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Leaf carbon isotope discrimination and nitrogen content for riparian trees along elevational transects

Received: 25 February 1996 / Accepted: 8 September 1996

Abstract Leaf carbon isotope discrimination (Δ), seasonal estimates of the leaf-to-air water vapor gradient on a molar basis (ω), and leaf nitrogen contents were examined in three riparian tree species (*Populus fremontii*, *P. angustifolia*, and *Salix exigua*) along elevational transects in northern and southern Utah USA (1500–2670 m and 600–1820 m elevational gradients, respectively). The ω values decreased with elevation for all species along transects. Plants growing at higher elevations exhibited lower Δ values than plants at lower elevations (*P. fremontii*, 22.9‰ and 19.5‰, respectively; *P. angustifolia*, 23.2‰ and 19.2‰, respectively; and *S. exigua*, 21.1‰ and 19.1‰, respectively). Leaf nitrogen content increased with elevation for all species, suggesting that photosynthetic capacity at a given intercellular carbon dioxide concentration was greater at higher elevations. Leaf Δ and nitrogen content values were highly correlated, implying that leaves with higher photosynthetic capacities also had lower intercellular carbon dioxide concentrations. No significant interannual differences were detected in carbon isotope discrimination.

Key words Stable isotope · Carbon isotope ratio · Carbon isotope discrimination · Riparian ecosystem · Water-use efficiency

Introduction

Leaf carbon isotope discrimination (Δ) reflects the ratio of leaf internal to external CO₂ concentration (c_i/c_a) and is an integrated, long-term measure of the effects of

factors affecting inward CO₂ diffusion (leaf conductance) and CO₂ consumption (photosynthetic rate) (Farquhar et al. 1989; Ehleringer et al. 1993). Intra- and inter-specific variations in leaf Δ values have been correlated with a diversity of related gas exchange components, including leaf conductance, hydraulic conductivity, water-use efficiency, and photosynthetic capacity (Woodward 1986; Körner et al. 1988; Farquhar et al. 1989; Ehleringer et al. 1993). Abiotic factors, such as soil moisture availability and humidity, have also been shown to exert a significant influence on leaf Δ values (Winter et al. 1982; Madhavan et al. 1991; Ehleringer et al. 1993).

Combining the results from a number of different herbaceous species, Körner et al. (1988) showed that Δ values generally decreased along an increasing elevation gradient. Marshall and Zhang (1993) showed a similar pattern for coniferous trees in North America. Over such elevational transects, plants encounter a variety of microclimates differing in temperature, soil moisture and vapor pressure gradient, each of which may influence Δ values. Increases in leaf thickness also occur along increasing elevational gradients (Wardlaw et al. 1983; Woodward 1986; Williams and Black 1993) and these changes have been correlated with both increased photosynthetic capacity per unit leaf area (Friend and Woodward 1990; Körner and Diemer 1987) and increased CO₂ diffusive pathway length (Vitousek et al. 1990). Distinguishing species-difference effects from water-stress, temperature, and/or humidity effects on Δ values along elevation gradients has been challenging with existing data sets.

The objectives of this study were to examine the responses of single species that exhibit a continuous distribution over a broad elevational transect. To control soil moisture environment along an elevational transect, we selected mature individuals of obligate riparian tree species growing immediately adjacent to streams: *Populus fremontii* (Fremont cottonwood), *P. angustifolia* (narrowleaf cottonwood), and *Salix exigua* (coyote willow). We predicted and evaluated two Δ -value responses

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to increased elevation. First, if stomatal conductance increased with elevation along this transect in response to decreasing leaf-air vapor pressure differences, then leaf c_i/c_a and Δ values would be greatest at highest elevations. Second, if increased photosynthetic capacity (as measured by increased leaf nitrogen concentrations) increased with elevation, then leaf c_i/c_a and Δ values would be lowest at highest elevations.

