

EFFECTS OF FOLIVORY ON SUBCORTICAL PLANT DEFENSES: CAN DEFENSE THEORIES PREDICT INTERGUILD PROCESSES?

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Abstract. The manner and extent to which physiological alterations resulting from folivory can affect the growth, survival, and resistance of trees against subsequent insects and fungi is poorly understood. Information obtained under natural conditions and with subcortically feeding insects is particularly lacking. We evaluated the effects of varying levels of natural feeding by a folivore on subsequent host growth, survival, and suitability to subcortical insects and fungi and also considered implications as to how source limitations caused by defoliation relate to current plant defense theories. The study system consisted of *Choristoneura pinus pinus*, the jack pine budworm, on *Pinus banksiana* Lamb., jack pine. We quantified a range of defoliation by *C. pinus pinus* in test trees and measured parameters of host defenses and colonization by bark beetles (Coleoptera: Scolytidae) and woodborers (Coleoptera: Cerambycidae). We also measured colonization and accompanying tree mortality attributable to these insects. Tree physiological parameters and insect colonization patterns were measured over a 24-mo period. Primary resin flow rates and the ability of active responses to confine the bark beetle's fungal symbiont *Ophiostoma ips* within the phloem, were reduced by high levels of defoliation. These patterns were further influenced by host seasonal phenology and time since defoliation. The predominant subcortical insects responding to defoliation by *C. pinus pinus* were *Ips grandicollis* and *Monochamus carolinensis*. Colonization by these insects together increased exponentially in relation to defoliation level, but the two species differentially exploited trees from particular defoliation levels. The loss of growth among surviving trees increased with defoliation intensity. However, growth and defensive capacity were not related, either negatively or positively, during any interval of this study. Depending on the length of time since defoliation stress, the relationship between plant defense and defoliation intensity was either parabolic, as predicted by growth differentiation theory, or inverse linear, as predicted by plant stress theory. Thus, differing models depicting how carbon allocation and overall carbon availability can influence secondary-chemical metabolism in plants may represent various stages along a temporal continuum. Our results suggest that the time since a stress is exerted is an important variant that should be incorporated into synthetic theories of plant defense. These results also suggest that integrative models of plant defense theory can be extended to describe impacts on community-level interactions.

Key words: *Choristoneura*; *defoliation*; *feeding guild*; *growth–differentiation balance hypothesis*; *Ips*; *Monochamus*; *Ophiostoma*; *Pinus*; *plant defense theory*; *plant stress*; *plant–insect interactions*; *source limitations*.

INTRODUCTION

A growing theoretical and empirical framework has greatly improved our understanding of direct interactions between species, but indirect effects remain poorly understood, despite their increasingly recognized importance to community-level processes (Strong 1983, Fowler and Rausher 1985, Rhoades 1985, Clay et al. 1993, Holt and Lawton 1993, Evans 1994, McDonald et al. 1999). Indirect interactions are often mediated by a common host, and can affect species that simultaneously or subsequently exploit this substrate (Damman 1993). Community-level effects can be manifested through competition between members of the

same feeding guild, or through host physiological processes that subsequently affect common or separate feeding guilds (Denno et al. 1995).

An important class of indirect interactions consists of perennial plants that are exploited by multiple herbivore species within the same or following growing seasons. Biotic stress agents, such as defoliators and root pathogens, have been shown to influence photosynthesis, water balance, and carbon and nutrient allocation (Horn 1971, Mooney 1972, Caldwell 1979, Chapin 1980, McNaughton et al. 1983, Waring and Schlesinger 1985, Lorio 1993, Gershenson 1994). The available data are varied, and include examples in which herbivory by one species has subsequent positive (Geri et al. 1988), negative (Schultz and Baldwin 1982, Karban and Myers 1989, Baldwin 1990, Ehrlen 1995, Krause and Raffa 1996), both positive and negative (Faeth 1992a, Rieske and Raffa 1998), or no (Niemela

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et al. 1991, Faeth 1992b) impact on subsequent herbivory by other species. The diversity of chemical and physical responses to herbivory, and of herbivore counteradaptations, makes it difficult to develop general predictive theories of interguild interactions (Belsky 1986, Larsson 1989). Characterizing these diverse patterns requires that a better linkage be made between ecological patterns and physiological processes, and that direct effects on plant growth and survival (McNaughton 1983, Krause and Raffa 1996) be integrated with indirect effects on subsequent susceptibility to other feeding guilds (Hunter and Price 1992, Power 1992, Hunter and Schultz 1993, Rieske and Raffa 1998, Raffa et al. 1999). We propose that current theories on allocation processes within plants, particularly on the relative allotment of resources to growth vs. defense (Coley et al. 1985, Bryant et al. 1991, Herms and Mattson 1992), provide a framework that can be extended to between-guild interactions.

Several theories generate seemingly divergent predictions of how plants respond to stress. The plant vigor (Honkanen et al. 1994), plant stress (Mattson and Haack 1987, Waring 1987), and growth–differentiation balance (Lorio 1986, Herms and Mattson 1992) hypotheses all assume that plant physiological processes are limited by the availability of carbon. They differ in that the plant vigor hypothesis emphasizes source–sink use conversions among carbon pools, the plant stress hypothesis emphasizes the overall size of the carbon pool that is available for allocation, and the growth–differentiation balance hypothesis emphasizes how the available carbon pool is allocated. Based on how various stresses affect carbon source–sink ratios, the plant vigor hypothesis predicts a positive relationship between defense and herbivore performance, the plant stress hypothesis predicts a consistent inverse relationship between defense and carbon availability, and the growth–differentiation balance hypothesis predicts a convex parabolic relationship. The growth–differentiation balance hypothesis further predicts an inverse relationship between growth and defense among plants, whereas the plant stress hypothesis recognizes trade-offs within plants but predicts that among-plant differences in overall carbon availability can generate positive correlations. There are numerous examples supporting various plant defense theories. However, recent reviews have found numerous exceptions to each model, and emphasized the need to better define the specific plant biochemical and insect behavioral conditions under which each is likely to operate, test underlying assumptions, and develop synthetic models (e.g., Larsson 1989, Gershenson 1994, Herms and Raffa 1995, Koricheva et al. 1998a).

