

Comparison of insect, fungal, and mechanically induced defoliation of larch: effects on plant productivity and subsequent host susceptibility

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Summary. Larch sawfly, *Pristiphora erichsonii* Hartig, and larch needlecast fungus, *Mycosphaerella laricina* (R. Hartig) Neg., are early season defoliators restricted only to *Larix* host trees. Larch defoliation (100%) by either the fungus or insect, but not mechanical removal, induced systemic responses that reduced sawfly consumption and digestion rates one year later. In a feeding behavior assay, larvae quickly abandoned seedlings previously defoliated by *M. laricina*. Adult female oviposition choice and egg deposition were unaffected. Seedling growth was not affected during the year of defoliation by *M. laricina*, but was significantly reduced one year later. Defoliation by *M. laricina* reduced stem volume, radial growth, root biomass and new shoot production. The latter tissue is the only oviposition resource for larch sawfly, and, in contrast, is not influenced by sawfly feeding. We hypothesize that *M. laricina* infection may limit larch sawfly populations where both species coexist. However, this reduction is at a substantial net cost to larch productivity.

Key words: *Larix decidua* – *Mycosphaerella laricina* – *Pristiphora erichsonii* – Carbon allocation

Defoliation can negatively influence insect folivores by reducing the quantity of plant tissue available for oviposition and consumption, decreasing foliage quality through induced defenses or nutrient depletion, and various combinations thereof. Such defoliation-induced changes within host plants may partially regulate the population dynamics of some leaf-feeding insects (Baltensweiler et al. 1977; Rhoades 1983). Although early studies focused on the impact of plant changes on the species causing plant injury (Whittaker and Fecny 1971; Levin 1976), evidence now indicates that herbivory can affect interspecific associates and competitors (Suzuki 1980; Karban et al. 1987). Local infections of plant

pathogens can also induce systemic antibiosis against insect folivores (McIntyre et al. 1981).

Fungal induced resistance to species of Coleoptera (Ahmad et al. 1985), Hemiptera (Mathias et al. 1990), and Lepidoptera (Funk et al. 1983) has been demonstrated for agronomic crops (Clay 1988). Trees infected with fungi may also be less susceptible to herbivory from gall-making species of Diptera (Bergdahl and Massola 1985), Homoptera (Lasota et al. 1983) and Hymenoptera (Taper et al. 1986). Little is known, however, on the effects of fungal induced defoliation on free-feeding insect folivores and the productivity of host trees.

European larch, *Larix decidua* Miller, is a shade intolerant, winter deciduous conifer (Olaczek 1986). After spring needle growth, succulent branch shoots grow from dormant buds for 4–6 weeks before becoming woody. *L. decidua* was introduced into the United States in 1850 (Nyland 1965), and is now widely planted because of its rapid growth rate, high genetic diversity, and favorable wood quality (Einspahr et al. 1984). However, *L. decidua* is among the most susceptible species to defoliation by larch needlecast fungi (Ostry and Nichols 1989).

Larch needlecast, *Mycosphaerella laricina* (R. Hartig) Neg., causes early season defoliation of larch in its native Europe (Hartig 1895), and was recently discovered in the United States (Patton and Spear 1983). Disease symptoms may appear before new shoot growth is complete. Ascospores and conidia predominate in May–July, and August–September, respectively (Palmer and Ostry 1986). The effects of *M. laricina* defoliation on *L. decidua* productivity and co-occurring insect folivores are unknown.

The larch sawfly, *Pristiphora erichsonii* Hartig (Hymenoptera: Tenthredinidae), is one of the major insect defoliators on larch (Kulman 1971). Following its apparent introduction from Europe (Coppel and Leius 1955; but see Wong 1974) *P. erichsonii* contributed to widespread mortality of larch throughout the northern United States and Canada (Nairn et al. 1962). Recent outbreaks of larch sawfly have occurred on *L. decidua* in Wisconsin and Canada (Drooz 1985).

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Larch sawfly biology is closely tied to characteristics of its host. *P. erichsonii* is monophagous on larch, univoltine, and parthenogenetic. Adult females emerge in spring from cocoons in the duff and oviposit only into succulent, current year branch shoots. Larvae emerge 7–10 days later, and feed on the foliage tufts present on older (1+ year) branches. Although needles on succulent shoots contain anti-feedant diterpenes (Wagner et al. 1983), trees are not immune to complete defoliation (Drooz 1960).

