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Foliar carbon isotope discrimination in *Larix* species and sympatric evergreen conifers: a global comparison

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Abstract Larches (*Larix* spp.), deciduous conifers, occur in the northern hemisphere in cold-temperate and boreal climates – an environment normally thought to favor evergreen tree species. We compare foliar carbon isotope discrimination (Δ), instantaneous water use efficiency, total foliar nitrogen concentration, and specific leaf area (for a subset of sites) between *Larix* spp. and co-occurring evergreen conifers at 20 sites throughout the natural range of larches. Except for *Larix occidentalis* in the xeric Intermountain West, USA, Δ is significantly ($P < 0.05$) greater for larches than co-occurring evergreen conifers at 77% of the sites, suggesting that larches use water less efficiently. At elevations greater than 3000 m, the Δ of *Larix* spp. and co-occurring conifers converge, suggesting that water is not the limiting resource. Foliar nitrogen concentration and specific leaf area are two ecophysiological characteristics that are positively correlated with high photosynthetic capacity. Foliar nitrogen concentration is significantly greater for larches than evergreen conifers at 88% of the sites and specific leaf area is approximately three times greater for larches than co-occurring conifers. Future studies should examine the potential effect that global warming may have on the distribution of larch forests because the water use efficiency of larches is commonly less than co-occurring evergreen conifers and the boreal and high-latitude environments are likely to experience the greatest climate warming.

Key words Foliar nitrogen · Needle age · Specific leaf area · Water use efficiency · δ^{13} Carbon

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Introduction

The role of leaf habit in the survival, carbon balance, and dominance of plants has received considerable attention since the 18th century. Typically, evergreen species prevail in regions where critical resources for plant growth are in short supply. Boreal and high-latitude subalpine forests, for example, are typically dominated by evergreen conifers (Axelrod 1966; Wolfe 1979; Kikuzawa 1991). The causes of evergreen dominance are not fully understood, but many scientists have speculated that evergreen plants use resources more efficiently and consequently have a more favorable carbon balance than deciduous plants in harsh climates (Mooney 1972; Waring and Franklin 1979; Kikuzawa 1991).

Larix, a deciduous conifer, is widespread in the cold temperate and boreal forests in North America and Eurasia and is an exception to theories related to leaf habit and climate. Ten species of larch are recognized and they typically occur in mixed stands with evergreen conifers, but they can occur in pure stands, especially in Siberia and Mongolia (Gower and Richards 1990; Schulze et al. 1995).

Only a few species of larch are well studied by ecophysiologists and this work has focused on leaf photosynthesis and nutrient use (see reviews by Gower and Richards 1990; Gower et al. 1995). Less is known about the water relations of larch and co-occurring evergreen conifers, but they appear to differ (Matyssek 1986; Gower and Richards 1990; Marshall and Zhang 1994). Gower and Richards (1990) speculated that *Larix* spp. are restricted to more mesic sites because of their less efficient water use in comparison to sympatric evergreen

conifers. They compared the foliar stable carbon isotope discrimination (Δ) of *Larix occidentalis*, *L. lyallii*, and sympatric evergreen conifers and found that larches consistently exhibited greater Δ, which is indicative of lower instantaneous water use efficiency.

Traditionally, instantaneous water use efficiency (WUE_i), defined as net photosynthesis/transpiration, was estimated in leaf cuvettes using portable gas analyzers. However, stomatal conductance and WUE_i both vary temporally and spatially in the canopy, making it difficult to extrapolate chamber-based WUE_i measurements to an annual basis for the entire canopy. Earlier publications were instrumental in establishing the theoretical links among stomatal conductance of water and CO_2, intercellular CO_2 concentration, biochemical discrimination, and the abundance of naturally occurring C isotopes in plant tissue (cf. O'Leary 1981; Farquhar et al. 1982; Evans et al. 1986; O'Leary 1988). The ratio of carbon isotope abundance in tissue is affected by greater stomatal conductance of CO_2, which increases intracellular CO_2 concentration and in turn allows greater biochemical discrimination against the heavier ^{13}C isotope. Since stomatal conductance is directly proportional to water loss (given similar ambient conditions), discrimination of ^{13}C is positively correlated with water loss per unit of carbon assimilated (Farquhar et al. 1982; Farquhar and Richards 1984). Carbon isotope discrimination (Δ) integrates water loss per unit of carbon assimilated (Ehleringer 1991) and is therefore a useful tool to compare water use by co-occurring species.

This study compares the Δ for deciduous *Larix* spp. and co-occurring evergreen conifers from 20 locations in the northern hemisphere where *Larix* occurs naturally. The analysis includes seven of the ten recognized species of *Larix* (Gower and Richards 1990). A second objective is to examine the interrelationships among several key leaf ecophysiological characteristics [N concentration, specific leaf area (SLA), and WUE_i] that are strongly correlated with maximum photosynthesis under optimal environmental conditions (i.e., physiological capacity). Based on the study conducted by Gower and Richards (1990), we hypothesize that Δ, foliar nitrogen concentration, and SLA are greater for *Larix* spp. than sympatric evergreen conifers.