Materials and methods

Field sites

Mature trees of *P. fremontii* Wats (Fremont Cottonwood) were sampled along a transect in southern Utah, USA (5–7 individuals per site). The transect was along the Virgin River drainage between Cedar City, Utah and Mesquite, Nevada (36°30' N, 114°10' W to 37°40' N, 112°58' W) (600–1820 m). Seven collection sites were selected at ca. 200 m elevation intervals along the transect. *P. angustifolia* James (narrowleaf cottonwood, 5–7 individuals per site) and *Salix exigua* Nutt. (coyote willow, 5 individuals per site) were sampled along a similar elevational transect in northern Utah. This second transect was along Big Cottonwood Canyon in the Wasatch Mountains east of Salt Lake City, Utah (40°50' N, 111°80' W to 40°50' N, 111°41' W) (1500–2670 m). Nine and seven collection sites were selected for *P. angustifolia* and *S. exigua*, respectively, at 100–200 m elevation intervals along the transect. All individuals of each species were growing adjacent to a perennial stream and all individuals of *P. fremontii* and *P. angustifolia* had a diameter at breast height (DBH) > 15 cm. *S. exigua* is a clonal shrub (2–3 m tall) and no DBH distinction was made, although apparent juveniles were not sampled.

Determination and expression of seasonal leaf-to-air water vapor mole fraction gradient

While weather station data were not continuously available along each transect, each transect was within 30 km of at least three long-term weather stations. For the southern transect (600–1820 m), the nearby weather stations used to calculate the climate at each elevation sampled were Cedar City, Utah (1713 m), New Harmony, Utah (1267 m), and St. George, Utah (812 m). For the northern transect (1500–2670 m), the nearby stations were Alta, Utah (2670 m), Silver Lake (Brighton), Utah (2664 m), and Salt Lake City, Utah (1287 m). Mean maximum air temperatures and precipitation values for these sites were calculated based on regression between altitude and the climatic parameter. In each case, the r^2 for the regressions exceeded 0.876.

To estimate the long-term evaporative gradients experienced by plants during the growing season at each site, we calculated the parameter ω as presented by Comstock and Ehleringer (1992). The ω value estimates the seasonally-weighted magnitude of the leaf-to-air water vapor mole fraction gradient (v) over the entire growing season, where v is the leaf-to-air-vapor pressure gradient divided by total atmospheric pressure. The ω value calculation assumes that the evaporative potential is related to the saturated vapor pressure gradient (i.e., a dry environment) and averages the saturation vapor pressure (e_{sat}) based on mean maximum daytime temperatures over each month of the year, scaled to the monthly ratio of precipitation (P) to potential evapotranspiration (E_p as calculated in Thornwaite 1948) as a weighting factor. Thus, the magnitude of the evaporative gradient only becomes relevant during those months when soil moisture is available for plants to transpire. The effective seasonal water vapor mole fraction gradient (ω) is then calculated as:

$$\omega = \frac{\left[\frac{1}{P_{\text{total}}} \sum_{\text{Jan}}^{\text{Dec}} \left(e_{\text{sat}} \frac{P}{E_p} \right) \right]}{\sum_{\text{Jan}}^{\text{Dec}} \frac{P}{E_p}},$$

ω is an index that ranks sites according to the mean evaporative demand experienced by plants during the growing season and has units of mbar bar⁻¹.

Plant sampling and analysis

P. angustifolia and *P. fremontii* were sampled twice during the summer of 1993 and once during the summer of 1994. *S. exigua* were sampled once in the summer of 1993. For each species at a sampling period, five sun-lit leaves were sampled from each individual (one leaf from each compass direction at a height of 2 m and one additional leaf from the crown of the main axis).

Leaf samples for carbon isotope analysis were dried for 48 h at 70°C and ground with a mortar and pestle. A 2-mg homogenized subsample of the tissue was combusted for 6 h at 850°C in sealed, evacuated Vycor tubes containing copper, cupric oxide, and silver foil, and then cooled to room temperature (Ehleringer and Osmond 1989). The CO₂ produced by combustion was purified cryogenically, and the $\delta^{13}\text{C}$ was measured on an isotope ratio mass spectrometer (delta S, Finnigan MAT, Bremen, Germany). The overall, long-term sample preparation and analysis error between repeated analyses of the same ground tissue was less than $\pm 0.11\%$.

Leaf nitrogen contents were measured on a separate subsample of the same ground leaf material. A 0.5–1.0 mg sample was analyzed using a CHN analyzer (Model 2400, Perkin-Elmer, Norwalk, Conn, USA). Leaf areas were measured using a leaf area meter (Licor Instruments, Lincoln, Neb, USA).

