

Insect herbivore relationship to the state of the host plant: biotic regulation of ecosystem nutrient cycling through ecological succession

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This paper provides a conceptual framework for increasing our understanding of the relationships between plant resistance to insect herbivores and insect herbivore influences on ecosystem nutrient cycling and succession. For a given plant species, adequate nutrient/light availability favors establishment and productivity; small insect herbivore populations regulated by plant biochemistry stimulate primary productivity and short-term nutrient cycling. As biomass and competition for nutrients and light increase during succession, plants become stressed as they approach their tolerance limits. Earlier successional plant species initially dominating the plant community have higher nutrient/light requirements and become stressed sooner than later successional plant species. Abundance and stress make the earlier plant species more apparent and susceptible, than later plant species, to insect herbivores. Insect herbivore populations increasing rapidly on stressed hosts tend to regulate long-term nutrient cycling patterns by accelerating changes in competitive relationships between plant species with different nutrient/light requirements.

Introduction

Intelligent management of ecosystems is a global problem requiring an understanding of the mechanisms governing ecosystem structure and function. Yet insect herbivores remain targets of control measures in managed ecosystems despite accumulating evidence that analysis of disturbance characteristics, including insect activity, is important to understanding ecosystem structure and function (Bormann and Likens 1979, Odum et al. 1979, Lorimer 1980). I suggest that studies of insect-plant interactions from an ecosystem viewpoint are critical to effective management of ecosystem resources.

Studies of insect-plant interactions have led to three general conclusions: (1) insect feeding, development and survival are often inhibited by host plant defenses (Cates 1980, Haukioja 1980, Mattson 1980), (2) insect herbivores change plant competitive relationships through selective herbivory, often accelerating the rate of ecological succession (Connell and Slatyer 1977,

Schowalter et al. 1981a), and (3) insect herbivores influence the rate and direction of nutrient transfer between vegetation and litter (Springett 1978, Schowalter et al. 1981b). However, the nature and consequences of insect-plant interactions within a changing environment remain poorly understood, largely because of the lack of a guiding conceptual framework for research relating these three aspects of insect-plant interactions to each other and to functional roles ascribed to vegetation.

My purpose in this paper is to integrate current views of insect-plant interactions and the ecosystem processes of succession and nutrient cycling. My objectives are: (1) to demonstrate how succession and nutrient cycling could result from insect relationships to the state of the host plant within a changing nutrient/light regime, and (2) to provide a focus for future research addressing the nature and consequences of insect-plant interactions at the ecosystem level. For the purposes of this paper, I will focus on the dynamics of forest ecosystems, from which most information is available, but my conclusions should be applicable to other ecosystem types.

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Insect-plant interactions

A large body of information has developed around plant resistance to insect herbivores. Research has established that plants have an array of mechanical and chemical defenses that inhibit feeding by or growth and survival of insect herbivores, and that these defenses vary between plants and with plant age, season, and environmental conditions (Cates 1980, Haukioja 1980, Macauley and Fox 1980, Mattson 1980). Circumstantial evidence suggests that plant metabolic pathways leading to growth/maintenance and defense are competitive, i.e. nutrient quality and quantity for herbivores vary as plant requirements for growth or defense change (Mattson 1980). Haukioja (1980), Schowalter and Whitford (1979) and Tilman (1978) suggested that plant biochemistry also has complex indirect influences on herbivore susceptibility to predators and parasites.

Insect feeding, growth and survival are generally concentrated on plants and/or plant species with either most suitable nutrient quality and quantity (Mattson 1980) or greatest degree of apparency or availability (Cates 1980). Populations of many insect herbivores periodically escape population modification and regulation by climate and host suitability, causing considerable damage, and often mortality, to host populations before being reduced (Isaev and Khlebopros 1976, Haukioja 1980). Such outbreaks by insect herbivore populations alter the competitive relationships between plant species and result in changes in plant community type such as those occurring during ecological succession (Connell and Slatyer 1977, Schowalter et al. 1981a).

Insect herbivore activity has also been related to changes in nutrient transfer rates between vegetation and litter. Insect herbivores have been shown to influence nutrient flows in the following ways: (1) stimulating net primary productivity and nutrient uptake by moderately-grazed plants, (2) increasing translocation of nutrients from plant reserves to sites of insect grazing, (3) increasing mass and nutrient content of litterfall during the growing season, (4) increasing leaching of foliar nutrients from chewed leaves, (5) stimulating (via nutrient-rich leachate, litterfall and insect feces) nitrification, nitrogen-fixation, litter decomposition and/or plant root growth rates within the litter/soil complex, and (6) altering long- and short-term nutrient cycling pathways through changes in the relative biomass of canopy and subcanopy plant species (Springett 1978, Owen 1980, Petelle 1980, Schowalter et al. 1981a, b). The importance of these insect herbivore effects at the ecosystem level has yet to be reported, although Schowalter et al. (1981b) found that forest insect herbivores on clearcut and undisturbed watersheds consumed an estimated 300% of foliar standing stock of sodium, 30% of foliar standing stock of potassium and 2-5% of foliar standing stocks of calcium and magnesium during the growing season.