Current outbreaks of larch needlecast and larch sawfly on their native host in Wisconsin provided an opportunity to determine whether fungal defoliation influences insect development and behavior and seedling productivity. Larch seedlings were experimentally defoliated (100%) by sawfly larvae, fungi, and hand shears to assess sawfly feeding performance and behavior. The root:shoot biomass of seedlings was measured to assess defoliation effects on productivity. Two supplemental experiments measured effects of artificial defoliation on sawfly oviposition choice, and the susceptibility of larch trees to *M. laricina*.

Materials and methods

Effect of defoliation agent on sawfly performance and seedling growth

Insects and seedlings. In October 1986, 3-year-old seedlings were bare-root lifted from the Department of Natural Resources state nursery, at Boscobel, WI and placed in dark storage at 4–5° C. In March 1987, trees were planted in 6 liter plastic pots containing quartz sand : field soil : compost : sphagnum peat in a 7:1:1:1 ratio, and held outdoors until use. Trees were watered regularly with a fertilizer solution of 17% ammoniacal nitrogen, 6% available phosphoric acid, 6% potash, and standard mixture of micronutrients at 0.25 t per 3.8 liter water.

Sawfly larvae were reared from egg-laden shoots collected in June, 1988 from a naturally infested *L. decidua* stand in Clark County, WI (T.24N.-R.4W., s. 18). Clipped shoots with eggs were placed in water until larval eclosion. Larvae were reared at 21–23° C, 40–60% relative humidity, 16 light: 8 dark, in plastic boxes (21.5 × 6.5 × 6.0 cm), and received fresh *L. decidua* foliage and a gentle spray of distilled water every 24–36 h (Heron and Drouin 1969).

Defoliation treatments. In June 1987, 25 seedlings were randomly assigned to each of four treatments. These consisted of 100% defoliation using *M. laricina*, *P. erichsonii*, or hand shears, or no defoliation (controls). Potted seedlings were transferred to the appropriate field site for defoliation. A natural outbreak of *M. laricina* infection on *L. decidua* at the Coulee Experimental Forest, LaCrosse Co., WI (T.16N.-R.5W., s. 16), provided inoculum for the fungal defoliation. Defoliation by sawflies was performed in a similar *L. decidua* plantation in Clark Co., WI (T.24N.-R.4W., s. 18), to avoid infection by *M. laricina*. A screen fence protected seedlings from native mammal herbivores at each site. Hand sheared and control seedlings were held outdoors in Madison, WI (T.7N.-R.9E., s. 16). All seedlings were exposed to full sunlight, and watered every 4–6 days during the treatments. Although the sites were 90–240 km apart, correlation analysis of weekly temperatures near the three field sites indicated that all seedlings experienced similar temperatures during the treatment period ($P < 0.0001$).

The rate of insect and manual defoliation was performed so as to correspond to the natural rate of leaf removal by *M. laricina*.

From 5–15 larvae (as needed) were placed on each seedling at any one time, to achieve the observed fungal defoliation rates. The appropriate level of defoliation with hand shears was estimated visually. The entire treatment period required approximately 28 days.

Following the defoliations, all seedlings were transported to Madison, WI and held in greenhouses at ambient conditions. On 18 October, seedlings were moved outdoors to topless coldframes, where they were held for the winter. Seedlings infected with *M. laricina* were held under similar conditions nearby (6 km) to prevent infection of the other seedlings.

In spring 1988, trees within treatments were randomly assigned to larval development, larval behavior, or larch biomass productivity analysis.

Larval development. Recently molted fifth instar larvae were held 12 h without food to allow emptying of their digestive tracts prior to assay. Each larva was weighed (± 0.1 mg), and housed in a transparent, plastic box (21.5 × 6.5 × 6.0 cm) with a known weight of foliage. After 48 h, the larva, frass and residual foliage were collected, oven dried for 72 h, and weighed. Larval consumption, digestion and feeding efficiency rates were determined gravimetrically (Waldbauer 1968). Experiments were performed in June in a growth chamber at 22–23° C, 55–60% relative humidity and constant light. There were 9 seedlings per treatment, with one insect per seedling.