Materials and methods

Site descriptions

Carbon isotope ratio ($^{13}C/^{12}C$), total nitrogen concentration, SLA, and WUE_i (net photosynthesis/transpiration) were measured for larch and sympatric evergreen conifer needles from 20 locations in cold-temperate and boreal forests in North America and Eurasia (Table 1). Except for the *L. decidua* site near Birmensdorf, Switzerland, all stands are mature, mixed forests containing *Larix* spp. and a sympatric evergreen conifer. If more than one evergreen conifer species was present at a site, only the most abundant was sampled. Table 1 summarizes physiographic information and sampling design for the 20 sites.

Foliar nitrogen and carbon isotope analysis

All needle samples were collected from sunlit foliage in the upper third of the tree canopy near the end of the growing season (August to October). Foliage subject to carbon isotope and total nitrogen analyses was ground to pass a 0.5-mm^2 mesh screen and dried at 70°C for 24 h. Foliage nitrogen concentration was determined on 300 mg of tissue that was digested using a wet oxidation procedure (cf. Parkinson and Allen 1975) and analyzed colorimetrically on a Lachat continuous-flow ion analyzer (Lachat, Mequon, Wisc.) (Lachat 1988). Results were calibrated against a wide range (0.70–2.94% total N) of plant tissue standards (National Bureau of Standards, Gaithersburg, Md.) that were digested to insure that the sample digestion was complete.

The carbon isotope ratio was determined for homogeneous foliage samples of approximately 3 mg that were sealed in heat-cleaned quartz tubing with approximately 1 g of purified CuO wire and 0.25 g of purified Ag. Samples were combusted at 850°C for 2 h to oxidize all tissue carbon to CO_2 and held at 520°C for 8 h to convert all N_2O to N_2. After cooling, CO_2 was purified cryogenically. The carbon isotope ratio ($^{13}C/^{12}C$) of the CO_2 was analyzed on a Finnigan Delta E mass spectrometer (Finnigan MAT, Bremen, Germany). All data were reported relative to PDB, a standard limestone fossil of *Belemnitella americana* from the Cretaceous Pee Dee formation in South Carolina, USA (Boutton 1991). The resulting delta notation, $\delta^{13}C$ after McKinney et al. (1950), was determined using the following equation:

$$\delta^{13}C(‰) = \left[\left(R_{sample} - R_{standard}\right)/R_{standard}\right] \times 10^3 \quad (1)$$

Carbon isotope discrimination,

$$\Delta = \left(\delta_{air} - \delta_{plant}\right)/\left(1 + \delta_{plant}\right) \quad (2)$$

was also calculated to remove the effect of varying $\delta^{13}C$ air concentrations from different latitudes so that a direct comparison of samples could be made (Farquhar and Richards 1984; Körner et al. 1991). An air $\delta^{13}C$ concentration of $-7.9‰$ was assumed for all calculations because all samples originated from the mid-latitudes in the northern hemisphere (45–69°N latitude) where global air $\delta^{13}C$ is relatively stable during the growing season (Körner et al. 1988). The use of Δ notation helped to focus the analysis on biological questions independent of source CO_2 variation. The calculation of Δ also facilitates data analysis (Körner et al. 1991) and direct inter-study comparison.

The precision of the analysis procedure was determined from repeated measurement of a common sample. Approximately 15 g of *L. occidentalis* foliage from the Lost Creek, Mont. site was ground and mixed thoroughly. Seven samples were analyzed on the same day with $\delta^{13}C$ values ranging from -26.44 to $-26.54‰$ with a mean and standard error of -26.51 and $0.014‰$, respectively. Thereafter, one *L. occidentalis* "standard" sample was included in each batch of evacuated samples and the value of all subsequent analyses of the larch "standard" was within the original observed range.

Needles from the long and short shoots of larch became mixed during shipment or, in some collections, needles from only one shoot morphology were of sufficient quantity for both carbon isotope discrimination and total nitrogen analysis. A comparison of three independent replicates of foliage samples from long and short shoots of *L. decidua* from Birmensdorf, Switzerland showed that the mean $\delta^{13}C$ ratio (± 1 SE) did not differ significantly ($P = 0.11$) between short and long shoots ($-26.72 \pm 0.14‰$ and $-26.42 \pm 0.04‰$, respectively). Furthermore, a comparison of foliage nitrogen concentration did not differ between long and short shoots from *L. occidentalis*, *L. laricina*, and *L. lyallii* (B.D. Kloeppel and S.T. Gower, in preparation). Therefore, combining foliage from long and short shoots likely did not affect results.

