level in deciphering broad patterns. Natural enemies of herbivores do not exert an overriding general pattern in insect herbivore population dynamics. This is a view expressed repeatedly for many major groups of insect herbivores as well as for individual cases: Berryman (1982) on bark beetles; galling sawflies on willows (Price et al. 1990); acridid grasshoppers (Dempster 1963; White 1976; Rainey 1982); ithomiine butterflies (Gilbert 1990; Vasconcellos Neto 1990); a thistle-feeding lady beetle (Ohgushi & Sawada 1985); a cone-feeding scolytid beetle (Mattson 1980).

Where, then, do the natural enemies of insect herbivores play their role in population dynamics? This is a very difficult question to address, with no certain answers (Price 1987). However, the general scenario in which natural enemies exert their influence is clear enough, as discussed in the next section.

THE THIRD TROPHIC LEVEL

The third trophic level is composed of the natural enemies of herbivores, represented by predators, parasitoids and microbial pathogens. In these trophic systems, in which components tend to be relatively large at the base and small or very small at the top, it is natural to assume that the enormous diversity of natural enemies of herbivores must have enormous impact on the population dynamics of herbivores. This is part of conventional wisdom established early in the sciences of biological control and insect herbivore population dynamics (Doutt 1964, on the biocontrol of the cottony cushion scale in 1889; Howard, 1897, on regulation of the brown-tail moth; and Lotka 1924, on models of herbivore-enemy interaction). But can we unravel the complex web of interactions among the components of nutrition, health, and vulnerability to enemies, that proved to be so vexing a case in human population eruptions accompanying the industrial revolution?

The building-block view of three-trophic-level interactions I advocate clarifies the approach to be taken in understanding the role of enemies of herbivores. Food is of paramount importance, and top-down effects generally only modify the food-feeder realationship, but do not dictate broad-scale population dynamics of the feeder. This is probably as true for most cases of plant demography, as for insect herbivore demography (Harper 1977, Solbrig et al. 1979; Silvertown 1982; Dirzo & Sarukhán 1984).

This broad generalization has many exceptions, with major evidence from the biological control of herbivorous insects (DeBach 1964; Huffaker 1971; Ridgway & Vinson 1977). But the major challenge is to detect pattern in the voluminous literature of idiosyncratic cases.

My personal preference, and I think the most constructive viewpoint, is to continue with a building-block approach to understanding the impact of the third trophic level on insect herbivores. Let us recognize again that food supplies are essential to the

existence of populations and species, and they depend on the passage of energy and nutrients up the trophic system.

Plant breeding and biological control

One approach to the question of the relative roles of plants and enemies in the population dynamics of insect herbivores would be to evaluate the frequency of successes in plant breeding programs for resistance to herbivores, compared to successes in applied biological control by introducing or otherwise manipulating enemies of herbivores. I have not seen such a comparison because, perhaps, these two major avenues to plant protection have, regrettably, never been adequately synthesized, even though the advantages are compelling (Price et al. 1980; Price 1986). My general view is that, where effective screening for resistant accessions of plants have been undertaken, improvements in herbivore control have been usually observed (Painter 1951; Maxwell & Jennings 1980). Such success is by no means as high in biological control by the introduction of enemies, remembering Varley (1959) estimate of 5 percent success in agricultural systems and 33 percent success in more stable orchard and forest habitats.

Plant succession and the landscape

Another view on bottom-up effects on natural enemies can be generated from a landscape perspective. Just as ecological succession provides a template for patterns in herbivory, so the effects pass on to impose pattern on the natural enemies. As succession develops from herbs to shrubs to trees, architectural complexity of plants increases, and the number of parasitoid species per insect herbivore host increases (Askew 1980; Hawkins & Lawton 1987; Hawkins 1988; Hawkins et al. 1990). On this gradient of vegetational change there is increasing habitat continuity and stability and decreasing diversity of dominant species in north temperate landscapes where most of the data originate. Therefore, the mechanisms

resulting in more parasitoid species per host species in later stages of succession may be multiple and correlated: plant architecture, area of habitat, stability of habitat, and simplicity of plant composition may all play a role. In the literature on agroecology most herbivore species (almost 70 percent of species studied) became more abundant in monocultures than polycultures (Risch et al. 1983; Altieri 1990). This suggests that not only are there more host herbivores in late succession but, in vegetations tending to be dominated by monocultures of trees, these herbivore hosts will be more abundant than hosts in more complex earlier successional stages. Not only is the biomass of plant food higher in late succession, but herbivores respond positively to resource concentration (Root 1973).

