

# Defoliation tolerance affects the spatial and temporal distributions of larch sawfly and natural enemy populations

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**Abstract.** 1. The monophagous larch sawfly, *Pristiphora erichsonii*, requires larch, *Larix* spp., shoots for oviposition and foliage for larval development. The hypothesis that chronic defoliation reduces shoot availability for adult females, causing shifts in host use within plantations of *L. decidua* and *L. leptolepis*, was evaluated over a 3-year period.

2. Larch productivity and sawfly abundance varied six- to 10-fold among individual trees within each plantation. Sawflies concentrated oviposition on the most rapidly growing trees, and had a marginal impact on shoot production. Consequently, sawfly herbivory on individual trees remained relatively constant for 3 years, failing to support the hypothesis that *P. erichsonii* defoliation causes shifts in host use.

3. *Pristiphora erichsonii* larval performance varied 20–30% among individual host trees. The oviposition event did not significantly affect larval performance or foliar nutrient content.

4. The relationship between cocoon survival and natural enemy abundance was evaluated among fifteen *L. leptolepis* trees. Parasites and predators killed over 65% of the 18 315 cocoons sampled. The proportion of cocoons killed by parasitoids declined significantly with *P. erichsonii* density, while predation rates increased under heavily infested trees. Overall, the proportion of cocoons killed by parasitoids and predators did not vary with sawfly density.

5. Results indicate that components of host vigour, herbivore performance and natural enemy guilds exhibit substantial spatial heterogeneity among trees within plantations of exotic *Larix* trees. Moreover, individual larch can tolerate repeated oviposition and herbivory without a rapid loss in shoot production. The potential for host plant physiological tolerance to herbivory to interact with natural enemy population dynamics and behaviour so as to stabilize herbivore population patterns is discussed.

**Key words.** *Larix*, larch, herbivory, tri-trophic, productivity, insect outbreak, plant insect interactions, *Pristiphora*.

## Introduction

Spatial and temporal variation in host plant quality can affect the performance and population behaviour of insect folivores (Edmunds & Alstad, 1978; Whitham, 1978; Denno & McClure, 1983; Denno *et al.*, 1990; Dicke & Dijkman, 1992; Power, 1992). Folivores, in turn, can influence host resource availability

during their feeding and oviposition phases (Carroll & Hoffman, 1980; Dussourd & Denno, 1991; McCullough & Wagner, 1993). Such interactions can be complicated by the actions of natural enemies, which in some cases can mediate outcomes of plant–insect associations at the individual and population levels (Price *et al.*, 1980; Weis & Abrahamson, 1985; Clancy & Price, 1989; Karban, 1989; Hunter & Price, 1992; Woodman & Price, 1992; English-Loeb *et al.*, 1993). Integrated, tri-trophic studies may improve understanding of folivore population behaviour, and are needed to place single-species interactions within an appropriate (co) evolutionary context. In addition, an understanding of how direct and indirect influences on

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plant–herbivore systems interact can contribute to the development of more effective and environmentally benign natural integrated pest-management strategies.

Larch sawfly, *Pristiphora erichsonii* (Hartig), is recognized as a major insect defoliator in North America on native eastern larch, *Larix laricina* (Du Roi) K. Koch (Drooz, 1985). *Pristiphora erichsonii* is monophagous on *Larix* spp. for both egg and larval development, and responsible for periodic, widespread mortality of *L. laricina* since 1780 (Graham, 1956). Oviposition occurs directly into newly elongating larch shoots, permanently damaging the cambium, and causing characteristic shoot scarring and curling (Drooz, 1960). The number of shoots infested with eggs is generally indicative of subsequent levels of defoliation (Ives & Prentice, 1958). Larvae feed primarily on hosts selected by adult females, and cannot disperse among host trees without suffering high mortality. Full grown larvae drop into duff, enter the soil, mostly within the drip line (Ives & Turnock, 1959), and overwinter. Pupation occurs within cocoons in spring. There is one generation per year (Turnock, 1960). Cocoon mortality from natural enemies and fluctuations in soil moisture can be locally significant (MacLeod & Heimpel, 1955; Muldrew, 1955; Buckner, 1959), and may influence larch sawfly population dynamics (Lejeune, 1955). Predation by small mammals in particular is well known to cause substantial *P. erichsonii* mortality throughout its North American range (Graham, 1928; Lejeune, 1951).

Current knowledge of larch sawfly ecology stems largely from studies in natural, lowland stands of *L. laricina*. However, North American plantings of exotic *Larix* spp. are becoming widespread for their value to the pulpwood industry. *Pristiphora erichsonii* colonization of *L. decidua* and *L. leptolepis* in north-eastern United States sometimes reaches population outbreak status (Drooz, 1959; Genys & Harman, 1976). Potential temporal and spatial variation in larch quality and sawfly abundance, and the potential degree to which such variation might contribute to sawfly outbreaks on exotic larch, are the focus of this research.

This study considered the following questions: (i) Does shoot availability vary among individuals within species of exotic larch trees? (ii) Does *P. erichsonii* affect subsequent year shoot availability? (iii) Is host quality influenced by sawfly oviposition? (iv) Are cocoon natural enemy guilds influenced by sawfly density? Results are discussed in terms of plant–insect interaction theory and forest pest management.

## Materials and Methods

The production of larch shoots and distribution of ovipositional scars by *P. erichsonii* was quantified in the field for 3 years using two larch species. Plant productivity and insect behaviour were analysed for spatial and temporal variation among thirty-six *L. decidua* and five *L. leptolepis* trees. Sawfly cocoon density and rates of natural enemy attack were determined from duff samples beneath an additional fifteen *L. leptolepis* trees.

## Study sites

The principal study site consisted of a rectangular 10-acre (~4 ha), 18-year-old *L. decidua* plantation in Clark County, Wisconsin, U.S.A. The site was bordered by three agricultural fields and a *Pinus resinosa* Ait. plantation. Trees were ≈ 8–10 m tall. Defoliation by *P. erichsonii* larvae was first noted in 1985, exceeding 50% on some trees between 1985 and 1988 (F. Morse, WIDNR, pers. comm.).