Foliar sample collection and gas exchange

WUE_i was measured at the five USA research sites using an open infrared gas analyzer system (Model LCA2, Analytical Development Corporation, Hoddesdon, UK) under saturating ambient light (>1000 μmol quanta m^{-2} s^{-1}) – a typical growing season condition. Net photosynthesis and transpiration were calculated following von Caemmerer and Farquhar (1981). Morning maximum and diurnal gas exchange were measured six to nine times for *L. occidentalis* and *L. laricina* sites in the USA during the 1992 and 1993 growing season while WUE_i was measured at the high-elevation *L. lyallii* site in western Montana, USA only once on 8 August 1993. After each photosynthesis measurement, foliage in the cuvette was refrigerated and returned to the laboratory. Projected leaf area was determined on the fresh samples using a DIAS II image analysis system (Decagon Devices, Pullman, Wash.) that was calibrated to a wire rod, simulating the size and shape of a coniferous needle. The leaf area sample was oven-dried at 70°C to a constant mass and weighed. SLA (cm^2 g^{-1}) was calculated and averaged for all sampling dates since no growing-season differences were detected among sampling dates (B.D. Kloeppel, unpublished data).

Statistical analysis

Statistical comparisons of carbon isotope discrimination, foliar nitrogen concentration, and SLA between *Larix* spp. and co-occurring evergreen conifers were conducted using a one-way general linear model (SAS 1985). Linear regression analysis was used to examine the relationships between site elevation, WUE_i, foliar nitrogen, SLA, and carbon isotope discrimination (SAS 1985). The mean value of the leaf ecophysiological characteristics at each study site was the experimental unit for all analyses except in the data for Fig. 1, where individual trees were the experimental unit because only one tree was available at each elevation in Fig. 1A and the analysis in Fig. 1B was conducted similarly to maintain consistency. Slopes and *y*-intercepts of linear regressions relating elevation and carbon isotope discrimination were compared using identification variables (Chatterjee and Price 1977).

Results and discussion

Environmental controls on carbon isotope discrimination

The ranking of mean carbon isotope data for deciduous and evergreen species within each site did not differ when expressed as $\delta^{13}C$ or on a carbon isotope discrimination (Δ) basis (Table 1); therefore, all ^{13}C isotope data are expressed as Δ following Körner et al. (1991). Carbon isotope discrimination is negatively correlated with elevation for *L. decidua* ($P = 0.027$ $r^2 = 0.95$) and *Picea abies* ($P = 0.008$ $r^2 = 0.98$) along the 1200-m elevation gradient in Switzerland (Fig. 1A). The *y*-intercept of the regression equation for each species is significantly different ($P = 0.001$) from 0 and is significantly greater for *L. decidua* than *P. abies* ($P = 0.041$), but the slopes are similar ($P = 0.251$). A weak, but significant, negative relationship exists between Δ and elevation for larches ($P < 0.001$, $r^2 = 0.25$) and evergreen conifers ($P = 0.015$, $r^2 = 0.09$) for all 20 sites (Fig. 1B). Other scientists have also shown that Δ is negatively related to elevation and concluded that this is due to increased stomatal resistance to carbon dioxide assimilation with increasing elevation (Körner et al. 1988, 1991; Marshall and Zhang 1993, 1994).

WUE_i and Δ are expected to be negatively related (O'Leary 1981, Farquhar et al. 1982, 1989). However, our estimates of mean growing season WUE_i are not correlated to foliage Δ for each site-species combination (*Larix* spp., $P = 0.684$, $r^2 = 0.06$; evergreen conifers, $P = 0.138$, $r^2 = 0.57$) when analyzed separately, or when data are pooled ($P = 0.174$, $r^2 = 0.22$). We speculate that the poor correlation between WUE_i and Δ is because of diurnal and seasonal variation in WUE_i resulting from variation in vapor pressure deficit, air temperature, and soil moisture. Zhang and Marshall (1994) reported that the correlation between WUE_i and Δ was more variable than the correlation with a more integrated measure of water use efficiency, seedling dry mass/total water use. Therefore, measures of water use efficiency integrated over a longer time period, such as foliage and stem wood Δ, may provide a more reliable and integrated measurement of environmental effects on transpirational water loss relative to carbon assimilation.

Comparison of Leaf N, SLA, and Δ between larch and evergreen conifers

Mass-based foliar nitrogen concentration is significantly greater ($P < 0.05$) for larches than evergreen conifers at 14 of 16 sites (Table 1, Fig. 2). SLA is significantly greater for larches than sympatric evergreen conifers for the five sites where fresh needles for SLA determination are available (Table 1). The large differences in SLA and mass-based leaf N concentration between larches and evergreen conifers in this study corroborate findings from earlier studies (Gower and Richards 1990; Gower et al. 1995). Mass-based foliar N concentration is positively correlated to SLA ($R^2 = 0.84$), but the relationship is largely the result of two groups of data (Fig. 3). The relationship, however, is in good agreement with the empirical relationship for plants of varying leaf longevity (Reich et al. 1992). A theoretical basis exists for the empirical relationship shown in Fig. 3. Thick leaves (i.e., leaves with a low SLA) contain moderate to high concentrations of secondary compounds (e.g., lignin) that deter herbivory and reduce winter desiccation, both of which are essential for long-lived leaves (Mooney and Gulmon 1982; Coley 1988; Gower and Richards 1990; Reich et al. 1992). High concentrations of structural constituents, however, dilute mass-based foliar N concentration (Fig. 2), which is a critical constituent of the photosynthetic machinery (Field and Mooney 1986; Reich et al. 1991, 1992). The reverse is true for deciduous or short-lived leaves: they have a high SLA, high mass-based foliar N concentration, and low concentrations of secondary compounds. The physiological capacity of plants to assimilate carbon dioxide is correlated with leaf N concentration and SLA, especially when environmental conditions do not limit photosynthesis. Because

Table 1 Mean (±SE) values for $\delta^{13}C$, carbon isotope discrimination (Δ), mass-based foliar nitrogen concentration (*Foliar N*), and specific leaf area (*SLA*) for *Larix* spp. and co-occurring evergreen conifers. Species comparisons within a site and sampling period that are significantly different at the 0.05, 0.01, or ≤0.001 *P*-level are indicated by *, **, and ***, respectively

Site (elevation)	Species	Needle age class sampled	Sample size	$\delta^{13}C$ (‰)	Δ (‰)	Foliar N (mg g^{-1})	SLA (cm^2 g^{-1})
Bonner, Mont. (46°51′N, 113°53′W) (1158 m)	*L. occidentalis*	Short shoots	5	−25.43 ± 0.06	17.98 ± 0.06	20.5 ± 0.6***	131.8 ± 2.2***
	Pseudotsuga menziesii	1 year old	5	−25.34 ± 0.44	17.89 ± 0.46	9.9 ± 0.4	43.7 ± 0.8
	L. occidentalis[a]	Short shoots	5	−27.28 ± 0.20**	19.93 ± 0.21**	19.8 ± 0.8***	
	P. menziesii[a]	1 year old	5	−25.94 ± 0.28	18.52 ± 0.29	10.3 ± 0.6	
Lost Creek, Mont. (47°55′N, 113°49′W) (1012 m)	*L. occidentalis*	Short shoots	5	−26.74 ± 0.06	19.36 ± 0.06	14.4 ± 1.0*	114.0 ± 1.8***
	P. menziesii	1 year old	5	−26.99 ± 0.18	19.62 ± 0.19	10.2 ± 0.8	43.8 ± 0.5
	L. occidentalis[a]	Short shoots	5	−27.37 ± 0.18	20.02 ± 0.18	14.2 ± 0.9**	
	P. menziesii[a]	1 year old	5	−26.71 ± 0.29	19.33 ± 0.31	10.1 ± 0.6	
Savage Lake, Mont. (48°25′N, 115°48′W) (706 m)	*L. occidentalis*	Short shoots	5	−27.33 ± 0.40	19.98 ± 0.42	15.5 ± 0.7**	120.2 ± 1.7***
	Pinus contorta	1 year old	5	−28.10 ± 0.14	20.79 ± 0.15	11.8 ± 0.6	48.8 ± 0.6
	L. occidentalis[a]	Short shoots	5	−28.01 ± 0.26	20.69 ± 0.28	16.0 ± 0.4**	
	P. contorta[a]	1 year old	5	−28.26 ± 0.36	20.96 ± 0.38	13.5 ± 0.4	
Carlton Ridge, Mont. (46°42′N, 114°10′W) (2130 m)	*L. lyallii*	Mixed shoots	5	−26.85 ± 0.20**	19.48 ± 0.21**	22.6 ± 1.0***	127.9 ± 4.2***
	Pinus albicaulis	3 years old	5	−25.63 ± 0.18	18.20 ± 0.19	8.0 ± 0.4	37.9 ± 2.3
Lake Tomahawk, Wisc. (45°46′N, 89°34′W) (482 m)	*L. laricina*	Short shoots	5	−28.77 ± 0.24***	21.49 ± 0.25***	16.5 ± 1.0***	123.9 ± 3.9***
	Picea mariana	Mixed ages	5	−26.70 ± 0.31	19.32 ± 0.32	8.2 ± 0.2	48.8 ± 0.8
Fredericton, Canada (45°56′N, 66°38′W) (72 m)	*L. laricina*	Long shoots	5	−28.58 ± 0.30***	21.29 ± 0.31***	14.8 ± 1.5	
	P. mariana	New	5	−25.53 ± 0.14	18.09 ± 0.15	12.3 ± 0.2	
Candle Lake, Canada (52°0′N, 105°0′W) (556 m)	*L. laricina*	Mixed shoots	5	−28.02 ± 0.14***	20.70 ± 0.14***	23.9 ± 0.2***	
	P. mariana	New	5	−27.01 ± 0.10	19.64 ± 0.10	9.8 ± 1.0	
Thompson, Canada (56°0′N, 98°30′W) (213 m)	*L. laricina*	Mixed shoots	5	−28.47 ± 0.05***	21.17 ± 0.05***	13.5 ± 1.0***	
	P. mariana	New	5	−27.29 ± 0.21	19.94 ± 0.22	7.8 ± 0.3	
Radenci, Slovenia (45°33′N, 15°9′E) (300 m)	*L. decidua*	Long shoots	2	−27.84 ± 0.10**	20.52 ± 0.11**	19.2 ± 1.0*	
	Picea abies	New	2	−25.81 ± 0.02	18.38 ± 0.02	12.0 ± 0.5	
Kamniska, Slovenia (46°15′N, 14°33′E) (1700 m)	*L. decidua*	Long shoots	3	−28.00 ± 0.52	20.68 ± 0.55	18.0 ± 0.6**	
	P. abies	New	2	−26.14 ± 0.24	18.73 ± 0.26	10.0 ± 0.4	
Birmensdorf, Switzerland[b] (47°22′N, 8°32′E) (550 m)	*L. decidua*	Long shoots	3	−26.42 ± 0.14	19.04 ± 0.04		
	L. decidua	Short shoots	3	−26.72 ± 0.14	19.34 ± 0.15		
Küblis, Switzerland[c] (46°24′N, 9°48′E) (800 m)	*L. decidua*	Long shoots	1	−28.61	21.32	14.9	
	P. abies	Mixed ages	1	−27.52	20.18	14.6	
Klosters, Switzerland[c] (46°24′N, 9°48′E) (1200 m)	*L. decidua*	Long shoots	1	−28.15	20.84	19.0	
	P. abies	*Mixed ages*	1	−27.11	19.75	11.1	
Dischma, Switzerland[c] (46°24′N, 9°48′E) (1600 m)	*L. decidua*	Long shoots	1	−27.48	20.13	16.8	
	P. abies	Mixed ages	1	−26.47	19.07	10.2	
Stillberg, Switzerland[c] (46°24′N, 9°48′E) (2000 m)	*L. decidua*	Long shoots	1	−26.19	18.78	21.1	
	P. abies	Mixed ages	1	−25.73	18.30	13.4	
Davos, Switzerland (46°24′N, 9°48′E) (2000 m)	*L. decidua*	Short shoots	5	−26.44 ± 0.19**	19.05 ± 0.20**	26.5 ± 3.0*	
	Pinus cembra	New	5	−24.48 ± 0.43	17.00 ± 0.45	18.2 ± 0.3	
Telnak, Russia (69°29′N, 88°23′E) (75 m)	*L. siberica*	Short shoots	3	−27.81 ± 0.36**	20.48 ± 0.37**	24.7 ± 2.0**	
	Picea obavata	New	3	−24.92 ± 0.25	17.45 ± 0.26	13.3 ± 0.3	