Defoliation can serve as a model of how source limitations affect allocation to plant defenses and growth. Source limitations result from the physical removal of leaf tissue, whereas sink limitations occur when carbon sinks such as meristematic tissue are removed. Since

some plant defense hypothesis propose curvilinear relationships between plant defense and growth (Herms and Mattson 1992), a range of quantifiable treatments is needed to evaluate source (carbon) limited impacts within the context of general plant defense theories. Given the limitations and difficulties in quantifying natural defoliation (e.g., Rieske and Raffa 1998), most such experiments have applied artificial defoliation under controlled conditions to achieve this range among closely related genotypes (e.g., Reich et al. 1993, Raffa et al. 1999). However, artificial defoliation experiments have certain limitations. For example, they do not always simulate natural feeding patterns accurately (Baldwin 1990), they can place artificial limitations on the age and size of test trees, and the extent to which they can be extrapolated to natural community-level processes is uncertain.

The purpose of this study was to evaluate the effects of natural defoliation on the tree's constitutive defenses and also on its rapidly induced host defenses against subcortical insects and fungi, and to use these results to evaluate current hypotheses relating to plant stress. Our overall goal was to use basic plant defense models to strengthen our understanding of community-level interactions. The specific objectives were to: (1) examine potential source limitations by quantifying natural defoliation levels and leaf photosynthesis of trees experiencing a range of folivory, (2) quantify growth and mortality of test trees over 24 mo following defoliation, (3) quantify effects of defoliation on parameters of constitutive and inducible defense against subcortical insects and fungi, and (4) quantify the colonization density of subcortical insect herbivores following defoliation. In a companion study (Wallin and Raffa 1999), we described changes in the concentrations and proportions of constitutive and induced subcortical monoterpenes in these trees, and relationships among host allelochemicals and insect colonization patterns.

MATERIALS AND METHODS

Study system

Our study system consisted of five native species: jack pine, *Pinus banksiana* (Lamb.), the folivore *Choristoneura pinus pinus* (Freeman) (Lepidoptera: Tortricidae), the bark beetle *Ips grandicollis* (Coleoptera: Scolytidae), the major fungal associate of *I. grandicollis*, *Ophiostoma ips* (Rumbold), and the wood borer *Monochamus carolinensis* (Olivier) (Coleoptera: Cerambycidae). *P. banksiana* is an early successional, shade-intolerant conifer widely distributed across Canada and the Great Lakes region of the United States (Yeatman 1967). *P. banksiana* communities are periodically subjected to area-wide population eruptions of *C. pinus pinus*. Severe infestations occur at 8–10-yr intervals, and persist for 2–4 yr (Clancy et al. 1980).

The bark beetle *I. grandicollis* usually attacks trees

that have been weakened by stress factors such as drought, disease, or lightning (Pearson 1931). The ability of bark beetles to exploit the subcortical stem tissue of living trees is facilitated by aggregation pheromones that coordinate mass attacks, mutualistic associations with moderately phytopathogenic fungi that help impede the tree's resistance mechanisms, and chemosensory abilities to detect tree physiology (Brandt et al. 1975, Wood 1982, Raffa et al. 1985, Raffa and Smalley 1995). Fungi vectored by bark beetles progress across tracheids through bordered pits or direct penetration of cell walls (Gibbs 1993). Together the beetles and fungi disrupt the vascular system of the tree by inducing aspiration of pits in the tracheids, and eventually render the xylem nonconducting (Berryman 1972, Hemmingway et al. 1977, Lieutier and Berryman 1988, Raffa and Smalley 1988, Klepzig et al. 1996). Sapwood occlusion and impeded water flow ultimately cause tree death.

Monochamus carolinensis colonizes some substrata in common with *I. grandicollis*, specifically living phloem tissue. Like *I. grandicollis*, they are usually associated with weakened or dead trees, but differ in that *M. carolinensis* adults chew ovipositional niches in the outer bark rather than enter hosts. Their larvae are substantially larger than those of *Ips* spp., do not feed in organized galleries, and develop as late instars in the sapwood (Raske 1972). No phytopathogenic fungi are known to be associated with *M. carolinensis*, although these beetles vector a nematode, *Barsaphelelenchus xylophilus*, which can be lethal to Asian and European, but not North American, pines (Linit 1986).

P. banksiana resists attacks by subcortical organisms through an integrative process of constitutive and inducible defenses (Raffa and Smalley 1995). Wounding of *P. banksiana*'s well-developed resin duct system results in the localized accumulation of oleoresin. Preformed resin flows into the wound site, forming a barrier against desiccation and repelling insects and pathogens. Trees respond actively to the presence of insects and fungi by rapidly forming necrotic lesions in advance of their growth, accumulating increased concentrations of terpenes and phenolics at the site of the invasion, and altering the proportions of various secondary chemicals in the phloem (Wallin and Raffa 1999).

Plot description and quantification of natural defoliation levels

We established three plots, spaced ~600 m from each other, of 66 trees each in a naturally generated *P. banksiana* forest in Jackson County, Wisconsin (T20N, R2W, S17) in August 1994. Trees within these plots had been naturally defoliated to varying degrees by *C. pinus pinus* during the previous month. Little defoliation occurred after this study commenced. The plots were relatively homogeneous with regard to soil (sandy loam), slope (minimal slope within and between plots),

and ground cover (primarily sedge), and selected trees were similar in size (11.52 ± 1.28 cm dbh [mean \pm 1 SE]), age (24 yr old), and phenotypic characteristics (dominant, closed-canopy).

We determined defoliation levels by a two-step process. First, three observers made independent estimates of defoliation for each tree using criteria established by the Wisconsin and Michigan Departments of Natural Resources (McCullough and Kulman 1991). Their estimates were averaged. The resultant categories were: (1) no visible defoliation, (2) $\leq 25\%$ defoliation, (3) 26–50% defoliation, (4) 51–75% defoliation, and (5) $> 76\%$ defoliation with the top half of the trees having dead and dying branches. These classes are subsequently referred to as none, light, moderate, heavy, and severe defoliation levels. Second, we verified and quantified these visual estimates by destructively sampling randomly chosen subsets of trees within each class. We used a modified method of Gower et al. (1993a) to quantify each defoliation level. The canopies of six randomly selected trees from each defoliation level were equally divided into upper and lower canopy lengths, and weighed. Each half was delimitted, and four branches were randomly selected from each crown section. These subsamples were immediately weighed, placed in plastic bags, sealed, placed on ice, and transported to the laboratory. The needles and branches were manually separated, weighed, dried at 70°C for 72 h, and reweighed. Needle and branch moisture was calculated for each canopy section. We calculated needle-to-branch dry mass ratios for each defoliation level. We compared means for moisture content and needle-to-branch dry mass ratio among defoliation levels, and between canopy sections within trees.

Effects of varying levels of defoliation on tree growth, mortality, and leaf photosynthesis

We permanently marked each tree 1.4 m above its base. We quantified growth following defoliation by measuring annual radial increment using an increment borer. We removed a core from each tree, placed each core into an individual plastic tube, sealed the tube, and placed the core on ice until analysis. Each core was secured onto a tray and sanded smooth to expose the growth rings, and the growth rings were measured using a Gaertner 6823-P dendrometer (Scientific Corporation, Chicago, Illinois, USA). Radial growth increments during the five years previous to August 1994 were also determined using a dendrometer. We calculated relative growth based on the ratio of growth during the 2-yr study period to cumulative growth during the 5-yr period prior to defoliation (Gower et al. 1993b). We determined mortality by visually assessing the tree crown. We analyzed potential growth differences using one-way ANOVA (Littrell et al. 1989).

We measured leaf water vapor and CO₂ exchange with an ADC LCA-Z portable infrared gas analyzer, Parkinson leaf chamber, and air supply unit (Analytical

Development, Hoddesdon, UK) using previously described methods (Farquhar et al. 1989, Reich et al. 1995, DeLucia et al. 1996, Green 1998). We measured net gas exchange and stomatal conductance to water vapor on needles during midday (0900–1400) on 20 May 1995. Five trees were selected from each defoliation level. One branch each from the upper and lower crown was removed at the branch collar using a pruning pole. The cut end of the branch was placed in water and measurements were made immediately. Gas exchange and stomatal conductance were measured using six intact and six detached needles, respectively. Measurements were recorded in high light conditions (photon flux density $>1500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Ambient temperature averaged 22°C , and ambient CO_2 concentration averaged $370 \mu\text{L/L}$. Immediately following a measurement, each needle sample was weighed and placed on ice for subsequent determination of dry mass.

Since there was no difference in gas exchange between the upper and lower crown ($P = 0.54$, $df = 1$) we pooled the results from the two crown locations. The potential influence of defoliation level on gas exchange rates of needles was analyzed using one-way ANOVA (Littrell et al. 1989).

Effects of defoliation levels on defenses against subcortical insects and fungi

We measured resin flow in early June 1995, early August 1995, and early June 1996 using techniques described by Lorio (1993). We sampled five randomly selected trees from each defoliation class with a 1.25-cm arch punch, avoiding injury to the face of the xylem. Aluminum troughs pinned to the bark below the wounds channeled resin flow into tapered graduated centrifuge vials. We placed three vials evenly around the circumference of each tree, at 1.4 m above the base. The average of these three samples provided one measurement. After 24 h, we collected the vials, and we determined total volume to the nearest 0.1 mL.

The fungus *O. ips* was isolated in February 1995 from *P. banksiana* phloem tissue colonized by *I. grandicollis* at the field sites, and cultured using methods described by Raffa and Smalley (1988). These cultures were grown in petri plates on potato dextrose agar at 22°C and 85% RH for 7–10 d and provided the source for hyphal tip transfer. We administered three inoculations evenly around the circumference of five randomly selected trees from each defoliation class in June 1995, August 1995, and June 1996, totaling 75 trees. Each inoculation of *O. ips* was administered into the main stem at 1.4 m above the tree's base to simulate its introduction by *I. grandicollis*. Host responses to such inoculations are chemically and histologically similar to those of natural single attacks (Raffa and Berryman 1982). We administered inoculations by first boring a hole to the sapwood with a 4 mm diameter cork borer without injuring the xylem tissue, then applying a mycelial plug into the sapwood using a 3 mm

diameter metal syringe, and finally resealing the bark (Raffa and Berryman 1982). We sampled host responses 3, 6, and 9 d following inoculation. At each sampling interval we removed the outer bark and phloem tissue from one of the three inoculations and measured the visible reaction lesions on the phloem–xylem interface. Phloem surface lesions are less variable than those on the xylem surface (Wallin 1996). The excised tissue was placed in a vial, immediately stored over dry ice in the field, and stored at -40°C until subsequent chemical analysis. Results of the chemical analysis are reported in Wallin and Raffa (1999).

The effects of defoliation on resin flow were analyzed by ANOVA (Littrell et al. 1989). Fungal colonization rates were analyzed using repeated-measures ANOVA (among days after inoculation) within each month, and split-plot ANOVA (within days after inoculation) among months. Homogeneity of variance was tested using the Levenes test. Results that indicated heterogeneous variances were log transformed prior to analysis.

Computation of potential relationships of growth and defense

We evaluated possible trade-offs between growth and defense by testing for relationships between resin volume or lesion length and increment radial growth within the same trees. Since we are interested in how a source stress impacted the relationship between growth and defense we conducted a separate analysis among defoliated trees. Radial growth measurements ($\{[\text{growth during test periods}] - [\text{growth from 1989 to 1994}]\} / [\text{growth from 1989 to 1994}]$) were separately regressed on resin volume and lesion length (day 6/9 ratio, see *Results: Effects of C. pinus pinus feeding . . .*, below) in June 1995, August 1995, and June 1996. Test periods were June 1995 to August 1995, June 1995 to June 1996, June 1996 to August 1996, and from August 1994 to August 1996. Data were log-linear transformed, and regression analyses were performed using SAS (Littrell et al. 1989).

Effects of defoliation intensity on subsequent colonization by subcortical insects

We visually assessed the bole of each tree ($N = 168$ remaining trees [198 trees initially, minus the 30 trees destructively sampled to quantify *C. pinus pinus* feeding]) for bark beetle entrance holes and wood borer (*Monochamus*) oviposition marks during March to November of each year (1994, 1995, and 1996). In addition, on August 1994, we marked a bark surface area of 200 dm^2 on each tree 1.4 m above the tree base. We counted the entrance holes and ovipositional marks of *I. grandicollis* and *M. carolinensis* within the predetermined 200-dm^2 sample space during daily checks of study trees. Each entrance hole and oviposition site was marked to designate time of attack. The density and sequence of insect presence were also quantified. The

counts were pooled into three periods: August 1994–June 1995, July–October 1995, and April–August 1996. These periods correspond to the three major flight periods of *I. grandicollis* and *M. carolinensis* (Raffa 1991) following the initial folivory by *C. pinus pinus* during July 1994. In addition, we examined the entire length of the bole of each tree daily using binoculars May–October 1995 and 1996. We examined each tree until the appearance of new entrance holes and oviposition marks ceased. The influence of moderate, heavy, and severe defoliation of trees on the densities of subcortical insects were analyzed using one-way ANOVA (Littrell et al. 1989).

All *F* values in this article have 167 degrees of freedom in the denominator.

RESULTS

Effects of C. pinus pinus feeding on the needle: branch ratio, photosynthesis, and growth of P. banksiana

Defoliation had no to minimal effect on the moisture content of the remaining needles (nondefoliated trees = 0.15 ± 0.04 mg/g [mean \pm 1 SE]; lightly defoliated trees = 0.08 ± 0.006 mg/g; moderately defoliated trees = 0.07 ± 0.05 ; heavily defoliated trees = 0.11 ± 0.04 mg/g; $F = 1.21$, $df = 3$, $P = 0.34$), or branches (nondefoliated = 0.37 ± 0.12 mg/g; lightly defoliated trees = 0.26 ± 0.07 mg/g; moderately defoliated trees 0.17 ± 0.08 mg/g; heavily defoliated trees 0.27 ± 0.03 mg/g; $F = 1.36$, $df = 3$, $P = 0.28$). Therefore, the same allometric ratio of needle:branch dry mass was effective in quantifying defoliation intensity. The amount of foliage remaining in tree canopies that were lightly, moderately, and heavily defoliated averaged 26%, 36%, and 50% less than trees that were not defoliated (Fig. 1A). These percentages correspond with our initial visual estimates of defoliation (Spearman rank correlation: $P < 0.001$, $r_s = 0.937$ [Littrell et al. 1989]).

Photosynthetic rates of the foliage in May 1995 were not influenced by defoliation level (nondefoliated trees 36.5 ± 2.3 nmol·g⁻¹·s⁻¹ [mean \pm 1 SE]; lightly defoliated trees 31.6 ± 9.3 nmol·g⁻¹·s⁻¹; moderately defoliated trees 32.2 ± 3.7 nmol·g⁻¹·s⁻¹; heavily defoliated trees 38.7 ± 3.8 nmol·g⁻¹·s⁻¹; $F = 1.5$, $df = 3$, $P = 0.3$). Likewise, defoliation did not affect leaf conductance (nondefoliated trees 107.3 ± 4.9 ; lightly defoliated trees 116.6 ± 5.8 ; moderately defoliated trees 103.1 ± 6.6 ; heavily defoliated trees 104.5 ± 6.5 ; $df = 3$, $F = 3.1$, $P = 0.09$).

Defoliation significantly affected tree radial growth from 1994 to 1996. This relationship showed an overall parabolic pattern (Fig. 1B). Moderately defoliated trees exhibited an overall increase in growth, and heavily and severely defoliated trees decreased in growth, relative to nondefoliated trees, during the study period. Trees from the various defoliation levels did not differ in predefoliation radial growth rates (1989–1994) (F

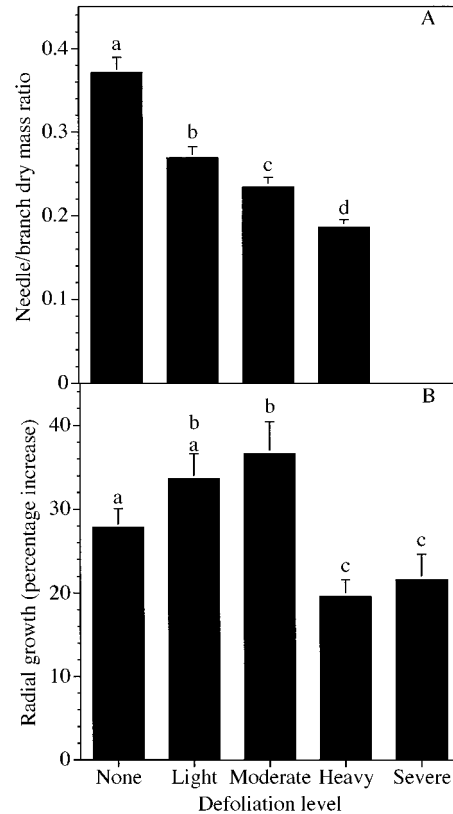


FIG. 1. Effects of feeding by *Choristoneura pinus pinus* on *Pinus banksiana*: (A) needle/branch dry mass ratios, and (B) growth rates over 2 yr ([ring width from 1996 to 1994]/[ring width of 1994]) ($F = 5.224$, $P = 0.0011$). Means with the same letter are not significantly different at $P < 0.05$ by Fisher's protected lsd. Error bars indicate 1 SE.

= 0.99, $df = 4$, $P = 0.42$). The radial growth rates of nondefoliated trees did not significantly differ between growing seasons during the study period ($F = 1.45$, $df = 1$, $P = 0.38$).

Effects of C. pinus pinus feeding on tree responses to subcortical insects and fungi

The volume of preformed resin was strongly influenced by defoliation level (Table 1A). Resin volume was also influenced by the length of time since defoliation. The rates of resin flow showed different relationships with defoliation level as the interval after defoliation increased; i.e., there were significant interactions between defoliation level and time since defoliation.

During the first period of tree growth following defoliation (June 1995), resin flow showed a parabolic relationship, with lightly defoliated trees producing the greatest resin volume and severely defoliated trees producing the least (Fig. 2A). In August 1995, resin volume was negatively associated with defoliation across all *C. pinus pinus* feeding intensities (Fig. 2B). At this time, the resin volume of nondefoliated trees was

TABLE 1. Variation in response of *Pinus banksiana* trees to inoculation with *Ophiostoma ips* fungus.

Dependent variable	Source	df	F	P
A) Preformed resin flow				
	Defoliation level (DL)	4	6.176	0.0034
	Time after defoliation (TD)	2	7.882	0.001
	(DL) × (TD)	5	4.117	0.035
B) Lesion length				
Time after inoculation (d)				
3	Defoliation level (DL)	4	0.844	0.506
	Time after defoliation (TD)	2	1.932	0.159
	(DL) × (TD)	6	1.662	0.168
6	Defoliation level (DL)	4	1.819	0.015
	Time after defoliation (TD)	2	11.054	0.0002
	(DL) × (TD)	6	1.356	0.126
9	Defoliation level (DL)	4	1.083	0.013
	Time after defoliation (TD)	2	8.119	0.001
	(DL) × (TD)	6	1.675	0.156
C) Fungal confinement rate				
Date of challenge				
June 1995	Defoliation level	4	8.88	0.044
August 1995	Defoliation level	3	5.27	0.091
June 1996	Defoliation level	2	10.12	0.005

Notes: Defoliation levels ranged from none to severely defoliated trees. The challenge in part C consisted of three inoculations of *Ophiostoma ips* hyphae evenly spaced around the circumference of five randomly selected trees. All *F* ratios given here have 167 df in the denominator.