As plant defensive chemicals tend to change through succession from toxins to digestibility reducers, so the host specificity of insect herbivores tends to decline (Feeny 1975, 1976). This probably results in the ability of parasitoids to become more general in host utilization as succession proceeds. This in part could account for the presence of more parasitoid species per host species in late succession.

More parasitoid species per host species is likely to translate into more impact on host population dynamics. This has been found in comparisons of sawflies (Price & Pschorn-Walcher 1988), *Tildenia* leaf miners (Gross & Price 1988), and in patterns in applied biological control in which the probability of success of a project increases as the number of parasitoids per host increases.

This pattern of increased impact of natural enemies as plant succession proceeds may well be reflected in predator effects also. Feeny (1975, 1976) predicted that digestibility reducers in late succession prolonged feeding times of insect herbivores and made them more vulnerable to enemy attack. Bernays (1989, Bernays & Graham 1988) has shown that generalized insect herbivore feeders are

more prone to predator attack than specialists, so we should expect heavier involvement of predators in the population dynamics of generalist herbivores on late successional plants. Successful cases of applied biological control also suggest much higher probability of effective natural enemy regulation in more stable habitats such as orchards and forests (Varley 1959).

These considerations suggest that natural enemies are more likely to play an important role in the population dynamics of late successional insect herbivores, including eruptive species, than in earlier stages of succession, including latent species. Endophagous latent species may well be effectively concealed from natural enemies in plant tissues, making search time consuming and attack slow. In the shoot-galling sawfly, *Euura lasiolepis*, for example, galls become too large for effective attack by small chalcidid parasitoids (Price & Clancy 1986b, Price 1988) and toughen too rapidly for larger ichneumonids (Craig et al. 1990). But in the population dynamics models for such epidemic species as the spruce budworm, *Choristoneura fumiferana*, natural enemies appear as important components (Morris 1963, 1969). Much more concern must be devoted to understanding the mechanisms resulting in such correlative models, in order to discover which is cause and which is effect (Morris 1959, 1969; McNeill 1973; Price 1987; Price et al. 1990). Are natural enemies simply responding to more food in the form of insect herbivore hosts, or are they causally involved in regulation of host populations? Whether natural enemies abundance in late successional host species is a consequence of host abundance or a cause of host regulation, the general pattern seems to be valid that natural enemies in late successional habitats inflict more mortality than those in earlier stages of succession, or less stable habitats.

Some support for this generalization comes from studies of tropical habitats. As noted earlier, one of five ithomiine butterflies was heavily impacted by natural enemies, and this species, *Mcclungia salonina*, was the only species restricted to a host plant living exclusively in permanently favorable sites for plant growth and butterfly reproduction (Vasconcellos Neto 1990). In another study, by Gilbert (e.g. 1990), *Heliconius charitonia* becomes abundant where disturbance is common but seems unable to colonize stable sites effectively, remaining very rare probably because of adult mortality caused by predators and dispersal to find more host plants for oviposition. Other species of *Heliconius* persisted more effectively in stable habitats.

Idiosyncratic differences in enemy impact among closely related species

These examples on tropical butterflies indicate that even among closely related species of insect herbivore the impact of natural enemies on their population dynamics may be remarkably different. Similar examples come from temperate latitudes also. One involves *Pieris* butterflies in Japan, each with different characteristics that minimize parasitoid impact (Ohsaki & Sato 1990). *Pieris rapae* cannot persist in permanent habitats because parasitism becomes too high, but it usually escapes heavy attack by exploiting small disturbed patches of weedy species, in which its crucifer hosts are common. *Pieris melete* can survive in stable habitats because of a strong encapsulation response to eggs of the major parasitoid, *Apanteles glomeratus*. A third congenor, *Pieris napi*, also survives in more stable habitats by exploiting inconspicuous hosts, the rock cresses *Arabis gemmifera* and *A. flagellosa*. These are frequently hidden below taller plants, and *Apanteles* females do not find hosts on them, even though the hosts would be suitable for larval survival. Although these species show idiosyncratic escape mechanisms relating to a parasitoid, they do illustrate the general pattern that selection by enemies imposes better defenses on insect herbivores in stable habitats, while in ephemeral habitats escape from enemies

may be an important strategy, not involving specific defense tactics.

