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Phytophagous Insects as Regulators of Forest Primary Production

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Phytophagous insects are common, ubiquitous elements of most terrestrial ecosystems. Occasionally some species become so abundant that they threaten the stability or output of systems having high ecological, esthetic, or economic value. Forest ecosystems, in particular, support myriads of phytophagous insects, but only few cause dramatic defoliations and widespread destruction of trees. These are termed outbreak species. Four such species currently are stirring public concern in North America: the Douglas fir tussock moth, the gypsy moth, the eastern spruce budworm, and the southern pine bark beetle.

Normal insect grazing (from 5 to 30 percent of annual foliage crops) usually does not impair annual plant (primary) production. In fact, it may accelerate growth. Although outbreaks (either local or extensive) do reduce plant production temporarily, they commonly occur in individual plants or in whole forest systems that are not particularly productive—that is, those which are under stress resulting from inadequate or excessive moisture, nutrient deficiencies, or pollution, or are senescent, having already passed their peak efficiencies in biomass production. Moreover, after an outbreak has subsided, there is evidence that the residual vegetation is more productive than the vegetation that was growing immediately before the outbreak.

For almost a century, research on phytophagous insects has focused primarily on aspects of their population biology and dynamics and their short-term impact on host plant growth and survival. Only recently has attention been directed at understanding and elucidating their long-term interactions with such fundamental ecosystem processes as primary production and nutrient cycling (*1–5*). This knowledge is necessary to achieve a holistic understanding of the functioning of ecosystems and to develop sound management strategies for insects that appear to threaten the vigor or stability of an ecosystem.

Our intent in this article is to examine the evidence for the hypothesis that insects can act as regulators of primary production and nutrient cycling and thus perform a vital function in ecosystem dynamics. Although we focus on outbreak phytophages of temperate and boreal forests, we think that other insect phytophages have similar but perhaps less obvious ecological interactions, regardless of the ecosystem in which they occur.

Interactions with Primary Production

Primary production (P) can be viewed as a product of the amount of photosynthetic biomass (leaf weight, or LWT) and the average rate of net photosynthesis (RNP) or net assimilation per unit of photosynthetic biomass: $P = LWT \cdot RNP$. Grazing insects influence P by directly and indirectly affecting LWT and RNP. For example, grazing directly reduces LWT, but indirectly affects LWT and RNP by altering the physiological status of plants and the distribution and relative availability of the abiotic flux (light, heat, moisture, nutrients, carbon dioxide concentrations, wind movements, and so forth). Specifically, grazing can affect the abiotic flux in such ways as by (i) increasing light penetration through the foliage canopy, (ii) reducing competition among plants for the abiotic flux, (iii) altering the plant species composition of a community, (iv) increasing the rate of nutrient leaching from foliage, (v) increasing the rate of fall of nutrient-rich litter, (vi) stimulating the redistribution of nutrients within plants from sinks (such as boles and branches) to components like leaves, buds, and flowers, with high turnover rates, and (vii) stimulating the activity of decomposer organisms.

Therefore, to evaluate the effects of grazing by insects on primary production, we must consider (i) intensity of grazing, (ii) quantity and distribution of photosynthetic biomass, and (iii) variations in the average rates of net photosynthesis under a broad spectrum of grazing and environmental conditions. Few (if any) studies of primary production have simultaneously considered all of these variables. In this article we refer only to aboveground primary production because little is known about belowground primary production and even less is known about belowground grazing.

Golley (*1*) and Wiegert and Owen (*6*) estimated that phytophages usually consume less than 10 percent of the total net primary production in forest ecosystems. Therefore, the bulk of energy that (forest) plants store as biomass is eventually utilized by heterotrophs other than phytophages—that is, the saprophages in the soil-litter system. In most temperate forest ecosystems, foliage-feeding insects usually consume 3 to 8 percent of the annual foliage production (*7*). However, some ecosystems, such as those that support species of outbreak phytophages, have higher than average foliage consumption, which may periodically reach 100 percent or more of the annual foliage production. Complete removal of the foliage on evergreen species represents consumption of 2 to 7 years of foliage production because most evergreen species can retain annual foliage yields for several years. Tadaki (*8*) reported that evergreen forests have three to seven times as much foliage as deciduous forests (700 to 1500 compared to 200 to 300 grams per square meter).

For herbaceous plants, P varies roughly as a domed quadratic function of density or leaf area index (LAI): $P = a \cdot LAI - b \cdot LAI^2$ (*9, 10*). This occurs because RNP decreases with increasing plant density or LAI. Blackman (*9*) showed that RNP decreases as a negative exponential function

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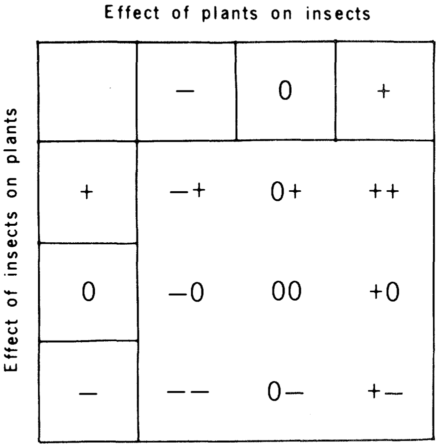
of plant density. Leaf area index is usually a positive linear or negatively accelerated curvilinear function of plant density. Hence, the product of LAI and RNP yields a curve (P) that looks like a quadratic function of plant density. For trees, on the other hand, Satoo (*11*) and Baskerville (*12*) reported that P was proportional to leaf surface area or LWT: $P = a \cdot LAI$ or $P = b \cdot LWT$. Baskerville questioned whether tree densities are ever high enough in natural regeneration to limit or reduce P, which Monsi (*10*) and Blackman (*9*) showed to occur in herbaceous plants.

Both RNP and LAI are ultimately related to the available abiotic flux and plant health (*13*). Blackman's (*9*) data indicate that RNP increases as a logistic function (sigmoidal curve) of solar radiation intensity. In relation to temperature and moisture, RNP increases to a maximum and then falls off. Nutrient levels also affect the rate of net photosynthesis. There have been several reports that RNP is always much greater on nutrient-rich than on poor soils (*14, 15*). Ghilarov (*16*) contends that P depends less on the amount of mineral nutrients in the soil than on the speed of organic matter turnover under the forest canopy—that is, the destruction and mineralization of dead and dying plants. Because insect grazers can respond to the nutrient levels in plants, nutrient availability becomes doubly important to our understanding of P, through its effects on RNP, LAI, and insect production.



Effect of plants on insects

Effect of insects on plants

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Fig. 1. The nine possible interactions between insects and plants.

The annual nutrient cycle is a balance between several inputs and outputs. Inputs to the available nutrient pool in the soil come primarily from weathering of parent minerals, decomposition of organic matter, and meteorological fallout. For most nutrients, the largest input is probably from the decomposition of organic matter (*17*), which seems to support Ghilarov's (*16*) hypothesis. Nutrient cycling is closely correlated with the rate of net primary production. Both seem to peak just before or when trees attain the so-called pole stage (3 to 9 inches in diameter) (*18, 19*). The time required for this to occur depends on the characteristics of the dominant tree species and the fertility of the site. Trees typically attain peak growth much sooner on nutrient-rich than on nutrient-poor sites (*18, 19*).

Kulman (*20*) concluded that, in general, losses in wood production are proportional to foliage losses. However, the relation is not linear over the whole range of defoliation intensities because plants can compensate for light defoliations of less than 40 to 50 percent with little if any loss in production (*21–23*). Harris (*22*) suggests that light defoliations can actually stimulate vegetative and reproductive growth of plants. Production losses may be proportional to foliage losses when defoliation exceeds 40 percent. However, this relation is confounded by such factors as cumulative defoliation effects, general health of the plants, and weather. These relationships appear to apply not just to forest ecosystems, but also to agro- (*24*), grassland (*25*), tundra (*26*), and marine (*6, 17*) ecosystems, where the dominant grazers may or may not be insects.

Table 1. Annual biomass production in two hypothetical aspen stands with and without forest tent caterpillar (FTC) populations. Y and X are the differences in total tree and FTC biomass production, respectively, between the forests without and with defoliation; C is the absolute magnitude of $Y + X$; $C/BP_0 = C/$(biomass production without FTC) = the distance from R0 as a proportion of radius; the coaction angle, arctan Y/X, is corrected in coaction space 90° to 180° and 270° to 360°.

Age (yr)	Annual biomass production (g/m², dry weight)						Difference				Corrected coaction angle (deg)
	Forest without FTC			Forest with FTC							
	Stemwood	Foliage	FTC	Stemwood	Foliage	FTC	Y	X	C	C/BP_0	
26	163	125	0	163	125	1	0	1	1	0.0035	0.00
27	165	125	0	165	125	2	0	2	2	0.0069	0.00
28	167	125	0	144	100	4	–48	4	44	0.1507	276.47
29	170	126	0	30	175	18	–91	18	73	0.2466	294.55
30	172	127	0	14	165	10	–120	10	110	0.3703	280.42
31	173	128	0	14	150	15	–137	15	122	0.4053	285.09
32	175	128	0	103	100	2	–100	2	98	0.3234	272.22
33	176	129	0	161	129	1	–15	1	14	0.0444	274.19
34	178	129	0	163	129	< 1	–15	< 1	14	0.0456	274.20
35	179	129	0	165	129	< 1	–14	< 1	13	0.0422	274.47
36	180	129	0	166	129	< 1	–14	< 1	13	0.0421	274.47
37	181	129	0	168	129	< 1	–13	< 1	12	0.0387	274.78
38	182	129	0	169	129	< 1	–13	< 1	12	0.0385	274.78
39	183	130	0	171	130	< 1	–12	< 1	11	0.0351	275.14
40	184	130	0	172	130	< 1	–12	< 1	11	0.0350	275.14

Simulating Insect–Overstory Plant Interactions

The nine possible interactions between plants and insects are portrayed in Fig. 1. Qualitatively, these interaction or coaction symbols denote enhancive or disenhancive effects that plants and insects have on one another (*27*). For example, ++ denotes a symbiotic or mutualistic relation, where both insects and plants benefit in some sense from the association, and +– a parasitic interaction, where the insects benefit at the plants' expense. Other symbols could be explained similarly. Many have become so engrossed with +– insect-plant coactions that they have ignored or dismissed any other possible relations.