Consumption and food conversion rates (mg/day) were log₁₀ transformed, and digestibility (aresin (sqrt %)) transformed to correct heteroscedasticity of variances. Oneway analysis of variance (ANOVA) using the general linear models (GLM) procedure was conducted for each performance variable (SAS 1990). Mean separation tests were performed using least-squares means (LSM) ($\alpha = 0.05$) (SAS 1990). A preliminary experiment demonstrated that these variables were not influenced by the solitary feeding conditions used in this assay.

Larval behavior. One second instar (4–5 d old) larva was placed on each of three randomly selected branches per seedling in June. Larvae were isolated by filter paper barriers secured to the base of each experimental branch. Thus, larvae could either feed on one branch, or abandon the food source by dropping from the branch. A cardboard skirt coated with petroleum jelly extended from the stem to the drip line around each seedling to capture dispersing larvae. Larvae were checked daily for 9 days. Because branches are likely to have individual properties (Graham 1931; Gill and Halverson 1984), the time spent on a branch was recorded for each larva ($N = 6$). There were two seedlings per treatment. Insects and trees were kept in a walk-in chamber at 21–22° C, 15 light: 9 dark, and misted daily with distilled water. Data were log₁₀ transformed and analyzed using GLM and LSM ($\alpha = 0.05$) (SAS 1990).

Larch productivity. Seedlings not used in either bioassay were harvested on 30–31 August 1988, 14 months after defoliation. Soil was carefully excavated and washed from the root mass with cold water. Roots had grown throughout the soil and were not pot bound. Terminal leader growth was measured (mm) in 1987 and 1988. Seedlings were then clipped at the root collar. Root collar radial growth was determined using a binocular microscope. Seedling stems are conical, so stem volume was estimated by the equation: $\text{vol} = \text{height} \times ((\pi \text{radius}^2)/3)$. Total foliage and shoots produced in 1988 were separated. All biomass was dried at 80° C for 5 days and weighed. Only seedlings defoliated by fungi or insects and controls were available for this analysis.

Productivity variables were log₁₀ transformed to normalize variances. Each variable was analyzed for treatment effects using GLM and LSM ($\alpha = 0.05$) (SAS 1990). Correlation coefficients were generated to measure the degree of association between plant height and biomass production. There were no significant differences in seedling height among treatments prior to the 1987 defoliations ($F = 1.05$, $df = 2,9$, $P < 0.39$).

Effect of artificial defoliation on *P. erichsonii* oviposition

To test whether defoliation influences ovipositional preference, females in 1988 were simultaneously offered shoots from control and previously mechanically defoliated trees. Defoliation was performed with hand shears with 75% of each leaf removed in 1987. Seedlings were maintained as described for the previous experiments. Females were reared from cocoons collected in April, 1988 from an infested *L. decidua* plantation in Wisconsin (T.24N.-R.4W., s. 18).

In 1988, shoot choice, egg number, and egg hatch were tested using a paired experiment. One shoot from each treatment was snipped from seedlings and inserted through cardboard into a 200 ml water cup. A 1 liter glass chimney lamp (Drooz 1960) was placed over each shoot pair and taped to the cardboard. One female < 24 h old was placed in each chimney lamp for 36 h at 23–25° C, 60–75% relative humidity, and 16 light: 8 dark. The chimney lamp top was covered with cheesecloth to prevent sawfly escape. Females and shoots were gently sprayed with distilled water every 12 h. After 36 h, females were dissected for the presence of eggs. Females that both did not contain eggs and did not oviposit were considered reproductively immature or sterile, and eliminated from further analysis.

Oviposition choice was analyzed using a Chi-Square test (Brower and Zar 1983). Number of eggs oviposited, percent egg hatch, and number of larvae were each tested for treatment effects using ANOVA (SAS 1990). Thirty-four females were tested.

Effect of defoliation on *M. laricina* infection

The potential effect of artificial defoliation on subsequent year infection by *M. laricina* was studied in a *L. decidua* plantation at the Coulee Experimental Forest in 1986 and 1987. Two-year-old seedlings were planted in 1978 at a spacing of 1.5 × 1.5 m. A 30 m × 60 m area consisting of 6 contiguous experimental blocks (30 × 10 m) was selected for study.