17.9× that of heavily defoliated trees. Resin volume was also negatively associated with defoliation intensity in June 1996 (Fig. 2C). The resin volume of non-defoliated trees was 5.7× that of moderately defoliated trees. Severely defoliated and heavily defoliated trees could not be sampled in August 1995 or June 1996, because *I. grandicollis* and/or *M. carolinensis* had colonized almost all of them and they were dead.

Trees responded to simulated insect–fungal attack by undergoing histological changes that confined fungal growth within resinous lesions. Reaction lesion lengths varied strongly with the number of days following the challenge inoculation ($F = 22.53$, $df = 2$, $P = 0.0001$), as is typically observed in such periodic samples (e.g., Raffa 1991, Raffa and Smalley 1995). Thus, subsequent analyses were based on separate postinoculation intervals. There were strong effects of both defoliation level and time after defoliation on lesion length at 6 and 9 d following challenge inoculation (Table 1B). There was no defoliation level × time after defoliation interactions on absolute lesion lengths. Host lesion lengths at 3 d did not vary and so are not considered hereafter.

Because lesion formation includes components of both host response and fungal growth, the significance of absolute lesion lengths has been subjected to conflicting interpretations (reviewed in Raffa [1991]). Thus, some authors have treated longer lesions as a measure of superior host defense, while others have considered them evidence of relatively higher fungal penetration, i.e., susceptibility. We report an integrated measure, fungal confinement rate (the day 6/9 ratio,

which is the ratio of lesion length at day 6 to that at day 9). Our rationale is that those trees capable of eliciting the most rapid autonecrotic responses will show larger lesions soon after inoculation (Raffa and Berryman 1982, Lieutier and Berryman 1988), but because lesions continue to expand as long as the attacking agent proceeds (Raffa and Berryman 1983), the more susceptible trees may have the longest ultimate lesion lengths. This interpretation is consistent with findings from numerous host–microbe interactions, in which resistant plant cultivars often show more rapid but ultimately less pronounced induced responses to fungal and bacterial pathogens than do susceptible hosts (Niemann et al. 1991, Reimers and Leach 1991, Cahill and McComb 1992).

Fungal confinement rates were influenced by the time after defoliation ($F = 6.345$, $df = 2$, $P = 0.0574$), so subsequent analyses are conducted separately for the three sampling periods (Table 1C). In addition, defoliation intensity had significant effects on fungal confinement rates, but the patterns of these relationships varied with time. In June 1995, there was a parabolic relationship between fungal confinement and defoliation intensity (Fig. 2D). Fungal confinement rate was highest in lightly defoliated trees. The fungal confinement rate was substantially lower in severely defoliated than nondefoliated trees. However, fungal confinement rate did not differ from the nondefoliated in moderately or heavily defoliated trees. In August 1995, fungal confinement rates were negatively related to defoliation across all intensities (Fig. 2E). Fungal growth was low in nondefoliated trees (day 6/9 ratio = 8.6), as indicated

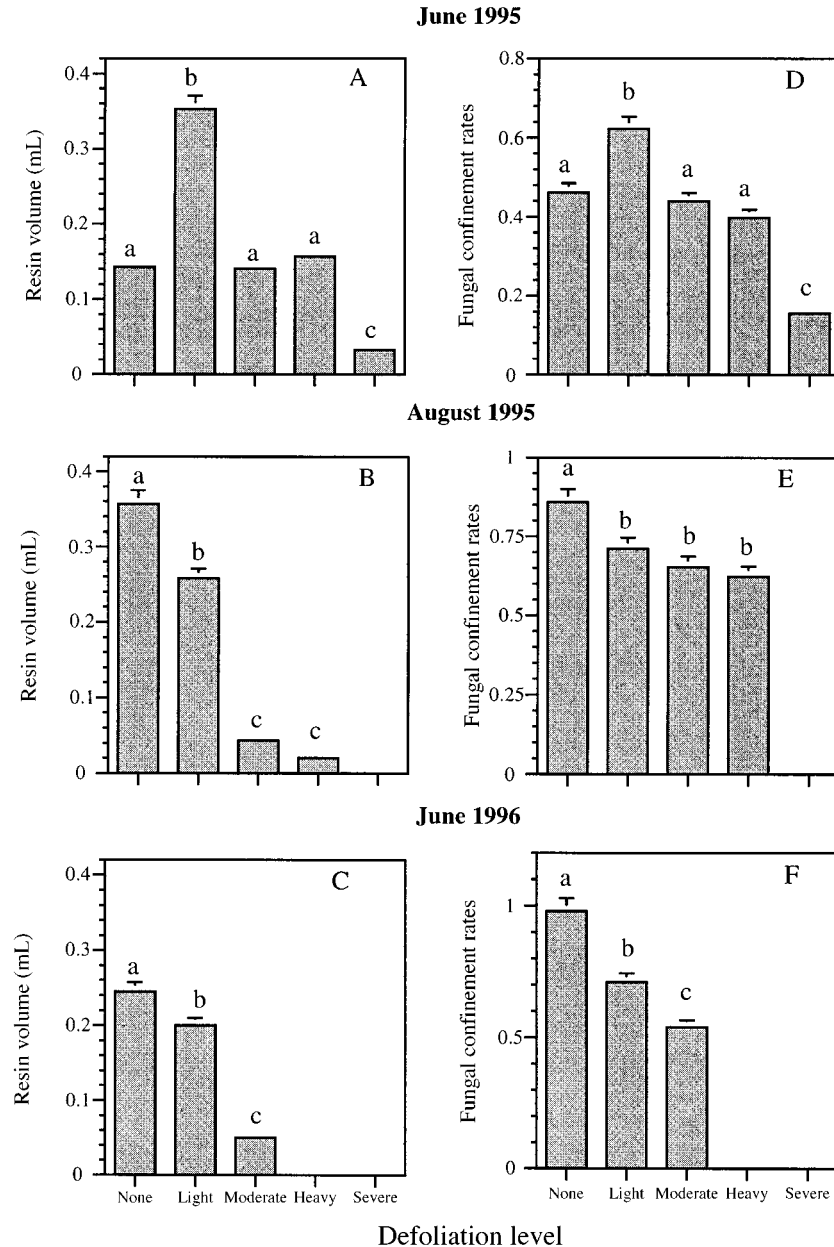


FIG. 2. Effects of feeding by *Choristoneura pinus pinus* on *Pinus banksiana* resin volume and fungal confinement rates in the phloem following inoculation with *Ophiostoma ips*: means within each month followed by the same letter are not significantly different at $P < 0.05$ by Fisher's protected lsd. Standard error bars are given for each mean but are not visible for all means.

by the high confinement ratio. Fungal growth was intermediate in lightly, moderately, and heavily defoliated trees. Severely defoliated trees could not be measured, due to host mortality associated with colonization by *I. grandicollis* and *M. carolinensis*. In June 1996, fungal confinement rates again showed a strong negative relationship with defoliation levels (Fig. 2F).