Ecosystem succession and nutrient cycling

Succession is the process of ecosystem organization through which a relatively stable community ultimately develops on a newly exposed or disturbed site. In forest ecosystems this process is typically an orderly sequence of community types beginning with an annual plant community and progressing sequentially through communities dominated by perennial grasses, shrubs, and finally trees (Connell and Slatyer 1977, Bazzaz 1979). In other ecosystems, succession is interrupted at earlier stages by disturbances, such as fire, or by geoclimatic conditions.

The process of ecological succession has recently been related to regulation of ecosystem nutrient budgets. Although different nutrients show different cycling patterns, mature ecosystems tend to have more closed nutrient cycles relative to successional ecosystems, with internal nutrient cycling greatly exceeding nutrient input and output (Bormann and Likens 1979). Studies of forested watersheds, however, have shown that successional stages tend to be more nutrient conservative than climax stages (Gorham et al. 1979). Succession occurs as nutrient-accumulating vegetation is replaced by later vegetation which is more tolerant of the low levels of nutrients and light, prevailing as a result of competition, and which cycles nutrients more efficiently (Bormann and Likens 1979, Gorham et al. 1979).

Biotic regulation of ecosystem processes

The evidence supporting current views of insect-plant interactions also supports a new model which integrates these views in order to describe the nature and consequences of insect-plant interactions for ecosystem succession and nutrient cycling. My hypothesis is that ecosystem succession and nutrient cycling are the net results of individual insect herbivore responses to changes in host plant biochemistry as environmental conditions change. Since contributions of insect herbivores to succession and nutrient cycling have not been evaluated experimentally, this model should stimulate research designed to evaluate insect herbivore effects and thereby increase our understanding of biotic regulation of ecosystem structure and function.

Plant species dominating early successional sites are characterized by wide tolerances to climatic conditions and high nutrient/light requirements (Bazzaz 1979, Bormann and Likens 1979, Boring et al. 1981). High nutrient/light requirements are initially met by normal nutrient/light supply to small plant biomass subject to relatively little competitive interaction. Plant biochemistry maintains small insect herbivore populations which stimulate primary productivity and short-term nutrient cycling (Mattson 1980). Growth of early plant species accumulates nutrients, increases ground

cover, and ameliorates microclimatic conditions, often permitting establishment of later successional plant species with somewhat narrower tolerances to climatic conditions and lower nutrient/light requirements (Bazzaz 1979, Bormann and Likens 1979, Boring et al. 1981). However, later successional plants are usually suppressed by the dominant plants until space, nutrients and light are made available by damage or death of an adjacent dominating plant (Connell and Slatyer 1977).

As plant size and biomass increase, competition for available nutrients and light increases, and the earlier plants approach their tolerance limits for nutrients and light sooner than the later plant species with lower requirements. Abundance, larger size, and stress make the dominant earlier plants more apparent and susceptible than later plants for insect herbivores (Mattson 1980); plant size may also protect insect herbivores from predators and parasites (Tilman 1978). Insect herbivore populations escape regulation by predators and host suitability and increase rapidly. Increased herbivory weakens or kills stressed plants and increases nutrient transfer from these nutrient-rich plants to the litter/soil complex. Space, nutrients and light made available through plant decline and mortality increase establishment and vigor of the replacing plant species. As biomass continues to increase through time, nutrient/light availability decreases relative to biomass, and current plant species approaching their tolerance limits become stressed, attacked by insect herbivores, and replaced in turn by plant species with lower nutrient/light requirements. In other words, insect herbivores accelerate the series of transitions from plant communities with smaller biomass and higher nutrient/light requirements to plant communities with larger biomass and lower nutrient/light requirements. Insect herbivores may thereby regulate ecological succession and nutrient cycling by altering plant competitive relationships in ways that more closely fit nutrient demand to nutrient availability. Population outbreaks of insect herbivores in climax forests may similarly reflect insect responses to changes in plant biochemistry as nutrient/light availability changes through time.

Tests of this model should compare plant biochemistry, nutrient cycling and succession between sites with normal and reduced insect herbivore abundance. Changes in nutrient uptake into vegetation, plant allocation of nutrients, nutrient transfer from vegetation to litter, and litter decomposition at sites with normal and reduced insect herbivore abundance could be compared to changes in plant species and biomass relations. Sites with reduced insect herbivore abundance should show lower rates of primary productivity, nutrient uptake and plant species replacement than sites with normal insect herbivore abundance.

Several systems, from which some information is presently available, might be particularly suitable for such tests. Included are the following four examples.