To evaluate the qualitative and quantitative nature of interactions between overstory trees and insects, we simulated and then compared annual biomass production in an aspen, *Populus tremuloides*, forest with and without forest tent caterpillars (FTC), *Malacosoma disstria*. For both situations, we calculated wood growth using equations for stand diameter growth (*28*) and height growth curves (*29*). We estimated foliage production using equations we had developed for similar aspen forests and caterpillar production using data reported by Witter *et al.* (*30*). The effects of insect defoliations on wood production were extracted from several studies (*20*). In this example, defoliations reduced wood growth by 14 to 92 percent. Leaf production increased temporarily because fully defoliated trees refoliated: the biomass of the second crop of leaves was about two-thirds that of a normal first crop.

The interactions portrayed in Table 1 can be mapped in the periodic coordinate system, as shown in Fig. 2a. The periodic coordinate system is particularly useful in studies of interaction because it permits detailed specification of the type and intensity of interaction and facilitates comparisons among the same interacting entities at different times or among different interacting entities. Type of interaction is specified by the angle θ (ranging between 0° and 360°) and intensity is specified by the proportional change from a standard reference value, represented by the circle, called reference zero (R0). This circle represents null interactions (0, 0) where systems with and without insects have equal biomass production. The axes of the coordinate system (0°, 90°, 180°, and 270°) represent interaction types +0, 0+, –0, and 0–, respectively. Angles between 0° and 90°, 90° and 180°, 180° and 270°, and 270° and 360° represent interaction types + +, – +, – –, and + –, respectively. Deviations either inward or outward from R0 indicate the intensity of interaction. To understand the intricacies of the periodic coordinate system the readers should consult Haskell (*27*), who invented the system, and Leary (*31*), who developed the mathematical foundations for mapping interactions.

At ages 26 and 27 (Fig. 2a), the FTC-aspen interaction (coaction) is commensalistic (+0), a little to the right of R0 at 0°. At age 28, the interaction moves into the parasitic coaction space (+–)—specifically, at a position of 276.5° and inward from R0 equal to 0.15 of the circle's radius. At ages 29 to 31, the interactions move inward to a maximum depth. Thereafter, the interaction intensity declines (as evidenced by movement toward R0) but remains in parasitic coaction space between 272° and 275°.

This mapping shows that the insects affected forest production most severely in the fifth and sixth years, after which the effect gradually diminished to become nearly negligible. Following defoliation, tree diameters and heights were smaller in the grazed stand than in the ungrazed stand. Consequently, the growth equations dictate that the annual growth rate in the grazed stand will always be somewhat smaller than in the ungrazed stand, unless tree diameter and height growth, for some reason, become larger than normal. However, there is evidence (*32, 33*) to suggest that aspen stands defoliated for 2 to 3 years may actually show larger height growth and slightly more diameter growth than that shown before defoliation. In such a situation, the insect-plant interaction could move into symbiotic coaction space (++)—that is, outside R0 and between 0° and 90°. Schlaegel (*32*) speculated that severely defoliated aspen stands can catch up, so to speak, with nondefoliated stands, given adequate time before future defoliations. This agrees with the principle of equifinality [described by Bertalanffy (*34*)] —namely, that the same final state may be reached from different initial conditions and by different pathways in open systems.

Wood production may increase after severe defoliations because the circulation of important growth elements such as nitrogen, phosphorus, and potassium is enhanced or the distribution of light and moisture is more equitable. Moderate to severe defoliations can increase normal nitrogen, phosphorus, and potassium contributions in the litter fall by 20 to 200 percent (*2, 3, 5, 34*). This occurs because litter fall is not only greater but also richer than normal due to the exceptionally high concentrations of nutrients in dead insect bodies, insect excrement, and wasted food parts. This enhances the soil organisms. The net result, perhaps, is increased plant growth.

Applications of sewage effluent and artificial fertilizers often can have the same effects: a spurt over normal tree growth for several years, presumably caused by the carryover of the added nutrients. Leaf surface area and the assimilation efficiency of leaves depend on the abundance of available soil nutrients, especially nitrogen and phosphorus (*13, 35*). Furthermore, Assmann (*15*) concluded that removal of suppressed trees (which can be accomplished by severe defoliations) will, as a rule, increase stand diameter growth in sites deficient in water and nutritive elements.

Our FTC-aspen example is typical for an FTC outbreak, which usually lasts for 2 to 3 years and then subsides. Such defoliations kill few if any trees, except those which are suppressed. There have been reports of unusual outbreaks which lasted for 4 to 6 years and caused tree mortality up to 50 percent (*20, 30*). In these outbreaks, the insects reduced height and stand diameter growth, as well as the growing stock. Such a severe interaction would almost certainly keep the relation in parasitic coaction space if primary production is a linear function of leaf biomass or plant density. If production is a quadratic function of plant density, theoretically, a thinning by insects could also cause production to increase in stands where density is more than optimal.