A second study site consisted of a 34-acre (~14 ha), 29-year-old plantation of Japanese larch, *Larix leptolepis*, in Fulton County, Pennsylvania, U.S.A. The larch were ≈ 10–15 m tall. An outbreak of *P. erichsonii* was first observed in the early 1980s.

## Spatial and temporal variation in larch vigour and sawfly abundance

Thirty-six *L. decidua* were randomly selected from three sections within the plantation: stand interior, adjacent to the pine plantation, and adjacent to an agricultural field. Two branches (north and south facing) were randomly sampled from the mid-canopy (3–6 m) on each tree. A preliminary experiment determined that mid-canopy was most frequently attacked by *P. erichsonii*. Per cent shoot oviposition averaged 12.2% ( $\pm 1.3$  SE) in mid-canopy, 7.11% ( $\pm 1.3$ ) in upper-canopy and 8.05% ( $\pm 1.3$ ) in lower-canopy branches (Krause, 1994). The numbers of new shoots and new shoots with oviposition scars were counted for 3 years.

The mean numbers of shoots and shoots attacked per tree were logarithmically transformed, and the proportions of shoots attacked were arcsine transformed, to normalize variances. Data were analysed to determine potential effects of stand position and individual trees on host productivity and sawfly distribution using nested-ANOVA (SAS Institute, 1985). Branches were nested within trees, and trees were nested within stand section.

Five randomly selected *L. leptolepis* were also sampled at mid-canopy height as described for *L. decidua*. The numbers of new shoots and new shoots with oviposition scars were counted for 3 years. Spatial and temporal variation in shoot production and sawfly oviposition density were analysed using linear regression (Abacus Concepts, 1987). Data from thirty-six *L. decidua* and five *L. leptolepis* were analysed separately. Data were expressed on a per tree basis.

## Effects of sawfly oviposition on larval host suitability

Effects of oviposition on sawfly performance were determined using ten *L. decidua* not used in the previous experiment. Trees were randomly selected and shoots were monitored for fresh oviposition scars. On each tree, three shoots with oviposition scars and three control shoots on separate branches were enclosed in dacron polyester sleeve cages within 24 h of oviposition to prevent further oviposition. Immediately prior to egg hatch, the six experimental shoots

per tree were coated with petroleum jelly. Five to seven days later, 1-year-old shoots were clipped, stored in water vials and returned to the laboratory for bioassays.

Bioassays consisted of placing two second-instar *P. erichsonii* with foliage from one shoot in a transparent plastic box (21.5 × 6.5 × 6.0 cm) at 22–23 °C, 55–60% relative humidity, and 16 : 8 h light : dark. Larval fresh weight was recorded prior to the assay, and after an 88-h feeding period. Oviposition treatment effect on larval growth was analysed using individual shoots as experimental units ( $n = 30$  per treatment) because within-tree variation in foliar physiology and suitability to herbivores is documented for various tree species (Marquis, 1988; Sprugel *et al.*, 1991; Suomela *et al.*, 1995). Fresh weight gain (mg/day) was logarithmically transformed and analysed for treatment effects using one-way ANOVA (Abacus Concepts, 1989). Mean larval performance per tree was calculated, logarithmically transformed, and analysed for host tree effect using one-way ANOVA.

#### *Effects of oviposition and leaf injury on larval feeding performance*

To eliminate potential effects of among-tree variation on larval performance, a second bioassay was conducted. On one tree three treatments were established: oviposition with no defoliation, oviposition with defoliation, controls. Eight days after oviposition (< 24 h prior to hatch), petroleum jelly was applied to all experimental shoots to prevent egg hatch. The defoliation treatment was administered by placing 5–10 larvae on foliage for 1 h, causing < 10% defoliation (Krause & Raffa, 1995). Shoots were then clipped and returned to the laboratory for bioassays as previously described. Three third-instar larvae were fed foliage from one shoot under non-choice conditions in transparent plastic boxes (Krause & Raffa, 1992). Survival and mean larval weight (mg) were recorded after 24, 72 and 120 h of feeding. Dependent variables were transformed to normalize variances. Data were analysed for treatment effects using repeated-measures and one-way analysis of variance techniques (Abacus Concepts, 1989). There were eight replicates.

Foliar nutrient contents were analysed for three shoots per treatment. Two distal foliage tufts on 1-year-old shoots were clipped prior to the bioassays, and immediately frozen in liquid nitrogen in the field. Frozen needles were transported in coolers to the laboratory where they were dried at 65–70 °C for 72 h. Samples were ground using a stainless steel Wiley mill with a #2 mesh screen. Concentrations of macronutrients (nitrogen, phosphorous, potassium, calcium, magnesium, sulphur), and micronutrients (zinc, boron, manganese, iron, copper, aluminium, sodium) were determined by the University of Wisconsin-Madison Soil and Plant Analysis Laboratory. Quantities were determined using an inductively coupled Plasma Emission Spectrophotometer, Model 34000 ARL (Applied Research Labs) coupled with a DEC (Digital Equipment Corporation) PDP 11/34 computer (Schulte *et al.*, 1987). Per cent nitrogen was analysed using a semi-micro Kjeldahl procedure (Schulte *et al.*, 1987). Micronutrients were expressed as parts per million,

and macronutrients as percentage element. Each nutrient was analysed for treatment effects using the Kruskal–Wallis test for non-parametric data (StatView, 1989)