□ Leaf-cutting ants (*Atta* spp.) are major defoliators of early successional vegetation in the tropical and subtropical Western Hemisphere (Haines 1978, Jonkman 1978). Colonies of leaf-cutting ants selectively harvest leaf, flower and fruit material for cultivation of underground fungus gardens. Degraded remains of the harvested plant material, together with dead and dying ants, are removed to refuse disposal areas (Haines 1978). In the case of *A. colombica* Guerin, above-ground refuse dumps stimulate tree root growth and nutrient uptake by surrounding trees (Haines 1978). The effect of increased nutrient cycling on tropical forest succession is not yet clear (Haines 1978), but Jonkman (1978) reported that abandoned *A. vollenweideri* Forel nests were sites of accelerated succession in old pastures in Paraguay.

□ Pin cherry *Prunus pennsylvanica* L., a successional tree, has been shown to contribute to nutrient conservation on disturbed watersheds at Hubbard Brook Experimental Forest, New Hampshire, USA (Bormann and Likens 1979). Insect herbivore effects on nutrient accumulation by pin cherry have not been investigated although the eastern tent caterpillar *Malacosoma americanum* Fabricius, an important defoliator of wild cherry and apple trees in the eastern U.S., probably contributes to the reduced importance of these trees in older forests. Tilman (1978) reported that young black cherry trees *Prunus serotina* Ehrh. in Michigan attract ants *Formica obscuripes* Forel to extrafloral nectaries produced by the trees during the post-budbreak period when tent caterpillar larvae are most vulnerable to ant predation. Tent caterpillar survivorship was positively correlated to distance between host tree and ant colonies for trees less than 5 cm diameter at ground level. Larger trees showed reduced ant foraging efficiency, reduced production of extrafloral nectaries, and increased oviposition by tent caterpillar adults. Larger trees may consequently be subjected to greater defoliation intensities. Since young pin cherries also produce extrafloral nectaries, attract ants, and are defoliated by the eastern tent caterpillar (Tilman 1978), the tent caterpillar-ant interaction potentially controls nutrient utilization and replacement of these successional trees.

□ Aphids attracting ants *Formica* spp. to nutrient-rich plants on a clearcut at Coweeta Hydrologic Laboratory, North Carolina, USA, may similarly control nutrient utilization and replacement of successional vegetation (Schowalter et al. 1981b). Black locust *Robinia pseudoacacia* L. closed the canopy over much of the clearcut (Boring et al. 1981) but eventually succumbs to attacks by locust borers *Megacyllene robiniae* (Forster) which are less vulnerable to ant predation. D. A. Crossley, Jr. and W. T. Swank (pers. comm.) recently observed an outbreak of the locust borer, at Coweeta, on a 15-yr-old clearcut watershed dominated by black locust. Coincident with this outbreak was an increase in stream concentration of nitrate, indicating important changes in ecosystem nutrient regime.

□ The successional transition from pine forests to hardwood forests may be regulated by pine bark beetles of the genus *Dendroctonus*. Pine forests typically occur in areas of high fire frequency necessary for establishment of pine seedlings and elimination of more shade-tolerant but less fire-tolerant hardwoods (Walter 1973). Bark beetles are normally restricted to scattered susceptible hosts in uncrowded pine forests (Coulson 1979). Pines become crowded when freedom from fire permitted accumulation of a large cone crop in the preceding generation (Peterman 1978) and/or hardwood growth in the present generation (Schowalter et al. 1981a). Pine stress and entrapment of attractive pheromones within the stem zone under continuous canopies increase with tree growth and facilitate bark beetle population expansion from refugia (Coulson 1979, Fares et al. 1980, Schowalter et al. 1981a). Bark beetle activity opens the canopy and increases nutrient/light availability to the hardwood understory but also contributes fuel in the form of abundant standing pine snags and woody litter, thereby increasing the probability of fire necessary for pine regeneration (Peterman 1978, Schowalter et al. 1981a). Since pines and hardwoods exploit nutrients differently (Waring and Franklin 1979), bark beetle mediation of competitive relationships between these two plant groups should have important consequences for succession and nutrient cycling (Schowalter et al. 1981a).

Conclusions

Ecosystem succession and nutrient cycling appear to be the net results of individual insect-plant interactions operating within a changing nutrient/light regime: unstressed plants support small insect herbivore populations which stimulate primary productivity and short-term nutrient cycling; stressed plants favor increased insect herbivore populations which accelerate plant decline and replacement. Although I have dealt specifically with successional transitions, insect outbreaks in climax communities may similarly reflect changes in plant biochemistry resulting from changes in nutrient/light supply.

Increased understanding of the nature and consequences of insect-plant interactions at the ecosystem level should contribute to effective ecosystem/resource management strategies. Trends in insect-plant interactions could, for example, provide an early indication of stressful conditions since plant species valued for crop and timber production are generally early successional species with high rates of primary production and high nutrient/light requirements. Knowledge of the ways in which ecosystems are self-managed will ultimately contribute to management practices which use or imitate natural regulatory mechanisms to enhance resource supply without disrupting ecosystem dynamics. Such knowledge, however, requires a strong conceptual

framework applied to ecosystem-level studies of changes in biotic interactions in response to specific changes in environmental conditions.

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