The two major components of host response to simulated subcortical insect and fungal attack, primary resin flow and induced fungal confinement, showed par-

allel responses to defoliation intensity, time since defoliation, and their interactions (Fig. 2).

Growth vs. defense

Parameters of tree defense were not significantly related to tree growth rate (Table 2A, B). Of 48 potential relationships between parameters of host tree resistance and intervals of tree growth, none were significant at $P < 0.05$. There were marginally significant relationships between growth and resin flow in June 1995 and

TABLE 2. Regressions of tree growth on two types of tree defenses following defoliations of *Pinus banksiana* in July 1994.

Growth interval	Resin volume								
	June 1995			August 1995			June 1996		
	r^2	F	P	r^2	F	P	r^2	F	P
A) Nondefoliated trees									
June 1995–August 1995	0.27	1.15	0.36	0.07	0.23	0.67	0.42	1.50	0.34
June 1995–June 1996	0.80	13.20	0.06	0.02	0.06	0.81	0.79	8.06	0.06
June 1996–August 1996	0.20	0.79	0.44	0.07	0.23	0.66	0.43	1.70	0.30
August 1994–August 1996	0.29	1.19	0.35	0.00	0.00	1.00	0.36	1.10	0.39
B) Defoliated trees									
June 1995–August 1995	0.022	0.294	0.596	0.016	0.195	0.665	0.158	1.120	0.330
June 1995–June 1996	0.016	0.208	0.656	0.058	0.739	0.407	0.010	0.060	0.814
June 1996–August 1996	0.020	0.325	0.657	0.045	0.725	0.431	0.025	0.215	0.626
August 1994–August 1996	0.061	0.840	0.376	0.040	0.506	0.491	0.096	0.639	0.454

Note: Resin volume is a constitutive defense of *P. banksiana*; confinement of the fungus by resin flow is an induced defense.

June 1996 and fungal confinement in August 1995 and June 1996, in nondefoliated trees only ($P = 0.06, 0.06, 0.06,$ and $0.07,$ respectively, with r^2 ranging from 0.70 to 0.86) (Table 2). In each of these four cases, the slope was positive.

Effects of foliar feeding by C. pinus pinus on insect colonization of host subcortical tissue and on host mortality

Colonization rates by *I. grandicollis* and *M. carolinensis* increased with defoliation intensity (Fig. 3A). Subcortical insects, while the three classes of damaged tree were differentially attacked, did not colonize non- and lightly defoliated trees. The defoliation level significantly influenced insect composition within a host. Of the trees colonized by *M. carolinensis* alone, 74% were heavily defoliated and the remainders were distributed among moderately (20%) and severely (6%) defoliated trees. The most common subcortical insect composition was a combination of *I. grandicollis* and *M. carolinensis*, which occurred in moderately, heavily, and severely defoliated trees. Severely defoliated trees had higher frequencies of both insects than did moderately or heavily defoliated trees. No folivores or sap-feeding insects were observed to be abundant on these trees during this period (Wallin 1996).

Trees that were colonized by subcortical insects were usually attacked by them relatively soon after defoliation (Table 3). Of the trees attacked by bark beetles, 57.1% were colonized either late in the year of defoliation or early in the next year, 43.9% were colonized during the second year, but none were colonized during the third year. Of the trees attacked by woodborers, 43.0% were colonized either late in the year of defoliation or early in the next year, 43.0% were colonized during the second year, and 14.9% were colonized during the third year. *I. grandicollis* completed colonization of a tree within days, whereas colonization of a tree by *M. carolinensis* extended over several years. Of trees colonized, the density of insect attack did not

vary significantly among defoliation levels ($df = 2, P = 0.07$).

Across study sites, *I. grandicollis* usually colonized trees before *M. carolinensis* ovipositional niches were observed. The likelihood of a tree initially colonized by *I. grandicollis* being subsequently colonized by *M. carolinensis* was 100.0% for moderately, 8.69% for heavily, and 95.05% for severely defoliated trees. The likelihood of a tree colonized first by *M. carolinensis* being subsequently colonized by *I. grandicollis* was 0% for moderately, 7.69% for heavily, and 0% for severely defoliation.

Mortality to *P. banksiana* during 1994–1996 was positively related to defoliation (Fig. 3B). There was no mortality among nondefoliated or lightly defoliated trees. There was 30% mortality of moderately defoliated trees. Among heavily and severely defoliated trees, mortality levels were 82% and 100%, respectively. No trees died without association with *I. grandicollis* or *M. carolinensis*.

DISCUSSION

These results indicate that removal of leaves by insect folivores can increase tree susceptibility to subcortical insects and their symbiotic fungi. Trees that were 26–100% defoliated had a higher incidence of subcortical insect colonization and associated host mortality than did non- or lightly defoliated trees (Fig. 3). We observed two types of host responses elicited by folivory: both the volume of resin within phloem tissue, and the inducible reactions to simulated subcortical beetle–fungal invasion, were altered. Non- and lightly defoliated trees produced a voluminous flow of resin and demonstrated rapid induced responses against the fungal pathogens, which together halted colonization by *Ips grandicollis* and *Monochamus carolinensis* under natural conditions (Table 3). The constitutive mechanism, resin volume, and subsequent induced defenses, histological responses to infection (Fig. 2) and allelochemical accumulation (Wallin and Raffa 1999),

TABLE 2. Extended.

Fungal confinement rate								
June 1995			August 1995			June 1996		
<i>r</i> ²	<i>F</i>	<i>P</i>	<i>r</i> ²	<i>F</i>	<i>P</i>	<i>r</i> ²	<i>F</i>	<i>P</i>
A) Nondefoliated trees								
0.01	0.00	0.99	0.03	0.07	0.78	0.34	1.00	0.42
0.34	1.50	0.30	0.70	11.05	0.06	0.86	12.20	0.07
0.14	0.48	0.54	0.03	0.08	0.79	0.33	1.00	0.45
0.40	2.12	0.24	0.00	0.00	1.00	0.32	0.94	0.43
B) Defoliated trees								
0.100	1.300	0.260	0.139	1.608	0.233	0.196	1.460	0.272
0.070	0.930	0.353	0.063	0.671	0.432	0.049	0.312	0.569
0.103	1.377	0.263	0.133	1.532	0.244	0.030	0.185	0.682
0.119	1.622	0.227	0.110	1.254	0.289	0.050	0.317	0.594

were influenced by defoliation intensity. Host seasonal phenology and time since defoliation compounded the patterns of these relationships. Defoliated *Pinus banksiana* had variable, but usually reduced, resin flow volumes and fungal confinement rates relative to nondefoliated trees. These parameters of defense accompanied changes in *P. banksiana* monoterpene concentrations and composition, which followed similar patterns.