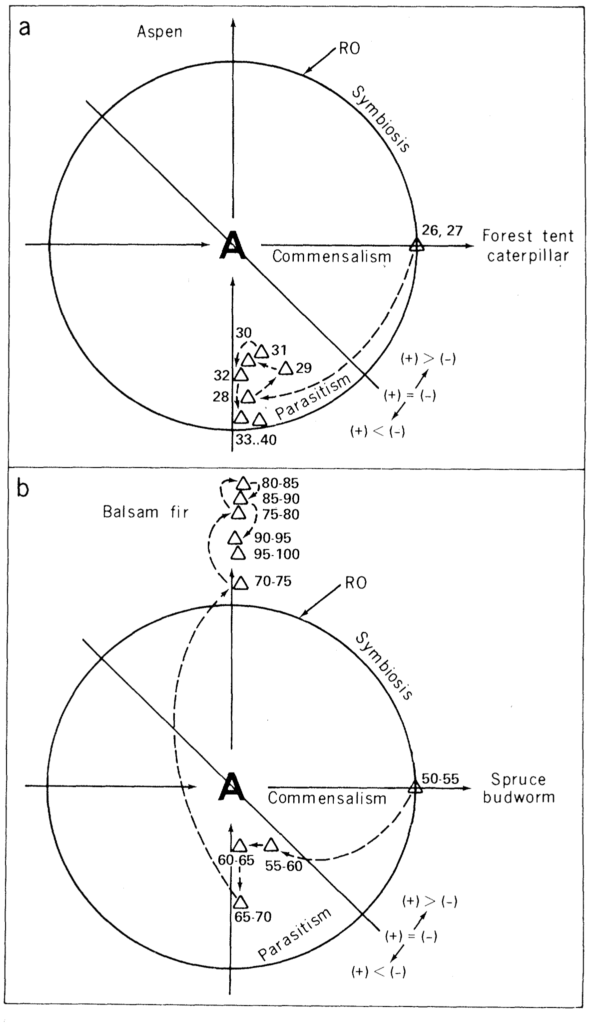

Fig. 2. Mappings of insect-plant interactions in the periodic coordinate system to demonstrate variations in the type and intensity of interactions: (a) forest tent caterpillar–aspen coactions, (b) spruce budworm–balsam fir coactions. The two circles, called reference zero (R0), represent cases where total production (insects plus vegetation) is the same in systems with and without insects. Positions inside and outside R0 represent cases where the system with insects has less and more total production, respectively, than the system without insects.

Simulating Insect–Overstory and Understory Plant Interactions

Logically, the impact of tree defoliations on total primary production depends in part on the kind and quantity of understory vegetation. Where there is little or no understory vegetation, the response to overstory defoliations will be small. Moreover, some plant species will respond more than others to overstory perturbations. Typically, understory trees and saplings respond with increased growth when the overstory trees are defoliated because competition with the overstory for the abiotic flux is decreased (*36, 37*). In general, we can assume that the understory vegetation, if it is not also defoliated, will reduce the differences in primary production between forests with defoliated and nondefoliated overstories. Therefore, insect–total vegetation coactions will probably map closer to R0 in the periodic coordinate system than insect–overstory tree coactions, but both should remain in roughly the same angular positions.

Little is known about the long-term relations between over- and understory plant growth. We were able to develop a partial picture of such a relation in spruce and fir (*Picea* spp. and *Abies balsamea*) forests of North America infested with spruce budworm, *Choristoneura fumiferana*. Middle-aged to mature forests commonly have little understory vegetation, except for their own seedlings and saplings (*38*). As in our aspen forest example, we compared stand growth and development with and without insect populations (Fig. 3 and Table 2). Although production information for tree foliage was not available, the example is useful because it portrays the understory response to overstory defoliations. During the first 5 years of observation, the outbreak destroyed most of the overstory, leaving only about 175 live trees per acre. Large numbers of understory seedlings and saplings survived after defoliation and grew, according to observations by Vincent (*39*).

For 10 years after the outbreak, wood production in the defoliated stand was less than in the undefoliated stand (Table 2). However, the difference in total primary production between the two stands was probably not as large as suggested by the data. By the 15th year after the outbreak, wood production in the defoliated forest actually surpassed that in the undefoliated forest. More likely than not, so did total primary production. This occurred because overstory trees in the undisturbed forest had become avigorous and inefficient producers due to old age and high incidences of debilitating diseases (*13, 38*). Nevertheless, such trees still continue to compete with the understory for the abiotic flux. Therefore, the data in Table 2 demonstrate how an outbreak can actually enhance one component of primary production, although this occurred 10 to 15 years after the major coaction.

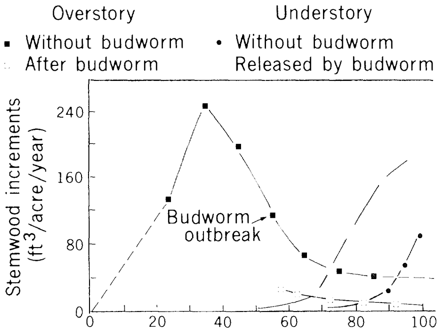

Fig. 3. Stemwood production by overstory and understory balsam fir in the northeastern United States and Canada with and without spruce budworm outbreaks. Data are derived from Bakuzis and Hansen (*38*, table 96), Vincent (*39*, table 8), and Baskerville (*12*, tables 7 and 8).

Such long-term effects are rarely considered in appraisals of the impact of insects on plant systems having high ecological, esthetic, or economic value. The coactions of spruce budworm and spruce-fir forest can also be mapped in the periodic coordinate system (Fig. 2b). These coactions are almost identical with the FTC-aspen coactions, except that the interaction was more intense (greater deviations from R0) during the spruce budworm outbreak and 15 or more years after. The spruce budworm's interaction with its hosts is more intense because this insect kills a large proportion of its hosts (*40*); the forest tent caterpillar usually does not.

We hypothesize that the angular positions for the insect-tree coactions (that is, either 0° or close to 90° or 270°) are probably typical of most invertebrate herbivore–woody plant coactions because they reflect basic energy level relations between a small, poikilotherm consumer and a large primary producer. Such a fundamental physical relation would not be expected to vary much among different species.

The results of the spruce budworm–vegetation interaction are not really surprising because other drastic disturbances (fires, windstorms, or logging) can produce the same effect: a recycling of forest succession to the younger, more efficient and productive stages. Loucks (*41*) concluded that drastic, natural, periodic perturbations (occurring at intervals of 50 to 100 years) are essential in forest ecosystems to recycle the waves of plant succession and the peaks in species diversity and primary production. He also concluded that modifications which preclude the perturbations and the subsequent recycling of plant succession would be detrimental to the forest system in the long run.

With Turnbull (*42*), we believe that outbreaks of native forest insects belong in the class of perturbations to which Loucks referred. Each plant species and forest system supports a variety of insects whose composition varies with the seasonal and ontogenetic development of the plants. At least a few of these insects are capable of making dramatic population responses to subtle changes in individual plant or ecosystem processes.

Insects as Regulators

In cybernetic systems, a regulator reduces the variety of actual outputs from a particular process, thereby making the outputs more consistent (*43*). The regulator or some part of it reacts to changes in the process or to its output and feeds back information to the process to keep the output within some target range.

Insects appear to share the following characteristics with cybernetic regulators: (i) phytophagous insects occupy the strategic position of a potential regulator; that is, they affect a plant's "nerve center," its primary site of energy and biochemical synthesis, by consuming foliage; (ii) several species of phytophagous insects are usually coextensive with every plant species; therefore, seldom, if ever, does the plant occur without its ubiquitous consumers; (iii) many foliage-feeding insects and their host plants have had a long history of association and coevolution (*44*); this implies that the insect-plant interactions are not haphazard or weak, but intricate and intensive; (iv) like regulators, insects can and do respond (negatively and positively) to variations in the state or condition of their host plant; and (v) plant systems react or respond physiologically and evolutionarily to variations in the state of their insect consumers (*20, 45–48*).

When insects respond with increased populations to changed host conditions, there is feedback to the hosts and other components of the ecosystem. For example, severe defoliations (i) further change the hosts' physiological status, and (ii) cause increased litter fall of insect excrement and bodies, tree leaves, leaf parts, small twigs, and branches. In addition, Kimmins (*2*) suggested that defoliations contribute more added nutrients to the soil-litter systems by the leaching pathway. Weakened, old, and suppressed plants almost always die after insect defoliations, which changes the distribution of abiotic flux among the remaining plants. This provides more available nutrients, light, heat, moisture, and so forth for the remaining live plants, which probably enhances their growth (*15*). The activity and numbers of soil organisms probably also increase after defoliations. Therefore, phytophagous insects may help to maintain nutrient cycling and primary production at the most optimal rates for a particular site. Odum (*49*), Ghilarov (*37*), and Golley (*1*) speculated that insects and other herbivores function much like regulators in cybernetic systems. Sukachev and Dylis (*3*) view phytophagous insects as processes that facilitate distribution of energy and circulation of matter.

Insect Response to Host Quality

Insects and plants must be viewed as coevolving, competing, interdependent, biochemical systems (*47, 48*). Because they have coevolved for eons, the balance between the two systems is often very fine. For example, Southwood (*48*) maintains that plant foliage is only marginally adequate nutritionally for its usual insect consumers. Therefore, insect grazers will respond to small biochemical changes in the plants, such as those caused by aging, fluctuations in soil moisture, pollution, or other stresses. Osborne (*46*) concluded that insects respond not just to the nutritional value of the ingested plant parts, but also to the presence and abundance of compounds that can regulate growth of insects and to special volatile products of plant metabolism.

Sensitivity of insects to their host plants is a basic premise in many agricultural plant management and breeding programs. These programs attempt to evoke negative responses (such as lowered oviposition, feeding, survival, fecundity, or vigor) by the insects to subtle manipulations in host quality (*50*). Occasionally, however, unexpected positive responses occur because of plant interactions with fertilizers, pesticides, and so forth (*51*).

The sensitivity of forest insects to variations in host quality has seldom been studied directly. Nevertheless, there is abundant circumstantial evidence that insects can detect and respond to subtle changes in host quality brought about by such factors as aging, nutrient deficiencies, and moisture stresses. This has led foresters and insect ecologists to conclude that insect population growth is inversely related to host plant vigor.

For example, many reports indicate that massive insect outbreaks typically begin in middle-aged to mature forests, which are in the waning end of their productivity cycle. Localized outbreaks (those occurring on scattered individual plants or small clusters of plants) seem to occur in forests of all ages, but typically are associated with the least vigorous, slowest growing plants.

