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The effect of defoliation intensity and history on photosynthesis, growth and carbon reserves of two conifers with contrasting leaf lifespans and growth habits

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SUMMARY

The effects of partial defoliation on photosynthesis, whole-seedling carbon allocation, partitioning and growth were studied for two species with contrasting foliar traits. Field-grown seedlings of deciduous Japanese larch (*Larix leptolepis*) and evergreen red pine (*Pinus resinosa*) were defoliated by hand in early summer for 2 consecutive years. In the first year (1990), seedlings were defoliated by removing the distal 0, 25, 50 or 75% of each needle. In the second year (1991), seedlings were defoliated either 0 or 50%, regardless of previous defoliation treatments. Defoliation had little effect on photosynthesis and starch concentration in whole seedlings of either species in the first year. In the second year, photosynthesis increased in both species in response to the 1991 defoliation treatment, and in red pine also increased in response to the 1990 defoliation treatment. Further, in 1991 both larch and pine had decreased whole-seedling total non-structural carbohydrate concentrations in all seedlings that were defoliated at least once over the 2-yr period. This decrease was noted mostly in the starch component of the non-structural carbohydrates, and was similar in both species. In 1991, biomass was similarly decreased in both species in response to 1991 defoliation. Both species showed overcompensation in total and component biomass in seedlings defoliated by 25% in 1990. Overall, the results do not support the widely held belief that evergreen trees are substantially more affected than deciduous trees by defoliation.

Key words: defoliation, leaf lifespan, *Pinus resinosa* (red pine), *Larix leptolepis* (Japanese larch), carbon allocation, carbohydrates, photosynthesis, starch.

INTRODUCTION

Efforts to understand plant responses to defoliation have focused on three related topics: the effect of defoliation on growth, carbon (C) allocation and partitioning; identification of common plant traits between species with similar defences; and the significance of compensatory responses to defoliation. The effect of defoliation on photosynthesis, growth, C allocation and partitioning in trees has received considerable attention (Kozlowski & Winget, 1964; Harris, 1974; Reich *et al.*, 1993), yet despite this research our overall understanding of plant responses to defoliation is weak (Haukioja, 1990).

Responses to defoliation have been characterized by plant types (Feeny, 1976; Mooney & Gulmon, 1982; Coley, 1988). Bryant *et al.* (1983) have proposed that plants can be grouped by their leaf longevities. A central tenet of their hypothesis is that evergreen plants are more sensitive to foliage loss than deciduous species, because evergreen foliage has a higher initial cost of production and a lower rate of return per (C) investment, and stores a proportionately larger amount of whole-plant C. Taken together, it has been proposed that evergreen plants will be more affected by defoliation than deciduous plants.

However, the hypotheses proposed by these authors do not appear to consider compensatory responses to defoliation (Trumble *et al.*, 1993). It has become apparent that plants compensate for lost

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leaf area in a number of ways (Harris, 1974; Heichel & Turner, 1983; Trumble *et al.*, 1993). In particular, rates of photosynthesis on residual or regrowth foliage often increase relative to non-defoliated controls (Heichel & Turner, 1983; Reich *et al.*, 1993). In addition, plant biomass is not necessarily reduced by the same percentage as leaf area (Harris, 1974; Bassman *et al.*, 1982; Reich *et al.*, 1993). In fact, there is evidence that lightly defoliated plants may increase sufficiently in biomass to end up larger in mass than non-defoliated controls (Harris, 1974; McNaughton, 1983).

Another possible shortcoming of the 'evergreen versus deciduous' hypothesis of plant–insect interactions is the assumption that evergreen plants store a significant proportion of their whole-plant C reserves in the foliage. There are few data to support or refute this claim, as until fairly recently most research on C pools of trees has been limited to above-ground components (but see Krueger & Trappe, 1967). The extent to which foliage can be considered a major storage organ for starch may be dependent on the age of the plant (Webb, 1975, 1980). Further, loss of reserves may be of little consequence to trees, depending on the timing of defoliation (McLaughlin *et al.*, 1980; Loescher *et al.*, 1990; Webb & Kilpatrick, 1993), and there is substantial evidence that currently produced photosynthates are primarily responsible for growth (Kozlowski & Winget, 1964; Gordon & Larson, 1970; Hogg & Lieffers, 1991).

Further confounding our understanding of plant responses to defoliation is a general lack of understanding of the impacts of defoliation intensity and history on plant physiology. Generally, studies have been conducted where either a set percentage of leaf area was removed (e.g. Lovett & Tobiessen, 1993) or a medium and severe amount of foliage were removed (e.g. Richards & Caldwell, 1985). In addition, only a few studies report the effect of previous defoliation (Reich *et al.*, 1993) or the effect of repeated defoliation (Ericsson *et al.*, 1980; Wallace *et al.*, 1984; Richards & Caldwell, 1985) on physiological responses. Multi-year defoliations are common in nature and may lead to responses otherwise not noted after 1 yr. For example, Ives & Nairn (1966) found that partial defoliation reduced growth initially in young tamarack (*Larix laricina*) trees, but that no further reduction occurred with additional years of defoliation. By contrast, Alfaro *et al.* (1982) found little to no effect of heavy defoliation ($>60\%$ needle loss) on growth of Douglas fir (*Pseudotsuga menziesii*) in the first 3 yr of defoliation in several outbreaks.

This paper presents an experiment to address defoliation and leaf longevity and their effects on photosynthesis, growth and C reserves. Seedlings of contrasting leaf lifespans and growth habits were grown and treated under similar conditions so that differences between species could be related without further inclusion of environmental and phenotypical variation (see Haukioja, 1990). A larch and a pine species were chosen for this experiment because of their presumed differences in dependence on currently produced and stored carbohydrates (Bryant *et al.*, 1988). Japanese larch (*Larix leptolepis*) and red pine (*Pinus resinosa*) are closely related conifers, but they differ in two important characteristics: Japanese larch is deciduous and indeterminate, while red pine is evergreen and determinate in growth habit. Consequently, Japanese larch potentially has the ability to offset loss of foliage incurred in mid-season by producing new foliage in the year of defoliation, whereas red pine produces only one flush of foliage in the spring. In addition, red pine will carry over affected foliage from one year to the next, while Japanese larch loses all its foliage each autumn.

MATERIALS AND METHODS

Plant material and growing conditions

Bare-root stock (2–0) of red pine (*Pinus resinosa* Ait.) and Japanese larch (*Larix leptolepis* (Sieb. and Zucc.) Gord.) seedlings were planted in rows within a 30 × 30 m enclosure at the University of Wisconsin Arboretum, Madison, Wisconsin. The red pine seedlings were obtained from a Wisconsin Department of Natural Resources nursery at Hayward, Wisconsin. The Japanese larch seedlings were obtained from a commercial nursery in Michigan. All of the seedlings were planted in the spring of 1989 in a completely random planting design and allowed to acclimate for 1 yr before treatments were applied.

Seedlings were planted in the ground in garbage bags (20, 55 or 110 l) with well mixed local soil (Kibbie sandy loam). Each bag was perforated at the bottom to allow for adequate drainage. In addition, a layer of pea-sized gravel 2–3 cm thick was put in the bottom of each bag to enhance drainage and to impede root penetration outside the bag. No root penetration was observed outside the bags in any of the samples in either year of the experiment. Initially it was planned to defoliate and harvest seedlings over a 3-yr period, but as a result of poor growth and survival in the first year the experiment was reduced to 2 yr. All of the seedlings harvested in 1990 were planted in the 20 l bags; all those harvested in 1991 were planted in 55 or 110 l bags. There were no significant effects of bag size on plant growth in 1991, thus the data are pooled throughout this paper. Seedlings were planted at an average density of 1.5 seedlings m^{-2}. None of the seedling crowns was touching at time of harvest. Seedlings were watered well in each year of the experiment and during acclimation.

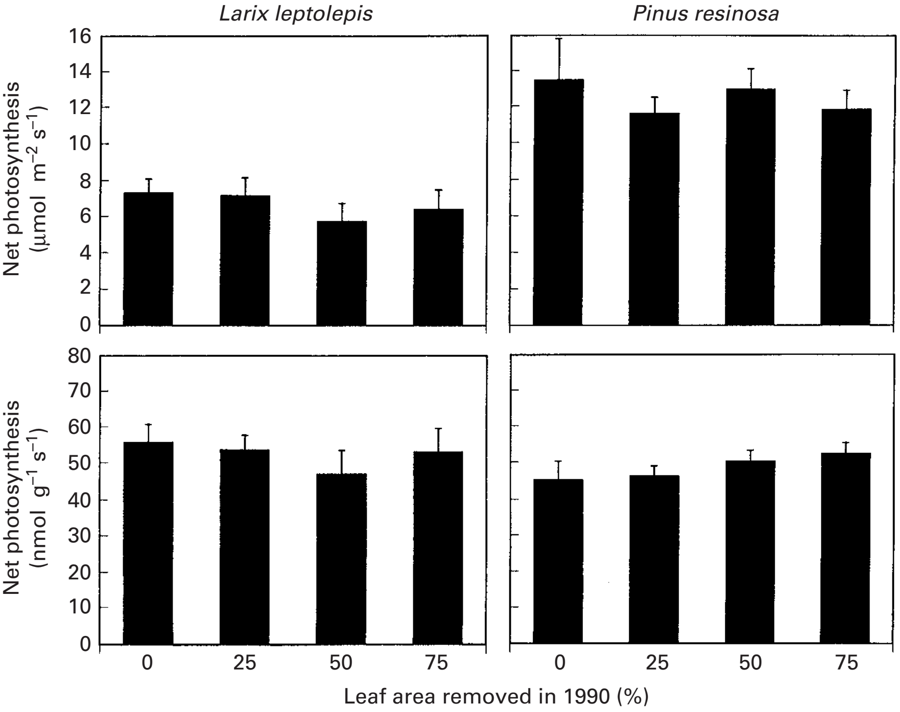

Fig. 1. Mean photosynthesis rates (±SE) per defoliation treatment in 1990 for *Larix leptolepis* and *Pinus resinosa* seedlings.

Treatments and sampling

In 1990, treatments consisted of removing the distal 0, 25, 50 or 75% of each needle on each seedling. Both species received the same treatments. In 1991, seedlings of both species (from all 1990 defoliation treatments) were equally and randomly allocated to one of two treatment groups: defoliated or non-defoliated (removing the distal half of each needle). In all cases, the designation 'control seedlings' refers to seedlings that were not defoliated in either year of the experiment. In both years, defoliation was done by hand using scissors in the first week of July. At that time, red pine seedlings had completed their needle expansion. A separate test of clipping accuracy showed that visual estimation was close to the desired levels (data not shown). Defoliation intensity refers to the increasing amount of foliage removed in 1990. Defoliation history refers to whether seedlings were defoliated in 1990, 1991, both years, or not at all.

Photosynthesis was measured using a portable photosynthetic gas-exchange system (ADC LCA-2, ADC Ltd, Hoddesdon, UK). One measurement per seedling per date was taken in such a manner that no seedling was measured twice during the study. In both years, measurements were taken on the residual current foliage in red pine and on the foliage growing on the current-year stem section in Japanese larch. In 1990, nine to 12 seedlings were measured per treatment for the summer (38 total measurements for red pine and 41 total measurements for Japanese larch). In 1991 some data were lost, and thus the usable number of measurements ranged from four to eight seedlings per treatment combination for the summer (32–64 total measurements for red pine and 52–62 total measurements for Japanese larch). Measurements took place in the late morning of each measurement date under high light conditions. This protocol was followed in order to be able to compare values when the seedlings were at similar diurnal stages. Further, it was assumed that during this time *in situ* rates of photosynthesis would be at or near maximum levels (cf. Reich *et al.*, 1993). Following each measurement on a seedling, needles were collected to determine the leaf area and mass in the cuvette at the time of measurement. These variables were used to calculate photosynthesis on a projected area or mass basis. The values reported in this paper are the averages of all measurements taken during the summer of each year. Generally, rates of photosynthesis increased from late July to the end of September, but the increase was consistent within each defoliation treatment and did not change the ranking of the treatment responses against each other. Further, using date or initial plant size as a covariate did not change the patterns of response.

In both years, seedlings were harvested in early October before autumnal foliage senescence. Seedlings were excavated from the soil, cleaned, divided into root, stem and foliage components, and dried at 70°C for several days. Subsamples from the dried components were collected and ground to pass a #40 mesh in order to determine starch and soluble sugar content. Soluble sugars were first extracted from the ground samples using a mixture of

Table 1. *Non-structural carbohydrate content per seedling tissue in defoliated and control* Larix leptolepis *and* Pinus resinosa *seedlings*

		Larix leptolepis				*Pinus resinosa*			
Fraction	Tissue	0	25	50	75	0	25	50	75
Starch	Roots	33.5 ± 2.3	27.0 ± 8.1	26.7 ± 3.1	40.1 ± 8.5	42.0 ± 10.7	54.0 ± 5.5	50.4 ± 18.0	52.3 ± 10.1
	Stem	29.5 ± 0.3	28.1 ± 8.6	22.9 ± 1.3	47.2 ± 14.1	12.5 ± 0.2	12.8 ± 0.2	11.8 ± 0.06	14.1 ± 2.1
	Foliage	14.6 ± 0.1	14.7 ± 0.1			12.8 ± 0.1	12.8 ± 0.1	11.9 ± 0.2	12.3 ± 0.3
	Rootprop*	0.45 ± 0.02	0.37 ± 0.13			0.65 ± 0.11	0.66 ± 0.02	0.70 ± 0.06	0.70 ± 0.06
	Stemprop	0.44 ± 0.03	0.56 ± 0.13			0.12 ± 0.03	0.12 ± 0.01	0.11 ± 0.02	0.15 ± 0.05
	Folprop	0.11 ± 0.02	0.08 ± 0.01			0.23 ± 0.07	0.21 ± 0.01	0.19 ± 0.04	0.15 ± 0.04
TNC†	Roots	150.6 ± 10.3	138.0 ± 24.8	114.5 ± 2.8	145.6 ± 13.0	124.2 ± 5.5	145.8 ± 17.2	154.2 ± 22.5	146.5 ± 19.6
	Stem	107.4 ± 11.0	101.5 ± 5.3	98.3 ± 5.6	115.1 ± 5.3	74.0 ± 5.9	79.6 ± 12.8	77.8 ± 5.4	77.2 ± 4.7
	Foliage	68.5 ± 5.1	74.3 ± 3.4			78.8 ± 12.3	79.3 ± 3.5	79.2 ± 6.4	73.8 ± 1.6
	Rootprop					0.51 ± 0.08	0.46 ± 0.04	0.56 ± 0.03	0.54 ± 0.08
	Stemprop					0.16 ± 0.02	0.20 ± 0.01	0.16 ± 0.01	0.22 ± 0.03
	Folprop					0.33 ± 0.06	0.34 ± 0.04	0.28 ± 0.02	0.24 ± 0.05

Values are means ± SE.

Non-structural carbohydrate content expressed as mg glucose equivalent g^{-1} d. wt tissue.

A blank cell is the result of lost tissue. $n = 3, 2, 3, 3$ and $n = 3, 3, 3, 3$ for 0, 25, 50 and 75% defoliated larch and pine, respectively. $n = 0$ for 50 and 75% defoliated larch foliage tissue. Each sample (except where tissue is missing) represents the combination of two to three seedlings.

*Prop, carbohydrate content in the tissue as a proportion of whole seedling content. Whole seedling content is the sum of all tissue contents (adjusted for biomass).

†TNC, total non-structural carbohydrates (starch and soluble sugars combined).

methanol, chloroform and water (12:5:3). Following extraction, soluble sugars were determined colorimetrically following digestion with sulfuric acid (Hanson & Möller, 1975). Starch content was determined colorimetrically following hot-water extraction of the residual sample tissue and enzymatic digestion of the extract (Haissig & Dickson, 1979).

All data for this experiment were analysed using ANOVA and regression procedures of the JMP statistical analysis software (version 3.1, SAS Institute, Cary, NC, USA). ANOVAs were used to assess the effect of defoliation in 1991. Contrasts within the ANOVAs were used to ascertain the effect of defoliation in general versus no defoliation in either year. Regression analysis was applied to analyse the effects of 1990 defoliation levels in either year of the experiment.

RESULTS

The effect of defoliation in 1990

Photosynthesis. Neither species was significantly affected by 1990 defoliation treatments. In general, both species had similar patterns of response for photosynthesis. Japanese larch seedlings had consistently lower ($P < 0.001$) rates of photosynthesis on an area basis than red pine, but had similar rates of photosynthesis on a mass basis (Fig. 1).

Non-structural carbohydrates. In 1990 there were no significant effects of defoliation on starch, soluble sugars or total non-structural carbohydrate (TNC) content in either species (Table 1). In larch, the roots had the highest TNC concentration as a result of high soluble sugar concentrations (Table 1). In red pine, the highest TNC concentration was also found in the roots, but as a result of high starch concentration (Table 1).

Biomass. There were no significant differences ($P = 0.178$) in mass between Japanese larch and red pine seedlings across defoliation treatments (Fig. 2). Red pine seedling mass did not change with increasing defoliation intensity. However, larch seedlings showed a pronounced response to the 25% defoliation treatment resulting in a doubling of mass relative to the control seedlings (Fig. 2). This is the result of increases in stem and root mass (Table 2). Larch and pine foliage mass at harvest were not significantly affected by defoliation treatments despite initial differences just after defoliation (Table 2), although mass was lowest in the 75% defoliated treatment.

In both species, proportional distribution of mass to stem and foliage, but not to roots, was affected by defoliation. In Japanese larch, leaf–weight ratio decreased markedly with increasing defoliation intensity ($P = 0.003$; Table 2) while allocation to the stem (stem–weight ratio) increased ($P = 0.054$; Table 2). In red pine, leaf–weight ratio was greater in the 25% defoliated seedlings than in controls or in 50% defoliated seedlings, and was least in the 75% defoliated ones (quadratic function: $P = 0.046$; Table 2). Similar to Japanese larch, stem–weight ratio in red pine increased with increasing defoliation intensity ($P < 0.001$; Table 2). For Japanese larch,

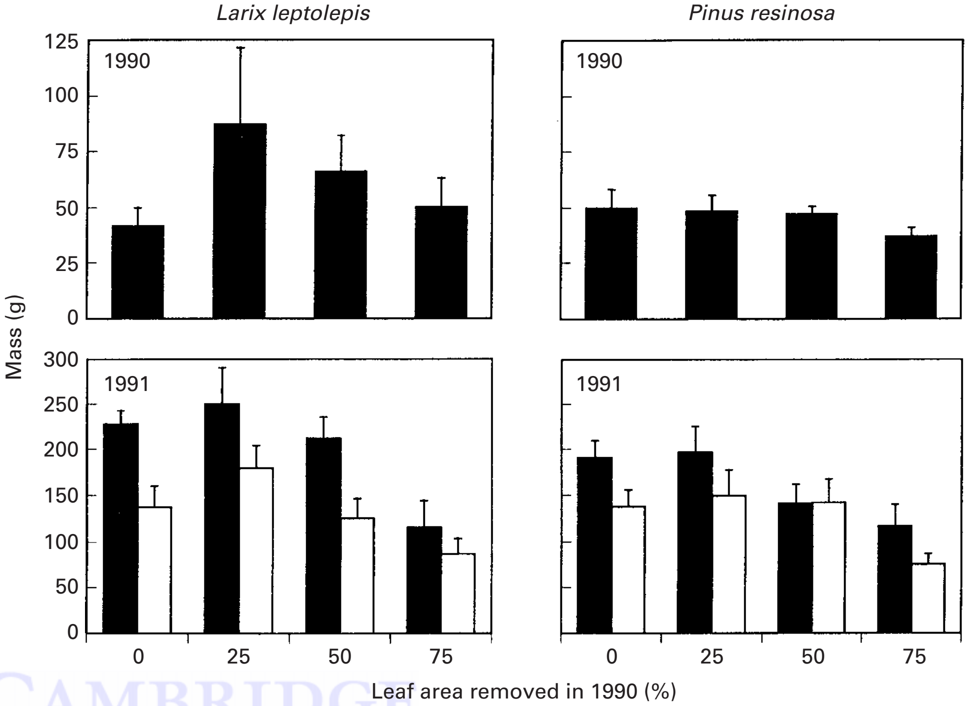

Fig. 2. Mean seedling mass (±SE) per defoliation treatment for *Larix leptolepis* and *Pinus resinosa* seedlings defoliated in 1990 and 1991. Means are plotted across 1990 treatments in both years. For 1991 data, solid bars indicate seedlings not defoliated in 1991; open bars indicate seedlings 50% defoliated in 1991.

Table 2. *Tissue dry weight for defoliated and control* Larix leptolepis *and* Pinus resinosa *seedlings in 1990*

	Larix leptolepis				*Pinus resinosa*			
Tissue	0	25	50	75	0	25	50	75
Roots	15.5 ± 3.1	30.0 ± 8.2	24.9 ± 5.6	17.1 ± 4.6	19.7 ± 3.1	16.6 ± 2.5	18.3 ± 1.7	12.8 ± 2.3
Stem	17.4 ± 3.8	44.9 ± 20.9	37.5 ± 8.7	26.8 ± 6.4	10.7 ± 2.2	11.6 ± 1.8	10.8 ± 1.2	11.3 ± 0.11
Foliage	8.7 ± 2.0	12.3 ± 5.6	9.7 ± 2.7	6.1 ± 2.2	19.3 ± 3.5	20.4 ± 2.9	18.2 ± 1.3	13.1 ± 1.4
RWR*	0.37 ± 0.03	0.41 ± 0.04	0.43 ± 0.08	0.34 ± 0.02	0.41 ± 0.03	0.34 ± 0.01	0.39 ± 0.02	0.34 ± 0.04
SWR	0.42 ± 0.02	0.46 ± 0.04	0.45 ± 0.07	0.56 ± 0.02	0.20 ± 0.01	0.24 ± 0.01	0.23 ± 0.01	0.31 ± 0.02
LWR	0.21 ± 0.03	0.13 ± 0.01	0.13 ± 0.02	0.10 ± 0.02	0.38 ± 0.02	0.42 ± 0.01	0.39 ± 0.01	0.35 ± 0.02
RT/FOL†	2.1 ± 0.3	3.4 ± 0.6	3.9 ± 1.0	4.4 ± 1.2	1.1 ± 0.2	0.8 ± 0.03	1.0 ± 0.1	1.0 ± 0.2

Values are means ± SE. Tissue weight expressed in g d. wt.
n = 9, 5, 7, 6 and *n* = 7, 8, 9, 6 for 0, 25, 50 and 75% defoliated larch and pine respectively.
*RWR, root weight ratio (ratio of root d. wt to seedling d. wt), SWR, stem weight ratio, LWR, leaf weight ratio.
†RT/FOL, root d. wt/foliage d. wt.

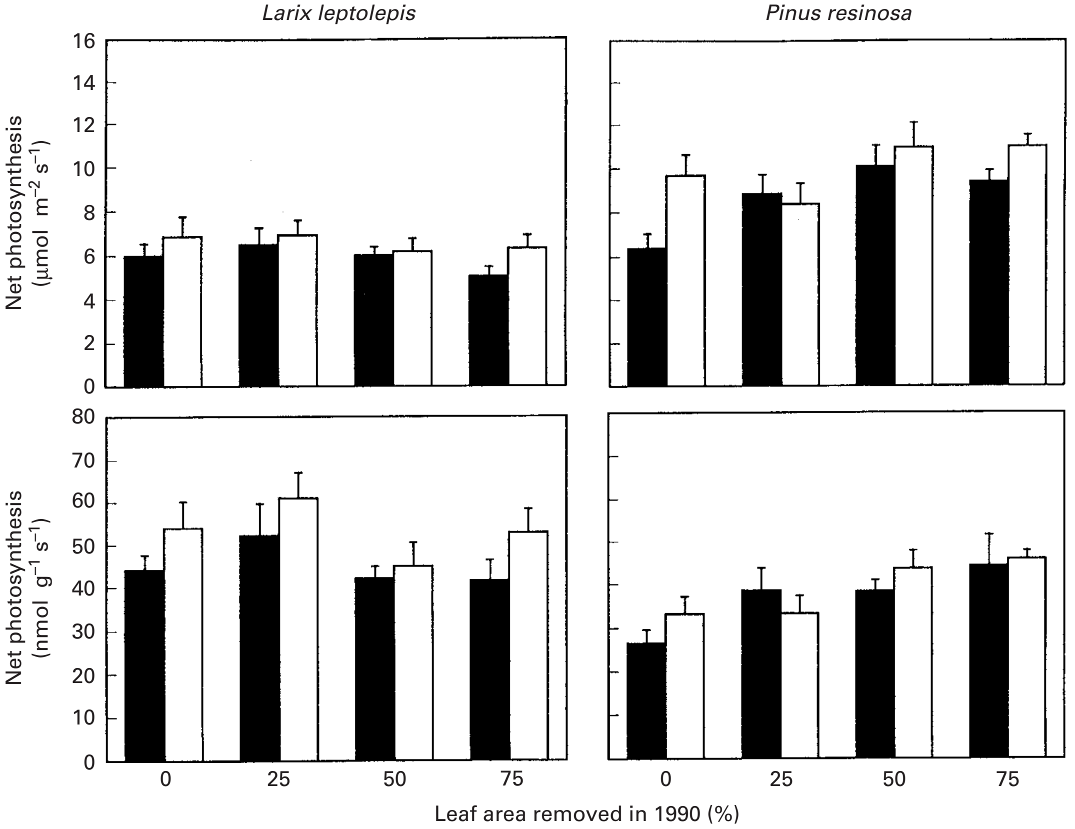

Fig. 3. Mean photosynthesis rates (± SE) per defoliation treatment in 1991 for *Larix leptolepis* and *Pinus resinosa* seedlings defoliated in 1990 and 1991. Means are plotted across 1990 defoliation treatments. For 1991 data, solid bars represent seedlings not defoliated in 1991; open bars represent seedlings 50% defoliated in 1991.

root-to-foliage ratios of defoliated seedlings (all treatments) were on average double those of the control seedlings. Root-to-foliage ratios of red pine did not change in response to defoliation intensity (Table 2).

The effect of 1990 and 1991 defoliation treatments on seedlings in 1991

Photosynthesis. As in 1990, defoliated red pine seedlings again had significantly higher photosynthesis rates on an area basis ($P < 0.001$) than defoliated Japanese larch (Fig. 3). In contrast to 1990, there was no significant difference between control larch and pine seedlings. Larch seedlings across treatments had higher rates of photosynthesis on a mass basis than red pine ($P < 0.001$; Fig. 3).

Larch seedlings defoliated in 1991 had significantly higher photosynthetic rates on a mass basis ($P = 0.054$; average increase 18%) than seedlings not defoliated in 1991 (Fig. 3). Red pine seedlings had significantly higher photosynthesis on an area basis ($P = 0.049$; average increase 15%), but not on a mass basis ($P = 0.515$) in response to 50% defoliation in 1991 (Fig. 3).

In 1991 there was no significant effect of 1990

Table 3. *Non-structural carbohydrate content per seedling tissue in defoliated and control* Larix leptolepis *and* Pinus resinosa *seedlings in 1991*

			Larix leptolepis				*Pinus resinosa*			
Fraction	Tissue	1991 TRT (%)	0	25	50	75	0	25	50	75
Starch	Roots	0	162.7±27.9	123.6±3.5	131.9±4.5	148.3±19.2	136.7±8.4a	53.7±18.8	83.8±3.6	51.5±7.3
		50	112.6±4.1	117.1±18.5	89.3±26.0	124.5±34.2	69.6±2.5b	60.9±5.2	68.3±11.4	70.0±9.5
	Stem	0	137.9±14.2a	91.0±22.5	73.6±2.3	95.0±6.6	26.2±3.2	21.9±0.1	30.6±12.0	19.0±1.0
		50	73.1±6.4b	68.4±14.0	70.5±10.0	94.6±14.3	23.9±1.4	19.4±1.1	20.3±2.7	21.5±0.2
	Foliage	0	31.3±8.6	15.4±3.0	19.2±2.5	15.1±1.2	34.2±1.5a	33.5±8.0	15.9±1.7	16.3±1.7
		50	17.5±1.7	15.1±0.6	15.9±0.4	18.4±2.7	18.9±4.2b	13.2±0.4	15.5±1.6	16.4±1.4
	Rootprop†	0	0.51±0.07	0.38±0.21	0.56±0.07	0.52±0.01	0.67±0.02a	0.45±0.07	0.58±0.07	0.58±0.03
		50	0.42±0.02	0.46±0.04	0.42±0.13	0.43±0.08	0.57±0.01b	0.65±0.01	0.65±0.03	0.61±0.04
	Stemprop	0	0.43±0.06	0.57±0.18	0.36±0.03	0.45±0.01	0.12±0.01a	0.21±0.02	0.24±0.10	0.24±0.05
		50	0.54±0.01	0.50±0.04	0.55±0.12	0.51±0.06	0.29±0.08b	0.21±0.01	0.20±0.00	0.23±0.04
	Folprop	0	0.06±0.02	0.05±0.02	0.08±0.04	0.03±0.01	0.21±0.02	0.34±0.05	0.17±0.02	0.17±0.04
		50	0.04±0.01	0.03±0.01	0.03±0.01	0.06±0.02	0.14±0.08	0.14±0.01	0.15±0.03	0.16±0.02
TNC‡	Roots	0	204.2±31.9	178.5±0.03	196.0±11.9	203.0±15.1	240.5±12.8	133.9±27.2	148.8±4.7	113.8±18.9
		50	161.1±1.3	167.5±21.3	146.5±26.6	169.6±35.0	112.9±8.0	122.5±7.6	130.9±6.8	116.0±11.6
	Stem	0	183.4±15.9	160.1±29.8	129.4±7.2	162.1±4.2	112.4±9.9	76.3±3.4	89.8±14.0	90.7±8.8
		50	127.8±12.9	122.0±19.8	134.8±14.4	148.0±14.5	55.0±4.5	76.4±0.5	78.2±14.3	69.8±1.7
	Foliage	0	116.1±21.4	101.4±2.6	130.6±21.6	108.2±12.3	118.1±4.5	102.3±8.5	78.9±0.7	80.3±9.9
		50	100.3±7.6	91.5±9.7	120.6±8.1	101.1±8.5	73.6±2.9	77.7±2.6	94.3±4.0	70.2±3.1
	Rootprop	0	0.45±0.07	0.29±0.16	0.47±0.07	0.42±0.01	0.49±0.02	0.40±0.05	0.40±0.06	0.39±0.04
		50	0.34±0.03	0.38±0.04	0.36±0.09	0.37±0.07	0.45±0.00	0.44±0.02	0.42±0.03	0.42±0.03
	Stemprop	0	0.40±0.05	0.52±0.13	0.35±0.02	0.46±0.00	0.21±0.01	0.24±0.00	0.27±0.06	0.35±0.08
		50	0.53±0.01	0.51±0.03	0.54±0.06	0.47±0.04	0.32±0.09	0.29±0.01	0.26±0.02	0.31±0.03
	Folprop	0	0.15±0.03	0.18±0.03	0.19±0.04	0.12±0.02	0.30±0.02	0.36±0.05	0.33±0.00	0.26±0.05
		50	0.13±0.02	0.11±0.01	0.11±0.03	0.16±0.04	0.24±0.09	0.27±0.03	0.32±0.02	0.27±0.02

Values are means±SE. Non-structural carbohydrate content expressed in mg glucose equivalent g^{-1} d. wt tissue.

$n = 4, 2, 2, 2$ and $n = 2, 2, 2, 5$ for 0, 25, 50 and 75% defoliated (in 1990) Japanese larch seedlings not defoliated in 1991 and seedlings defoliated in 1991, respectively. $n = 4, 2, 2, 4$ and $n = 2, 2, 2, 6$ for 0, 25, 50 and 75% defoliated (in 1990) red pine seedlings not defoliated in 1991 and those defoliated in 1991, respectively. Each sample represents the combination of two to three seedlings except where $n \geqslant 4$.

*Amount of foliage removed in 1991; significant differences (Student's t-test) between 1991 treatment responses are designated with a letter.

†Prop, carbohydrate content in the tissue as a proportion of whole seedling content. Whole seedling content is the sum of all tissue contents (adjusted for biomass).

‡TNC, total non-structural carbohydrates (starch and soluble sugars combined).

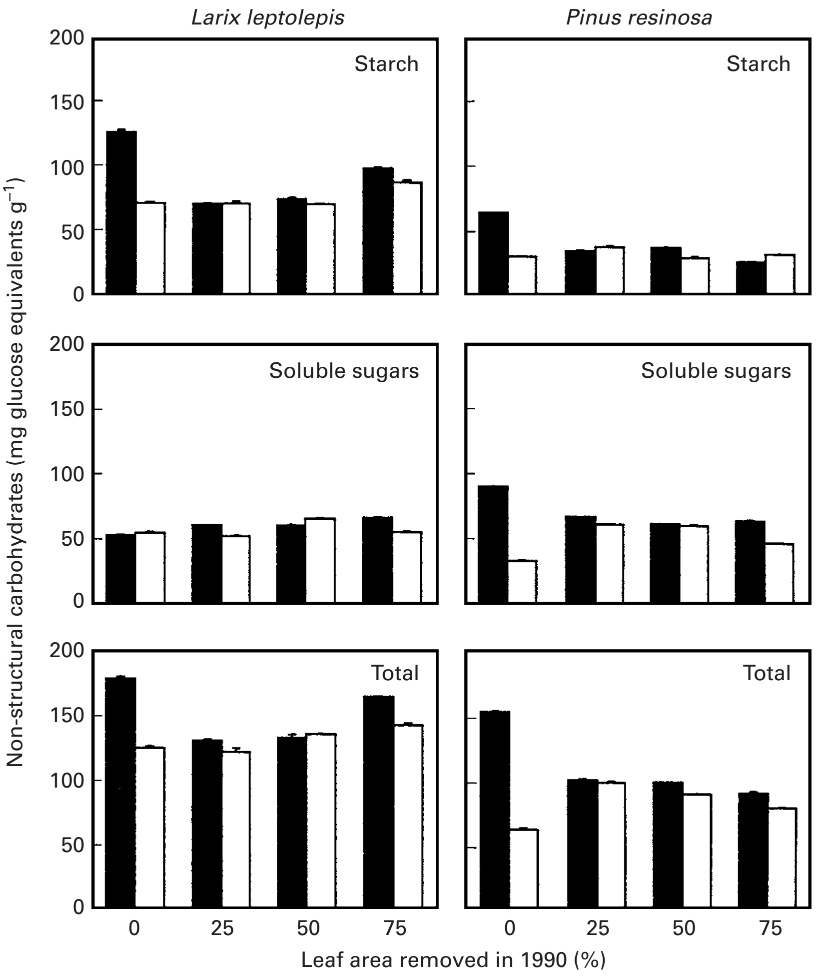

Fig. 4. Mean starch, soluble sugar and total non-structural carbohydrate concentrations of whole seedlings (±SE) per defoliation treatment for *Larix leptolepis* and *Pinus resinosa* seedlings defoliated in 1990 and 1991. Means are plotted across 1990 defoliation treatments. Solid bars indicate seedlings not defoliated in 1991; open bars indicate seedlings 50% defoliated in 1991.

defoliation treatments on photosynthesis in larch seedlings (Fig. 3). By contrast, red pine seedlings showed a linear increase (by as much as 50%) in photosynthesis on a mass and area basis with increasing 1990 defoliation intensity in 1991 (Fig. 3). A similar, but non-significant, pattern was seen in 1990 in photosynthesis on a mass basis (Fig. 1).

Non-structural carbohydrates. In both species, TNC concentrations showed similar patterns of response to defoliation (Table 3). Defoliation of any kind (in the current or previous year) caused about a 50% decrease in whole-seedling starch concentration, but neither the year of defoliation, nor the amount or number of years of defoliation, mattered otherwise (Fig. 4). This same pattern of response was generally seen in all seedling components in both species, although it was most pronounced in the foliage and stem in Japanese larch, and in the foliage and roots in red pine (Table 3). Soluble sugars displayed different patterns of response to defoliation depending on the species. In larch, soluble sugar concentrations were unaffected by defoliation (Fig. 4); in pine, soluble sugar concentrations followed the same patterns of response as starch, being lower in all defoliation treatments than in controls (Fig. 4).

The proportional allocation of starch or soluble sugars between seedling components differed between species. There was a significant difference between defoliated Japanese larch and red pine in the amount of starch proportionately allocated to their root systems (larch 44%, pine 55%, $P = 0.019$; Table 3). In addition, Japanese larch had proportionately less starch or soluble sugars in the foliage and more starch or soluble sugars in the stem than red pine (Table 3). In Japanese larch, the proportional allocation of starch or soluble sugars to a particular seedling component was not significantly or consistently affected by 1990 or 1991 defoliation (Table 3). Red pine seedlings defoliated in 1991 had proportionately more starch in the stem ($P = 0.026$) and proportionately less sugar in the roots ($P = 0.036$) relative to non-defoliated seedlings. No other effect of defoliation in 1991 was noted for starch or soluble sugar allocations to other seedling components.

Table 4. *Tissue dry mass (g) for defoliated and control* Larix leptolepis *and* Pinus resinosa *seedlings in 1991*

		Larix leptolepis				*Pinus resinosa*			
Tissue	1991 TRT (%)	0	25	50	75	0	25	50	75
Roots	0	87.9 ± 8.2a	81.6 ± 13.0	80.0 ± 9.3a	41.2 ± 9.8	55.7 ± 7.0	61.5 ± 12.1	38.8 ± 7.4	35.9 ± 7.8
	50	49.0 ± 8.9b	63.0 ± 9.7	40.3 ± 6.4b	27.7 ± 6.0	42.0 ± 6.8	50.8 ± 9.9	44.8 ± 8.7	23.0 ± 3.3
Stem	0	83.4 ± 9.5	106.0 ± 17.6	78.2 ± 11.6	54.4 ± 14.4	58.3 ± 5.9	62.7 ± 12.8	43.3 ± 5.4	37.7 ± 6.5
	50	65.2 ± 11.2	90.4 ± 14.0	70.8 ± 13.6	41.3 ± 9.0	56.2 ± 11.4	51.6 ± 8.2	49.3 ± 9.2	29.6 ± 4.5
Foliage	0	56.3 ± 4.4a	62.0 ± 12.0a	62.2 ± 7.3a	20.0 ± 5.2	76.5 ± 7.2a	71.9 ± 8.2	58.6 ± 8.2	43.1 ± 10.0
	50	23.2 ± 5.0b	25.1 ± 4.3b	14.6 ± 1.9b	17.8 ± 3.3	46.6 ± 7.5b	46.5 ± 10.5	47.6 ± 7.7	22.3 ± 4.5
RWR†	0	0.39 ± 0.02	0.33 ± 0.02	0.38 ± 0.02	0.36 ± 0.01	0.29 ± 0.01	0.30 ± 0.02	0.26 ± 0.02	0.30 ± 0.02
	50	0.36 ± 0.03	0.35 ± 0.02	0.32 ± 0.02	0.32 ± 0.03	0.22 ± 0.02	0.34 ± 0.02	0.31 ± 0.02	0.31 ± 0.01
SWR	0	0.36 ± 0.03a	0.43 ± 0.01a	0.30 ± 0.05a	0.47 ± 0.02	0.31 ± 0.01a	0.32 ± 0.03	0.32 ± 0.01	0.34 ± 0.04
	50	0.48 ± 0.03b	0.51 ± 0.03b	0.55 ± 0.02b	0.47 ± 0.02	0.41 ± 0.03b	0.36 ± 0.03	0.35 ± 0.01	0.40 ± 0.02
LWR	0	0.25 ± 0.03a	0.24 ± 0.01a	0.32 ± 0.04a	0.18 ± 0.02	0.40 ± 0.01	0.39 ± 0.03a	0.42 ± 0.01a	0.36 ± 0.04
	50	0.16 ± 0.02b	0.14 ± 0.01b	0.13 ± 0.02b	0.21 ± 0.03	0.37 ± 0.03	0.30 ± 0.03b	0.34 ± 0.02b	0.29 ± 0.03
RT/FOL‡	0	1.61 ± 0.16	1.43 ± 0.14a	1.41 ± 0.23a	2.42 ± 0.50	0.72 ± 0.05	0.81 ± 0.11	0.64 ± 0.07a	1.03 ± 0.24
	50	2.57 ± 0.46	2.65 ± 0.29b	2.89 ± 0.44b	1.71 ± 0.33	0.94 ± 0.13	1.38 ± 0.37	0.94 ± 0.10b	1.21 ± 0.24

Values are means ± SE. $n = 8, 7, 9, 8$ and $n = 9, 8, 7, 7$ for 0, 25, 50 and 75% defoliated (in 1990) Japanese larch seedlings not defoliated in 1991 and seedlings defoliated in 1991, respectively. $n = 8, 8, 9, 8$ and $n = 8, 7, 8, 7$ for 0, 25, 50 and 75% defoliated (in 1990) red pine seedlings not defoliated in 1991 and those defoliated in 1991, respectively.

*Amount of foliage removed in 1991; significant differences (Student's *t*-test) between 1991 treatment responses are designated with a letter.

†RWR, root weight ratio (ratio of root d. wt to seedling d. wt); SWR, stem weight ratio; LWR, leaf weight ratio.

‡RT/FOL, root d. wt/foliage d. wt.

Biomass. Both larch and pine seedlings defoliated in 1991 had significantly less mass than those not defoliated in 1991 (larch, $P < 0.001$; pine, $P = 0.030$; Fig. 2). In larch this response was the result of significant reductions in both foliage mass ($P < 0.001$) and root mass ($P < 0.001$), whereas in pine it was primarily due to a reduction in foliage mass ($P < 0.001$; Table 4). The residual effect of 1990 defoliation treatments was also similar in both species (Fig. 2). Relative to control seedlings, total mass was similar (pine) or greater (larch) in 25% defoliated seedlings and less in 50% and especially 75% defoliated seedlings (larch, quadratic function, $P < 0.001$; pine, quadratic function, $P = 0.003$). This pattern was generally shown by all components (foliage, stem and roots) in both species (Table 4).

In both species there were significant ($P < 0.001$) decreases in leaf–weight ratio and increases in stem–weight ratio in response to defoliation in 1991 (Table 4). As a result, root-to-foliage ratios were higher in seedlings defoliated in 1991 (larch, $P = 0.005$; pine, $P = 0.018$). There was no significant residual effect of 1990 defoliation treatments on leaf–, stem– or root–weight ratios in pine (Table 4). In larch seedlings defoliated in 1991, leaf–weight ratio decreased in seedlings defoliated by 25 and 50% in 1990 (quadratic function, $P = 0.018$). Despite this response, root-to-foliage ratios were not affected. In all other cases, there was no residual effect of 1990 defoliation treatments on proportional allocation of mass to seedling components.

DISCUSSION

Physiological and morphological differences between deciduous and evergreen species have been described and debated for some time (Chapin, 1980; Gower & Richards, 1990). The relative cost of defoliation in terms of whole-plant C economy is hypothesized to be higher for evergreen than deciduous species (Mooney & Gulmon, 1982; Bryant *et al*., 1988). Compensation for lost foliage, however, may alter these expectations (Harris, 1974; Heichel & Turner, 1983; Trumble *et al*., 1993).

Photosynthesis

In all combinations of treatments, years and species, defoliation either stimulated photosynthesis or had no significant effect (Figs 1, 3). Stimulatory effects on gas exchange were noted in 1991 in response to 1991 (larch and red pine) and 1990 (red pine only) defoliation treatments (Fig. 3). The residual effect of 1990 defoliation treatments on red pine photosynthesis is an interesting response both in occurrence and pattern. The delay in response and linear increase in gas exchange with increasing residual defoliation intensity are generally inconsistent with the literature (Wareing *et al*., 1968; Lubbers & Lechowicz, 1989). Reported responses often include an increase in photosynthesis, but not necessarily linearly with increasing defoliation intensity (e.g. Lincoln & Mooney, 1984; Reich *et al*., 1993). These reported responses were measured in the year of defoliation, although Prudhomme (1982) and Reich *et al*. (1993) found a residual enhancement of photosynthesis 1 yr after defoliation. Other residual effects of defoliation, such as on plant defensive chemistry, have received considerable attention (Karban & Myers, 1989). In addition, Alfaro *et al*. (1982) noted that effects of defoliation on growth and mortality could be delayed and may have a residual effect several years after defoliation. These results have been discussed mostly in the light of possible adaptive significances; an actual mechanism to explain them has not been identified.

Non-structural carbohydrates

Total non-structural carbohydrates form the pool of reserve C which can be partitioned to growth when demand exceeds supply of currently produced photosynthates (Kramer & Kozlowski, 1979; Waring & Schlesinger, 1985). Both species had similar response patterns for TNC content in both years of the study. In 1990 there was no response to defoliation, whereas in 1991 TNC concentrations were reduced in defoliated seedlings (Tables 1, 3). The reductions were less in larch than in red pine, primarily because there were no reductions in soluble sugar concentrations in defoliated larch seedlings.

Slightly higher TNC levels were allocated to the roots in red pine seedlings than in Japanese larch, but the main difference between the species was noted in the above-ground components. Japanese larch allocated proportionately more TNC to the stem, whereas red pine allocated proportionately more to its foliage (Table 3). These allocation patterns are consistent with the literature and underline the relative importance of the storage function of foliage in red pine seedlings (Chapin, 1980; Bryant *et al*., 1988). However, it is important to recognize that by far the largest pool of TNC (proportional or absolute) was located in the roots in both species. Thus, while loss of foliage constituted a greater loss of TNC to pine than to larch, the proportion of total seedling TNC lost in red pine was still fairly low (*c*. 15% in 50% defoliated seedlings), and lower still when regarding just the starch pool.

Within the TNC pool, starch concentrations have been shown to be well correlated with the ability of trees to survive defoliation events (Waring & Schlesinger, 1985). It is expected that any changes in the C balance of a seedling will be noted first in the starch pool, as in theory partitioning to this pool is of low priority (Chung & Barnes, 1980). Consequently, the differences in response pattern between species may reflect differences in their abilities to withstand defoliation. In both years of the study, both species responded similarly with regard to starch content. In 1990, starch concentrations were not affected in either species. In 1991, whole-seedling starch levels were reduced the same amount (*c.* 50%) by defoliation in both species, regardless of defoliation intensity or frequency relative to control seedlings (Fig. 4). In addition to the similarity in response patterns, both species had a minimum level of starch that was maintained or that could not be used (cf. Chapin *et al.*, 1990). The fact that starch levels were not reduced in 1990 is consistent with our results showing no negative impact of defoliation on photosynthesis or mass (Figs 1, 2). That defoliation induced reduction in starch levels in 1991 but not in 1990 may be a result of increased seedling size. Both red pine and Japanese larch seedlings increased fourfold in mass from 1990 to 1991 (Fig. 2). Reich *et al.* (1993) noted that smaller seedlings had shorter-lived responses to defoliation. Therefore the smaller seedlings in 1990 may have shown some response, but it may have been too short in duration to have had an impact on final starch concentrations.

How could defoliation cause a decrease in starch concentrations, but apparently independently of intensity or frequency of defoliation? Work with different tree species suggests that regardless of leaf longevity, C reserves are used in the spring only in the early phases of growth. Most biomass accumulation during the summer is dependent on current photosynthate production (Kozlowski & Winget, 1964; Little, 1974; Webb & Kilpatrick, 1993). Thus whole-seedling starch concentrations reflect the amount of reduction early in the spring, as well as the amount of replacement during the summer or early autumn. A plausible explanation for the response pattern of whole-seedling starch concentration in both species is that growth may have ceased sooner in controls than in defoliated seedlings. Consequently, any further acquisition of C in control seedlings could be partitioned to storage.

Biomass accumulation

In response to defoliation there was no particular advantage to being deciduous or evergreen in terms of total net C gain. There was no difference between species in total seedling mass in seedlings defoliated in both years of the experiment ($P < 0.766$), nor was there a difference between species in the proportional decrease in mass between seedlings defoliated in 1990 versus those defoliated in 1991 ($P < 0.149$).

Other similarities in response pattern were noted with regard to changed allocation patterns following defoliation. In response to current defoliation in both years of the experiment, both species showed a proportional shift in mass to the stem (Tables 2, 4). The result of this shift in allocation was that C was allocated to support the crown, but in a component that could not be removed by further defoliation. This pattern of response contradicts the predictions of van der Meijden *et al.* (1988), but is in keeping with results reported by Caldwell *et al.* (1981) and Reich *et al.* (1993).

The focus of this study was on adverse affects of defoliation on deciduous and evergreen conifer seedlings. The results presented in this paper show that the patterns and relative magnitude of response to defoliation were generally similar in the two species. Since there is some agreement that plant mass can increase in defoliated plants (i.e. overcompensate) relative to undefoliated ones (Harris, 1974; McNaughton, 1983; Reich *et al.*, 1993), the question can be posed whether defoliation had a more positive effect in either species. Larch seedlings lightly defoliated in 1990 showed no apparent change in photosynthesis, but did have a greater total biomass than controls in both years (Figs 1, 2, Table 4). By contrast, red pine seedlings had increased photosynthetic rates, but total mass was unchanged. Japanese larch seedlings may be better able to compensate for light defoliation than red pine. Whether a greater compensatory response confers an advantage in the long run remains to be seen, and is highly debated (Belsky *et al.*, 1993). In conclusion, this study does not support the widely held belief that evergreen species are more adversely affected by defoliation than deciduous ones. In this study, we found that despite differences in leaf lifespan and growth habit, both red pine and Japanese larch treated under the same conditions had similar patterns and relative magnitude of response.

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REFERENCES

Alfaro R, Van Sickle G, Thomson A, Wegwitz E. 1982. Tree mortality and radial growth losses caused by the western spruce budworm in a Douglas-fir stand in British Columbia. *Canadian Journal of Forest Research* **12**: 780–787.

Bassman J, Myers W, Dickman D, Wilson L. 1982. Effects of simulated insect damage on early growth of nursery-grown hybrid poplars in northern Wisconsin. *Canadian Journal of Forest Research* **12**: 1–9.

Belsky AJ, Carson WP, Jensen CL, Fox GA. 1993. Overcompensation by plants: herbivore optimization or red herring? *Evolutionary Ecology* **7**: 109–121.

Bryant JP, Chapin III FS, Klein DR. 1983. Carbon/nutrient balance of boreal plants in relation to vertebrate herbivory. *Oikos* **40**: 357–368.

Bryant JP, Tuomi J, Niemala P. 1988. Environmental constraint of constitutive and long-term inducible defenses in woody plants. In: Spencer KC, ed. *Chemical mediation of coevolution*. New York, USA: American Institute of Biological Sciences, 367–389.

Caldwell MM, Richards JH, Johnson DA, Nowak RS, Dzurec RS. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunchgrasses. *Oecologia* **50**: 14–24.

Chapin III FS. 1980. The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**: 233–260.

Chapin III FS, Schultze E-D, Mooney HA. 1990. The ecology and economics of storage in plants. *Annual Review of Ecology and Systematics* **21**: 423–427.

Chung HH, Barnes RL. 1980. Photosynthate allocation in *Pinus taeda*. II. Seasonal aspects of photosynthate allocation to different biochemical fractions in shoots. *Canadian Journal of Forest Research* **10**: 338–347.

Coley PD. 1988. Effects of plant growth rate and leaf lifetime on the amount and type of anti-herbivore defense. *Oecologia* **74**: 531–536.

Ericsson A, Helkvist J, Hillerdal-Hagstromer K, Larsson S, Mattson-Djos E, Tenow O. 1980. Consumption and pine growth – hypotheses on effects on growth processes by needle-eating insects. *Ecological Bulletins* **32**: 537–545.

Feeny P. 1976. Plant apparency and chemical defense. In: Wallace JW, Mansell RL, eds. *Biochemical interactions between plants and insects*. New York, USA: Plenum, 1–40.

Gordon JC, Larson PR. 1970. Redistribution of ^{14}C-labeled reserve food in young red pines during shoot elongation. *Forest Science* **16**: 14–20.

Gower ST, Richards JH. 1990. Larches: deciduous conifers in an evergreen world. *BioScience* **40**: 818–826.

Haissig BE, Dickson RE. 1979. Starch measurement in plant tissue using enzymatic hydrolysis. *Physiologia Plantarum* **47**: 151–157.

Hanson J, Möller I. 1975. Percolation of starch and soluble carbohydrates from plant tissue for quantitative determination with anthrone. *Annals of Biochemistry* **68**: 87–94.

Harris P. 1974. A possible explanation of plant yield increases following insect damage. *Agro-Ecosystems* **1**: 219–225.

Haukioja E. 1990. Induction of defenses in trees. *Annual Review of Entomology* **36**: 25–42.

Heichel GH, Turner NC. 1983. CO$_2$ assimilation of primary and regrowth foliage of red maple (*Acer rubrum* L.) and red oak (*Quercus rubra* L.): response to defoliation. *Oecologia* **57**: 14–19.

Hogg EH, Lieffers VJ. 1991. Seasonal changes in shoot regrowth potential in *Calamagrostis canadensis*. *Oecologia* **85**: 596–602.

Ives WGH, Nairn LD. 1966. Effects of defoliation on young upland tamarack in Manitoba. *Forestry Chronicle* **42**: 137–142.

Karban R, Myers JH. 1989. Induced plant responses to herbivory. *Annual Review of Ecology and Systematics* **20**: 331–348.

Kramer PJ, Kozlowski TT. 1979. *Physiology of woody plants*. New York, USA: Academic Press.

Kozlowski TT, Winget CH. 1964. The role of reserves in leaves, branches, stems and roots on shoot growth of red pine. *American Journal of Botany* **51**: 522–529.

Krueger KW, Trappe JM. 1967. Food reserves and seasonal growth of Douglas-fir seedlings. *Forest Science* **13**: 192–202.

Lincoln DE, Mooney HA. 1984. Herbivory on *Displacus aurantiacus* shrubs in sun and shade. *Oecologia* **64**: 173–176.

Little CHA. 1974. Relationship between the starch level at budbreak and current shoot growth in *Abies balsamea* L. *Canadian Journal of Forest Research* **4**: 268–273.

Loescher WH, McCamant T, Keller JD. 1990. Carbohydrate reserves, translocation and storage in woody plant roots. *HortScience* **25**: 274–281.

Lovett GM, Tobiessen P. 1993. Carbon and nitrogen assimilation in red oaks (*Quercus rubra* L.) subject to defoliation and nitrogen stress. *Tree Physiology* **12**: 259–269.

Lubbers AE, Lechowicz MJ. 1989. Effects of leaf removal on reproduction vs. below ground storage in *Trillium grandiflorum*. *Ecology* **70**: 85–96.

McLaughlin SB, McConathy RK, Barnes RL, Edwards NT. 1980. Seasonal changes in energy allocation by white oak (*Quercus alba*). *Canadian Journal of Forest Research* **10**: 379–388.

McNaughton SJ. 1983. Compensatory plant growth as a response to herbivory. *Oikos* **40**: 329–336.

Meijden E van der, Wijn M, Verkaar HJ. 1988. Defense and regrowth, alternate plant strategies in the struggle against herbivores. *Oikos* **51**: 355–363.

Mooney HA, Gulmon SL. 1982. Constraints on leaf structure and function in reference to herbivory. *BioScience* **32**: 198–205.

Prudhomme TI. 1982. The effect of defoliation history on photosynthesis rates in mountain birch. *Report of the Kevo Subarctic Research Station* **18**: 5–9.

Reich PB, Walters MB, Krause SC, Vanderklein DW, Raffa KF, Tabone T. 1993. Growth, nutrition and gas exchange of *Pinus resinosa* following artificial defoliation. *Trees* **7**: 67–77.

Richards JH, Caldwell MM. 1985. Soluble carbohydrates, concurrent photosynthesis and efficiency in regrowth following defoliation: a field study with *Agropyron* species. *Journal of Applied Ecology* **22**: 907–920.

Trumble JT, Kolodny-Hirsch DM, Ting IP. 1993. Plant compensation for arthropod herbivory. *Annual Review of Entomology* **38**: 93–119.

Wallace LL, McNaughton SJ, Coughenour MB. 1984. Compensatory photosynthetic responses of three African graminoids to different fertilization, watering and clipping regimes. *Botanical Gazette* **145**: 151–156.

Wareing PF, Khalifa MM, Treharne KJ. 1968. Rate-limiting process in photosynthesis at saturating light intensities. *Nature* **220**: 453–457.

Waring RH, Schlesinger WH. 1985. *Forest ecosystems: concepts and management*. Orlando, FL, USA: Academic Press.

Webb WL. 1975. Dynamics of photoassimilated carbon in Douglas-fir seedlings. *Plant Physiology* **56**: 455–459.

Webb WL. 1980. Starch content of conifers defoliated by the Douglas-fir tussock moth. *Canadian Journal of Forest Research* **10**: 535–540.

Webb WL, Kilpatrick KJ. 1993. Starch content in Douglas-fir: diurnal and seasonal dynamics. *Forest Science* **39**: 359–367.