Leaf carbon isotope discrimination

Leaf carbon isotope ratio is expressed in delta notation as:

$$\delta^{13}\text{C}_{\text{sample}} (\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000,$$

where $\delta^{13}\text{C}_{\text{sample}}$ is the isotope ratio in parts per mil (‰), R_{sample} and R_{standard} are the $^{13}\text{C}/^{12}\text{C}$ molar abundance ratios of the leaf material and the PDB standard, respectively. Although δ provides information on the $^{13}\text{C}/^{12}\text{C}$ of tissues, it is often preferable to express the values as leaf carbon isotope discrimination (Δ) (Farquhar and Richards 1984):

$$\Delta (\text{‰}) = \frac{\delta^{13}\text{C}_{\text{air}} - \delta^{13}\text{C}_{\text{sample}}}{1 + \delta^{13}\text{C}_{\text{sample}}},$$

where $\delta^{13}\text{C}_{\text{air}}$ is -8% .

Results

Seasonal water vapor mole fraction gradient

The highest ω values were found at the lowest elevation for all transects (Fig. 1). The northern transect ranged from 34.0 mbar bar⁻¹ at 1580 m to 18.5 mbar bar⁻¹ at 2670 m. The southern transect ranged from 61.8 mbar bar⁻¹ at 600 m to 28.8 mbar bar⁻¹ at 1820 m. The southern transect exhibited a slightly steeper trend in seasonal water vapor mole fraction difference compared to the northern transect. Values decreased with elevation at a greater rate along the southern transect compared to

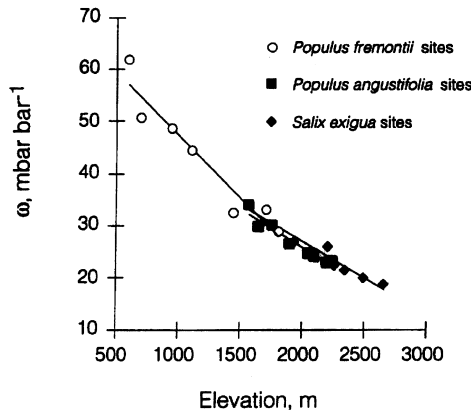


Fig. 1 Trends in seasonally integrated leaf-air humidity gradients (ω) along elevational transects in northern and southern Utah. *Populus angustifolia* and *Salix exigua* were sampled along the northern Utah transect ($y = 53.74 - 0.014x$, $r^2 = 0.930$, $P < 0.0001$). *P. fremontii* were sampled along the southern Utah transect ($y = 71.37 - 0.024x$, $r^2 = 0.926$, $P < 0.0001$)

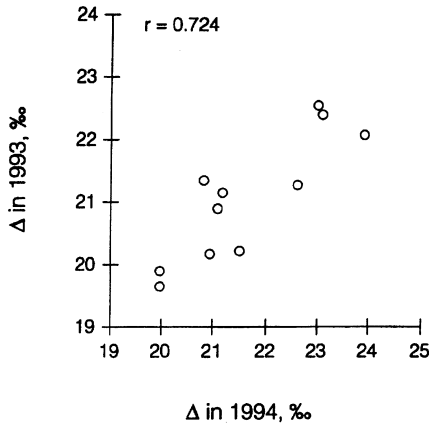
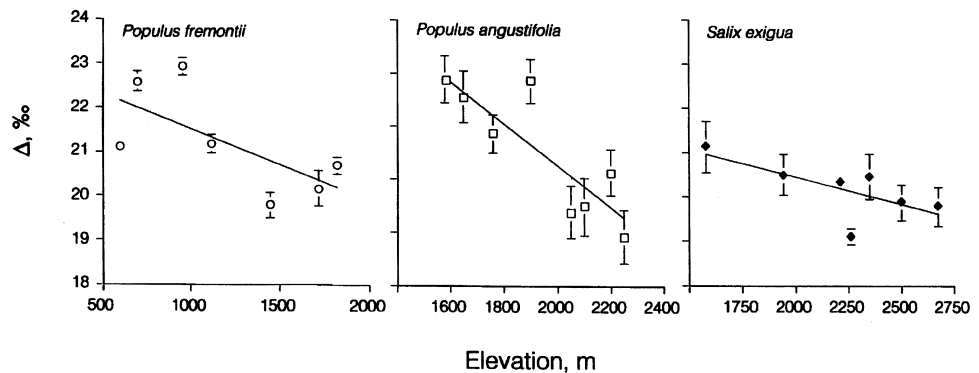