Table 1 (contd.)

Site (elevation)	Species	Needle age class sampled	Sample size	$\delta^{13}C$ (‰)	Δ (‰)	Foliar N (mg g^{-1})	SLA (cm^2 g^{-1})
Norilsk, Russia (69°24′N, 88°17′E) (75 m)	*L. siberica*	Short shoots	5	−27.07 ± 0.29**	19.70 ± 0.31**	22.4 ± 0.9**	
	P. obavata	New	5	−25.39 ± 0.28	17.95 ± 0.30	17.6 ± 1.0	
Haukadalur, Iceland (69°24′N, 20°25′W) (200 m)	*L. siberica*	Mixed shoots	5	−29.47 ± 0.22***	22.22 ± 0.23***	26.9 ± 0.6***	
	Picea sitchensis	Mixed ages	5	−27.62 ± 0.29	20.28 ± 0.30	11.4 ± 0.9	
Chengdu, China (3000–4000 m)	*L. gmelinii*	Mixed shoots	2	−27.55 ± 0.41	20.21 ± 0.43	17.8 ± 0.1**	
	Picea sp.	Mixed ages	3	−27.56 ± 0.10	20.21 ± 0.11	12.6 ± 0.4	
Shanxi, China	*L. olgenisis*	Mixed shoots	2	−27.82 ± 0.08	20.48 ± 0.08	15.3 ± 1.9	
	Pinus sylvestris	Mixed ages	2	−26.86 ± 1.10	19.49 ± 1.16	17.6 ± 0.1	

[a] Resampled in August 1996
[b] Data used only for shoot morphology comparison
[c] Data used for elevational gradient displayed in Fig. 1A

