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Influence of stand structure on carbon-13 of vegetation, soils, and canopy air within deciduous and evergreen forests in Utah, United States

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Abstract Carbon isotope ratios ($\delta^{13}C$) were studied in evergreen and deciduous forest ecosystems in semi-arid Utah (*Pinus contorta, Populus tremuloides, Acer negundo* and *Acer grandidentatum*). Measurements were taken in four to five stands of each forest ecosystem differing in overstory leaf area index (LAI) during two consecutive growing seasons. The $\delta^{13}C_{leaf}$ (and carbon isotope discrimination) of understory vegetation in the evergreen stands (LAI 1.5–2.2) did not differ among canopies with increasing LAI, whereas understory in the deciduous stands (LAI 1.5–4.5) exhibited strongly decreasing $\delta^{13}C_{leaf}$ values (increasing carbon isotope discrimination) with increasing LAI. The $\delta^{13}C$ values of needles and leaves at the top of the canopy were relatively constant over the entire LAI range, indicating no change in intrinsic water-use efficiency with overstory LAI. In all canopies, $\delta^{13}C_{leaf}$ decreased with decreasing height above the forest floor, primarily due to physiological changes affecting c_i/c_a (> 60%) and to a minor extent due to $\delta^{13}C$ of canopy air (< 40%). This intra-canopy depletion of $\delta^{13}C_{leaf}$ was lowest in the open stand (1‰) and greatest in the denser stands (4.5‰). Although overstory $\delta^{13}C_{leaf}$ did not change with canopy LAI, $\delta^{13}C$ of soil organic carbon increased with increasing LAI in *Pinus contorta* and *Populus tremuloides* ecosystems. In addition, $\delta^{13}C$ of decomposing organic carbon became increasingly enriched over time (by 1.7–2.9‰) for all deciduous and evergreen dry temperate forests. The $\delta^{13}C_{canopy}$ of CO_2 in canopy air varied temporally and spatially in all forest stands. Vertical canopy gradients of $\delta^{13}C_{canopy}$, and $[CO_2]_{canopy}$ were larger in the deciduous *Populus tremuloides* than in the evergreen *Pinu contorta* stands of similar LAI. In a very wet and cool year, ecosystem discrimination (Δ_e) was similar for both deciduous *Populus tremulodies* (18.0 ± 0.7‰) and evergreen *Pinus contorta* (18.3 ± 0.9‰) stands. Gradients of $\delta^{13}C_{canopy}$ and $[CO_2]_{canopy}$ were larger in denser *Acer* spp. stands than those in the open stand. However, ^{13}C enrichment above and photosynthetic draw-down of $[CO_2]_{canopy}$ below tropospheric baseline values were larger in the open than in the dense stands, due to the presence of a vigorous understory vegetation. Seasonal patterns of the relationship $\delta^{13}C_{canopy}$ versus $1/[CO_2]_{canopy}$ were strongly influenced by precipitation and air temperature during the growing season. Estimates of Δ_e for *Acer* spp. did not show a significant effect of stand structure, and averaged 16.8 ± 0.5‰ in 1933 and 17.4 ± 0.7‰ in 1994. However, Δ_e varied seasonally with small fluctuations for the open stand (2‰), but more pronounced changes for the dense stand (5‰).

Key words CO_2 · $\delta^{13}C$ · Ecosystem discrimination · Soil respiration · Temporal and spatial variation

Introduction

The influence of stand structure on ecophysiological processes in forest ecosystems is critical for our understanding of what controls carbon fluxes in evergreen and deciduous forests (Valentini et al. 1996). Leaf carbon isotope ratios ($\delta^{13}C_{leaf}$) integrate plant ecophysiological processes over time, and often show large differences between deciduous and evergreen plants (for recent reviews see Farquhar et al. 1989; Ehleringer et al. 1993). These leaf-type differences are also manifested as differences in the stand structure of deciduous and evergreen forests, which vary not only depending on the dominant species or tree age, but also in response to resource availability or site management (Gholz 1982; Parker

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1995). Moreover, feedback mechanisms of stand structure on forest vegetation influence the environment a plant is living in, for example by rain interception, light attenuation and resistance to turbulent mixing with the troposphere (Raupach 1989; Baldocchi and Vogel 1996). These abiotic factors themselves have profound effects on the leaf discrimination (Δ_{leaf}) against the heavier ^{13}C isotope, due to changes in the ratio of internal CO_2 concentration in the mesophyll airspaces to the ambient atmospheric concentration of carbon dioxide (c_i/c_a; Farquhar et al. 1982). Few studies have examined the influence of stand leaf area index (LAI) on leaf carbon isotope composition. Gutiérrez and Meinzer (1994) found that carbon isotope discrimination of sun leaves of coffee hedgerows decreased by about 2‰ with increasing LAI and age of the hedgerow as stomatal conductance decreased. However, Harrington et al. (1995) reported increasing Δ_{leaf} of *Acacia koa* with increasing LAI across several sites, but changes in elevation and precipitation may have confounded interpretation of these patterns. Walcroft et al. (1996) observed a negative correlation between stocking density and lower canopy $\delta^{13}C_{\mathrm{leaf}}$ for *Pinus radiata* that was associated with increased leaf shading. However, they provided no data on upper canopy leaves which are likely to contribute more of the overall canopy carbon gain.