#### *Natural enemy guild composition and spatial variation*

*Pristiphora erichsonii* cocoons were collected from fresh duff beneath fifteen randomly selected *L. leptolepis*, in Fulton Co., PA, U.S.A. Duff samples were collected 28–30 March 1989. An area 4 m<sup>2</sup> was sampled within the dripline of each tree. From the base of each tree, paths 0.5 m wide and up to 4 cm deep were dug in each cardinal direction for 2 m. Cocoons within 4 cm of the soil surface appeared light brown and fresh compared with cocoons below this depth, suggesting that they were 1–2 years old. Samples were bagged in 50-L plastic garbage bags, and returned to the laboratory in Madison, Wisconsin. Cocoons were separated from the duff, and scored for successful adult sawfly emergence or the likely source of mortality. Criteria for categorizing cocoon fate were based on characteristic appearance and holes in cocoons using previously described methods (Morris, 1949; Holling, 1955; Buckner, 1958, 1959; Schoenfelder *et al.*, 1978): (i) smooth, spherical exit hole on cocoon's end = sawfly emergence; (ii) jagged, shredded opening, variable size = predation; (iii) very small, spherical exit hole = parasitoid, and (iv) intact cocoons: mummified adult or larval sawfly = desiccation; fungal hyphae, bacterial spores = diseased. Cocoons that did not easily fit into one category were discarded and not recorded. Total number of cocoons and the proportion of cocoons apparently killed by various natural enemies were analysed using linear and polynomial regression techniques (Abacus Concepts, 1987).

## Results

#### *Spatial and temporal variation in larch vigour and sawfly abundance*

*Larix decidua* productivity and distribution of *P. erichsonii* were generally uniform throughout the plantation during the 3-year study. Variability in new shoot production and number of oviposition wounds were not significantly affected by experimental block (Table 1). Individual trees varied significantly in productivity and suitability to larch sawfly oviposition [Tree(Block)  $P < 0.0001$ ]. In year 3, plantation-wide reductions in sawfly oviposition activity and host productivity occurred independent of block (Block × year interaction, NS), most likely caused by the record heat and low precipitation that spring in Wisconsin. Year 1 and year 2 results were equivalent. Direction of branch growth did not affect shoot productivity or oviposition.

Individual trees varied little temporally in their vigour and host suitability. Regression analysis showed that the number of new shoots within trees was directly correlated with previous shoot production for both *Larix decidua* and *L. leptolepis* (Fig. 1). Previous year shoot production accounted for over 80% of the variation in subsequent productivity each year.

**Table 1.** Nested ANOVA results for effects of experimental block, individual trees, direction of branch growth, and year on variation in *Larix decidua* productivity and sawfly oviposition. Productivity measured as new shoots per branch and oviposition as number of shoots with oviposition scars for 3 years on thirty-six larch trees in Clark Co., WI., U.S.A.

	df	Type I SS	F	P
New shoots				
Experimental block	2	1.10	0.37	0.89
Tree (block)	33	49.56	38.24	0.0001
Branch direction	1	0.16	1.09	0.31
Block direction	2	1.07	3.58	0.045
Tree direction (block)	22	3.28	3.80	0.0001
Year	2	2.12	26.94	0.003
Direction year	2	0.15	1.85	0.163
Block year	4	0.19	1.24	0.298
Block direction year	4	0.02	0.15	0.96
Shoots with oviposition wounds				
Experimental block	2	5.00	2.39	0.11
Tree (block)	33	34.88	4.28	0.0001
Branch direction	1	0.06	0.12	0.73
Block direction	2	0.89	1.82	0.40
Tree direction (block)	20	9.30	1.88	0.02
Year	2	8.35	19.51	0.0001
Direction year	2	0.22	0.45	0.64
Block year	4	0.42	0.43	0.79
Block direction year	4	0.86	0.87	0.48

*Larix decidua* (df = 1,34) results were: year 1 vs. 2,  $F = 260.06$ ,  $P < 0.0001$ ; year 1 vs. 3,  $F = 146.23$ ,  $P < 0.0001$ ; year 2 vs. 3,  $F = 428.71$ ,  $P < 0.0001$ . Similar results were noted for *L. leptolepis* (df = 1,3): year 1 vs. 2,  $F = 60.08$ ,  $P < 0.005$ ; year 1 vs. 3,  $F = 23.31$ ,  $P < 0.02$ ; year 2 vs. 3,  $F = 126.44$ ,  $P < 0.002$ . Between tree productivity varied sixfold in *L. decidua*, and 10-fold in *L. leptolepis*. Thus, larch productivity varied strongly spatially, but not temporally, in each plantation. *Pristiphora erichsonii* oviposited repeatedly in individual trees of both species during the 3 years studied. Spatial variation between trees ranged from six- to 10-fold within each larch plantation, with females completely avoiding some individual trees (Fig. 2). The spatial pattern remained generally stable for 3 years. The mean number of oviposition wounds per tree was significantly related to previous oviposition history in *L. decidua*: year 1 vs. 2,  $F = 220.12$ ,  $P < 0.0001$ ; year 1 vs. 3,  $F = 7.22$ ,  $P < 0.01$ ; year 2 vs. 3,  $F = 8.83$ ,  $P < 0.005$ . There was a similar but less consistent relationship in *L. leptolepis*: year 1 vs. 2,  $F = 8.31$ ,  $P < 0.06$ ; year 1 vs. 3,  $F = 2.13$ ,  $P > 0.2$ ; year 2 vs. 3,  $F = 17.74$ ,  $P < 0.03$ . Two years after oviposition (year 1 vs. year 3), the predictability remained significant in *L. decidua*, but not *L. leptolepis*, suggesting possible host shifts among *L. leptolepis*.