In June 1986, five 10-year-old trees, approximately 2 m tall, within each block were selected based on uniform size and shape, and randomly assigned to a defoliation treatment of 0%, 33% 66%, 33+33% or 66+33%. Percentages indicate the approximate leaf length removed from each needle using hand shears. The latter two treatments refer to an initial defoliation of either 33% or 66%, followed by another 33% of the original needle length clipped 30 days later. Defoliation treatments were completed between July 3 and August 10. All trees were surveyed September 30 for *M. laricina* defoliation and found to be symptom-free.

On 7 July and 15 August 1987, trees were visually monitored for defoliation by *M. laricina*. Percent defoliation was recorded as the average estimate of two observers to the nearest 10% (Ostry and Nichols 1989). Effects of artificial defoliation on subsequent year natural *M. laricina* defoliation were analyzed using ANOVA (SAS 1990).

Results

Effect of defoliation agent on sawfly performance and seedling growth

Larval development. Larval and fungal defoliation had significant effects on the relative consumption rate of larch sawfly ($F=9.49$, $df=3,32$, $P<0.001$). Larval consumption rates were reduced 56.2% and 42.7% by prior defoliation due to fungi and sawfly larvae, respectively (Table 1). Fungal and insect defoliations also significantly reduced the approximate digestion rates of larvae by

Table 1. Feeding and development by *P. erichsonii* on *L. decidua* one year after 100% defoliation by various treatment agents

Treatment	RCR (mg)	AD (%)	RGR (mg)
Control	8.9 ± 1.0 a	92.6 ± 2.7 a	0.02 ± 1.0 a
Hand shears	7.3 ± 0.8 ab	88.8 ± 3.0 ab	0.05 ± 0.8 a
Sawfly larvae	5.1 ± 0.6 bc	76.8 ± 3.9 bc	0.07 ± 0.6 a
Fungi	3.9 ± 0.4 d	70.7 ± 9.1 c	0.05 ± 0.6 a

Mean ± SEM within columns followed by different letters are significantly different; $\alpha=0.05$, $N=9$

Table 2. *P. erichsonii* feeding times on seedlings before host abandonment one year after 100% defoliation by various agents

Treatment	Days feeding (means ± sem)
Control	4.3 ± 1.1 a
Hand shears	5.8 ± 1.4 a
Sawfly larvae	3.2 ± 0.7 ab
Fungi	2.3 ± 1.1 b

Data followed by different letters are significantly different; $\alpha=0.05$, $N=6$

23.7%, and 17.1%, respectively ($F=4.27$, $df=3,32$, $P<0.013$).

The relative growth rate of larvae was not significantly affected by previous defoliation ($F=1.12$, $df=3,32$, $P>0.36$). Similarly, there were no significant differences in the ability of larvae to convert ingested foliage to biomass ($F=1.58$, $df=3,32$, $P>0.22$) or digested food to biomass ($F=1.36$, $df=3,32$, $P>0.28$).

Mechanical defoliation did not significantly affect any parameter of larch sawfly performance. However, values were consistently between those on control and biotically defoliated plants.

Larval behavior. Larvae remained on seedlings that were previously defoliated by *M. laricina* only about half as long as on controls ($F=3.68$, $df=3,19$, $P<0.031$) (Table 2). Over 83% dispersed from previously fungal infested seedlings within 24 h. Larval dispersal from sawfly defoliated trees was statistically equivalent to those on fungal treatments and controls.

Larch productivity. Seedling growth was not affected during the year of defoliation by insects or fungi. However, fungal defoliation significantly reduced productivity during the following year (Table 3). New shoot biomass was reduced by 71.4% on treated seedlings. Estimated stem volume growth was only 41% that observed on control and sawfly defoliated seedlings. *M. laricina* defoliation also significantly reduced root collar diameter and root weight. Total seedling biomass was significantly less following fungal infection than for control or sawfly defoliated seedlings. Leader growth and final plant height were not significantly affected by sawfly or fungal defoliation. Sawfly defoliation had no significant impact on any measure of tree productivity.