Fig. 2 The correlation of population-level means of leaf carbon isotope discrimination values (Δ) for *P. angustifolia* and *P. fremontii* in 1993 and 1994 ($r = 0.724$, $P < 0.001$)

Fig. 3 The relationship between leaf carbon isotope discrimination (Δ) and elevation in *P. fremontii*, *P. angustifolia*, and *S. exigua*. Regressions are based on the mean values for plants sampled at a given elevation; error bars represent ± 1 SE. See Tables 1 and 2 for regression statistics and tests of heterogeneity of slope and intercept difference



the northern transect (slopes = -0.024 and -0.014 mbar bar $^{-1}$ m $^{-1}$, respectively, heterogeneity of slope test, $P < 0.05$).

Leaf carbon isotope discrimination

There were no significant interannual differences in leaf carbon isotope discrimination values for either of the *Populus* species (Fig. 2, $r = 0.724$, $P < 0.001$, $n = 11$). The data were therefore pooled between years for *P. fremontii* and *P. angustifolia* (*S. exigua* were sampled only in 1993). Plants of all species growing at higher elevation discriminated less against ^{13}C compared to plants at lower elevations (Fig. 3, Table 1). Carbon isotope discrimination for *P. fremontii* ranged from 22.9 ‰ to 19.5 ‰ over an elevational range of 1220 m (2.8‰ km^{-1} , $r^2 = 0.417$, $P < 0.0001$, $n = 75$). Similarly, Δ values for *P. angustifolia* ranged from 23.2 ‰ to 19.2 ‰ over an elevational range of 750 m (5.3‰ km^{-1} , $r^2 = 0.362$, $P < 0.0001$, $n = 45$). Discrimination in *S. exigua* leaves ranged from 21.1 ‰ to 19.1 ‰ over a 1090-m elevational range (1.8‰ km^{-1} , $r^2 = 0.174$, $P < 0.05$, $n = 30$). The slopes of leaf carbon isotope discrimination across elevation were significantly different when all species were compared (Table 2). However, if the *S. exigua* data were excluded (i.e., when only the two poplar species were compared) there was no significant difference in slope between the two species of *Populus* indicating the response over elevation was similar. However, the Δ intercept values for each species were significantly different (*P. fremontii*, 24.07 ‰, *P. angustifolia*, 29.07 ‰, and *S. exigua*, 22.82 ‰, Table 2), implying there were species differences in Δ value at any given elevation.

Leaf nitrogen contents

Leaf nitrogen content increased with elevation for both *P. fremontii* and *P. angustifolia* (Fig. 4, Table 1). Leaf nitrogen contents of *P. fremontii* increased more than 85% over 1300 m from 112 mmol N m $^{-2}$ at 600 m to

Table 1 Regression parameters for changes in leaf carbon isotope discrimination with elevation ($\Delta \times$ elevation), change in leaf nitrogen contents (N) with elevation (N \times elevation), change in leaf carbon isotope discrimination with leaf nitrogen content ($\Delta \times$ N), change in specific leaf weight (SLW) with leaf nitrogen contents

(SLW \times N), and the change in leaf carbon isotope discrimination with specific leaf weight ($\Delta \times$ SLW) (symbols: b_0 intercept, b_1 slope and F calculated F -ratio). Regression equations are of the form $Y = b_0 + b_1(x)$

Regression	Species	b_0	b_1	r^2	F
$\Delta \times$ Elevation	<i>Populus fremontii</i>	24.07	-0.0028	0.417	51.60 ^{*4}
	<i>P. angustifolia</i>	29.07	-0.0053	0.362	24.45 ^{*4}
	<i>Salix exigua</i>	22.82	-0.0018	0.174	5.89 ^{*1}
N \times Elevation	<i>P. fremontii</i>	73.92	0.075	0.479	21.11 ^{*4}
	<i>P. angustifolia</i>	-9.93	0.082	0.190	5.39 ^{*1}
$\Delta \times$ N	<i>P. fremontii</i>	24.95	-0.024	0.536	26.54 ^{*4}
	<i>P. angustifolia</i>	24.50	-0.023	0.424	16.95 ^{*3}
SLW \times N	<i>P. fremontii</i>	11.14	0.584	0.673	47.30 ^{*4}
	<i>P. angustifolia</i>	45.20	0.302	0.644	43.34 ^{*4}
$\Delta \times$ SLW	<i>P. fremontii</i>	23.68	-0.022	0.311	10.37 ^{*2}
	<i>P. angustifolia</i>	26.52	-0.061	0.432	18.25 ^{*3}