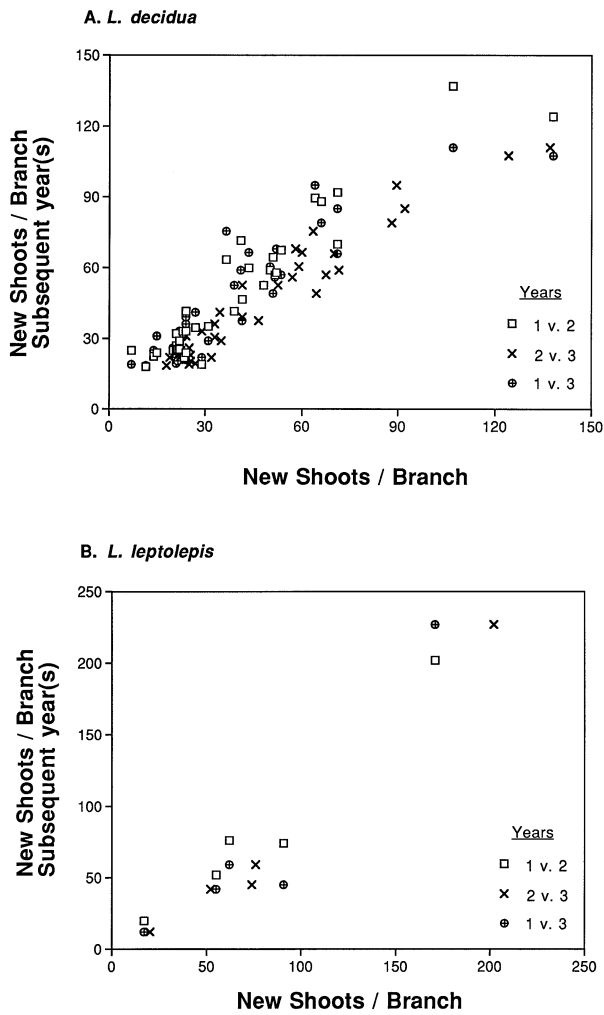
*Pristiphora erichsonii* oviposition occurred most frequently in those larch trees with the greatest abundance of new shoots. The number of oviposition wounds per tree was significantly related to shoot abundance in each host species (Fig. 3). Linear

regression results for effects of *L. decidua* shoot production on oviposition scar abundance were: year 1,  $F = 24.24$ ,  $P < 0.0001$ ; year 2,  $F = 11.74$ ,  $P < 0.002$ ; year 3,  $F = 1.96$ ,  $P < 0.18$ . Variability in year 3 may be due, in part, to the record heat that caused reductions in shoot production and sawfly oviposition standwide. Effects of shoots on oviposition were strong for *L. leptolepis*: year 1,  $F = 7.81$ ,  $P < 0.07$ ; year 2,  $F = 33.11$ ,  $P < 0.01$ ; year 3,  $F = 223.09$ ,  $P < 0.0007$ .

The percentage of shoots scarred by oviposition reflects a general degree of defoliation and subsequent host stress. Increased defoliation moderately reduced new shoot production in *L. decidua*, but the variation among trees was very high ( $r^2 < 0.11$  for between year comparisons) (Fig. 4). However, the minimum amount of shoot productivity by *L. decidua* was relatively independent of prior defoliation. Branches produced at least twenty shoots even at the highest defoliation intensities measured. In contrast, *L. leptolepis* shoot production was not influenced by a single year of previous sawfly defoliation, despite higher levels of oviposition (17–50%) than in *L. decidua* (0–38%). Repeated defoliation may have some effect, as combining percentage shoots infested in years 1 and 2 produced a marginal reduction in year 3 ( $F_{1,3} = 8.51$ ;  $P < 0.061$ ).

#### Effects of sawfly oviposition on larval host suitability

Oviposition did not significantly influence *P. erichsonii* larval growth rate. Second-instar growth averaged 38.3 mg/day (1.9)

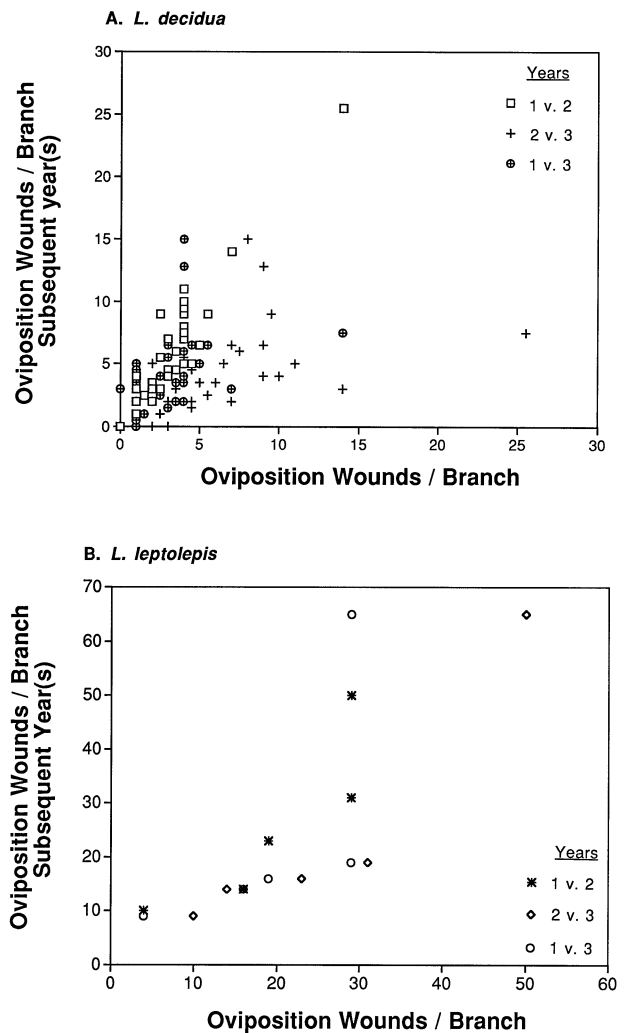


**Fig. 1.** Spatial and temporal variation in larch new shoot growth over 3 years. Spatial variation among individual trees was high, ranging sixfold for *Larix decidua* ( $n = 36$ ) (A), and 10-fold for *Larix leptolepis* ( $n = 5$ ) (B). Temporal variation between years, however, was very low for each species. Linear relationships in between-year shoot production per tree were highly significant for all comparisons. All statistical analyses were performed using single comparisons only, but these are illustrated collectively to depict the overall pattern.

for controls and 39.2 (9.3) for larvae on shoots with oviposition wounds ( $F_{1,57} = 0.201$ ;  $P > 0.6$ ). Treatments were pooled per tree, and analysed for tree effects on larval growth and survival. Growth varied 30% among trees, but this difference was not statistically significant ( $F_{9,49} = 1.51$ ;  $P < 0.172$ ). Similarly, larval survival varied from 80 to 100% among trees, but was not significant ( $F_{9,49} = 0.497$ ;  $P > 0.8$ ).