However, these reports are not as specific in establishing cause and effect as are the numerous reports that link outbreaks to soil-litter substrates in which nutrient and moisture regimes are less than optimal. For examples, Zwölfer (*52*) and Voûte (*23*) observed that massive outbreaks of defoliating insects in Europe usually occur in forests growing on nutrient-poor soils in which impoverished microfauna are found. McLeod (*53*) observed that outbreaks of the Swaine jack-pine sawfly, *Neodiprion swainei*, usually appear as foci on the poorer, sandy soils. Mason and Tigner (*54*) found that outbreaks of the lodgepole needle miner, *Coleotechnites milleri*, typically occur on nutrient-poor soils that have poor moisture-holding capacity. Shepherd (*55*) concluded that outbreaks of the spruce budworm *Choristoneura biennis* are restricted to drier, poorer sites. Averill and Fowler (*56*) found that the red-headed pine sawfly is most abundant on trees growing (i) in soils with poorly developed or disturbed profiles and low moisture-holding capacity, and (ii) in competition with other vegetation. Grimal'skii (*57*) observed that outbreaks of several species of pine defoliators occurred primarily in stands growing on soils deficient in nitrogen. Therefore, he compared insect survival and feeding on plots in which nitrogen was and was not deficient. Survival and feeding activity were substantially greater on the deficient soils. Feeding activity, he found, was enhanced by lower concentrations of essential oils in foliage of physiologically weakened trees. Goyer and Benjamin (*58*) found that conifer plantations infested with root weevils had significantly less nitrogen and more available phosphorus in their roots than did adjacent noninfested plantations.

Furthermore, outbreaks are often preceded by predisposing extrinsic stresses to plant systems, such as pollution, drought, or excessive moisture (*59*). For example, Siewniak (*60*) reported that the stem coccid, *Matsucoccus pini*, on Scotch pine occurs most frequently in areas with polluted air. Morris (*61*) and Ives (*62*) concluded that several summers of warm, dry weather appear to cause outbreaks of the spruce budworm *Choristoneura fumiferana* in mature forests. Similarly, Carroll (*63*) speculated that outbreaks of the hemlock looper, *Lambdina fiscellaria*, were stimulated by climatic conditions that limited tree growth for several years. Bejer-Peterson (*64*) reported that outbreaks of the nun moth, *Lymantria monacha*, in Denmark usually occurred in the drier areas after 2 to 3 years of hot, dry summers. Others have reported that outbreaks of numerous defoliators occur first and most commonly on ridgetops and at higher elevations, where soil moisture depletions and other climatic stresses may be most severe and occur most frequently (*65*). Of course, extrinsic stresses affect not only the quality of the host but also the physiology and behavior of the phytophages and their predators. These combined effects are probably synergistic in promoting rapid growth of phytophage populations.

In general, the developmental, survival, and fecundity rates of forest insects show a negative correlation with the age of the foliage consumed. For example, Morris (*66*) reported that the survival and fecundity of the fall webworm, *Hyphantria cunea*, which may have three generations a year in Europe, are always highest in the spring and lowest in the fall generation. In eastern Canada, where the fall webworm has one

Table 2. Annual biomass production in two hypothetical spruce-fir forests with and without spruce budworm (SBW) populations. *Y* and *X* are differences in total stemwood and SBW biomass production, respectively, between the defoliated and undefoliated stands; *C*, C/BP_0, and corrected coaction angle are defined as for Table 1; tr. = trace.

Age (yr)	Annual biomass production (g/m^2, dry weight)						Difference				Corrected coaction angle (deg)
	Forest without SBW			Forest with SBW							
	Overstory stemwood	Understory stemwood	SBW	Overstory stemwood	Understory stemwood	SBW	*Y*	*X*	*C*	C/BP_0	
50–55	320	2	0	320	2	2	0	2	2	0.006	0.00
55–60	242	3	0	58	11	25	–176	25	151	0.616	308.44
60–65	194	3	0	48	17	tr.	–132	tr.	132	0.670	271.76
65–70	139	3	0	35	59	tr.	–48	tr.	48	0.338	271.22
70–75	122	6	0	29	121	tr.	22	tr.	22	0.172	89.99
75–80	111	11	0	28	236	tr.	142	tr.	142	1.164	89.99
80–85	99	17	0	23	305	1	212	1	213	1.836	89.73
85–90	92	50	0	16	357	2	231	2	233	1.641	89.50
90–95	90	103	0	12	367	3	186	3	189	0.979	89.07
95–100	88	161	0	2	413	3	166	3	169	0.679	88.96

generation a year, larvae reared on early season foliage had greater survival rates and produced six times more eggs per female than did those reared on late season foliage. Similarly, Feeny (*67*) found that the growth rates and weights of winter moth, *Operophtera brumata*, larvae were higher when the larvae were reared on early rather than late season foliage. Moreover, when extracts from late season leaves were added to artificial diets, they reduced normal larval growth rates and pupal weights.

Fertilizer applications in forests generally seem to cause changes in food quality that reduce larval feeding and survival rates (*68*). This is symptomatic of nutrient imbalances in their diets (*69*). However, fertilization has been shown to increase the weight and probably the fecundity of some grazing insects (*70*) and populations of mites and sucking insects (*51*).

High populations of foliage feeders appear to be associated with the same conditions that typically have been associated with high populations of bark beetles—that is, declining or stressed host plants (*71*). For example, Moore and Thatcher (*72*) concluded that the following stand conditions favor population eruptions of the southern pine bark beetle, *Dendroctonus frontalis*: (i) excessive damage to residual stands during timber harvest and other cultural operations, (ii) poor internal drainage and low fertility of soil, (iii) prolonged moisture stress, and (iv) slow growth and dense stocking conditions. Wambolt (*73*) also showed that plant competition for moisture increases sharply with stand density.