The responses to defoliation were more pronounced in induced than constitutive defenses against subcortical organisms (Wallin and Raffa 1999).

The observation that photosynthetic rates were not influenced by defoliation is somewhat surprising, given that such changes have been observed in other systems (Nowak and Caldwell 1984, Waring 1987, Krause and Raffa 1996). Our measured photosynthetic rates of nondefoliated trees are similar to those reported for other pines (Gower et al. 1993b, Reich et al. 1995, Stenberg et al. 1995), including jack pine (Green 1998). Based on the absence of changes in photosynthetic rates, removal of leaf area by *Choristoneura pinus pinus* (Fig. 1A) likely reduced the total amount of photosynthate produced by a tree, and therefore generated source limitations. However it should be noted that we only measured photosynthetic rates once during the study and perhaps subsequent measurements would modify these conclusions.

Radial growth decreased at high defoliation intensities, which agrees with observations by Kulman (1971) and Volney (1992). Because there were no differences in growth rates prior to defoliation between subsequently defoliated and nondefoliated trees, and because growth of nondefoliated trees remained constant during the study period, the differential growth rates observed among defoliation levels can likely be attributed to feeding by *C. pinus pinus*. However, the effect of defoliation on tree growth was not negative across all defoliation intensities. Moderately defoliated trees grew significantly more over the two-year study period than trees that were not defoliated, which agrees in part with models of overcompensation (Ericsson et al. 1980).

Our data do not indicate a consistent trade-off between growth and defense (i.e., resin flow or fungal confinement vs. growth) as predicted by the growth differentiation balance hypothesis (Table 2). The absence of such a trend may reflect the involvement of multiple processes and costs, such as transport, storage, and enzymatic conversions that affect the accumulation

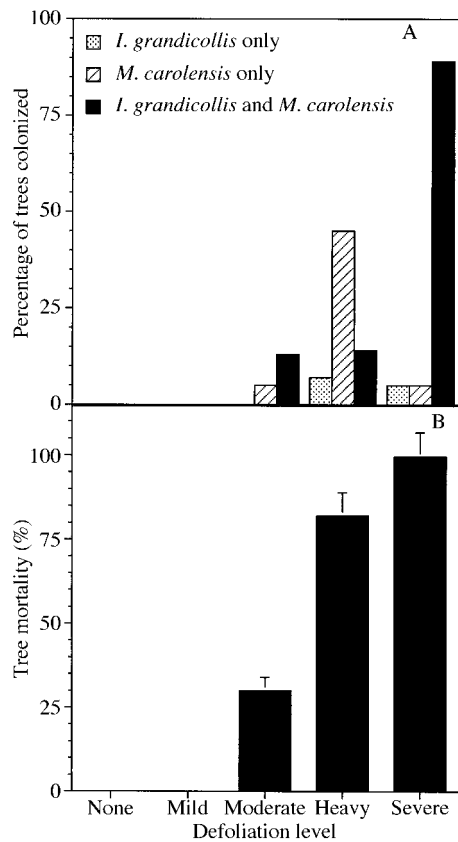


FIG. 3. Effects of *Choristoneura pinus pinus* feeding on *P. banksiana*: (A) Subcortical insect compositions two years following defoliation and (B) mortality two years following defoliation ($\chi^2 = 54.56, P < 0.001$). Error bars indicate 1 SE.

TABLE 3. Effects of foliage feeding by the budworm *Choristoneura pinus pinus* on *Pinus banksiana* trees and on the trees' colonization by the bark beetle *Ips grandicollis* and the wood borer *Monochamus carolinensis*.

Defoliation level	August 1994–June 1995				June 1995–October 1995			
	<i>I. grandicollis</i>		<i>M. carolinensis</i>		<i>I. grandicollis</i>		<i>M. carolinensis</i>	
	Dead trees	Entrance sites	Dead trees	Entrance sites	Dead trees	Entrance sites	Dead trees	Entrance sites
None	0	0	0	0	0	0	0	0
Light	0	0	0	0	0	0	0	0
Moderate	7	5.3 (1.2)	9	10.9 (4.2)	5	2.5 (0.4)	3	8.9 (4.2)
Heavy	12	5.0 (1.0)	10	9.7 (5.3)	7	10.3 (4.6)	9	17.9 (4.2)
Severe	14	6.5 (3.5)	16	6.7 (2.1)	5	6.45 (3.2)	4	8.9 (2.6)

Note: Data are number of trees dying per defoliation level and number of entrance sites per 200 dm² bark surface area (mean and 1 SE) on newly colonized trees during the stated time interval.

of allelochemicals in plants, as opposed to substrate availability only (Gershenson 1994, Steele et al. 1995). It may also reflect the important role of monoterpenes in conifer defense against subcortical insects and pathogens, as the growth–differentiation balance hypothesis frequently does not predict the outcome of systems in which products of 1-deoxy *d*-xylulose 5-phosphate pathway (Lichtenthaler 1999) and mevalonic acid pathway synthesis are important (Gershenson 1994, Koricheva et al. 1998b).

Resin flow and fungal confinement rates responded to defoliation and simulated bark-beetle attack in a relatively similar fashion (Fig. 2). Host physiological responses differed within the growing season. These responses may relate to changes in allocation patterns and physiological requirements of the host (Mooney 1972, Chapin et al. 1990, Lewinsohn et al. 1991, Lorio 1993). Seasonal patterns in tree responses may also relate to phenologically based histological changes. Early in the growing season, fungi can grow through newly formed large-diameter, thin-walled phloem cells; conversely the transition to thick-walled, flattened-diameter cells later in the growing season can slow fungal penetration (Lieutier and Berryman 1988).

I. grandicollis and *M. carolinensis* differed in their colonization patterns. *I. grandicollis* did not independently colonize moderately defoliated trees, suggesting either that *I. grandicollis* was unable to exploit this resource, or that the substrate was rapidly colonized by *M. carolinensis* following *I. grandicollis* attack. Field observations on the sequence of arrival (Wallin 1996) and the known responses of *M. carolinensis* to *Ips* pheromones (Wood 1982, Raffa 1991) support the latter conclusion. Conversely, *M. carolinensis* commonly occurred alone in heavily defoliated trees, suggesting that their full exploitation of this resource competitively excluded *I. grandicollis*. This agrees with previous reports that competition with cerambycids can substantially reduce the reproductive potential of bark beetles in weakened trees (Flamm et al. 1993, Schroeder and Weslien 1994). Results of our companion study (Wallin and Raffa 1999) indicate that bark beetle arrival

rates were more strongly associated with the chemical composition of constitutive than reaction phloem chemistry.