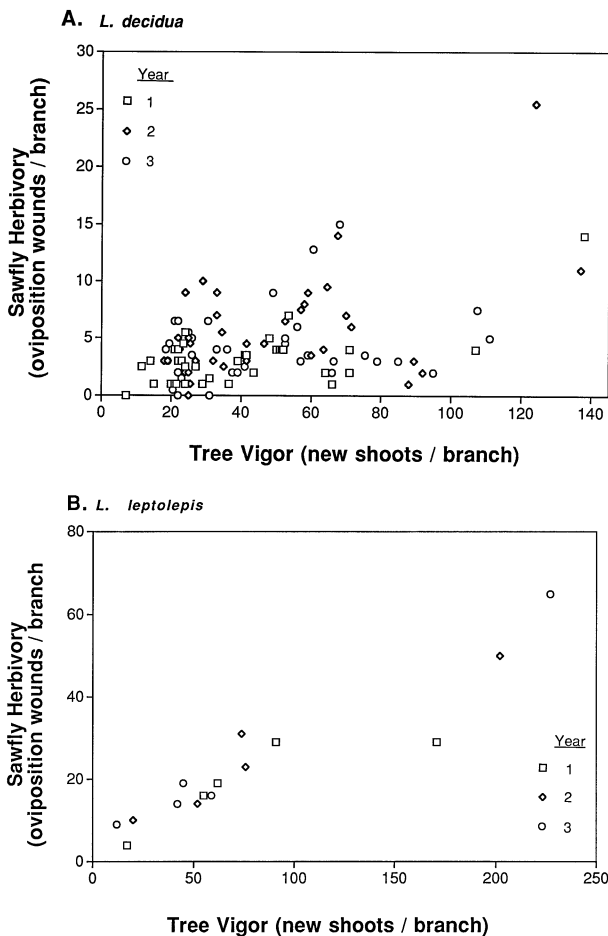
#### *Effects of oviposition and leaf injury on larval feeding performance*

Results from the second bioassay also indicate little effect of oviposition on short-term larval performance. Larval growth and survival over 120 h was similar for all treatments. However,



**Fig. 2.** Variation in *Pristiphora erichsonii* herbivory among individual larch trees. Spatial variation among individual trees was high, ranging at least 10-fold for *Larix decidua* (A), and sixfold for *Larix leptolepis* (B). The number of oviposition wounds per branch was significantly linearly related to previous sawfly attack in *L. decidua*, while the relationship was significant for year 2 vs. year 3 only in *L. leptolepis*, suggesting possible host shifts among *L. leptolepis*. All statistical analyses were performed using single comparisons only, but these are illustrated collectively to depict the overall pattern.

defoliation in combination with oviposition had a modest effect on initial growth after 24 h (Table 2). This suggests a possible induced response in foliage that is eliminated with longer feeding periods. However, the pattern of larval development did not change through time on the three treatments (repeated-measures time  $\times$  treatment interaction: larval growth  $F_{4,42} = 1.31$ ,  $P > 0.28$ ; survival  $F_{4,42} = 0.38$ ,  $P > 0.8$ ). Similarly, oviposition and defoliation had no significant effects on foliar nutrient content (Table 3). However, nutrient results should be interpreted with caution due to low sample size.

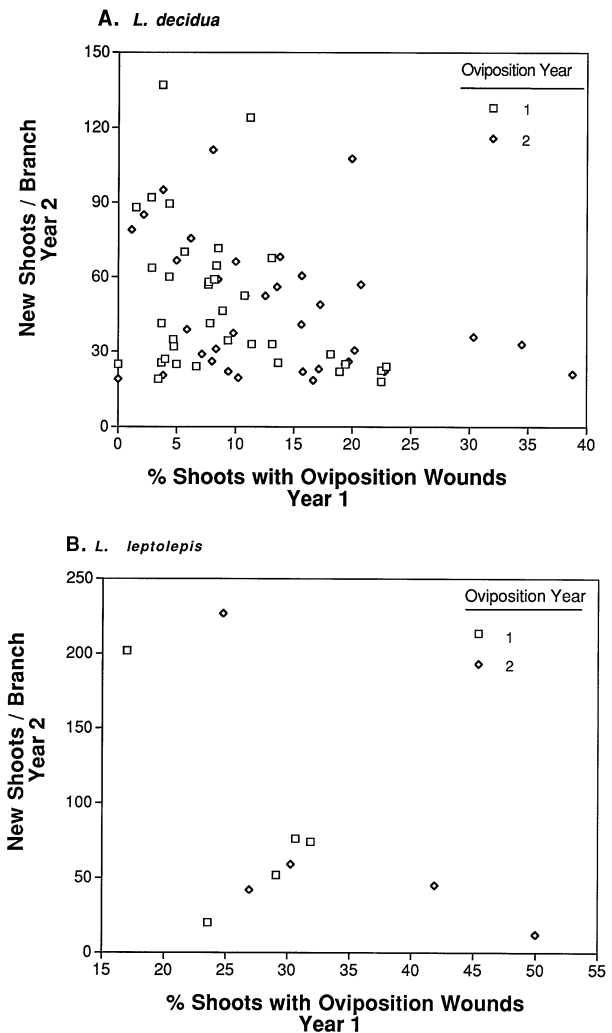


**Fig. 3.** Effects of shoot production on sawfly colonization. *Larix decidua* (A) productivity ranged from six to 135 shoots per branch, with a proportional increase in the number of oviposition wounds in years 1 and 2. Significant linear effects of shoot production on sawfly oviposition in *Larix leptolepis* (B) were found in 2 of 3 years. New shoot production accounted for over 91% of the variation in sawfly attack in years 1 and 2 (Table 5). All statistical analyses were performed using single comparisons only, but these are illustrated collectively to depict the overall pattern.