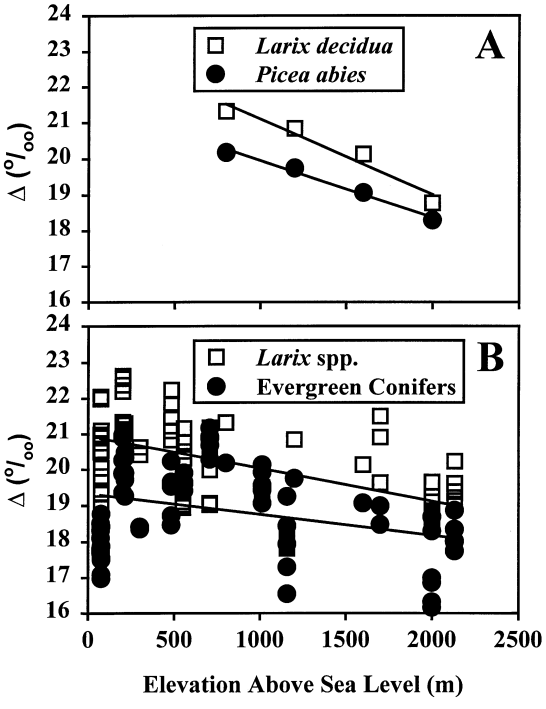

Fig. 1 **A** Foliar carbon isotope discrimination (Δ) of the deciduous conifer *Larix decidua* and the evergreen conifer *Picea abies* growing in mixed forest stands along an elevational transect in the Swiss Alps. Linear regressions: *L. decidua*, $y = 23.18 - 0.00208x$, $r^2 = 0.95$, $P = 0.027$; *P. abies*, $y = 21.53 - 0.00157x$, $r^2 = 0.98$, $P = 0.008$. **B** Foliar carbon isotope discrimination (Δ) of 20 mixed species stands containing *Larix* spp. and a co-occurring evergreen conifer from all sampling sites in North America and Eurasia. Linear regressions: *Larix* spp., $y = 20.88 - 0.00088x$, $r^2 = 0.25$, $P < 0.001$; evergreen conifers, $y = 19.31 - 0.00052x$, $r^2 = 0.09$, $P = 0.015$

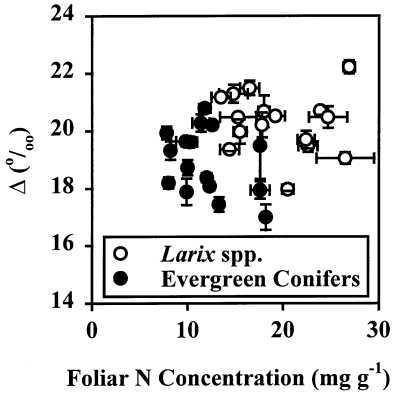

Fig. 2 Foliar carbon isotope discrimination (Δ) versus mass-based foliar nitrogen concentration (mean ± SE of both variables) of samples collected from 16 mixed *Larix* spp. and evergreen conifer forest study sites located in North America and Eurasia

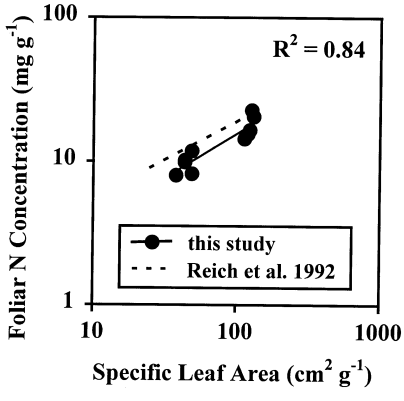

Fig. 3 Mass-based foliar nitrogen concentration versus specific leaf area for two species at each of five US sites in this study (*filled circles*). The $\log_{10}$-transformed regression for this relationship is $y = 0.6170x - 0.04094$, $r^2 = 0.84$, $P < 0.001$. The *dashed line* represents the relationship reported in Reich et al. 1992

carbon dioxide uptake and water vapor loss are strongly controlled by stomatal conductance, leaf characteristics that imply high photosynthetic rates are likely to be correlated to transpiration. They are also likely to facilitate greater water loss per unit of carbon assimilated due to high stomatal conductance and hence higher Δ.

Although other scientists have reported a negative correlation between carbon isotope discrimination and leaf N concentration (Körner et al. 1991; Högberg et al.

1993; Lajtha and Getz 1993), we did not observe a significant correlation for all samples ($P = 0.152$, $r^2 = 0.04$), or for *Larix* spp. or evergreen conifers analyzed separately (Fig. 2). The wide range of environmental conditions, especially elevation, may confound this relationship. Our results corroborate those of Damesin et al. (1997) who observed a similar result for mass-based nitrogen in Mediterranean evergreen and deciduous *Quercus* spp.