It is conceivable that *M. carolinensis* and *I. grandicollis* preferred the same trees as *C. pinus pinus* for reasons independent of *C. pinus pinus* feeding. However this seems unlikely for several reasons: first, trees that are predisposed to colonization by bark beetles and wood borers typically show reduced growth rates prior to colonization (e.g., Mahoney 1978, Raffa and Berryman 1983, Waring 1987, Klepzig et al. 1991, Waring and Cobb 1992). Conversely, no such pattern has been observed for *C. pinus pinus*, despite the high degree of attention given to this insect from a pest-management perspective (Clancy et al. 1980, McCullough and Kulman 1991, Volney 1992). Thus, the identical growth rates prior to defoliation between subsequently defoliated and nondefoliated trees, and the absence of any correlation between predefoliation growth rate and woodborer attack, argue against the likelihood of an unknown covariant. Secondly, there was a clear sequence of herbivory, in which defoliation by *C. pinus pinus* occurred first, followed by subcortical colonization by *I. grandicollis* and *M. carolinensis*. If these trees were simultaneously susceptible to all three herbivores, such as due to a common genotype that conferred low resistance against all of these organisms, a random temporal pattern would be expected. Furthermore, if susceptibility were independent of folivory, the fact that seasonal flight activities by *I. grandicollis* and *M. carolinensis* begin before and extend through the flight period of *C. pinus pinus* (Clancy et al. 1980, Raffa 1991) would likely yield the opposite sequence, in which subcortical insects attacked first. Third, the spatial distribution of bark beetles and wood borers such as *Ips* and *Monochamus* is usually aggregated in response to stresses that are likewise clustered in nature (Klepzig et al. 1991, Bentz et al. 1996). However, these subcortical insects showed a scattered distribution, which coincided with defoliation in our study sites.

General models of response to stress have received extensive attention in recent years, and provide a basis

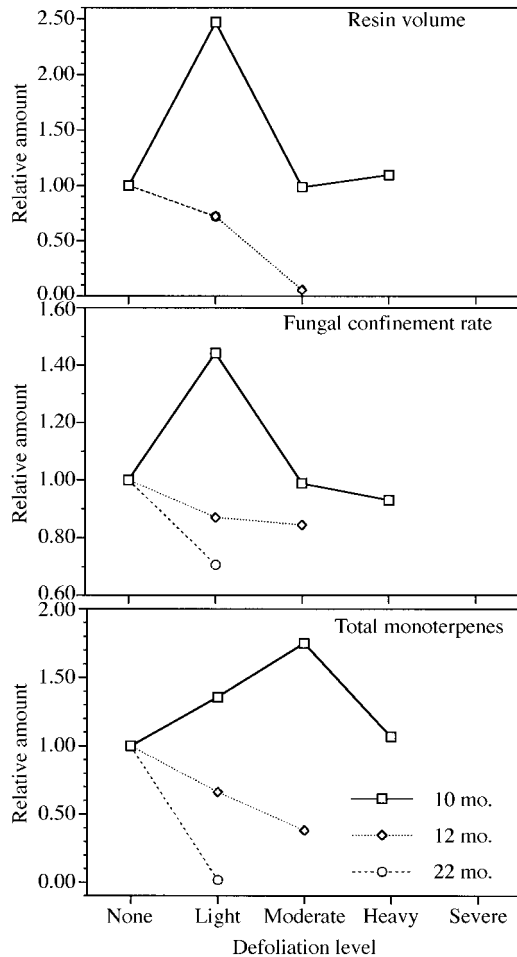


FIG. 4. Influence of stress duration on the effects of defoliation intensity on *Pinus banksiana* resistance to subcortical insects and fungi. Three parameters of resistance are shown, across four intensities of natural defoliation, and at three post-defoliation sampling intervals. Data are normalized for comparative purposes, so that the value in the absence of defoliation is always 1.0. Data are from Fig. 2, and from Wallin and Raffa (1999). When mortality within a defoliation level prior to a sample was $\geq 20\%$, values are excluded, due to potential biases arising from elimination of trees from the sampling pool.

for our overall understanding of resource allocation to various functions (e.g., Mooney 1972, Coley et al. 1985, Lorio 1986, Mattson and Haack 1987, Chapin et al. 1990, Herms and Mattson 1992, Koricheva et al. 1998a). Our observation that the same defense parameters can respond to defoliation in both parabolic and uniformly inverse fashions (Fig. 2), with time since defoliation as a crucial variant, provides support for both the growth-differentiation (Lorio 1986, Herms and Mattson 1992) and plant stress (Mattson and Hack 1987, Waring 1987, Koricheva et al. 1998b) models of plant resistance. That is, what are often viewed as competing interpretations might in fact represent a continuum along a time scale, at least in some systems (see Fig. 4). Three parameters of host resistance, resin flow

rate, fungal confinement rate in response to challenge inoculation, and induced monoterpene concentration in response to challenge inoculation (data from Fig. 2 and Wallin and Raffa [1999]), are plotted against defoliation intensity at three intervals after initial defoliation stress. The data are normalized for comparative purposes, so that each parameter's value in the absence of defoliation is one. Because mean observations could be biased by high mortality eliminating trees prior to sampling, intervals at which mortality was $\geq 20\%$ are not included in this figure. The same pattern was observed for each defense parameter: there was an initial parabolic relationship between stress and defense, but as the effects of stress continued, these relationships became inverse linear. Available physiological information on tree responses to defoliation suggests possible mechanisms, such as decreased resin volume (sink) and allelochemicals (Wallin and Raffa 1999) that could occur over time in defoliated (source-limited) trees (Webb 1981, Gregory and Wargo 1986). Patterns such as those in Fig. 4 will surely differ among various species interactions, stresses, and chemical groups. However, our results suggest that for at least one form of source-limiting stress, defoliation, integrative models among supposedly competing theories can advance our understanding of plant-herbivore interactions.

These temporal patterns may partially explain why various studies on plant-mediated effects on interguild interactions have yielded conflicting results. If the pattern of plant response to increasing biotic stress changes with time since the onset of stress, then a few relatively simple physiological relationships can generate a multitude of complex relationships at the population and community levels. Incorporating a dynamic temporal component into general models of plants defense theory can thus improve their robustness and applicability to natural systems.

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