*Natural enemy guild composition and spatial variation*

Cocoon abundance ranged from 104 to 4355 per tree, averaging 1221.0 (264.4) (Fig. 5A). Mortality attributed to natural enemies was high. Parasitoids killed an estimated 34.6% (3.4), and rodents killed 31.0% (2.3), of the 18 315 cocoons sampled. Desiccated sawfly larvae and adults were observed in 12.4% (1.5) of the cocoons, while disease was evident less frequently 7.7% (1.0). The estimated number of adult sawflies emerging from cocoons ranged from 10 to 769 per tree.

The proportion of cocoons killed by various natural enemies varied substantially among host trees (Fig. 5B). Parasitoids were the most common mortality agent on nine trees. On seven trees, parasitoids killed at least 40% of the sawflies. Rodents were the most abundant source of mortality under four trees, while cocoon desiccation was predominant under one tree.



**Fig. 4.** Effects of *Pristiphora erichsonii* herbivory on subsequent *Larix* shoot production. *L. decidua* (A) produced at least twenty shoots per branch regardless of previous percentage rates of oviposition. Significant linear effects indicate an overall negative effect of sawfly herbivory on larch productivity. However, herbivory explained less than 11% of the variation in shoot production, indicating high tolerance in shoot production among individual trees. Oviposition had no significant effect on *L. leptolepis* shoot production (B). All statistical analyses were performed using single comparisons only, but these are illustrated collectively to depict the overall pattern.

The influence of host density on the proportion of cocoons killed showed a different pattern between parasitoids and predators. Rates of parasitism declined significantly with *P. erichsonii* density. Both linear and quadratic relationships were significant (linear:  $F_{1,13} = 8.387, P < 0.0125, r^2 = 0.345, y = -8.04E-5x + 0.448$ ; quadratic:  $F_{2,12} = 6.713, P < 0.011, r^2 = 0.446, y = 2.42E-4x + 2.315E-8 \times 2 + 0.548$ ) (Fig. 6A). Parasitism rates exceeded 20% for fourteen of fifteen trees. Conversely, the rate of predation increased with host density in a generally linear fashion (linear:  $F_{1,13} = 5.26, P < 0.039, r^2 = 0.233, y = 4.7E-5x + 0.253$ ; quadratic:  $F_{2,12} = 2.813, P < 0.1, r^2 = 0.206, y = 9.60E-5x - 1.11E-$

**Table 2.** Effects of *Pristiphora erichsonii* oviposition and defoliation on larval growth and survival. Mean  $\pm$  SE growth (mg, fresh wt) and percent survival were measured after 24, 72 and 120 h. Data followed by different letters within rows are statistically significant (Fischer's Protected LSD;  $P < 0.05$ ) (df = 2,18).

Time (h)	Treatment			F	P
	Control	Oviposition	Oviposition + defoliation		
Larval growth					
24	12.01 $\pm$ 0.97 ab	12.99 $\pm$ 1.16 a	10.08 $\pm$ 0.65 b	3.39	0.056
72	26.17 $\pm$ 1.48	27.47 $\pm$ 4.04	24.59 $\pm$ 2.21	0.27	0.767
120	34.96 $\pm$ 3.67	45.47 $\pm$ 6.69	37.67 $\pm$ 5.35	1.19	0.324
% Survival					
24	100.00 $\pm$ 0.0	100.00 $\pm$ 0.0	100.00 $\pm$ 0.0	–	–
72	78.80 $\pm$ 6.2	91.50 $\pm$ 5.6	87.3 $\pm$ 6.2	0.28	0.759
120	45.50 $\pm$ 12.5	58.0 $\pm$ 12.2	57.9 $\pm$ 8.3	0.74	0.49

**Table 3.** Effects of *Pristiphora erichsonii* oviposition and defoliation on *Larix decidua* foliar nutrient concentrations. Foliage from 1-year-old shoots was analysed 8 days after oviposition into distal current-year shoots. Data  $\pm$  SE were analysed using the Kruskal–Wallis *H*-test for nonparametric data.

Nutrient	Treatment			H	P
	Control	Oviposition	Oviposition + defoliation		
N	1.88 $\pm$ 0.19	1.82 $\pm$ 0.93	1.87 $\pm$ 0.19	0.156	0.925
P	0.20 $\pm$ 0.02	0.22 $\pm$ 0.01	0.21 $\pm$ 0.01	1.762	0.414
K	0.44 $\pm$ 0.05	0.47 $\pm$ 0.04	0.46 $\pm$ 0.07	0.156	0.925
Ca	0.76 $\pm$ 0.13	0.86 $\pm$ 0.06	0.84 $\pm$ 0.09	0.622	0.733
Mg	0.28 $\pm$ 0.04	0.31 $\pm$ 0.02	0.33 $\pm$ 0.04	1.098	0.575
S	0.16 $\pm$ 0.01	0.16 $\pm$ 0.01	0.16 $\pm$ 0.01	0.601	0.741
Zn	23.35 $\pm$ 0.93	26.23 $\pm$ 1.93	56.00 $\pm$ 30.15	4.356	0.113
B	37.4 $\pm$ 5.67	28.9 $\pm$ 6.08	33.99 $\pm$ 3.94	0.649	0.556
Mn	1111.33 $\pm$ 46.16	769.48 $\pm$ 385.36	1121.2 $\pm$ 106.3	0.622	0.732
Fe	90.11 $\pm$ 7.43	119.4 $\pm$ 6.06	99.82 $\pm$ 10.79	3.822	0.148
Cu	25.89 $\pm$ 8.86	117.84 $\pm$ 98.18	33.04 $\pm$ 10.81	1.156	0.561
Al	97.75 $\pm$ 2.08	114.67 $\pm$ 8.57	138.27 $\pm$ 27.48	3.467	0.177
Na	562.00 $\pm$ 276.68	443.13 $\pm$ 142.19	551.97 $\pm$ 46.39	0.622	0.733