^{*4} $P < 0.0001$, ^{*3} $P < 0.001$, ^{*2} $P < 0.01$, ^{*1} $P < 0.05$

Table 2 Tests of heterogeneity of slope (F_1) for regressions in Table 1 within a given series of regressions. Whenever the result of this analysis was not significant (i.e., there was no statistical differences between slopes), then a test of intercept difference (F_2) was performed (Littel et al. 1991)

Regression series	F_1 (heterogeneity of slope)	F_2 (intercept difference)
$\Delta \times$ Elevation (all species)	3.92 ^{*1}	-
$\Delta \times$ Elevation (<i>Populus</i> only)	3.15 ^{N.S.}	53.02 ^{*4}
N content \times elevation	0.05 ^{N.S.}	20.88 ^{*4}
$\Delta \times$ N content	< 0.001 ^{N.S.}	1.48 ^{N.S.}
SLW \times N content	8.32 ^{*3}	-
$\Delta \times$ SLW	5.86 ^{*1}	-

^{*4} $P < 0.0001$, ^{*3} $P < 0.001$, and ^{*1} $P < 0.05$

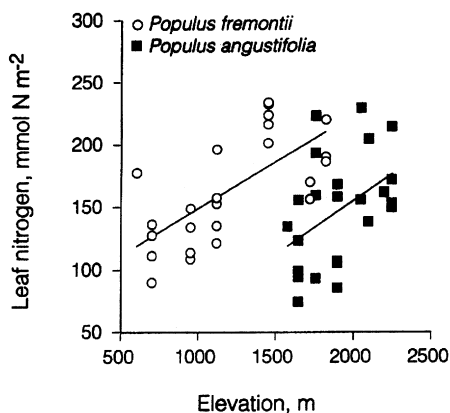


Fig. 4 The relationships between leaf nitrogen content (mmol N m⁻²) and elevation in *P. fremontii* and *P. angustifolia*. See Tables 1 and 2 for regression statistics and tests of heterogeneity of slope and intercept difference

210 mmol N m⁻² at 1820 m ($r^2 = 0.479$, $P < 0.0001$, $n = 23$). Leaf nitrogen contents of *P. angustifolia* in-

creased approximately 50% over 750 m elevation from 107 mmol N m⁻² at 1580 m to 163 mmol N m⁻² at 2250 m ($r^2 = 0.190$, $P < 0.05$, $n = 24$). The rate of change in nitrogen content of leaves over elevation was not different between *P. fremontii* and *P. angustifolia* (slopes = 0.075 and 0.082 mmol m⁻³, respectively, Table 2). However, there was a difference between *P. fremontii* and *P. angustifolia* in the nitrogen content of leaves at any given elevation (intercepts = 73.92 and -9.93 mmol m⁻³, respectively, Table 2).

Leaf carbon isotope discrimination decreased with increasing leaf nitrogen contents (Fig. 5, top panel, Table 1) for both *P. fremontii* ($r^2 = 0.536$, $P < 0.0001$, $n = 24$) and *P. angustifolia* ($r^2 = 0.424$, $P < 0.001$, $n = 23$). The relationship between leaf Δ values and nitrogen content was not different between *P. fremontii* and *P. angustifolia* (slopes = -0.024 and -0.023, respectively, Table 2). Also, there was no difference between the two species in leaf carbon isotope discrimination at a given leaf nitrogen content (intercepts = 24.95 and 24.50‰, respectively, Table 2). Specific leaf weight (SLW) tended to increase with leaf nitrogen content (Fig. 5, bottom panel) for both *P. fremontii* ($r^2 = 0.673$, $P < 0.0001$, $n = 24$) and *P. angustifolia* ($r^2 = 0.644$, $P < 0.001$, $n = 23$). The relationship between SLW and leaf nitrogen contents was significantly different between *P. fremontii* and *P. angustifolia* (slopes = 0.584 and 0.302 g mmol⁻¹, respectively, Table 2), implying a species level difference in leaf thickness for a given leaf nitrogen content.