Another example shows that, even in the same habitat, impact by natural enemies can be very different on hosts utilizing different host plants that impose a strong effect on herbivore behavior and enemy attack. Two solanaceous plants, *Physalis heterophylla*, and *Solanum carolinense*, grow together in sandy fields in Illinois, USA, the first having simple trichomes, and the second with stellate trichomes (Gross & Price 1988). Trichome differences impose differences in herbivore behavior, such that the leaf miner in the genus *Tildenia* on *Physalis* freely initiates and leaves several mines in a lifetime, but its congenor on *Solanum* lives in a single mine because the stellate trichomes prevent mine initiation except for very small larvae. These evolved behavioral differences in *Tildenia* species imposed by plant characters have their impact on the community of parasitoids able to exploit these leaf miners. The *Physalis* leafminer can escape from a mine during parasitoid attack and successful parasitoid species number only about four, that inflict about 14 percent mortality. In contrast the *Solanum* leafminer, limited to a single mine, can be attacked by 10 parasitoid species that inflict about 40 percent mortality (Gross & Price 1988).

These examples of idiosyncratic differences in enemy attack among closely related species of insect herbivore do reinforce the view that plant and vegetation variation impose dramatic influences up the trophic system, to the natural enemies of herbivores. They also illustrate the difficulty in discovering generality when rather small differences in plants can inflict large differences on natural enemy communities. This means that we must approach the search for generality with caution, and expect to find many exceptions to general pattern. The challenge is to find patterns that are generally valid even though exceptions are numerous.

IMPLICATIONS FOR BIOLOGICAL CONTROL

If the generalizations summarized in the preceding sections are reinforced by more studies then their implications for the practice of applied biological control are extensive and worth reviewing here. I will concentrate on the biological control of insect herbivores.

1. Environmental complexity - Natural enemies of insect herbivores live in a complex environment in which hosts and prey are frequently hidden by the plant that provides a safe habitat for the herbivore. The herbivore may well have sequestered toxins from the host plant which act as defenses against enemies. Other defensive traits are effective, such as encapsulation of parasitoid eggs, mechanical defenses and *de novo* synthesis of toxic chemicals. Escape in time and space is also a possible strategy to minimize impact by natural enemies, as in *Pieris rapae*. All these complexities make searching, attacking and surviving very difficult for natural enemies, with strong potential for reducing functional and numerical responses to increasing host or prey density. Therefore, we should not expect regulation to occur commonly, and if it does occur in a predictable way this is likely to be only in the most favorable environments.

2. Habitat stability - A recurring theme in this chapter has been the apparent success of natural enemies in stable habitats. Natural enemies seem to be more common in terms of species present and abundance per species, making impact on insect herbivores stronger. The features of stable habitats that are closely correlated are the large areas occupied by late successional vegetations and the complex architecture of large trees. As habitats become less stable, through ecological succession inducing rapid change, or through habitat disturbance caused by humans, the efficacy of natural enemies is likely to weaken, and biological control may have a much lower probability of success.

3. Bottom-up effects - Where bottom-up effects of plants on the trophic system are minimized, then top-down impact by natural

enemies should be predictably stronger. Generalized chewing herbivores that remain unconcealed from natural enemies, and that have broad tolerances to plant food quality variation, are probably members of a group on which enemy impact can be strong. In general plants will have less mediating effects on herbivore-enemy interactions when the herbivores are exophytic and feed in exposed locations. Many homopteran pests such as scale insects and aphids fall into this class, where biological control has proved to be effective.

4. **Ephemeral habitats** - Habitats subject to rapid change and disturbance, as in early successional locations, and agricultural systems, appear to be very limiting on the efficacy of natural enemies, both in terms of the numbers of species that have colonized hosts in these habitats and the abundance of individuals per species. The relatively small spatial settings and the short times over which they are available for colonization and population growth for natural enemies, work against a high probability of herbivore population regulation by natural enemies. Frequent disruption by agricultural practices reduces the probability of observing effective enemies even below that expected for natural early succession after disturbance.

5. **Manipulation of natural enemies** - In agricultural systems unfavorable for the regulatory action of natural enemies on insect herbivores, the applied manipulation of biocontrol agents seems to offer considerable promise. This can take two forms. One involves the provision of stable sites in and around agricultural fields, such as strips of cover in the fields, which can harbor alternative hosts or prey, and a holdover habitat during agricultural disturbance. The other involves the use of sophisticated husbandry techniques such as mass releases of natural enemies, supply of supplemental food, and use of attractants that reduce dispersal including kairomones, or chemicals that enemies have learned to associate with hosts or prey. Whatever the method employed in biocontrol, research must generate a detailed understanding of the biology of each species involved in these three-trophic-level interactions. Only then can the best approaches for regulation be deduced and appropriate biocontrol initiated.

These implications for biological control have converged on conventional wisdom based on empirical observations. However, the patterns discussed in this chapter do have mechanistic underpinnings, at least conceptually, if not empirically. And the probable mechanisms involved are multiple and interactive in complex ways not generally recognized in conventional wisdom. If these patterns and mechanisms remain valid after much more research they will provide the basis for a theory of three-trophic-level interactions and biological control.

REFERENCES

ALTIERI, M.A. Ecology of tropical herbivores in polycultural agroecosystems. In: PRICE, P.W.; LEWINSOHN, T.M.; FERNANDES, G.W.; BENSON, W.W. ed. **Plant-animal interactions**: evolutionary ecology in tropical and temperate regions. New York: Wiley, 1990. pp. 607-617.

ASKEW, R.R. The diversity of insect communities in leaf-mines and plant galls. **Journal of Animal Ecology**, v.49, p.817-829, 1980.

BACH, C.E. Plant successional stage and insect herbivory: flea beetles on sand-dune willow. **Ecology**, v.71, p.598-609, 1990.

BARBOSA, P.; KRISCHIK, V.; LANCE, D. Life-history traits of forest-inhabiting flightless Lepidoptera. **American Midland Naturalist**, v.122, p.262-274, 1989.

BARBOSA, P.; LETOURNEAU, D.K. ed. **Novel aspects of insect-plant interactions**. New York: Wiley, 1988.

BERGMAN, J.M.; TINGEY, W.M. Aspects of interaction between plant genotypes and biological control. **Bulletin of the Entomological Society America**, v.25, p.275-279, 1979.

BERNAYS, E.A. Host range in phytophagous insects: the potential role of generalist predators. **Evolutionary Ecology**, v.3, p.299-311, 1989.

BERNAYS, E.; GRAHAM, M. On the evolution of host specificity in phytophagous arthropods. **Ecology**, v.69, p.886-892, 1988.

BERRYMAN, A.A. population dynamics of bark beetles. In: MITTON, J.B.; STURGEON, K.B. ed. **Bark beetles in North American conifers**: a system for the study of evolutionary biology. Austin: University of Texas Press, 1982. p.264-314.

CARPENTER, S.R.; KITCHELL, J.F.; HODGSON, J.R. Cascading trophic interactions and lake productivity. **BioScience**, v.35, p.634-639, 1985.

COLEY, P.D. Herbivory and defensive characteristics of tree species in a lowland tropical forest. **Ecological Monographs**, v.53, p.209-233, 1983.

COLEY, P.D.; AIDE, T.M. Comparison of herbivory and plant defenses in temperate and tropical broad-leaved forests. In: PRICE, P.W.; LEWINSOHN, T.M.; FERNANDES, G.W.; BENSON, W.W. ed. Plant-animal interactions: evolutionary ecology in tropical and temperate regions. New York: Wiley. 1990. p.25-49.

COLEY, P.D.; BRYANT, J.P.; CHAPIN, F.S. Resource availability and plant antiherbivore defense. **Science**, v.230, p.895-899, 1985.

CRAIG, T.P.; ITAMI, J.K.; PRICE, P.W. A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. **Ecology**, v.70, p.1691-1699, 1989.

CRAIG, T.P.; ITAMI, J.K.; PRICE, P.W. The window of vulnerability of a shoot-galling sawfly to attack by a parasitoid. **Ecology**, v.71, p.1471-1482, 1990.

CRAIG, T.P.; PRICE, P.W.; ITAMI, J.K. Resource regulation by a stem-galling sawfly on the arroyo willow. **Ecology**, v.67, p.419-425, 1986.

DARWIN, C. **The origin of species**. London: Murray, 1859.

DE BACH, P. ed. **Biological control of insect pests and weeds**. New York: Reinhold, 1964.

DEMPSTER, J.P. The population dynamics of grasshoppers and locusts. **Biological Review**, v.38, p.490-529, 1963.

DIRZO, R.; SARUKHÁN, J., ed. **Perspectives on plant population ecology**. Sunderland: Sinauer, 1984.

DOUTT, R.L. The historical development of biological control. In: DE BACH, P. ed. **Biological control of insect pests and weeds**. New York: Reinhold, 1964. p.21-42.

FEENY, P. Biochemical coevolution between plants and their insect herbivores. In: GILBERT, L. E.; RAVEN, P.H. ed. **Coevolution of animals and plants**. Austin: University of Texas Press, 1975. p.3-19.

FEENY, P. Plant apparency and chemical defense. In: WALLACE, J.W. & MANSELL, R.L. ed. **Biochemical interaction between plants and insects**. New York: Plenum, 1976. p.1-40.

FUTUYMA, D.J. Evolution of host specificity in herbivorous insects: genetic, ecological, and phylogenetic aspects. In: PRICE, P.W.; LEWINSOHN, T.M.; FERNANDES, G.W.; BENSON, W.W. ed. **Plant-animal interactions**: evolutionary ecology in tropical and temperate regions. New York: Wiley, 1990. p.431-453.

GILBERT, L.E. Biodiversity of a Central American *Heliconius* community: pattern, process, and problems. In: PRICE, P.W.; LEWINSOHN, T.M.; FERNANDES, G.W.; BENSON, W.W. ed. **Plant-animal interactions**: evolutionary ecology in tropical and temperate regions. New York, Wiley, 1990. p.403-427.

GOEDEN, R.D.; LOUDA, S.M. Biotic interference with insects imported for weed control. **Annual Review of Entomology**, v.21, p.325-342, 1976.

GROSS, P.; PRICE, P.W. Plant influences on parasitism of two leafminers: a test of enemy-free space. **Ecology**, v.69, p.1506-1516, 1988.

HARPER, J.L. **Population biology of plants**. London, Academic Press, 1977.

HAWKINS, B.A. Species diversity in the third and fourth trophic levels: patterns and mechanisms. **Journal of Animal Ecology**, v.57, p.137-162, 1988.

HAWKINS, B.A.; LAWTON, J.H. Species richness for the parasitoids of British phytophagous insects. **Nature**, v.326, p.788-790, 1987.

HAWKINS, B.A., ASKEW, R.R., & SHAW, M.R. Influences of host feeding-niche and food plant type on generalist and specialist parasitoids. **Ecol. Entomol.** 15, 275-280, 1990.

HOWARD, L.O. **A study of insect parasitism.** USDA, 1897. p.1-57. (USDA Bur. Entomol. Tech. Ser. 5).

HUFFAKER, C.B. Ed. **Biological control** New York: Plenum, 1971.

KEARSLEY, M.J.C.; WHITHAM, T.G. Developmental changes in resistance to herbivory: Implications for individuals and populations. **Ecology**, v.70, p.422-434, 1989.

KOGAN, M. Contemporary adaptations of herbivores to introduced legume crops. In: PRICE, P.W.; LEWINSOHN, T.M.; FERNANDES, G.W.; BENSON, W.W. ed. **Plant-animal interactions:** evolutionary ecology in tropical and temperate regions. New York: Wiley, 1990. p.591-605.

LANDSBERG, J. Dieback of rural eucalypts: Response of foliar dietary quality and herbivory to defoliation. **Australian Journal Ecology**, v.15, p.89-96, 1990.

LANDSBERG, J. Feeding preferences of common brushtail possoms, *Trichosurus vulpecula*, on seedlings of a woodland eucalypt. Australian Wildlife Research, v.14, p.361-369, 1987.

LANDSBERG. J.; WYLIE, F.R. Dieback of rural trees in Australia. **GeoJournal**, v.17, p.231-237, 1988.

LANDSBERG, J.; WYLIE, F.R. Water stress, leaf nutrients and defoliation: A model of dieback of rural eucalypts. **Australian Journal Ecology**, v.8, p.27-41, 1983.

LAWTON, J.H. Plant architecture and the diversity of phytophagous insects. **Annual Review of Entomology.** v.28, p.23-39, 1983.

LAWTON, J.H.; MCNEILL, S. Between the devil and the deep blue sea: On the problem of being a herbivore. In: ANDERSON, R.M.; TURNER, B.D.; TAYLOR, L.R. ed. **Population dynamics.** 1979. p.223-244. (Symp. Brit. Ecol. Soc., nº 20)

LOTKA, A.J. **Elements of physical biology.** Baltimore: Williams and Wilkins, 1924.

MATTSON, W.J. Cone resources and the ecology of the red pine cone beetle, *Conophthorus resinosae* (Coleoptera: Scolytidae). Annals of Entomological Society of America, v.73, p.390-396, 1980.

MAXWELL, F.G.; JENNINGS, P.R. **Breeding plants resistant to insects.** New York: Wiley, 1980.

MCKEOWN, T. **The modern rise of population.** New York: Academic Press, 1976.

MCNEILL, S. The dynamics of a population of *Leptopterna dolabrata* (Heteroptera: Miridae) in relation to its food resources. **Journal of Animal Ecology.** v. 42, p. 495-507, 1973.

MCNEILL, W.H. **Plagues and peoples.** New York: Doubleday, 1976.

MCNEILL, W.H. **The human condition.** Princeton: Princeton University Press, 1980.

MESSINA, F.J. Plant protection as a consequence of an ant-membracid mutualism: interactions on goldenrod (*Solidago* sp.). **Ecology,** v.62, p.1433-1440, 1981.

MESSINA, F.J. Comparative biology of the goldenrod leaf beetles, *Trirhabda virgata* Leconte and *T. borealis* Blake (Coleoptera: Chrysomelidae). **Coleopterists Bulletin,** v.36, p.255-269, 1982.

METCALF, C.L.; FLINT, W.P.; METCALF, R.L. **Destructive and useful insects.** New York: McGraw-Hill, 1962.

MORAN, V.C. Interactions between phytophagous insects and their *Opuntia* hosts. **Ecological Entomology.** v.5, p.153-164, 1980.

MORRIS, R.F. Approaches to the study of population dynamics. In: WATERS, W.E. ed. **Forest insect population dynamics.** USDA, Agr. For. Serv. Res. Paper, NE-125) p.9-28. 1969.

MORRIS, R.F. The dynamics of epidemic spruce budworm populations. **Memoirs of Entomological Society of Canada,** v.31, p.1-332, 1963.

MORRIS, R.F. Single-factor analysis in population dynamics. **Ecology,** v.40, p.580-588, 1959.

NORDLUND, D.A.; JONES, R.L.; LEWIS, W.J., ed. Semiochemicals: their role in pest control. New York, Wiley, 1981.

OHGUSHI, T.; SAWADA, H. Population equilibrium with respect to available food resource and its behavioural basis in the herbivorous lady beetle, *Henosepilachna niponica*. Journal of Animal Ecology, v.54, p.781-796, 1985.

OHSAKI, N.; SATO, Y. Avoidance mechanisms of three *Pieris* butterfly species against the parasitoid wasp *Apanteles glomeratus*. Ecological Entomology, v.15, p.169-176, 1990.

PAINTER, R.H. Insect resistance in crop plants. Lawrence: Kansas University Press, 1951.

PRESZLER, R.W.; PRICE, P.W. Host quality and sawfly populations: A new approach to life table analysis. Ecology, v.69, p.2012-2020, 1988.

PRICE, P.W. Clonal development of coyote willow, *Salix exigua* (Salicaceae), and attack by the shoot-galling sawfly, *Euura exiguae* (Hymenoptera: Tenthredinidae). Environmental Entomology, v.18, p.61-68, 1989.

PRICE, P.W. Ecological aspects of host plant resistance an biological control: Interactions among three trophic levels. In: BOETHEL, D.J.; EIKENBARY, R.D. ed. Interactions of plant resistance and parasitoids and predators of insects. Chichester: Horwood, p.11-30, 1986.

PRICE, P.W. Evolutionary biology of parasites. Princeton: Princeton University Press, 1980.

PRICE, P.W. General concepts on the evolutionary biology of parasites. Evolution, v.31, p.405-420, 1977.

PRICE, P.W. Inversely density-dependent parasitism: the role of plant refuges for hosts. Journal of Animal Ecology, v.57, p.89-96, 1988.

PRICE, P.W. The role of natural enemies in insect populations. In: BARBOSA, P.; SCHULTZ, J.C. ed. Insect outbreaks. New York: Academic Press, p.287-312, 1987.

PRICE, P.W.; BOUTON, C.E.; GROSS, P.; MCPHERON, B.A.; THOMPSON, J.N.; WEIS, A.E. Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annual Review of Ecology and Systematics, v.11, p.41-65, 1980.

PRICE, P.W.; CLANCY, K.M. Interactions among three trophic levels: Gall size and parasitoid attack. Ecology, v.67, p.1593-1600, 1986b.