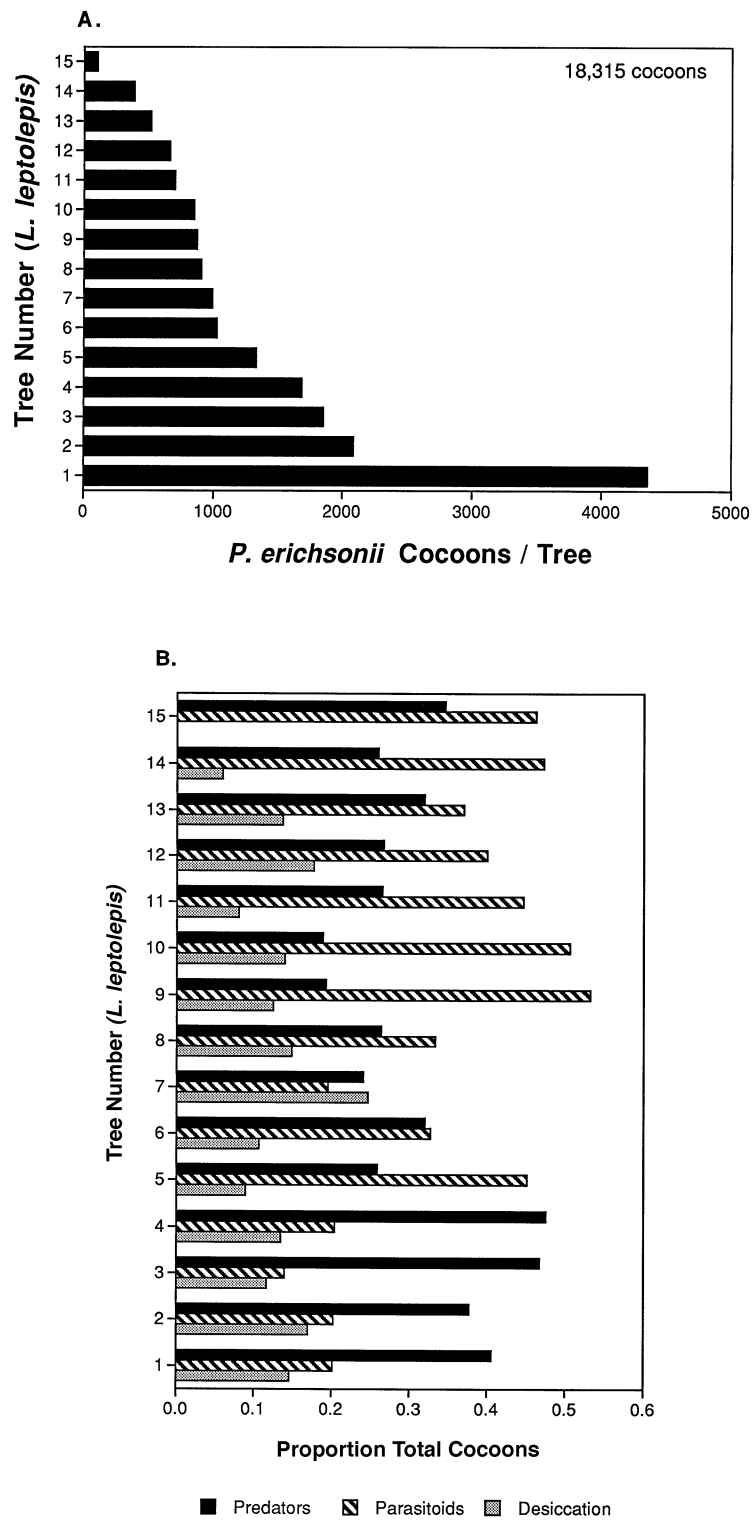
8  $\times$  2 + 0.22) (Fig. 6B). The combined effects of parasitoids and predators did not vary with host density ( $F_{1,13} = 2.43$ ;  $P > 0.143$ ) Likewise, natural enemy efficiency varied widely among host trees, particularly at lower (< 1200) cocoon densities.

## Discussion

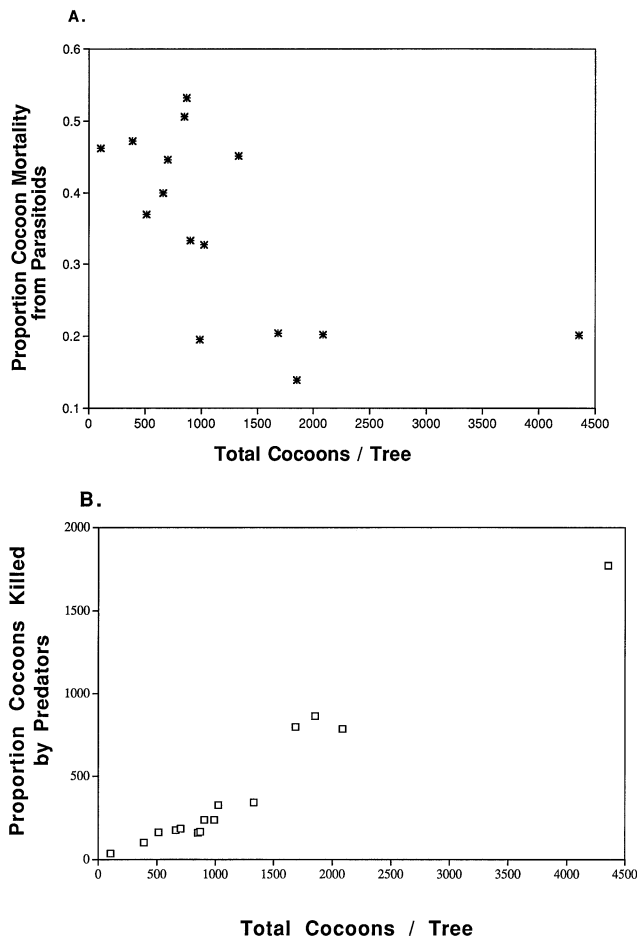
The hypothesis that chronic defoliation leads to reduced host suitability as a resource for larch sawfly oviposition was generally not supported in either *L. decidua* or *L. leptolepis*. Individual tree productivity was highly correlated between years during the 3-year study. Sawfly herbivory also remained relatively constant on individual trees. Spatial heterogeneity in plant quality and herbivore distributions is well known in