Leaf carbon isotope discrimination also tended to decrease with increasing specific leaf weight (Fig. 6, Table 1) for both *P. fremontii* ($r^2 = 0.311$, $P < 0.01$, $n = 24$) and *P. angustifolia* ($r^2 = 0.432$, $P < 0.001$, $n = 24$). The relationships between leaf Δ and specific leaf weight was different between *P. fremontii* and *P. angustifolia* (slopes = 0.022 and 0.061‰ g m⁻², respectively, Table 2), suggesting a species level difference in Δ values for a given specific leaf weight.

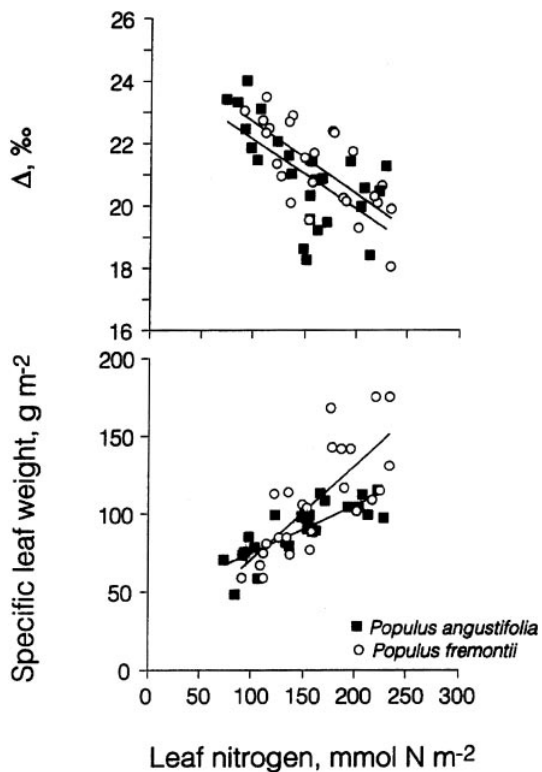


Fig. 5 The relationships between leaf carbon isotope discrimination (Δ , ‰) and specific leaf weight (g m^{-2}) versus leaf nitrogen content (mmol N m^{-2}) in *P. fremontii* and *P. angustifolia*. See Tables 1 and 2 for regression statistics and tests of heterogeneity of slope and intercept difference

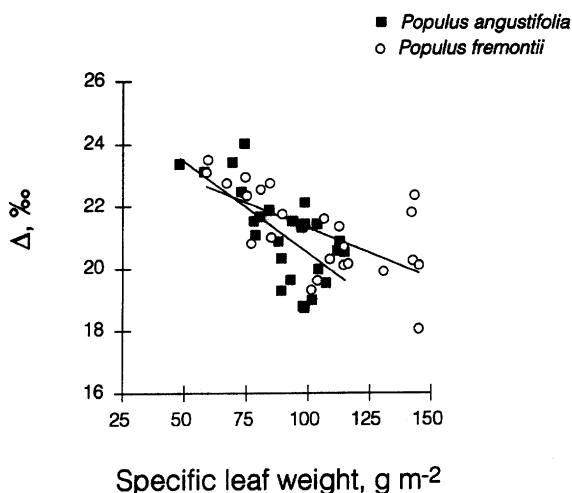


Fig. 6 The relationships between leaf carbon isotope discrimination (Δ , ‰) and specific leaf weight (g m^{-2}) in *P. fremontii* and *P. angustifolia*. See Tables 1 and 2 for regression statistics and tests of heterogeneity of slope and intercept difference