Table 3. Effects of 1987 defoliation (100%) by insects and fungi on *L. decidua* seedling growth over two years

	Control (n=5)	Insects (n=4)	Fungi (n=3)	P ≤ 0.05
a. 1987				
Leader (cm)	10.7 ± 1.9	9.0 ± 3.1	4.2 ± 1.6	no
Root Collar (mm)	9.2 ± 0.5	8.3 ± 0.5	7.5 ± 0.7	no
Stem volume (cm ³)	16.0 ± 1.9	12.3 ± 2.1	10.3 ± 2.2	no
b. 1988				
Leader (cm)	10.0 ± 5.8	5.8 ± 1.8	4.2 ± 1.6	no
Root: Shoot	1.02 ± 0.2	0.86 ± 0.2	0.74 ± 0.0	no
New Shoots (g)	2.1 ± 0.4 a	1.7 ± 0.3 a	0.6 ± 0.3 b	0.007
Root Collar (mm)	11.7 ± 0.7 a	11.6 ± 0.5 a	9.1 ± 0.8 b	0.032
Stem volume (cm ³)	30.0 ± 3.5 a	25.5 ± 3.1 a	15.9 ± 2.6 b	0.032
Total Height (cm)	61.0 ± 2.9	64.3 ± 3.8	57.4 ± 3.3	no
Total Biomass (g)	55.5 ± 1.7 a	58.2 ± 1.8 a	29.8 ± 1.5 b	0.004

Means ± SEM within rows followed by different letters are significantly different; α = 0.05

Table 4. Pearson product-moment correlations (r) between *L. decidua* height and biomass following defoliation (* P < 0.0001)

Treatment	Root: Shoot	New shoots	Foliage
Control	0.55	-0.21	-0.67
Insects	-0.97*	0.48	0.83
Fungi	-0.99*	0.70	0.07

Correlation analysis indicated a strong negative relationship between seedling height and the ratio of root: shoot biomass following larval and fungal defoliation (Table 4).

Effect of artificial defoliation on *P. erichsonii* oviposition

Defoliation did not influence subsequent year oviposition choice by larch sawfly. Of the 21 females that oviposited, only two oviposited in both shoots. Shoot choice between treatments did not differ from the expected 1:1 ($\chi^2 = 0.81$, $P > 0.05$). Over 64% of the females were alive after the 36 h experiment.

No significant impact from 75% defoliation was observed on the number of eggs oviposited per shoot, percent egg hatch, or number of progeny (Table 5). Number of eggs oviposited and progeny produced varied con-

Table 5. Effects of artificial defoliation (75%) on subsequent year *P. erichsonii* egg and larval production (means ± SE)

Treatment	Eggs per shoot	% Egg Hatch's	No. Larvae
Control	8.6 ± 6.3	65.5 ± 45.9	7.6 ± 1.8
Hand shears	12.3 ± 8.3	86.8 ± 17.7	11.1 ± 13.7
Significance level	P < 0.40 F _{1,20} = 0.82	P < 0.22 F _{1,20} = 1.63	P < 0.57 F _{1,16} = 0.34

siderably within each treatment. Females oviposited from 2–26 and 3–18 eggs in shoots from defoliated and undefoliated seedlings, respectively. Egg hatch varied from 0–100% within each treatment. Consequently, the number of first instar progeny varied from 0–26 on defoliated shoots and 0–16 on control shoots.

Effect of defoliation on *M. laricina* infection

Previous defoliation did not alter the susceptibility of *L. decidua* to needlecast disease. On July 7, fungal induced defoliation ranged from 20–40% among treatments (F = 0.99, df = 4,25, $P > 0.43$). On August 15, all trees were completely defoliated.

Discussion

Prior defoliation can affect both larch sawfly performance and *L. decidua* productivity. Larvae consumed less foliage on treated seedlings, particularly following defoliation caused by *M. laricina* infection. Similar results have been observed with larch bud moth, *Zeiraphera diniana*, which consumed less foliage on previously defoliated branches, possibly due to reduced protein levels and increased fiber content in needles (Baltensweiler et al. 1977). The reduced consumption exhibited by *P. erichsonii* larvae, however, did not influence their growth rate. This suggests that even though larvae consume less foliage following *M. laricina* defoliation, they may be more efficient at converting foliage to biomass than those larvae feeding on other seedlings.

Increased larval efficiency of converting ingested and digested food to biomass on fungal-infected larch suggests that the nutritional quality of foliage may increase following defoliation. However, the relationships between feeding rates and efficiencies are complex (Scriber and Slansky 1981), and may be regulated by the simul-

tanous induction of nutrients and allelochemicals following defoliation (Wagner and Evans 1985).