PRICE, P.W.; CLANCY, K.M. Multiple effects of precipitation on *Salix lasiolepis* and populations of the stem-galling sawfly, *Euura lasiolepis*. Ecological Research, v.1, p.1-14, 1986a.

PRICE, P.W.; PSCHORN-WALCHER, H. Are galling insects better protected against parasitoids than exposed feeders?: a test using tenthredinid sawflies. Ecological Entomology, v.13, p.195-205, 1988.

PRICE, P.W.; ROININEN, H.; TAHVANAINEN, J. Plant age and attack by the bud galler, *Euura mucronata*. Oecologia, v.73, p.334-337, 1987a.

PRICE, P.W.; ROININEN, H.; TAHVANAINEN, J. Why does the bud-galling sawfly, *Euura mucronata*, attack long shoots? Oecologia, v.74, p.1-6, 1987b.

RAINEY, R.C. Putting insects on the map: spatial heterogeneity and the dynamics of insect populations. Antenna, v.6, p.162-169, 1982.

READSHAW, J.L. A theory of phasmatid outbreak release. Australian Journal of Zoology, v.13, p.475-490, 1965.

RIDGWAY, R.L.; VINSON, S.B. ed. Biological control by augmentation of natural enemies. New York: Plenum, 1977.

RISCH, S.; ANDOW, D.; ALTIERI, M. Agroecosystem diversity and pest control: data, tentative conclusions and new research directions. Environmental Entomology, v.12, p.625-629, 1983.

ROOT, R.B. Organization of a plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). Ecological Monographs, v.43, p.95-124, 1973.

SACCHI, C.F.; PRICE, P.W.; CRAIG, T.P.;

ITAMI, J.K. Impact of shoot galler attack on sexual reproduction in the arroyo willow. Ecology, v.69, p.2021-2030, 1988.

SERVICE, P. Genotypic interactions in an aphid-host plant relationship: *Uroleucon rudbeckiae* and *Rudbeckia laciniata*. Oecologia, v.61, p.271-276, 1984a.

SERVICE, P. The distribution of aphids in response to variation among individual host plants: *Uroleucon rudbeckiae* (Homoptera: Aphididae) and *Rudbeckia laciniata* (Asteraceae). Ecological Entomology, v.9, p.321-328, 1984b.

SERVICE, P.M.; LENSKI, R.E. Aphid genotypes, plant phenotypes, and genetic diversity: A demographic analysis of experimental data. Evolution, v.36, p.1276-1282, 1982.

SHUGART, H.H. Dynamic ecosystem consequences of tree birth and death patterns. BioScience, v.37, p.596-602, 1987.

SHUGART, H.H.; WEST, D.C. Long-term dynamics of forest ecosystems. American Scientist, v.69, p.647-652, 1981.

SILVERTOWN, J.W. Introduction to plant population ecology. London: Longman. 1982.

SOLBRIG, O.T.; JAIN, S.; JOHNSON, G.B.; RAVEN, P.H. Topics in plant population biology. New York: Columbia University Press, 1979.

STRONG, D.R.; LAWTON, J.H.; SOUTHWOOD, R. Insects on plants: community patterns and mechanisms. Cambridge: Harvard University Press, 1984.

THOMPSON, J.N. Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomologia Experimentalis et Applicata, v.47, p.3-14, 1988.

VARLEY, G.C. The biological control of agricultural pests. Journal of the Royal Society of Arts, v.107, p.475-490, 1959.

VASCONCELLOS NETO, J. Dinâmica de populações de Ithomiinae (Lepidoptera, Nymphalidae) em Sumaré-SP. Campinas: Universidade Estadual de Campinas, 1980. 264p. Tese mestrado.

VASCONCELLOS NETO, J. Interactions between ithomiine butterflies and Solanaceae: feeding and reproductive strategies. In: PRICE, P.W.; LEWINSOHN, T.M.; FERNANDES, G.W.; BENSON, W.W. ed. Plant-animal interactions: evolutionary ecology in tropical and temperate regions. New York: Wiley, 1990. p.291-313.

WALLNER, W.E. Factors affecting insect population dynamics: differences between outbreak and nonoutbreak species. Annual Review of Entomology, v.32, p.317-340, 1987.

WHITE, T.C.R. Weather, food and plagues of locusts. Oecologia, v.22, p.119-134, 1976.