Discussion

Seasonal δ values were highest at lower elevations for all transects, implying high growing-season evaporative differences could constrain plant gas exchange at the lower elevations through reduced stomatal conductances. If leaf-level photosynthetic capacity remained constant along the elevational transect (i.e., a constant leaf nitrogen content), we would expect a decrease in discrimination against ¹³C with increasing elevation associated with reduced stomatal conductances in leaves exposed to low-humidity environments. However, we observed that Δ values showed the opposite trend. All three species (*P. fremontii*, *P. angustifolia*, and *S. exigua*) exhibited their highest Δ values at the lowest elevation. This suggests internal leaf CO₂ concentrations (c_i) are highest at low elevation and that stomatal limitations are having a lesser impact on constraining gas exchange in low humidity environments than at the higher elevation, more humid habitat. Instead it appears that the major factor contributing to the decreased c_i values with increased elevation may be increased photosynthetic capacity (as observed by leaf N values). Decreased leaf carbon isotope discrimination with increasing elevation has been observed elsewhere over elevational ranges (Woodward 1986; Körner et al. 1988, 1991).

Körner et al. (1991) have suggested that changes in the partial pressures of CO₂ and O₂ may be a causative factor over elevation. However, it is unlikely that the decrease in partial pressure of CO₂ over the transect can fully explain the observed trend in Δ values. First, the change in partial pressure of CO₂ over a transect of this size is small. Second, even if the change in partial pressure is significant, photosynthetic rates would tend to decrease and leaf conductances increase with decreasing partial pressure of CO₂ and decreasing evaporative gradients. This would lead to an increase in c_i/c_a with elevation and a subsequent increase in Δ , the opposite of the trend observed. However, it is possible that leaf conductances remained at some constant value, while photosynthetic capacity increased. Such a response would lead to lower c_i/c_a values at higher elevations and decreased leaf carbon isotope discrimination.

Körner and Diemer (1987) and Friend et al. (1989) suggested that at higher elevations plants exhibit unusually high carboxylation capacities in relation to their stomatal conductances. This would decrease c_i/c_a leading to a decrease in Δ over elevation. Our data support this hypothesis. We observed an increase in foliar nitrogen over elevation for both species (Fig. 4). Because the majority of leaf nitrogen is bound in photosynthetic enzymes, this implies that photosynthetic capacity may also be increasing over these transects. Furthermore, the strong correlation between specific leaf weight and foliar nitrogen content (Fig. 5, bottom panel) suggests that as specific leaf mass increases the ratio of nitrogen to carbon concentration remained constant. There is a robust correlation between leaf carbon isotope discrimination

and foliar nitrogen contents (Fig. 5, top panel) implying that high leaf nitrogen contents corresponded to increased photosynthetic capacities and decreased internal leaf CO₂ concentrations.

Vitousek et al. (1990) speculated that decreasing leaf carbon isotope discrimination with elevation may be due to increases in leaf thickness. Increases in leaf thicknesses could increase the diffusional pathway length for CO₂ from the atmosphere to the site of carboxylation and potentially decrease Δ . Similarly, we found significant increases in specific leaf weight (SLW) over elevation (Fig. 6). We observed similar ranges in leaf carbon isotope discrimination (ca. 3‰ per km elevation) with very different changes in specific leaf weight for our species (ca. 85–150 g m⁻² in *Populus* spp.) compared to *Metrosideros polymorpha* (120 to 490 g m⁻², Vitousek et al. 1990). An increased diffusive pathway length for CO₂ cannot be eliminated using our data.

Comstock and Ehleringer (1992) reported significant variation in leaf Δ values in the desert shrub *Hymenoclea salsola* that were correlated with water vapor mole fraction gradient values of the origin habitat, when plants were grown in a common garden. Similar patterns have been observed with other desert shrubs (J. Comstock, unpublished work). While plants in this study were not grown under common environment conditions, the Δ pattern we observed was opposite to that previously observed for *Hymenoclea*. The discrepancy in patterns observed in desert studies and those observed here and in other elevational studies may relate to seasonal constraints on productivity. In desert environments, productivity is usually constrained by water limitations and not season length per se. In contrast, productivity in mesic environments (such as along the elevational gradients in this study) is often constrained by the length of the frost-free period. Thus, while our data are not satisfactory to test the ω versus Δ hypothesis as proposed by Comstock and Ehleringer (1992), they nonetheless extend the elevational patterns first observed by Körner and colleagues to now include riparian environments where soil moisture availability is constant.

Acknowledgements We are grateful to David Williams and R. Alan Black who commented on earlier drafts of this article. This study was supported by a grant from the National Science Foundation and funds from the University of Utah Hughes Undergraduate Initiative.

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