After an outbreak of the fir engraver beetle, *Scolytus ventralis*, Berryman (*74*) concluded that "epidemics . . . erupt when food supply increases substantially, i.e., when large numbers of trees are weakened by catastrophic events (defoliation, competition, drought, disease, etc.) or when stands become overmature and senescent."

Source of Variation in Host Plant Quality

The causal mechanisms eliciting responses are not fully understood, but they are undoubtedly related to reductions in the plants' defensive mechanisms coupled with alterations in the nutrient balance and abundance. The general consensus is that most plants produce a distinct set of chemicals (so-called secondary compounds, of which more than 1000 are known) that affect the plants' susceptibility to and degree of utilization by herbivores (*75, 76*). For example, the quality and quantity of the resin exudations of the Pinaceae have long been known to be significant factors in their defensive mechanism against bark beetles (*77*). The susceptibility of pines to foliage feeders is also apparently related to the rate of resin exudation from the needles and to concentrations of monoterpenes (*57, 78*).

Little is known about variations in the quality and quantity of secondary compounds in relation to plant age or physiological condition. However, it is probably safe to assume that they vary in abundance during the course of a plant's seasonal and ontogenetic development (*45, 46, 67*). Furthermore, it is suspected that what Hanover (*76*) termed a plant's "chemical halo" is significantly altered when the plant is stressed or declining. For example, Grimal'skii (*57*) found that concentrations of essential oils in pine foliage were reduced in physiologically weakened trees.

The food quality of plants depends on complex interactions among such factors as stage of plant development, soil fertility, and soil moisture. Foliar concentrations of macro- and micronutrients and carbohydrates change dramatically during the course of a growing season. For example, nitrogen and phosphorus concentrations in new foliage typically peak in the early season and thereafter fall off steadily (*67, 79*). However, sugar concentrations tend to gradually increase over time (*67, 80*).

Moisture stress can significantly alter food quality through its impact on nutrient uptake and carbohydrate and nitrogen metabolism. Such an impact may favor insect grazers by creating a more optimal balance of nutrients or by increasing the percentage of utilizable substances in the plant. Most woody and many nonwoody plants exhibit increased concentrations of sugars in foliage and other tissues when subjected to moisture stresses (*81–83*). Coincidentally, the concentrations of amino-N often increase, along with changes in the relative abundance of individual amino acids (*84, 85*). However, concentrations of protein-N may decrease because of its breakdown and translocation (*81–85*).

The nutritional requirements of insects are probably most critical during the earliest and latest feeding stages. For example, White (*86*) speculated that nitrogen concentrations are a determining factor in survival of early larvae—a key stage in the population dynamics of many important forest defoliaters. Sugar concentrations apparently are not as critical in survival of early larvae because Otto (*82*) and Feeny (*67*) concluded that they are usually sufficiently abundant. For late larvae, however, increased sugar levels may produce increased feeding, growth, survival, and fecundity (*87*).

Grazers and Saprophages

Both grazers and saprophagous heterotrophs (saprophages) degrade plant materials into smaller, simpler substances. In so doing, they enhance the circulation of vital nutrients needed for plant growth. However, there are differences among ecosystems in the fraction of plant biomass production consumed directly by these two trophic groups. In most forest ecosystems, for example, grazers consume only about 5 to 10 percent of the aboveground biomass production, and the remainder goes directly to saprophages. In natural African grassland, grazers may use up 50 or 60 percent of the annual aboveground biomass production; in marine ecosystems they may utilize up to 90 percent of total production (*6, 25*).

Insect grazers may also greatly accelerate the rate of leaching of mobile nutrients from plant foliage (*2*). In addition, grazers have a direct and immediate feedback linkage to autotrophs (*1–6, 45, 46*). For example, grazing can cause plants to quickly react physiologically, thereby bringing about changes in (i) the mobilization and utilization of stored reserves and nutrients trapped in sinks, (ii) the efficiency of photosynthetic processes, (iii) the initiation and differentiation of bud primordia (*13, 20, 88*), and (iv) the metabolism and growth of cells (*45, 46*). Furthermore grazers can influence the evolution of various reproductive and defensive strategies by their host plants (*47, 48*). This can have manifold effects on ecosystems. For example, the development of high concentrations of secondary compounds in plant tissues can affect (i) phytophages and their predators, (ii) the rate of litter processing by saprophages, (iii) the *p*H of soil-litter systems, (iv) the *p*H and quality of percolation and runoff water, and ultimately (v) soil development.

Besides these direct effects, grazers interact indirectly by altering the abiotic flux to both grazed and nongrazed plants. For example, grazers can change the vertical distribution of biomass production in ecosystems. Ghilarov (*37*) cited an instance where the understory vegetation produced enough biomass to compensate for the production lost by the severely defoliated overstory trees. Therefore, the total importance of grazers in the processes of primary production and nutrient cycling has probably been underrated in most terrestrial ecosystems because it has been assumed, until recently, that their influence is limited primarily to reductions in leaf surface area and degradation of consumed plant material, which typically is a small share of the annual primary production.