Canopy air, the carbon source for photosynthetic fixation, also influences $\delta^{13}C_{\mathrm{leaf}}$ (Vogel 1978; Francey et al. 1985; Schleser and Jayasekara 1985; Sternberg 1989; Broadmeadow et al. 1992; Brooks et al. 1996; Buchmann et al. 1997a). The carbon isotope ratio of canopy air ($\delta^{13}C_{\mathrm{canopy}}$) is the result of turbulent mixing of tropospheric and respired CO_2 as well as carbon isotope discrimination during photosynthesis. Thus, changes in stand leaf area or stand density will indirectly influence $\delta^{13}C_{\mathrm{canopy}}$ and ecosystem discrimination (Δ_e; Buchmann et al. 1997b). For example, Buchmann et al. (1996) found profound differences in carbon dioxide concentrations ($[CO_2]_{\mathrm{canopy}}$) with stand structure (presence or absence of understory vegetation, LAI) as well as between deciduous and evergreen ecosystems. Eddy correlation measurements in deciduous and evergreen ecosystems demonstrated that carbon flux densities were about three times larger over the temperate deciduous than over the boreal evergreen forest (Baldocchi and Vogel 1996). Hence, changes in $\delta^{13}C_{\mathrm{canopy}}$ with stand structure are expected because of strong linear relationships between $\delta^{13}C_{\mathrm{air}}$ and $1/[CO_2]_{\mathrm{air}}$ (Keeling 1958). The intercept of these regressions represents the δ^{13}C of respired CO_2 and can be used to estimate Δ_e. Whether or not the δ^{13}C of respired CO_2 (and therefore Δ_e) changes with stand structure is unknown. However, one might expect stand structure to affect δ^{13}C of foliage and therefore the isotopic signature of litter and soil organic carbon as well.

In this study, we address the questions of how stand structure (e.g., presence or absence of understory vegetation, canopy leaf area and its development) affects the carbon isotope composition of soil organic carbon and foliage as well as carbon isotopic composition of canopy air along vertical canopy profiles. We are further interested how carbon isotope discrimination of forest ecosystems changes temporally and whether Δ_e differs with stand structure or between vegetation types (deciduous and evergreen forests).

Materials and methods

Sites

Mature mountain forest stands of the evergreen *Pinus contorta* Dougl. ex Loudon (lodgepole pine) and the deciduous *Populus tremuloides* Michx. (aspen) were selected in the Uinta Mountains (Broadhead Meadows and Soapstone Basin, respectively), approximately 80 km east of Salt Lake City, Utah, United States (Table 1). Five individual stands for each species were studied during the 1993 growing season, with the overstory leaf area index ranging from 1.5 to 2.2 for *Pinus contorta*, and from 1.5 to 2.9 for *Populus tremuloides*. Mature stands of a riparian community comprised of *Acer negundo* L. (box elder) and *A. grandidentatum* Nutt. (bigtooth maple) were chosen in Red Butte Canyon Research Natural Area (Parley's Fork), east of Salt Lake City, Utah, United States (Ehleringer et al. 1992). Four stands with overstory LAIs ranging from 1.5 to 4.5 were studied during the 1993 growing season; two of these stands (LAI 1.9 and 3.6 after full canopy development) were used in 1994 (for more details see Buchmann et al. 1996). Leaf area index was measured in September 1993 and four times during the 1994 growing season using two plant canopy analyzers (LAI-2000; LiCor, Lincoln, Neb., USA).

Collection of canopy air for isotopic analyses

Canopy air was sampled from different heights within the canopy (0.02, 0.30, 1.00, 3.30, 5.60 and 9.60 m for most of the stands in 1993; 0.02, 0.30, 1.00, 5.90, 9.60 m and 14.0 m in 1994). Different heights were used for one *Populus tremuloides* stand (LAI 1.5) and one *Pinus contorta* stand (LAI 2.2) in 1993 (0.02, 0.30, 3.30, 7.00, 13.20 and 16.50 m). Dry air (dried with magnesium perchlorate) was drawn through tubing (Dekoron 1300, 0.625 cm outer diameter, non-buffering ethylene copolymer coating; Aurora, Ohio, USA), which was attached to portable masts. Using a battery-operated 12-V pump (TD-3LS, Brailsford and Company Inc., