Functional Ecology 2000
14, 281–292

Leaf-level resource use for evergreen and deciduous conifers along a resource availability gradient

B. D. KLOEPPEL,*† S. T. GOWER,† J. G. VOGEL†‡ and P. B. REICH§

†*Department of Forest Ecology and Management, 1630 Linden Drive, University of Wisconsin–Madison, Madison, WI 53706, USA, and* §*Department of Forest Resources, 115 Green Hall, 1530 North Cleveland Avenue, University of Minnesota, St Paul, MN 55108, USA*

Summary

1. We compared leaf-level carbon, nitrogen and water use for a deciduous (*Larix occidentalis* Nutt.) and sympatric evergreen (*Pseudotsuga menziesii*, Beissn., Franco, or *Pinus contorta* Engelm.) conifer along a resource availability gradient spanning the natural range of *L. occidentalis* in western Montana, USA.

2. We hypothesized that leaf photosynthesis (A), respiration (r), specific leaf area (SLA) and foliar nitrogen concentration (N) would be higher for deciduous than sympatric evergreen conifers in mixed stands, and that these interspecies differences would increase from high to low resource availability. We also hypothesized that leaf-level nitrogen and water-use efficiency would be higher for the co-occurring evergreen conifer than *L. occidentalis*.

3. In general, mass-based photosynthesis (A_m) was significantly higher for *L. occidentalis* than co-occurring evergreen conifers in the drier sites, but A_m was similar for evergreen and deciduous conifers at the mesic site.

4. Mass-based foliar nitrogen concentration (N_m) was positively correlated to SLA for all species combined across the gradient ($R^2 = 0{\cdot}64$), but the relationship was very weak ($R^2 = 0{\cdot}08$–$0{\cdot}34$) for evergreen and deciduous species separately. Mass-based A_m and r_m were poorly correlated to N_m for all species combined across the gradient ($R^2 = 0{\cdot}28$ and $0{\cdot}04$, respectively).

5. For each site-species combination, daily maximum A_m was negatively correlated to vapour pressure deficit (VPD) ($R^2 = 0{\cdot}36$–$0{\cdot}59$), but was poorly correlated to twig predawn water potential ($R^2 < 0{\cdot}04$).

6. Instantaneous nitrogen-use efficiency (NUE$_i$; A_m divided by N_m) and water-use efficiency ($\delta^{13}C$) increased significantly ($P = 0{\cdot}05$) from high to low resource availability for both evergreen and deciduous conifers, except for NUE$_i$ in *L. occidentalis*.

Key-words: *Larix occidentalis*, photosynthesis, *Pinus contorta*, *Pseudotsuga menziesii*, resource-use efficiency, respiration

Functional Ecology (2000) **14**, 281–292

Introduction

High resource availability favours plants with a deciduous leaf habit, while low resource availability favours an evergreen leaf habit (Bazazz 1979; Chapin 1980; Coley, Bryant & Chapin 1985; Kikuzawa 1991; Monk 1966). The physiological mechanisms responsible for the different distributions of evergreen and deciduous plants are not completely understood, but ecophysiological characteristics may be important. Higher resource-use efficiency confers a more positive plant carbon balance when the resource is limiting (Chabot & Hicks 1982; Givnish 1986; Sheriff *et al.* 1995). Many leaf-level ecophysiological characteristics that influence resource use are correlated to leaf habit (Coley 1988; Reich, Walters & Ellsworth 1991). For example, net photosynthesis (A_m – mass basis), nitrogen concentration (N_m – mass basis) and specific leaf area (SLA) are often higher for deciduous than evergreen trees (Chabot & Hicks 1982; Coley 1988; Mooney & Gulmon 1982; Reich *et al.* 1995b; Reich, Walters & Ellsworth 1997). Past studies have often compared species with widely

---

*Present address and correspondence: Institute of Ecology, University of Georgia, Coweeta Hydrologic Laboratory, 3160 Coweeta Lab Road, Otto, NC 28763, USA.
‡Present address: Department of Forest Sciences, University of Alaska Fairbanks, PO Box 757200, Fairbanks, AK 99775, USA.

varying leaf longevity growing in different environments (i.e. resource availability; Reich *et al.* 1997). However, few studies have capitalized on the relatively high control of the evergreen and deciduous conifer model where foliage morphology (i.e. needles), canopy architecture (i.e. conical) and xylem water conducting elements (i.e. tracheids) are all similar (Gower & Richards 1990; Gower, Reich & Son 1993). Isolated studies have shown that *Larix* spp., deciduous conifers, compared with evergreen conifers have higher photosynthetic rates, higher foliar nitrogen concentration, higher specific leaf area and lower water-use efficiency (Dang *et al.* 1991; Gower & Richards 1990; Gower *et al.* 1993; Gower, Kloeppel & Reich 1995; Kloeppel *et al.* 1998; MacDonald & Lieffers 1990; Matyssek 1986). However, such comparisons have not been made between *Larix* spp. and evergreen conifers across a range of edaphic conditions.

Resource availability influences many ecophysiological characteristics of individual leaves of evergreen and deciduous conifers. Photosynthesis is positively correlated to foliage nitrogen concentration for *Larix laricina*, but the impact is larger on evergreen conifers (Dang *et al.* 1991) which typically have a lower nitrogen concentration (Gower & Richards 1990; Gower *et al.* 1993; Kloeppel *et al.* 1998). More available water favours higher growth in *L. laricina* compared with evergreen conifers (Montague & Givnish 1996) because *Larix* spp. generally use water less efficiently (Gower & Richards 1990; Kloeppel *et al.* 1998). *Larix* spp. are very shade intolerant, therefore they must maintain their canopy above competitors to maximize incident light and support a favourable carbon balance (Dang, Lieffers & Rothwell 1992; Gower & Richards 1990). The interaction of these three resources (nitrogen, water and light) and the efficiency of their use is critical to the understanding of the exception of *Larix* spp. to the leaf habit axiom (Gower & Richards 1990; Lambers & Poorter 1992; Sheriff *et al.* 1995). Previous studies have compared leaf-level water- and nitrogen-use efficiency of *Larix* spp. and sympatric evergreen conifers at single or replicated sites (Dang *et al.* 1991; Gower *et al.* 1993; MacDonald & Lieffers 1990), but we are not aware of any studies that have compared water- and nutrient-use efficiency of *Larix* spp. and sympatric evergreen conifers along a gradient of water and nitrogen availability.

In this study we compared key leaf-level ecophysiological characteristics for *Larix occidentalis* (Western Larch) and the dominant sympatric evergreen conifer, *Pseudotsuga menziesii* (Douglas Fir) or *Pinus contorta* (Lodgepole Pine), at three sites spanning the natural gradient of *L. occidentalis* in western Montana, USA. We hypothesized that A_m, r_m (foliar respiration – mass basis), N_m and SLA would be higher for *L. occidentalis* than evergreen conifers, and that these ecophysiological characteristics would differ less between *L. occidentalis* and sympatric evergreen conifers when resource availability was high. To test directly the effect of nutrient availability on leaf-level ecophysiological characteristics that influence carbon balance, we compared A_m, r_m, N_m and SLA in control and fertilized plots of mixed *L. occidentalis* and co-occurring evergreen conifers at each location.

Methods

STUDY SITES

Three study sites were established along a 230-km transect spanning an edaphic gradient in western Montana, USA (Table 1), that encompasses a large portion of the natural range of *Larix occidentalis* Nutt. (Burns & Honkala 1990). The Bonner, Lost Creek and Savage Lake sites are located near Bonner, Swan Lake and Troy, Montana, respectively. The edaphic gradient, Bonner to Savage Lake, is the result of both increasing precipitation and soil water-holding capacity. Mean annual precipitation ranges from 340 mm at Bonner to 763 mm at Savage Lake. Total soil depth ranges from 0·5 m at Bonner to 1·2 m at Savage Lake. Volcanic ash depth increases markedly across the gradient from Bonner to Savage Lake as a result of long-range deposition via the predominant westerly wind patterns from volcanoes in the states of Oregon and Washington (Baker 1944). Potential soil available water was determined at each site for both the A and B horizons by multiplying the soil horizon depth, horizon bulk density and horizon water-holding capacity and summing for both horizons. The water-holding capacity for each soil horizon was determined from soil water-release curves developed using a pressure plate apparatus. Three soil cores, 10 cm in diameter and 10 cm deep, from both the A and B horizons were utilized from each site. Potential soil available water ranged from 0·022 m m^{-2} at Bonner to 0·150 m m^{-2} at Savage Lake (Table 1). Available soil nutrient concentration was higher at Bonner, but total available nutrient content (concentration × bulk density × rooting depth) was higher at Savage Lake. This resource availability gradient provides a unique experimental design to compare resource-use efficiency between coniferous evergreen and deciduous trees.

All sites support closed-canopy forests of similar tree diameter (Table 1) and stage of development (stem exclusion; *sensu* Smith 1986), but not age, because important structural and functional characteristics occur at different ages, depending upon site quality (Ryan, Binkley & Fownes 1997; Vogt *et al.* 1983, 1987). The most common evergreen tree species for the drier forests (i.e. Bonner and Lost Creek) is *Pseudotsuga menziesii* var. *glauca*, Beissn., Franco (Douglas Fir), while *Pinus contorta* var. *latifolia* Engelm. (Lodgepole Pine) is a more common co-occurring species in mesic forests (i.e. Savage Lake) (Daubenmire 1943; Schmidt, Shearer & Roe 1976). *Larix occidentalis* and the co-occurring evergreen conifer each comprise about one-half of the total basal area in each stand for a

Table 1. Location, climate, soil and vegetation summary for three western Montana, USA, study sites supporting mixed *Larix occidentalis* (Western Larch) and evergreen conifer forests. For soil chemistry, means within a row followed by the same letter are not significantly different using the LSD mean separation technique at the $\alpha = 0{\cdot}05$ level

Site	Bonner*	Lost Creek†	Savage Lake‡
Location			
Latitude	N 46°51′30″	N 47°55′10″	N 48°25′10″
Longitude	W 113°53′45″	W 113°49′00″	W 115°48′30″
Elevation (m)	1158	1012	706
Climate			
Mean January air temperature at 1 m (°C)	–5·6	–4·8	–3·9
Mean July air temperature at 1 m (°C)	19·4	16·3	19·0
Mean total annual precipitation (mm)	340	490	763
Growing season (May–September) precipitation (mm)	168	190	226
Soil			
Texture	loam	sandy loam	silt loam
Rooting depth (m)	0·5	0·7	1·2
Available water			
A Horizon (m m^{-2})	0·009	0·014	0·044
B Horizon (m m^{-2})	0·013	0·024	0·106
Total (m m^{-2})	0·022	0·038	0·150
Chemistry			
pH	5·9 (0·2) a	5·4 (0·1) b	5·6 (0·1) ab
Total N (% mass)	0·11 (0·01) a	0·09 (0·01) a	0·04 (0·01) b
Extractable P (mg g^{-1})	22 (7) a	24 (4) a	26 (4) a
Exchangeable Ca (mg g^{-1})	1317 (148) a	950 (33) b	608 (28) c
Exchangeable Mg (mg g^{-1})	133 (13) a	100 (11) ab	87 (6) b
Exchangeable K (mg g^{-1})	223 (64) a	144 (22) ab	104 (9) b
Vegetation			
Dominant species			
Deciduous	*Larix occidentalis*	*Larix occidentalis*	*Larix occidentalis*
Evergreen	*Pseudotsuga menziesii*	*Pseudotsuga menziesii*	*Pinus contorta*
Stand age (years)	92	66	34
Tree density [number ha^{-1} (SE)] (*Larix*, EC§)	533 (102), 640 (68)	427 (33), 397 (36)	461 (41), 283 (29)
Basal area [m^2 ha^{-1} (SE)] (*Larix*, EC§)	16 (3), 23 (2)	13 (1), 15 (1)	12 (1), 10 (1)
d.b.h.¶ range (cm) (*Larix*, EC§)	7·9–33·7, 6·8–43·5	8·8–32·7, 10·6–36·1	6·2–27·8, 10·5–35·4
Mean tree d.b.h.¶ [cm (SE)] (*Larix*, EC§)	18·9 (0·4), 20·0 (0·4)	19·2 (0·4), 21·3 (0·4)	17·8 (0·5), 22·3 (0·7)

Climate data sources: *30-year average (1967–96), Missoula Airport, Missoula, MT; †30-year average (1964–93) for Swan Lake, MT, National Climate Data Center, Asheville, NC; ‡30-year average (1962–91), Fire Weather Station, Three Lakes Ranger District, Kootenai National Forest, Troy, MT.
§EC, evergreen conifer.
¶d.b.h., stem diameter at breast height (1·37 m).

total of 97·2%, 89·4% and 93·1% of the stand basal area at Bonner, Lost Creek and Savage Lake, respectively (Table 1). Other tree species found at the three sites include *Pinus ponderosa* Laws. (Ponderosa Pine), *Picea engelmannii* Parry (Engelmann Spruce) and *Abies grandis* (Dougl.) Lindl. (Grand Fir).

Six 25 × 25-m plots were established at the Bonner and Lost Creek sites, and eight 15 × 15-m plots were established at the Savage Lake site. The smaller and higher number of plots at the Savage Lake site were used because the stand structure was more heterogeneous at Savage Lake than at the other two sites. All live trees larger than 1 cm diameter at breast height (d.b.h.; 1·37 m) in each plot were permanently tagged and the species and d.b.h. were recorded. Half of the plots at each site were randomly selected to be a control or fertilized treatment. Plots at the Bonner site were stratified by slope position before randomization to limit the possibility that all lower or upper slope plots would be allocated to the same treatment.

The fertilized plots, including the 5-m treated buffer strip, were fertilized in June 1992, October 1992 and May 1993. All fertilizer applications consisted of a balanced nutrient addition of N, K, P, Fe, S and Mn at the following rates: 100, 90, 80, 4, 2, 0·4 kg ha^{-1}, respectively, based on extensive experience of a local forest soil scientist (J. Mandzak, Champion International).

GAS EXCHANGE MEASUREMENTS

Branches were sampled with a pole pruner or shotgun. To test the effect of measuring photosynthesis on foliage from cut branches, net photosynthesis was compared for three cut and intact branches at Lost Creek, where a scaffolding tower was erected. Net photosynthesis (mean ± SE in nmol g^{-1} s^{-1}) of the same attached and cut shoots (within 5 min) did not differ significantly ($P > 0{\cdot}05$) for *L. occidentalis* (24·69 ± 9·26 *vs* 28·35 ± 11·82, respectively) or *Ps. menziesii* (8·05 ± 1·36 *vs* 8·21 ± 1·86, respectively).

Our results are consistent with other studies that have compared photosynthetic rates of leaves from cut and intact branches (Meng & Arp 1993).

The gas exchange of both *L. occidentalis* and *Ps. menziesii* foliage was measured on excised shoots, except *Pi. contorta* for which only needles were placed in the cuvette. After each measurement, the twig inside the cuvette was dried (65 °C) and weighed. In addition, twigs of both species were measured at a variety of temperatures without foliage attached. A respiration–temperature response function was derived from these data and used to predict the respiration of the twig mass for each photosynthesis measurement. Net photosynthesis of the foliage mass was increased by the predicted respiration rate of the twig mass.

A calibrated open-flow infrared gas analyser system (Model LCA-2; Analytical Development System, Hoddesdon, Herts, UK) was used to measure foliar gas exchange. Gas exchange parameters (net photosynthesis, stomatal conductance to water vapour, transpiration, leaf temperature and leaf-to-air vapour pressure deficit) were calculated following von Caemmerer & Farquhar (1981). Gas exchange was measured on sunlit foliage (> 1000 μmol quanta m^{-2} s^{-1}) from the upper third of the tree crown for five to seven trees of both *L. occidentalis* and the dominant evergreen conifers in the control and fertilized plots at each site.

The objectives of the gas exchange measurements were to: (i) examine the maximum instantaneous gas exchange rates of evergreen and deciduous species over the growing season; (ii) compare the light response of both evergreen and deciduous species; and (iii) compare the effects of nutrient availability on the leaf chemistry and gas exchange of evergreen and deciduous species. Daily maximum photosynthesis (A_{max}) was measured from shortly after dew on the foliage evaporated until a consistent 20% decline in CO_2 differential values was observed (e.g. approximately from 08.00 to 11.00 hours local standard time) or until all measurements were complete. All gas exchange measurements, except where noted, were made on the false whorls of needles on *L. occidentalis* and on 1-year-old foliage on evergreen conifers. Gas exchange measurements were conducted during nine sample dates: May, early June, late June, July, August and October 1992, May and August 1993, and May 1994. Net photosynthesis of evergreen conifers was also measured at all sites in March 1993 to assess the potential winter carbon gain by evergreen conifers while *L. occidentalis* was leafless. At that time, soils were thawed and maximum air temperatures had exceeded 10 °C for several preceding days. Net photosynthesis of different aged needles was examined on the evergreen species at each site in May 1993 and May 1994, when soil water availability was relatively high. Gas exchange sampling was measured at one study site per day because of the extensive travel time between sites. Photosynthesis measurements were completed at all three sites in 3–10 days for each sample date.

Net photosynthesis was also measured five times during the day, approximately 2 h apart, in early June and August 1992, corresponding to periods of relatively high and low soil water availability, respectively. Foliage dark respiration was measured once in July 1992 when all leaf tissue was mature.

Light-response curves were generated for both species at each site using foliage from the false whorls of needles (*vs* the single needles on terminal shoots) on *L. occidentalis* and 1-year-old foliage on evergreen conifers. Both *L. occidentalis* and *Ps. menziesii* needle clusters were measured with foliage at their natural angles, whereas *Pi. contorta* needles were measured by placing them in a single plane in the cuvette. In May 1993, neutral density shade cloth screens were used to reduce the ambient light level; measurements were conducted after a 5-min adjustment period. In May 1994, varying light levels were achieved with a red-light emitting diode system (Q-Beam 1000 A; Quantum Devices, Barneveld, WI). Light-response data were fitted to a Michaelis–Menten model (Givnish 1988; Kloeppel, Abrams & Kubiske 1993; Sheve 1984) using a non-linear curve fitting procedure (Proc NLIN; SAS Institute Inc., Cary, NC). This model can be solved for $A = 0$ to estimate the light compensation point:

$$A = [(A_{max} \times Q)/(Q + K)] - r_s,$$

where A is net photosynthesis (nmol g^{-1} s^{-1}), A_{max} is maximum asymptotic photosynthesis (nmol g^{-1} s^{-1}), Q is photosynthetically active radiation (PAR; μmol m^{-2} s^{-1}), K is the light saturation constant at one half of predicted A_{max} (μmol m^{-2} s^{-1}), and r_s is dark respiration equal to negative A when $Q = 0$ (nmol g^{-1} s^{-1}).

MICROENVIRONMENT MEASUREMENTS

Environmental parameters were measured along with all gas exchange data. Predawn and diel xylem water potentials were measured using a pressure bomb (PMS Instrument Co., Corvallis, OR) on twigs from five to seven overstorey *L. occidentalis* and evergreen conifers on each sampling date, except for October 1992 and March 1993 when predawn air temperatures were < 0 °C. Bulk xylem water potential of most twigs was quantified immediately after photosynthesis was measured. Leaf temperature and vapour pressure deficit were calculated for each gas exchange measurement.

LEAF MEASUREMENTS

Specific leaf area (SLA) and leaf nitrogen concentration (N_m) were determined for all needles that were sampled for A_m or r_m. SLA could not be obtained immediately after A_m or r_m measurement because an image analysis system was not available near the field sites. Needles were refrigerated at 5 °C for less than 1 week until they could be photocopied on acetate sheets and dried to a constant mass at 65 °C. Upon returning to the University of Wisconsin–Madison laboratory, the one-sided projected area of the foliage image on the acetate sheets was determined using a leaf area meter (Decagon Devices Inc., Pullman, WA). One-sided SLA was calculated as the ratio of the one-sided leaf area of fresh needles : needle dry mass. One complete set of fresh samples from all sites was photocopied as well as digitized. A linear regression equation (SAS Institute 1985) was applied to all photocopied samples to correct for the increase in leaf area due to the magnification of photocopiers (actual leaf area = photocopy leaf area × 0·840 + 0·587; $R^2 = 0{\cdot}932$; $P = 0{\cdot}002$; $n = 60$).

Needles for N analysis were ground to pass a 1-mm^2 mesh screen and redried at 65 °C. Approximately 300 mg of tissue was digested using a wet oxidation procedure (Parkinson & Allen 1975) and nitrogen concentration was determined colorimetrically using a Lachat continuous-flow ion analyser (Lachat Inc., Mequon, WI) (Lachat Inc. 1988). Plant tissue standards (National Bureau of Standards, Gaithersburg, MD) spanning a wide range of N concentration (7·0–29·4 mg g^{-1} total N) were also digested and analysed for *N* to insure that the digestion and colorimetric analysis were accurate.

STATISTICS

Statistical comparisons of means between *L. occidentalis* and co-occurring evergreen conifers were conducted using a one-way general linear model (SAS Institute 1985). Mean comparisons were conducted using the LSD mean separation technique at the $\alpha = 0{\cdot}05$ level. For Fig. 6, the insets include $\log_{10}$-transformed data to linearize the relationships. Linear regression analysis was used to examine the relationships between specific leaf area, leaf nitrogen, predawn water potential, net photosynthesis, vapour pressure deficit and dark respiration (SAS Institute 1985). Slopes and *y*-intercepts of linear regressions were compared using identification variables (Chatterjee & Price 1977).

Results and Discussion

INFLUENCE OF ENVIRONMENT ON GAS EXCHANGE AND SPECIFIC LEAF AREA

Daily maximum mass-based net photosynthesis (A_m) was significantly higher ($P < 0{\cdot}05$) for *L. occidentalis* than *Ps. menziesii* for all sampling dates at Bonner and Lost Creek, and was significantly higher for *L. occidentalis* than *Pi. contorta* at Savage Lake for five of the eight sampling dates (Fig. 1). In 1992, maximum net photosynthesis for both species occurred in June at Bonner and Lost Creek and from July through August at Savage Lake. Net photosynthesis, expressed on an area basis (A_a), did not differ ($P > 0{\cdot}05$) between *L. occidentalis* and *Ps. menziesii* for all sample dates at Lost Creek, and for five of eight sampling dates at Bonner (Kloeppel 1998). However, A_a was significantly higher ($P > 0{\cdot}05$) for *Pi. contorta* than *L.*

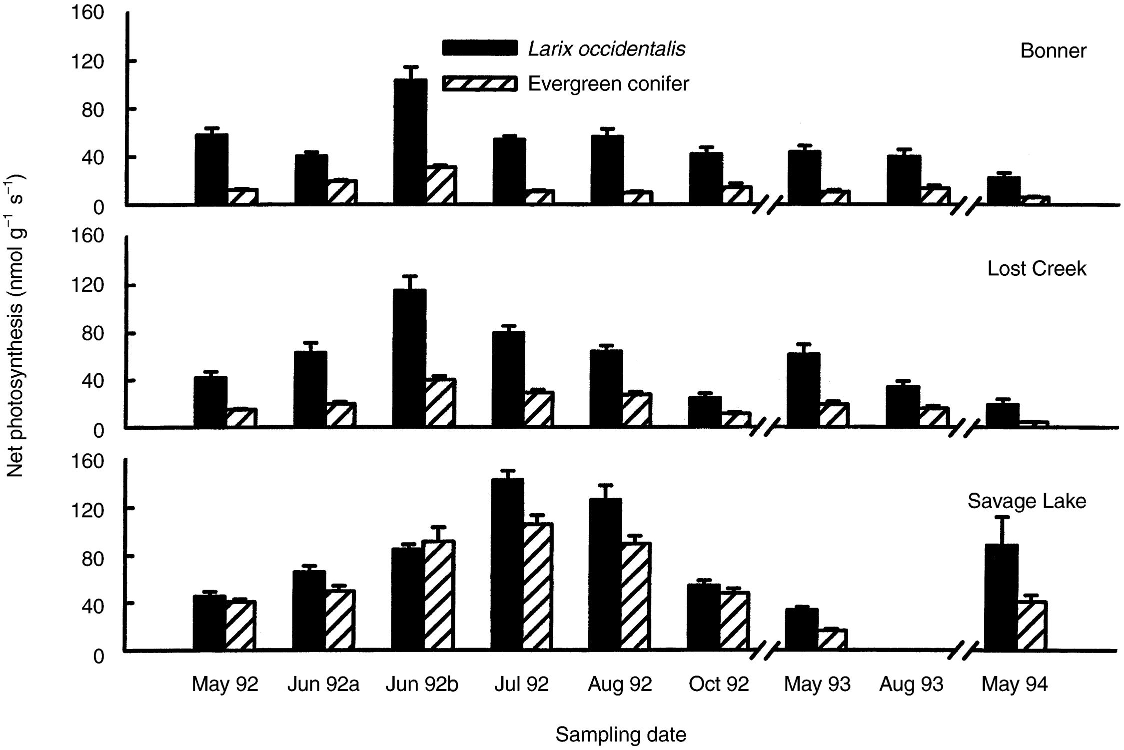

Fig. 1. Mean (± SE) daily maximum growing season net mass-based photosynthetic rates over 3 years at three western Montana, USA study sites. The evergreen conifer at Bonner and Lost Creek is *Pseudotsuga menziesii* whereas *Pinus contorta* is the evergreen conifer at Savage Lake.

Table 2. Foliar nitrogen concentration (N_m; mass basis) and specific leaf area (SLA) for *Larix occidentalis* and co-occurring evergreen conifers in control and fertilized treatments at three western Montana, USA study sites

		Larix occidentalis		Evergreen conifer	
Site	Treatment	N_m (mg g^{-1})	SLA (m^2 kg^{-1})	N_m (mg g^{-1})	SLA (m^2 kg^{-1})
Bonner	Control	25·9 ± 0·8	18·1 ± 0·9	8·0 ± 0·2	5·0 ± 0·2
	Fertilized	29·7 ± 0·6	17·0 ± 0·9	9·3 ± 0·5	4·6 ± 0·1
Lost Creek	Control	17·0 ± 0·7	11·4 ± 0·3	7·8 ± 0·2	4·7 ± 0·2
	Fertilized	20·5 ± 0·8	12·9 ± 0·3	11·8 ± 0·4	5·4 ± 0·1
Savage Lake	Control	15·7 ± 0·6	14·2 ± 0·7	8·6 ± 0·3	4·7 ± 0·2
	Fertilized	16·7 ± 0·5	16·4 ± 0·7	11·4 ± 1·0	4·4 ± 0·1

occidentalis at Savage Lake for seven of eight sampling dates. Bulk leaf water potential (both predawn and sampling), leaf temperature, vapour pressure deficit, specific leaf area and leaf nitrogen concentration for all sampling dates were presented in Kloeppel (1998).

Specific leaf area was approximately three times higher for *L. occidentalis* than *Ps. menziesii* or *Pi. contorta* (Table 2; Kloeppel 1998), corroborating previous comparisons of SLA between *Larix* spp. and co-occurring evergreen conifers (Gower & Richards 1990; Gower *et al.* 1995; Reich *et al.* 1999). The large differences in SLA explained the observed differences in area-based net photosynthesis between *Larix* spp. and evergreen conifers, but this inter- and intraspecies SLA effect was reduced when net photosynthesis was expressed on a mass basis (Kloeppel *et al.* 1993). Expressing photosynthesis on a mass basis was a more direct comparison among species for water- and nitrogen-use efficiency to resource investment in foliage production (i.e. carbon and nitrogen). Therefore, for the remainder of this paper, gas exchange results will be presented on a mass basis.

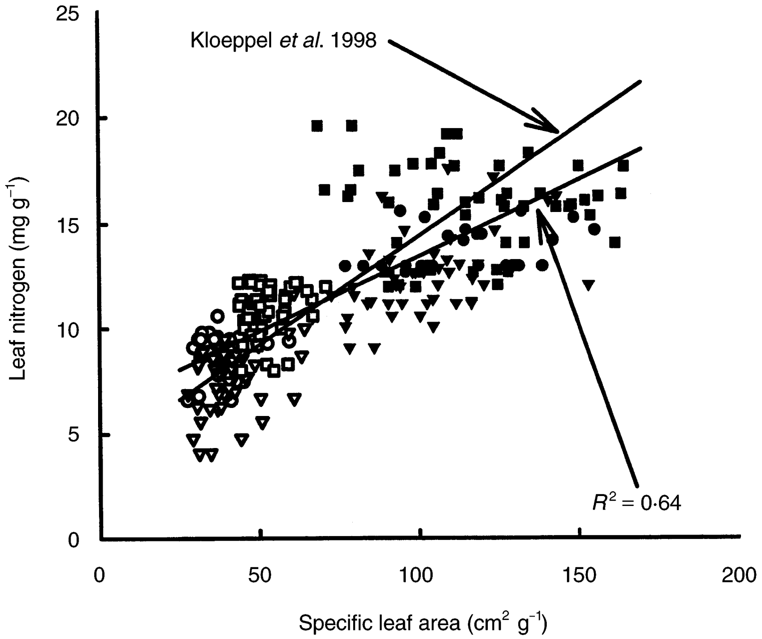

Fig. 2. Foliar nitrogen *vs* specific leaf area for all growing season daily maximum photosynthesis data. The overall regression equation ($y = 0·072x + 6·25$, $P < 0·001$, $R^2 = 0·64$) is compared to the equation from Kloeppel *et al.* 1998 ($y = 0·109x + 4·58$, $P < 0·001$, $R^2 = 0·80$), which characterized the same relationship for a global survey of *Larix* spp. and co-occurring evergreen conifers. Filled symbols represent *Larix occidentalis* while open symbols represent evergreen conifers at Bonner (circles), Lost Creek (triangles) and Savage Lake (squares).

Specific leaf area was highly correlated ($P < 0·001$, $R^2 = 0·64$) to leaf N_m (Fig. 2), corroborating a global pattern reported previously for species in general (Reich, Walters & Ellsworth 1992, 1997) as well as more specifically for *Larix* spp. and sympatric evergreen conifers (Kloeppel *et al.* 1998). Although the *y*-intercepts and slopes of both regressions were statistically similar ($P > 0·05$), the slope of 0·072 in this study was somewhat lower than the slope of 0·109 reported by Kloeppel *et al.* (1998). Leaves with a thinner cuticle have a lower C : N ratio and hence a higher leaf N concentration that correlates to higher rates of net photosynthesis (Reich *et al.* 1992; Reich, Ellsworth & Walters 1998a). These interrelationships may be responsible for the consistently higher gas exchange rates of *L. occidentalis* than *Ps. menziesii* at the Bonner and Lost Creek sites.

Mass-based net photosynthesis for both species at all three sites declined after mid-morning for both early and late growing season measurement periods (Fig. 3). Early morning A_m was significantly lower ($P < 0·05$) for both species at the Bonner and Lost Creek than Savage Lake site during the mid to late growing season. Predawn water potential (Ψ_p) was significantly lower (more negative Ψ_p) at Bonner and Lost Creek during the late *vs* early growing season, but no consistent seasonal pattern existed between species (Fig. 4). In general, A_m was higher for *L. occidentalis* than co-occurring evergreen conifers (*Ps. menziesii* or *Pi. contorta*) during the day (Fig. 3). Overall, A_m was similar for all sites early in the growing season, but A_m was significantly higher at Savage Lake than Bonner and Lost Creek later in the growing season.

Predawn Ψ did not differ consistently between *L. occidentalis* and *Ps. menziesii* at Bonner and Lost Creek, but it was significantly lower (more negative Ψ_p) for *Pi. contorta* than *L. occidentalis* at Savage Lake (Fig. 4). As expected, water availability increased

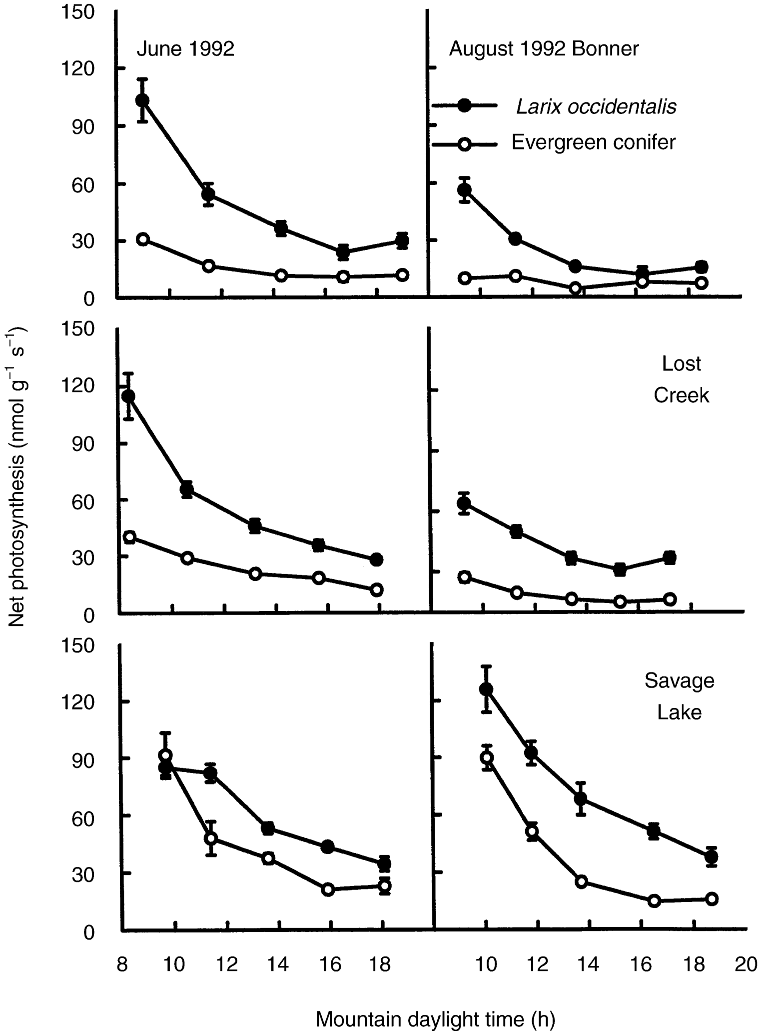

Fig. 3. Diurnal patterns of net mass-based photosynthesis (mean ± SE) of *Larix occidentalis* and evergreen conifers at three study sites in western Montana, USA. The June data were collected during the relatively moist early growing season, while the August data were collected at the peak of the seasonal late summer drought.

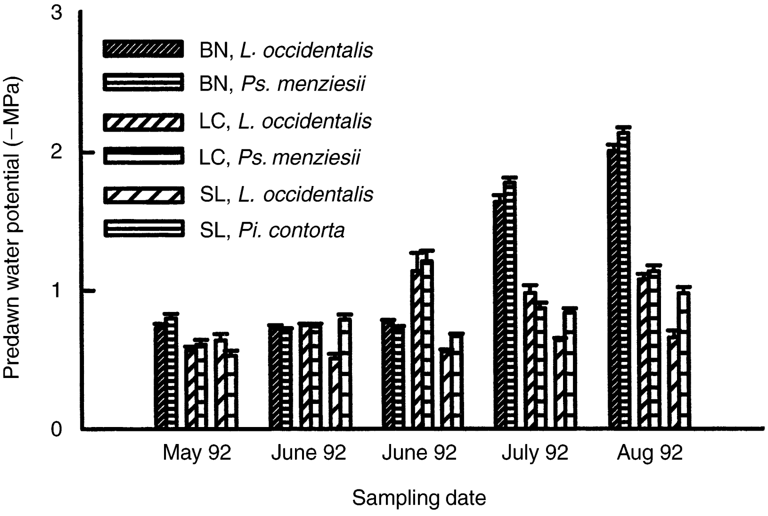

Fig. 4. Twig predawn water potential of *Larix occidentalis* and co-occurring evergreen conifers at three study sites (BN, Bonner; LC, Lost Creek; SL, Savage Lake) for five 1992 seasonal sampling dates in western Montana, USA. Data within each sampling date (left to right) are arranged in the same order as the legend (top to bottom).

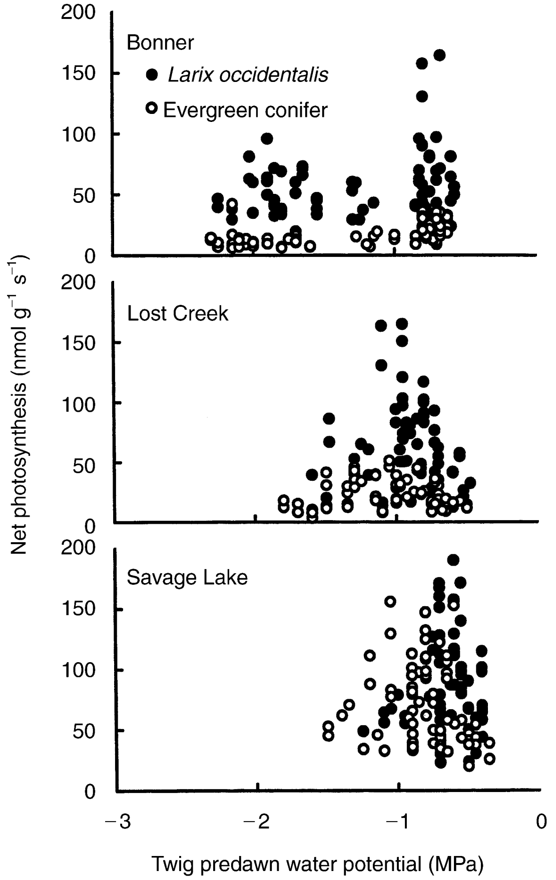

Fig. 5. Net photosynthesis *vs* twig predawn water potential at three Montana, USA study sites. The relationship for both species combined was significant at Bonner ($P = 0{\cdot}007$), but the $R^2 = 0{\cdot}04$. The relationship was not significant at either Lost Creek ($P = 0{\cdot}53$) or Savage Lake ($P = 0{\cdot}98$).

from Bonner to Savage Lake, as evidenced by Ψ_p. The mean growing season (and range) Ψ_p (in MPa) for both species pooled at Bonner, Lost Creek and Savage Lake was –1·30 (–2·33 to –0·58), –0·96 (–1·80 to –0·48) and –0·73 (–1·50 to –0·35), respectively. Mass-based net photosynthesis was not correlated to Ψ_p at any study site when both species were pooled ($P = 0{\cdot}07 – 0{\cdot}98$), even though Ψ_p ranged from –0·35 to –2·33 MPa during the growing season (Fig. 5). Higgins *et al.* (1987) reported that A_m was negatively correlated to Ψ_p for *L. occidentalis* seedlings.

Mass-based net photosynthesis was inversely correlated to vapour pressure deficit (VPD) for each species at all sites ($R^2 = 0{\cdot}36 – 0{\cdot}55$, Fig. 6), corroborating earlier research with *Larix* spp. (Dang *et al.* 1991; Higgins *et al.* 1987). Comparison of these regression lines between species at each site (Bonner and Lost Creek $\log_{10}$ transformed, Savage Lake untransformed) indicated that the slope of the regression line relating A_m to VPD did not differ between *L. occidentalis* and the sympatric evergreen conifer, but the *y*-intercept was significantly higher for *L. occidentalis* than *Ps. menziesii* at Bonner ($P < 0{\cdot}001$) and Lost Creek ($P < 0{\cdot}001$). A_m was not correlated to Ψ_p, in contrast

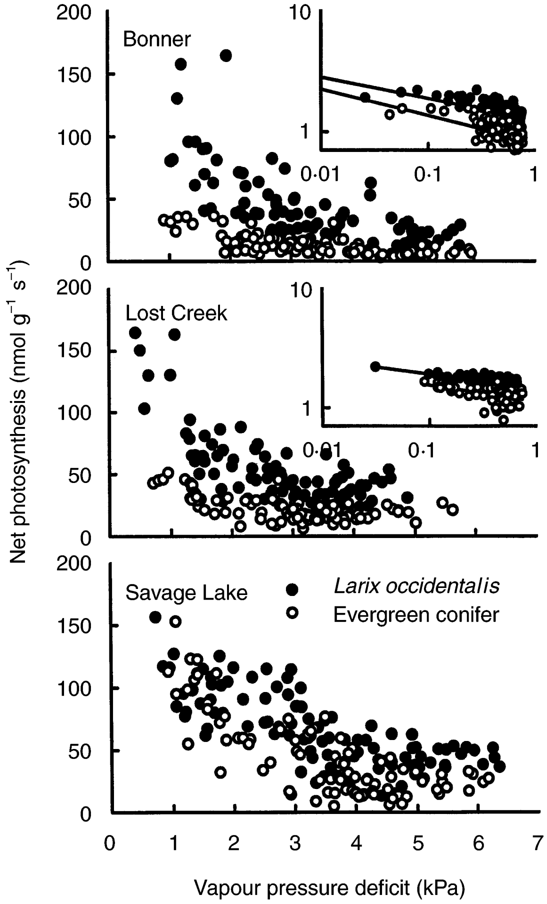

Fig. 6. Net photosynthesis *vs* vapour pressure deficit at three Montana, USA study sites. The correlation coefficients of the $\log_{10}$-transformed data for the six site–species combinations ranged from 0·36 to 0·55. See the Results and discussion for equation parameters.

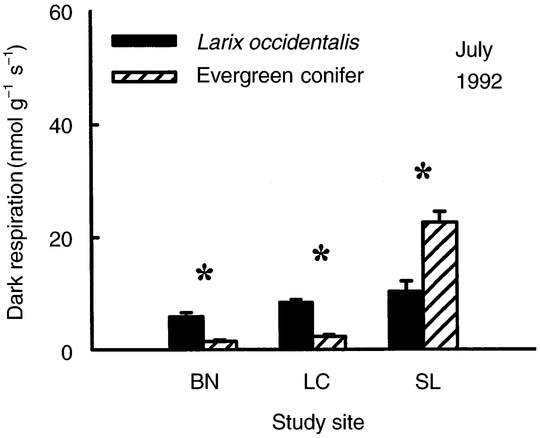

Fig. 7. Predawn mass-based dark respiration (mean ± SE) of *Larix occidentalis* and evergreen conifer foliage at three western Montana, USA study sites (BN, Bonner; LC, Lost Creek; SL, Savage Lake) in July 1992. Pairs of means with an asterisk overhead are significantly different ($P \leq 0·05$).

to the *L. occidentalis* seedling study in eastern Washington by Higgins *et al.* (1987) where both Ψ_p and VPD were negatively correlated to A_m.

Mass-based net photosynthesis did not differ significantly ($P = 0·20$) among different needle age cohorts (1–4 years) for *Ps. menziesii* at Bonner and Lost Creek in May 1993 and May 1994 (Kloeppel 1998). However, at Savage Lake A_m decreased significantly ($P = 0·03$) from current to 4-year-old needles of *Pi. contorta* in May 1994; the decline ranged from 48% in 1994 to a statistically insignificant 33% decline in May 1993. Mass-based leaf nitrogen concentration declined from current to 4-year-old needles by 1·5, 0·5 and 1·3 mg g^{-1} at Bonner ($P = 0·08$), Lost Creek ($P = 0·15$) and Savage Lake ($P = 0·04$), respectively. Other studies have found that A_m declined with leaf age (Freeland 1952; Reich *et al.* 1995a; Schoettle 1994; Teskey, Grier & Hinckley 1984; Woodman 1971). The inverse relationship between A_m and needle age was often attributed to decreasing nitrogen and phosphorous concentration with leaf age.

In general, interspecies differences of foliage dark respiration rates (r_m) followed A_m patterns (Figs 7 and 1). Dark respiration was significantly higher for *L. occidentalis* than *Ps. menziesii* at Bonner and Lost Creek, but was significantly higher for *Pi. contorta* than *L. occidentalis* at Savage Lake (Fig. 7). These results corroborated the findings of the light response respiration parameter presented in Table 3, except that the difference between species at Savage Lake was not significant in Table 3.

Table 3. Light-response curve parameter estimates (mean ± asymptotic standard error) for two species at three sites in western Montana, USA. Maximum photosynthesis (A_{max}), dark respiration (r_s), saturation constant (K), residual degrees of freedom (residual d.f.), and residual mean squares (RMS) were estimated with Proc NLIN in SAS, while the light compensation point (LCP) was determined by solving the overall net photosynthesis equation for $A = 0$. Means in a column followed by the same letter are not significantly different utilizing the LSD mean separation technique at the $\alpha = 0·05$ level. Units for A_{max} and r_s are nmol g^{-1} s^{-1} while units for K and LCP are µmol m^{-2} s^{-1}

Site	Species	A_{max}	r_s	K	LCP	Residual d.f.	RMS
Bonner	*Larix occidentalis*	75 ± 12 b	3·5 ± 6·5 b	421	20	46	260
Bonner	*Pseudotsuga menziesii*	14 ± 3 c	0·9 ± 2·3 c	214	14	49	24
Lost Creek	*Larix occidentalis*	79 ± 11 b	3·4 ± 5·8 b	516	23	45	176
Lost Creek	*Pseudotsuga menziesii*	14 ± 2 c	0·7 ± 2·2 c	220	11	45	19
Savage Lake	*Larix occidentalis*	126 ± 11 a	7·7 ± 5·8 ab	100	13	65	910
Savage Lake	*Pinus contorta*	110 ± 15 a	16·9 ± 5·6 a	204	37	58	776

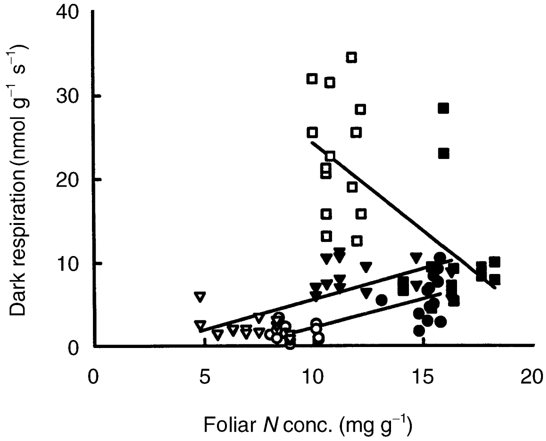

Fig. 8. Mass-based dark respiration *vs* foliar nitrogen concentration at three western Montana, USA study sites. Species and site symbols follow those in Fig. 2. The overall relationship is significant (P = 0·036), but the R^2 = 0·04. Study sites exhibited significant relationships (Bonner: P < 0·001, R^2 = 0·56; Lost Creek: P < 0·001, R^2 = 0·47; Savage Lake: P < 0·001, R^2 = 0·38), but they are forced by species clustering at each site.

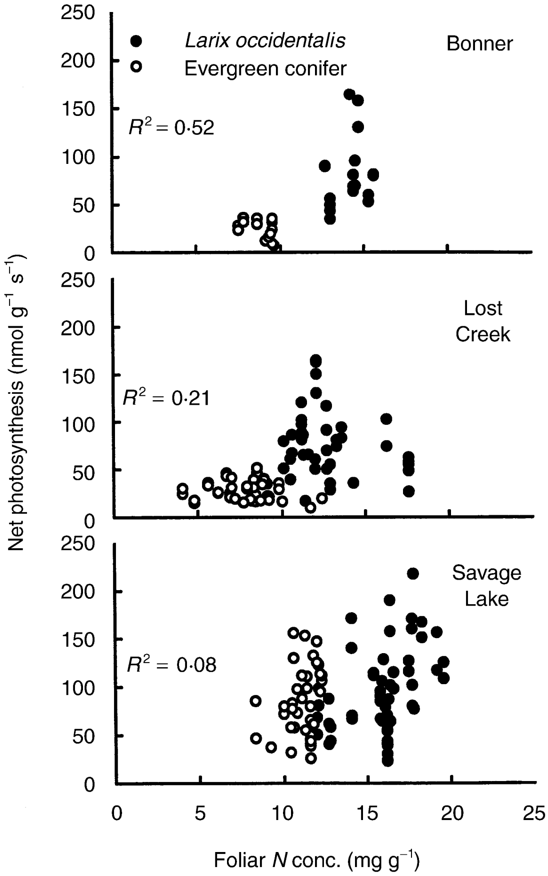

Fig. 9. Net mass-based photosynthesis *vs* foliar N concentration at three western Montana, USA study sites. Data are restricted to a vapour pressure deficit < 2·0 kPa and a predawn water potential > –1·5 MPa. The equation for all pooled data is $y = (6{\cdot}65x) - 12{\cdot}81$, P < 0·001, R^2 = 0·28.

Light-response curves indicated that the light compensation point for *L. occidentalis* was not different among sites and was similar to the light compensation points for sympatric evergreen conifers at Bonner and Lost Creek, but was much higher for *Pi. contorta* at Savage Lake (Table 3).

RELATIONSHIPS BETWEEN PHOTOSYNTHESIS, RESPIRATION, AND LEAF NITROGEN

Both r_m and A_m were poorly correlated to foliar nitrogen concentration for data from all sites (R^2 = 0·28 and 0·04, respectively) (Figs 8 and 9). Leaf respiration was positively and significantly correlated to N_m (R^2 = 0·36–0·56) for each individual study site (lines shown in Fig. 8), but the slopes for each site were extremely different. Moreover, all three correlations were the result of two clusters of data for *L. occidentalis* and the evergreen conifer. Leaf photosynthesis was poorly correlated (R^2 = 0·08–0·52) to foliar nitrogen concentration for each site, unlike the results from previous studies (Field & Mooney 1986; Reich & Walters 1994; Reich *et al.* 1995b). The relationship between A_m and N_m was not improved by restricting the data to observations with a $\Psi_p > -1{\cdot}5$ MPa and a VPD < 2·0 kPa. The lack of a strong positive relationship suggested that other resources, perhaps water or other nutrients, are more limiting at these sites. This conclusion is supported by the fact that A_m was not consistently higher for fertilized than control trees (Fig. 10). When fertilized, foliage N_m increased 1·3–3·5 mg g^{-1} in 1-year-old evergreen conifer tissue and increased only marginally in *L. occidentalis* short shoots (Kloeppel 1998).

The lack of a strong relationship between foliar N_m with both r_m and A_m suggested that other environmental variables, rather than N_m, constrain gas exchange. Indeed, the strong relationship of VPD with A_m (Fig. 6) appeared to exhibit a much stronger influence on carbon assimilation than tissue nitrogen concentration. In contrast, literature reviews by Ryan (1991a, 1991b) and Reich *et al.* (1998b) presented data that indicated a strong positive correlation between N_m and r. The different results are likely explained by Ryan's use of a variety of plant growth forms ranging from coniferous tree species to agricultural crops with corresponding tissue N_m ranging from 4·0 to 60·0 mg g^{-1}, respectively. Any relationship between leaf N_m and r_m or A_m may be obscured or non-existent when the range of values of N_m are restricted to that observed for a single species or plant growth form (i.e. 10·2–29·7, 6·9–11·8, and 8·6–11·6 mg g^{-1} N_m for *L. occidentalis*, *Ps. menziesii* and *Pi. contorta*, respectively).

RESOURCE-USE EFFICIENCY

Instantaneous nitrogen-use efficiency (NUE_i), defined as A_m divided by N_m, was significantly higher in evergreen conifers than *L. occidentalis* at all study sites.

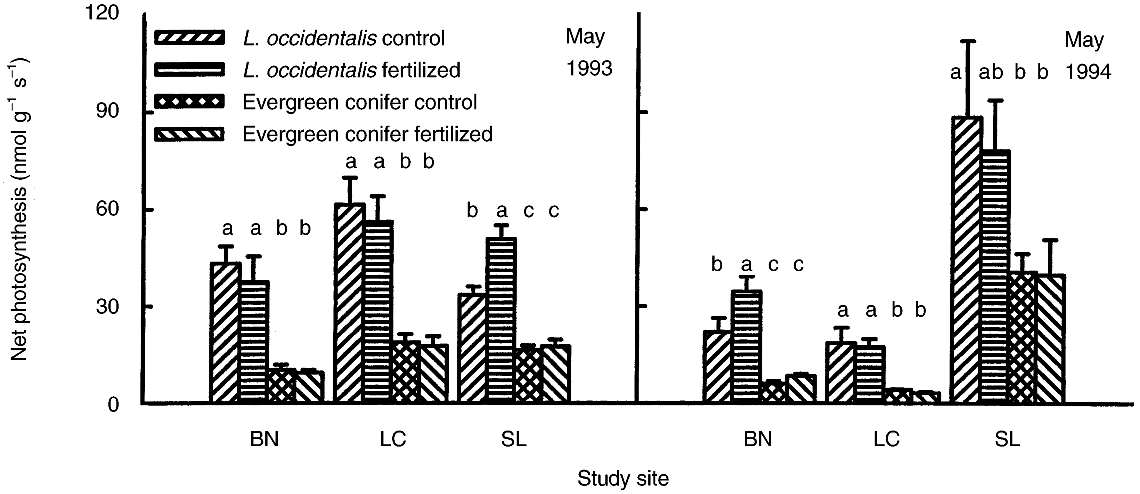

Fig. 10. Net mass-based photosynthesis (mean ± SE) of control and artificially fertilized foliage of both *Larix occidentalis* and co-occurring evergreen conifers at three western Montana, USA study sites. Sampling was conducted in both May 1993 and May 1994 during the early growing season when water was less limiting than later in the season. Means below the same letter within each group of species–treament combinations are not significantly different using the LSD mean separation technique at the $\alpha = 0{\cdot}05$ level.

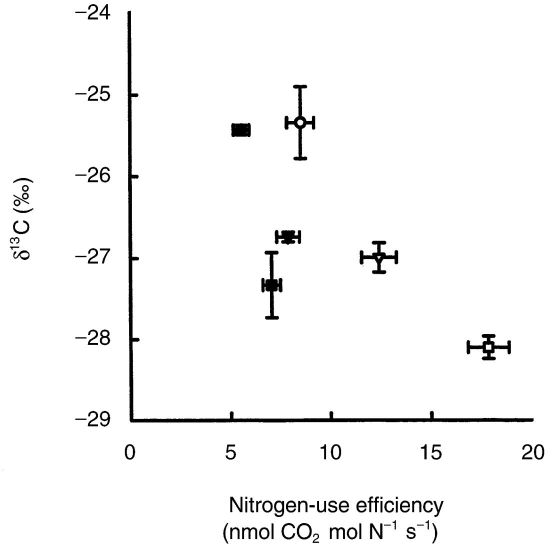

Fig. 11. Study site mean instantaneous nitrogen-use efficiency (NUE) *vs* study site mean foliar carbon isotope ratio for both *Larix occidentalis* (closed symbols) and evergreen conifers (open symbols) at three western Montana study sites (Bonner, circles; Lost Creek, triangles; Savage Lake, squares). NUE data are summarized from all growing season daily maximum sampling dates with no other restrictions whereas δ^{13}C data are from Kloeppel *et al.* 1998.

Instantaneous nitrogen-use efficiency by evergreen conifers increased significantly ($P < 0{\cdot}001$) along the edaphic gradient from Bonner to Savage Lake (Fig. 11), but NUE$_i$ of *L. occidentalis* did not differ consistently across study sites. Evergreen conifers have lower foliar N_m than *L. occidentalis*, providing a higher NUE$_i$ if A_m is similar. The increase in A_m from Bonner to Savage Lake for evergreen conifers compared to *L. occidentalis* resulted in significantly higher NUE$_i$ for evergreen conifers, relative to *L. occidentalis*. Because species substitution occurs for the evergreen conifers along the gradient we cannot determine if the increase in NUE$_i$ reflects species differences or physiological differences in response to increasing trade-offs of resource availability. The NUE$_i$ index does not account for the well-documented more efficient withdrawal of nitrogen from senescing needles by *Larix* spp. than sympatric evergreen conifers (Gower & Richards 1990; Gower *et al.* 1995). Nor does the index account for the use of nitrogen over several years by evergreen conifers.

The relationship of nitrogen-use efficiency and foliar carbon isotope discrimination, an index of water-use efficiency (Kloeppel *et al.* 1998), was examined to explore resource-use efficiency between deciduous and evergreen conifer trees along the edaphic gradient (Fig. 11). Evergreen conifers exhibited significant differences in both variables across the edaphic gradient, whereas *L. occidentalis* exhibited differences in carbon isotope discrimination only. Therefore, *L. occidentalis* and the co-occurring evergreen conifers used water more efficiently in drier environments, but only evergreen conifers used nitrogen less efficiently in drier environments. *Larix occidentalis* and co-occurring evergreen conifers had similar water-use efficiency in contrast to earlier studies (Gower & Richards 1990; Marshall & Zhang 1994; Kloeppel *et al.* 1998).

When generalizing about leaf habit and resource availability, seasonal carbon gain on a weight basis was higher in evergreen *vs* deciduous trees in mild temperate environments because evergreens tended to have a longer assimilation season and higher leaf area, despite lower photosynthetic rates (Gower & Richards 1990). However, in cold temperate ecosystems, winter photosynthesis by evergreen conifers contributed little to the annual carbon budget (Tranquillini 1979; Matyssek 1986). Net photosynthesis (mean ± SE in nmol g^{-1} s^{-1}) was not significantly different than zero for *Ps. menziesii* at either Bonner (0·31 ± 0·67) or Lost Creek (0·31 ± 0·76); however, *Pi. contorta* was significantly higher than zero at Savage Lake (6·28 ± 1·29). In the spring and autumn, evergreen conifers may gain a carbon advantage over *L. occidentalis* when *L. occidentalis* is foliage free, but this advantage is probably small based on the low A_m values in evergreen conifers in March and October compared to the middle growing season (Fig. 1).

In summary, A_m, r_m, N_m and SLA were higher for *L. occidentalis* than for co-occurring evergreen conifers. However, increasing resource availability across the natural range of *L. occidentalis* resulted in decreasing differences in these variables between leaf habits. Furthermore, resource-use efficiency differed between leaf habits, suggesting that evergreen conifers use nitrogen more efficiently than *L. occidentalis*. Both species were apparently equally limited by water across the observed gradient and exhibited similar water-use efficiency at each study site.

Acknowledgements

This project was supported by NSF grant BSR 91-07419 to S. T. Gower and P. B. Reich. B. D. Kloeppel acknowledges financial support from NSF grant DEB 96-32854 to the Coweeta Long-Term Ecological Research programme during preparation of this manuscript. An earlier draft of this manuscript was improved with edits from Eric L. Kruger. We thank the following individuals who assisted with field data collection and laboratory sample processing: Jim Gries, Brent Haynes, Yolanda Lukaszewski, Dan Meyer, Jim Piesz, Sylvia Quideau, Jeremy Rich, Jairo Rivera, Leslie Ross, Tom Steele and Ken Walz.

References

Baker, F.S. (1944) Mountain climates of the western United States. *Ecological Monographs* **14**, 223–254.

Bazazz, F.A. (1979) The physiological ecology of plant succession. *Annual Review of Ecology and Systematics* **10**, 351–371.

Burns, R.M. & Honkala, B.H. (1990) *Silvics of North America. Volume 1: Conifers*. Agriculture Handbook 654. USDA Forest Service, Washington, DC.

von Caemmerer, S.& Farquhar, G.D. (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta* **153**, 376–387.

Chabot, B.F. & Hicks, D.J. (1982) The ecology of leaf life spans. *Annual Review of Ecology and Systematics* **13**, 229–259.

Chapin, F.S. III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics* **11**, 233–260.

Chatterjee, S. & Price, B. (1977) *Regression Analysis by Example*. John Wiley and Sons, New York, NY.

Coley, P.D. (1988) Effects of plant growth rate and leaf lifetime on the amount and type of antiherbivore defense. *Oecologia* **74**, 531–536.

Coley, P.D., Bryant, J.P. & Chapin, F.S. III (1985) Resource availability and plant anti-herbivore defense. *Science* **230**, 895–899.

Dang, Q.L., Lieffers, V.J. & Rothwell, R.L. (1992) Effects of summer frost and subsequent shade on foliage gas exchange in peatland tamarack and black spruce. *Canadian Journal of Forest Research* **22**, 973–979.

Dang, Q.L., Lieffers, V.J., Rothwell, R.L. & MacDonald, S.E. (1991) Diurnal variation and interrelationships of ecophysiological parameters in three peatland woody species under different weather and soil moisture conditions. *Oecologia* **88**, 317–324.

Daubenmire, R. (1943) Vegetation zonation in the Rocky Mountains. *Botanical Review* **9**, 325–393.

Field, C. & Mooney, H.A. (1986) The photosynthesis–nitrogen relationships in wild plants. *On the Economy of Plant Form and Function* (ed. T. J. Givnish), pp. 25–55. Cambridge University Press, Cambridge, UK.

Freeland, R.O. (1952) Effect of age on leaves upon the rate of photosynthesis in some conifers. *Plant Physiology* **27**, 685–690.

Givnish, T.J. (1986) Optimal stomatal conductance, allocation of energy between leaves and roots, and the marginal cost of transpiration. *On the Economy of Plant Form and Function* (ed. T. J. Givnish), pp. 171–213. Cambridge University Press, Cambridge, UK.

Givnish, T.J. (1988) Adaptation to sun and shade: a whole plant perspective. *Australian Journal of Plant Physiology* **15**, 63–92.

Gower, S.T. & Richards, J.R. (1990) Larches: deciduous conifers in an evergreen world. *Bioscience* **40**, 818–826.

Gower, S.T., Kloeppel, B.D. & Reich, P.B. (1995) Carbon, nitrogen, and water use by larches and co-occurring evergreen conifers. *Ecology and Management of Larix Forests: A Look Ahead* (eds W. C. Schmidt & K. J. McDonald), pp. 110–117. Proceedings of an International Symposium, Technical Report GTR-INT-319. USDA Forest Service, Washington, DC.

Gower, S.T., Reich, P.B. & Son, Y. (1993) Canopy dynamics and aboveground production of five tree species with different leaf longevities. *Tree Physiology* **12**, 327–345.

Higgins, S.S., Black, R.A., Radamaker, G.K. & Bidlake, W.R. (1987) Gas exchange characteristics and water relations of *Larix occidentalis*. *Canadian Journal of Forest Research* **17**, 1364–1370.

Kikuzawa, K. (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *American Naturalist* **138**, 1250–1263.

Kloeppel, B.D. (1998) *Carbon and nitrogen allocation and resource use efficiency in mixed* Larix *spp. and evergreen conifer forests along a resource availability gradient*. PhD Dissertation. University of Wisconsin–Madison, Madison, WI.

Kloeppel, B.D., Abrams, M.D. & Kubiske, M.E. (1993) Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barrens species in open versus understorey environments. *Canadian Journal of Forest Research* **23**, 181–189.

Kloeppel, B.D., Gower, S.T., Treichel, I.W. & Kharuk, S. (1998) Foliar carbon isotope discrimination in *Larix* species and sympatric evergreen conifers: a global comparison. *Oecologia* **114**, 153–159.

Lachat Inc. (1988) *Total Kjeldahl Nitrogen as* NH_3. Quikchem Method no. 13-107-06-2-A. Lachat Inc., Mequon, WI.

Lambers, H. & Poorter, H. (1992) Inherent variation in growth-rate between higher plants – a search for physiological causes and ecological consequences. *Advances in Ecological Research* **23**, 187–261.

MacDonald, S.E. & Lieffers, V.J. (1990) Photosynthesis, water relations, and foliar nitrogen of *Picea mariana* and *Larix decidua* from drained and undrained peatlands. *Canadian Journal of Forest Research* **20**, 995–1000.

Marshall, J.D. & Zhang, J. (1994) Carbon isotope discrimination and water-use efficiency in native plants of the North-Central Rockies. *Ecology* **75**, 1887–1895.

Matyssek, R. (1986) Carbon, water and nitrogen relations in evergreen and deciduous conifers. *Tree Physiology* **2**, 177–187.

Meng, F.R. & Arp, P.A. (1993) Net photosynthesis and stomatal conductance of red spruce twigs before and after twig detachment. *Canadian Journal of Forest Research* **23**, 716–721.

Monk, C.A. (1966) An ecological significance of evergreenness. *Ecology* **47**, 504–505.

Mooney, H.A. & Gulmon, S.L. (1982) Constraints on leaf structure and functions in reference to herbivory. *Bioscience* **32**, 198–206.

Montague, T.G. & Givnish, T.J. (1996) Distribution of black spruce versus eastern larch along peatland gradients: relationships to relative stature, growth rate, and shade tolerance. *Canadian Journal of Botany* **74**, 1514–1532.

Parkinson, J.A. & Allen, S.E. (1975) A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. *Communications in Soil Science and Plant Analysis* **6**, 1–11.

Reich, P.B. & Walters, M.B. (1994) Photosynthesis–nitrogen relations in Amazonian tree species. II. Variation in nitrogen vis-a-vis specific leaf area influences mass- and area-based expressions. *Oecologia* **97**, 73–81.

Reich, P.B., Ellsworth, D.S. & Walters, M.B. (1998) Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: evidence from within and across species and functional groups. *Functional Ecology* **12**, 948–958.

Reich, P.B., Ellsworth, D.S., Walters, M.B., Vose, J.M., Volin, J. & Bowman, W. (1999) Generality of leaf trait relationships: a test across six biomes. *Ecology* **80**, 1955–1969.

Reich, P.B., Kloeppel, B.D., Ellsworth, D.S. & Walters, M.B. (1995a) Different photosynthesis–nitrogen relations in deciduous hardwood and evergreen coniferous tree species. *Oecologia* **104**, 24–30.

Reich, P.B., Koike, T., Gower, S.T. & Schoettle, A.W. (1995b) Causes and consequences of variation in conifer leaf life-span. *Physiological Ecology: Ecophysiology of Coniferous Forests* (eds W. K. Smith & T. M. Hinckley), pp. 225–254. Academic Press, San Diego, London.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1991) Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species. *Oecologia* **86**, 16–24.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**, 365–392.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: global convergence in plant functioning. *Proceedings of the National Academy of Sciences of the USA* **94**(25), 13730–13734.

Reich, P.B., Walters, M.B., Ellsworth, D.S., *et al.* (1998) Relationships of dark respiration to leaf N, SLA, and life-span: a test across biomes and functional groups. *Oecologia* **114**, 471–482.

Ryan, M.G. (1991a) Effects of climate change on plant respiration. *Ecological Applications* **1**, 157–167.

Ryan, M.G. (1991b) A simple method for estimating gross carbon budgets for vegetation in forest ecosystems. *Tree Physiology* **9**, 255–266.

Ryan, M.G., Binkley, D. & Fownes, J.H. (1997) Age-related decline in forest productivity: pattern and process. *Advances in Ecological Research* **27**, 213–262.

SAS Institute (1985) *SAS User's Guide: Statistics, Version 5*. SAS Institute, Cary, NC.

Schmidt, W.C., Shearer, R.C. & Roe, A.L. (1976) *Ecology and Silviculture of Western Larch Forests*. Technical Bulletin no. 1520. USDA Forest Service, Washington, DC.

Schoettle, A.W. (1994) Influence of tree size on shoot structure and physiology of *Pinus contorta* and *Pinus aristata*. *Tree Physiology* **14**, 1055–1068.

Sheriff, D.W., Margolis, H.A., Kaufmann, M.R. & Reich, P.B. (1995) Resource use efficiency. *Resource Physiology of Conifers* (eds W. K. Smith & T. M. Hinckley), pp. 143–178. Academic Press, San Diego, London.

Sheve, L.G. (1984) *Elements of Biochemistry*. Allan and Bacon Inc., Newton, MA.

Smith, D.M. (1986) *The Practice of Silviculture*, 8th Edn. John Wiley & Sons, New York, NY.

Teskey, R.O., Grier, C.C. & Hinckley, T.M. (1984) Change in photosynthesis and water relations with age and season in *Abies amabilis*. *Canadian Journal of Forest Research* **14**, 77–84.

Tranquillini, W. (1979) *Physiological Ecology of the Alpine Timberline*. Springer, New York, NY.

Vogt, K.A., Moore, E.E., Vogt, D.J., Redlin, M.J. & Edmonds, R.L. (1983) Conifer fine root and mycorrhizal root biomass within the forest floors of Douglas fir stands of different ages and site productivities. *Canadian Journal of Forest Research* **13**, 429–441.

Vogt, K.A., Vogt, D.J., Moore, E.E., Redlin, M.R., Fatuga, B.A. & Edmonds, R.L. (1987) Conifer and angiosperm fine root biomass in relation to stand age and site productivity in Douglas fir forests. *Journal of Ecology* **75**, 857–864.

Woodman, J.N. (1971) Variation of net photosynthesis within the crown of a large forest-grown conifer. *Photosynthetica* **5**, 50–54.

Received 26 November 1998; revised 6 September 1999; accepted 16 September 1999