Larches have a significantly greater Δ ($P < 0.05$) than co-occurring evergreen conifers at 10 of the 16 study sites (Table 1). The small number of trees sampled ($n \leq 3$) may have prevented us from detecting a significant difference in Δ between larches and evergreen conifers in Slovenia and the two sites in China. The only other sites where Δ does not differ between larches and co-occuring evergreen conifers are the three *L. occidentalis* sites (Bonner, Lost Creek, and Savage Lake) in Montana. We resampled these three sites in 1996 because we were concerned that a sampling error may have occurred. For 1996, the Δ differed significantly between *L. occidentalis* and *Pseudotsuga menziesii* at the Bonner site, but it did not differ between larch and the sympatric evergreen conifer at the other two sites. An inadequate number of trees were sampled at each location in Switzerland to perform statistical comparisons between larch and co-occuring evergreen conifers; however, the significantly greater ($P < 0.041$) *y*-intercept of *L. decidua* than *P. abies* in Fig. 1A suggests that water use efficiency is lower in *L. decidua* than *P. abies*. Similarly, the *y*-intercept in Fig. 1B was significantly greater ($P < 0.001$) for *Larix* spp. than the co-occurring evergreen conifer line, but the slopes were similar ($P = 0.291$).

Other scientists have also reported significantly lower Δ for evergreen conifers than broad-leaved deciduous hardwood species in the southern USA (Garten and Taylor 1992) and *L. occidentalis* in Idaho, USA (Marshall and Zhang 1994). Our data corroborate the initial findings by Gower and Richards (1990) and suggest that on a unit leaf area basis, larches, and deciduous species in general, use water less efficiently than evergreen conifers (cf. Lloyd and Farquhar 1994).

Our data suggest that at high elevations, Δ would be similar for both *Larix* spp. and co-occurring evergreen conifers. The equations for the Swiss transect (Fig. 1A) would yield the same Δ at an elevation of 3235 m. Similarly, in Fig. 1B, the equations for all data generate the same Δ at 4361 m. Finally, the Chengdu sample site in China, at an elevation of 3000–4000 m, resulted in no difference in Δ values between *L. gmelinii* and *Picea* spp.: 20.21‰ for both species. Thus, it appears that water availability is not the most limiting resource at high elevations, but rather the low partial pressure of CO_2 and extreme cold limit the photosynthesis of both evergreen and deciduous species (Tranquillini 1979).

Efficient use of critical resources, such as water and nutrients, benefits plant growth and survival (Bloom et al. 1985; Givnish 1986). The less efficient use of water by larches than evergreen conifers may limit where larches can effectively compete with sympatric evergreen conifers. For example, subalpine larch (*L. lyallii*) typically occurs in mesic microsites of north-facing alpine slopes and the base of talus slopes where snow accumulates, thus providing a water source during snow melt (Arno and Habeck 1972; Richards and Bliss 1986). *L. occidentalis* occurs on deeper soils on north-facing exposures and the edges of stream drainages in the more xeric portions of its range (Schmidt et al. 1976). Little is known about the ecophysiology of other larch species, but this study demonstrates that in general larches use water less efficiently than evergreen conifers. Future studies should examine the potential effects climate warming may have on water use efficiency and its effects on the growth and distribution of larch forests.

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References

Arno SF, Habeck JR (1972) Ecology of alpine larch (*Larix lyalli* Parl.) in the Pacific Northwest. Ecol Monogr 42:417–450

Axelrod DI (1966) Origin of deciduous and evergreen habits in temperate forests. Evolution 20:1–15

Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants – an economic analogy. Annu Rev Ecol Syst 16:363–392

Boutton TW (1991) Stable carbon isotope ratios of natural materials. I. Sample preparation and mass spectrometric analysis. In: Coleman DC, Fry B (eds) Carbon isotope techniques. Academic Press, San Diego, Calif, pp 155–171

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

Chatterjee S, Price B (1977) Regression analysis by example. Wiley, New York

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

Damesin C, Rambal S, Joffre R (1997) Between-tree variations in leaf $\delta^{13}C$ of *Quercus pubescens* and *Quercus ilex* among Mediterranean habitats with different water availability. Oecologia 111:26–35

Ehleringer JR (1991) $^{13}C/^{12}C$ fractionation and its utility in terrestrial plant studies. In: Coleman DC, Fry B (eds) Carbon isotope techniques. Academic Press, San Diego, Calif, pp 187–200

Evans JR, Sharkey TD, Berry JA, Farquhar GD (1986) Carbon isotope discrimination measured concurrently with gas exchange to investigate CO_2 diffusion in leaves of higher plants. Aust J Plant Physiol 13:281–292

Farquhar GD, Richards RA (1984) Isotopic composition of plant carbon correlates with water-use efficiency of wheat genotypes. Aust J Plant Physiol 11:539–555