diverse plant-insect systems (Denno & McClure, 1983). Individual conifer host trees are differentially attacked by sawflies annually, while adjacent trees remain uninfested (Henson *et al.*, 1970; Genys & Harmon, 1976; Higashiura, 1988).

Larch sawfly spatial distribution and abundance were directly associated with tree growth vigour. Shoot production and number of oviposition wounds per tree were highly correlated in both larch plantations. These results do not support the application of plant stress theory (White, 1974) to folivores, but rather agree with results from some other insect guilds that prefer more rapidly growing hosts (Craig & Price, 1986; Kimberling *et al.*, 1990; Price, 1991). It is impossible to extrapolate whether this relationship arises from increased substrate availability or reduced defensive chemistry associated with more rapid growth, as predicted by growth differentiation



**Fig. 5.** Spatial variation in *Pristiphora erichsonii* cocoon numbers and survival within a *Larix leptolepis* plantation. Cocoons were not evenly distributed among the fifteen host trees (A). Number of cocoons collected varied from 150 to 4400 per tree. Adult sawfly emergence was low, averaging less than 20% (B). Mortality was caused primarily by parasitoids (ten trees), and rodent predators (four trees), while desiccation was the greatest cause of cocoon mortality beneath tree no. 7.



**Fig. 6.** Efficiency of predators and parasitoids based on *Pristiphora erichsonii* cocoon density. As host density increases, parasitism rates decline (A), and predation rates increase (B). Combined effects are not significantly affected by host density.

theory (Loomis, 1953; Herms & Mattson, 1992; Krause *et al.*, 1993).

The production and architecture of new shoots are essential to the optimization of canopy light capture and carbon assimilation (Remphrey & Powell, 1984, 1988). However, the expected plant growth benefits following new shoot production appear to be offset by the increased resource availability that new shoots offer female *P. erichsonii*. The high proportion of infested shoots on some *L. decidua* and *L. leptolepis* was sufficient to cause defoliation and larch dieback. *Pristiphora erichsonii* population levels of 20% infested shoots are capable of causing severe defoliation (Ives & Prentice, 1958; Ives, 1976). In tundra regions of Québec, *L. laricina* suffered reduced growth and branch dieback following 20–35% infested shoots (Cloutier & Filion, 1991). The ability to tolerate folivory without sacrificing shoot production is based, in part, on the availability of resources such as soil nutrients and light. Variation in such resources was not apparent in this study. *L. decidua* productivity was similar among three sections within the stand, suggesting that differential productivity among

individual trees is not caused by local variation in abiotic resources.

Insect folivores may be partially responsible for maintaining high levels of plant productivity (Mattson & Addy, 1975). *Pristiphora erichsonii* sawfly oviposition into rapidly growing long shoots can stimulate axillary buds to produce multiple short shoots, thereby creating additional oviposition resources for females. Defoliation by *P. erichsonii* larvae did not significantly reduce subsequent year shoot production (Krause & Raffa, 1992). Sawfly oviposition behaviour may also improve larval performance by cutting cambial tissues, thereby restricting the flow of plant resins distally into growing shoots (McCullough & Wagner, 1993). Similarly, cambial wounding may improve foliar quality for larvae by shunting nutrients to needles rather than growing shoots. *Pristiphora erichsonii* oviposition increased foliar iron, copper and aluminium, although increased replication is required to test this hypothesis. Foliar nutrients are strongly correlated with cocoon weight and potential fecundity in *Neodiprion lecontei* (Hymenoptera: Diprionidae) (Krause, 1994). Further testing of the effects of *P. erichsonii* oviposition on foliar quality and larval performance will improve understanding of larch sawfly ecology and plant–insect interactions.

Although some defoliation might enhance sawfly performance without affecting host productivity (Krause & Raffa, 1992, 1995), chronic defoliation can eventually exhaust plant resources for shoot and leaf production, leading to host decadence, decline and death. In the relatively defoliation tolerant *Larix*, high defoliation of  $\approx 50\%$  for 5 years is usually accompanied by host decline, death, or heightened susceptibility to other stress agents (Butcher, 1951; Graham, 1956; Drooz, 1960; Ives, 1976; Tailleux & Cloutier, 1993). However, defoliation tolerance in larch may allow sufficient time for natural enemies to exert pressure on sawfly populations before the onset of severe negative impacts on the host.

The spatial heterogeneity in herbivore abundance resulting from variations in host plant quality also contributed to high variation in natural enemy abundance. The absolute number and proportion of cocoons attacked by predators increased significantly with sawfly abundance. This could be caused largely by the positive functional responses exhibited by these generalists on conifer sawflies (Holling, 1959, 1965). However, proportionate rates of parasitism declined. Competition by predators seems the most likely cause for this relationship. Predators may prevent *P. erichsonii* from maintaining high herbivore pressure on larch. This relationship between host-plant tolerance and the requisite time delay needed for natural enemy impact could contribute to the overall stability of this tri-trophic interaction, by preventing overexploitation of the host resource and subsequent collapse of *P. erichsonii* populations. Additional studies are required to test this view.

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