Foliage produced following *M. laricina* infection also induced second instar larvae to abandon their host plants. Host abandonment under natural conditions can cause high larval mortality, and thus reduce sawfly populations. Larch sawfly larvae are poorly adapted for dispersal between trees, and mortality of early instars increases substantially with the distance travelled (Lejeune 1955; Ives 1963). Host abandonment may also affect sawfly population dynamics through delays in larval feeding. Brief periods of starvation increase larval mortality, decrease the lipid concentration and size of eonymphs, and decrease egg production (Heron 1955; Graham 1956).

Food availability is especially critical during the fourth and fifth instars when peak larval feeding occurs. Larval consumption peaks in July (Drooz 1960), when *M. laricina* may cause substantial defoliation. In this study, fungal induced defoliation was extensive and severe, causing 100% defoliation throughout the plantation by mid-August. An intensive outbreak of *M. laricina* might leave little food available for larch sawfly development, significantly reducing the vigor of local sawfly populations. This effect on *P. erichsonii* could continue for several years, as we found no evidence that prior defoliation affects host susceptibility to *M. laricina*.

Larch sawfly larvae could conceivably avoid *M. laricina* infected host plants if females preferentially select healthy larch for oviposition. However, oviposition choice, egg number, and larval production were not influenced by mechanical defoliation. Defoliation by larvae probably does not affect shoot choice either, as annually repeated, concentrated oviposition into individual trees has been noted for *P. erichsonii* and other sawflies. This occurs despite the availability of undefoliated, apparently healthy trees (Henson et al. 1970; Genys and Harman 1976). The possibility that *M. laricina* infection can directly influence sawfly oviposition behavior requires formal testing.

M. laricina infection may reduce the availability of ovipositional sites for sawflies, however, through its impact on shoot growth. Females oviposit into succulent shoots growing from terminal buds. In this study, *M. laricina* infection greatly reduced new shoot biomass. This contrasts with host response to equivalent levels of defoliation caused by sawflies, which did not affect shoot parameters. Moreover, sawfly induced defoliation reduces the length of individual larch shoots (Butcher 1951; Drooz and Meyer 1955), but also stimulates the production of lateral shoots from axillary buds (Nairn et al. 1962). The latter effect could increase the available ovipositional resource.

Reduced shoot production following *M. laricina* defoliation may impact long-term growth and survival of larch. Shoot growth contributes significantly to larch architecture, which is believed to optimize photosynthetic area and biomass productivity throughout the tree (Remphrey and Powell 1984, 1988). Shoot loss may have contributed to the 46% reduction in plant biomass fol-

lowing *M. laricina* infection. Therefore, *M. laricina* may seriously threaten commercial production of European larch in the United States.

Some tree species may respond to defoliation by allocating resources into shoot and height growth with a simultaneous decreased allocation to roots (Mooney 1972; Chapin et al. 1987). Rapid height growth is especially important to deciduous woody plants such as *Larix* found in early successional stages (Marks 1975). Shade intolerant species like larch may have evolved allocation pathways that maintain canopy dominance at an energy cost to root production. Our results suggest that fungal and insect defoliation induces seedlings to allocate resources into aboveground productivity and height growth. Mature trees may respond similarly, but the root: shoot dynamics for mature larch are difficult to study and requires further attention (Gower and Richards 1990).

The greater impact on larch productivity and sawfly performance caused by *M. laricina* than other methods of defoliation suggests that the duration between injury and abscission may affect host tolerance. Defoliation is often expressed on a per plant basis, but it may be best characterized as a rate of individual leaf loss (Brown and Allen 1989). Leaves remain on shoots for weeks following infection with *M. laricina*, but only minutes during sawfly feeding. Fungi infect leaves through stomates, invade neighboring cells, and cause lesions and chlorosis before leaf drop, whereas larvae quickly chew entire leaves. Mechanical defoliation using hand shears removed individual leaves most rapidly among the treatments, and had no significant effect on subsequent sawfly performance. The relatively slow rate of individual leaf loss that accompanies *M. laricina* infection may cause reduced productivity, perhaps due to cell repair and maintenance, but also allow the translocation of elicitors that stimulate systemic defense against herbivores (Ryan 1983).

These results also have implications to defoliation studies that attempt to simulate herbivory. The differential effects caused by equivalent levels of leaf removal support the view (Baldwin 1990), that phytochemical and insect responses to artificial defoliation may not adequately reflect natural conditions. Thus, the appropriate biotic agent should be used where possible, at least as a supplement to controlled, artificial treatments.

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