Farquhar GD, O'Leary MH, Berry JA (1982) On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Aust J Plant Physiol 9:121–137

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Physiol Plant Mol Biol 40:503–537

Field C, Mooney HA (1986) The photosynthesis-nitrogen relationship in wild plants. In: Givnish TJ (ed) On the economy of plant form and function. Cambridge University Press, New York, pp 25–55

Garten CT, Taylor GE Jr (1992) Foliar $\delta^{13}C$ within a temperate deciduous forest: spatial, temporal, and species sources of variation. Oecologia 90:1–7

Givnish TJ (1986) (ed) On the economy of plant form and function. Cambridge University Press, New York

Gower ST, Richards JH (1990) Larches: deciduous conifers in an evergreen world. Bioscience 40:818–826

Gower ST, Kloeppel BD, Reich PB (1995) Carbon, nitrogen, and water use by larches and co-occurring evergreen conifers. In: Ecology and management of *Larix* forests: a look ahead, USDA For Serv Gen Tech Rep INT-GTR-319, Ogden, Utah, pp 110–117

Högberg P, Johannisson C, Hallgrën JE (1993) Studies of ^{13}C in the foliage reveal interactions between nutrients and water in forest fertilization experiments. Plant Soil 152:207–214

Kikuzawa K (1991) A cost benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. Am Nat 138:1250–1263

Körner CH, Farquhar GD, Roksandic Z (1988) A global survey of carbon isotope discrimination in plants from high altitude. Oecologia 74:623–632

Körner CH, Farquhar GD, Wong SC (1991) Carbon isotope discrimination by plants follows latitudinal and altitudinal trends. Oecologia 88:30–40

Lachat (1988) Total Kjeldahl nitrogen as NH_3. Quikchem method No 13-107-06-2-A. Lachat, Mequon, Wisc

Lajtha K, Getz J (1993) Photosynthesis and water-use efficiency in pinyon-juniper communities along an elevation gradient in northern New Mexico. Oecologia 94:95–101

Lloyd J, Farquhar GD (1994) ^{13}C discrimination during CO_2 assimilation by the terrestrial biosphere. Oecologia 99:201–215

Marshall JD, Zhang J (1993) Altitudinal variation in carbon isotope discrimination by conifers. In: Ehleringer JR, Hall AE, Farquhar GD (eds) Stable isotopes and plant carbon-water relations. Academic Press, San Diego, Calif, pp 187–199

Marshall JD, 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 Physiol 2:177–187

McKinney CR, McCrea JM, Epstein S, Allen HA, Urey HC (1950) Improvements in mass spectrometers for the measurement of small differences in isotope abundance ratios. Rev Sci Instrum 21:724–730

Mooney HA (1972) The carbon balance of plants. Annu Rev Ecol Syst 3:315–346

Mooney HA, Gulmon SL (1982) Constraints on leaf structure and functions in reference to herbivory. BioScience 32:198–206

O'Leary MH (1981) Carbon isotope fractionation in plants. Phytochemistry 20:553–567

O'Leary MH (1988) Carbon isotopes in photosynthesis. BioScience 38:328–336

Parkinson JA, Allen SE (1975) A wet oxidation procedure suitable for the determination of nitrogen and mineral nutrients in biological material. Commun Soil Sci Plant Anal 6:1–11

Reich PB, Walters MB, Ellsworth DS (1991) Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area, and photosynthesis in maple and oak trees. Plant Cell Environ 14:251–259

Reich PB, Walters MB, Ellsworth DS (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecol Monogr 62:365–392

Richards JH, Bliss LC (1986) Winter water relations of a deciduous timberline conifer, *Larix lyallii* Parl. Oecologia 69:16–24

SAS (1985) SAS user's guide: statistics, version 5 edition. SAS Institute, Cary, NC

Schmidt WC, Shearer RC, Roe AL (1976) Ecology and silviculture of western larch forests. Tech Bull No 1520. USDA Forest Service, Washington

Schulze ED, Schulze W, Kelliher FM, Vygodskaya NN, Ziegler W, Kobak KI, Koch H, Arneth A, Kusnetsova WA, Sogatchev A, Issajev A, Bauer G, Hollinger DY (1995) Aboveground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian *Larix* stands in eastern Siberia. Can J For Res 25:943–960

Tranquillini W (1979) Physiological ecology of the alpine timberline. Springer, New York

Waring RH, Franklin JF (1979) The evergreen coniferous forests of the Pacific Northwest. Science 204:1380–1386

Wolfe JS (1979) Temperate parameters of humid to mesic forests of eastern Asia and relation to forests of other regions of the northern hemisphere and Australasia. USGS Professional Paper 1106, Washington, DC

Zhang J, Marshall JD (1994) Population differences in water-use efficiency of well-watered and water-stressed western larch seedlings. Can J For Res 24:92–99