Grazers appear to have much more potential than decomposers to significantly alter the availability and distribution of the abiotic flux in ecosystems. Furthermore, through their feeding on and selective destruction of some plants and plant propagules, they have a strong influence on community composition, density, and succession (*89*). Although tremendously important, saprophages are more passive than grazers in their regulative effects on nutrient cycling and primary production. Grazers interact with autotrophs more directly and through more channels than do decomposers. Furthermore, grazers can affect the activity of decomposers both directly and indirectly, but the reverse interaction between decomposers and grazers is only possible through an intermediary—the host plant.

Summary

Insect grazers function much like cybernetic regulators of primary production in natural ecosystems. That is, they tend to ensure consistent and optimal output of plant production over the long term for a particular site. Their actions or activities seem to vary inversely with the vigor and productivity of the system. This inverse relation is probably a consequence of the long history of coevolution between plant systems and their usual consumers.

Increases in the quality of host food and decreases in host resistance are apparently brought about by interactions of host age, stressful climatic conditions, low fertility of the site, and bottlenecks in the flow of certain vital nutrients. The combination of these events enhances insect survival or fecundity, and increases the probability of escape from natural enemies. In short, it increases the environmental set point (average level of abundance) for grazers. The initial result is usually a change in the distribution and relative availability of the abiotic flux for the plant system. The ultimate result may be a recharge of the cycling nutrient pool. Other perturbances, such as cutting, blowdown, and fire, may produce both of these results, but the effects brought about by grazing occur more slowly. Therefore, they may be more conservative.

If insect-plant relations are mutualistic in the long term, despite temporary parasitic coactions, serious modifications must be made in the management of grazers in many forest ecosystems.

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Self-Inhibition by Dopaminergic Neurons

An alternative to the "neuronal feedback loop" hypothesis for the mode of action of certain psychotropic drugs.

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The mechanisms of action of amphetamine and the antipsychotic drugs have been the subject of intense empirical and theoretical interest for a number of years. Amphetamine appears to act, in large measure, by promoting the release of catecholamines from central and peripheral nerve endings and blocking their reuptake across the presynaptic membrane (*1, 2*). Antipsychotic drugs such as the phenothiazines and butyrophenones are currently believed to act in part by blocking catecholaminergic transmission, especially synaptic transmission in dopaminergic pathways in the central nervous system (*3–5*). These findings support the view that alterations in catecholaminergic transmission in the central nervous system may be significant in drug-induced or idiopathic psychotic disorders (*6, 7*).

One prominent behavioral effect of amphetamine administration in experimental animals is an induction of "stereotyped behaviors" which, in the rat, include compulsive stereotyped biting, licking, gnawing, and sniffing (*8, 9*). When amphetamine is administered for periods of days or weeks, various components of these stereotyped behaviors become progressively more intense (*10, 11*) while a variety of the other effects of amphetamine, such as anorexia and hyperthermia, show evidence of tolerance following long-term administration (*12*). In humans, long-term amphetamine abuse may result in a clinical disorder termed amphetamine psychosis, which is sufficiently similar to paranoid schizophrenia that the former has been regarded as a valuable heuristic model for the latter, and the progressive augmentation of stereotyped behavior that occurs in experimental animals following long-term amphetamine administration has been regarded as a useful experimental model for understanding the mechanisms by which amphetamine psychosis develops (*5, 7, 9, 11, 13*).

It is currently believed, on the basis of several lines of evidence (*14, 15*), that the stereotyped behavior produced by amphetamine is dependent in part on the integrity of catecholaminergic transmission in a pathway arising principally from cell bodies in the pars compacta of the substantia nigra in the brainstem and projecting ipsilaterally to the caudate-putamen, often termed the nigro-neostriatal bundle (*16*). This pathway has also been implicated in the etiology of Parkinson's disease, in which it shows progressive degeneration (*17*). Amphetamine acts on the nigro-neostriatal projection in part by releasing dopamine from the terminals of this pathway and blocking its reuptake across the presynaptic membrane (*2, 18, 19*). Release of dopamine from these terminals by amphetamine is accompanied by a marked inhibition of the activity of many neurons in the caudate-putamen (*20–24*), which is consistent with the role of dopamine as an inhibitory neurotransmitter (*24–26*). Many antipsychotic drugs block dopaminergic transmission in the nigro-neostriatal system and produce increased neuronal firing in elements postsynaptic to dopaminergic nerve terminals (*23*).

The "neuronal feedback loop" hypothesis, proposed initially by Carlsson and Lindqvist (*27*), is one of several theoretical models currently used to account for the regulation of dopaminergic transmission and biosynthesis in the nigro-neostriatal pathway (*28, 29*). Systemic administration of pharmacological agents that facilitate dopaminergic transmission, such as amphetamine, produce a marked inhibition of neuronal activity in the neostriatum (*20–23*) and a similar depression of neuronal firing in dopaminergic neurons in the substantia nigra (*21, 30, 31*). In contrast, systemic treatments with agents that block dopaminergic transmission, such as the antipsychotic drug haloperidol, produce an increase in neuronal firing in the caudate-putamen and in the dopaminergic neurons of the substantia nigra; such agents also block the depression of neuronal firing in both regions produced by prior amphetamine administration (*23, 29, 30, 32*). The effects of amphetamine and the antipsychotic drugs on the activity of dopaminergic neurons of the substantia nigra, located principally within the pars compacta region of this nucleus, have been presumed to occur at least in large measure by means of a neuronal feedback loop from the basal ganglia to the substantia nigra (*4, 21, 29,*

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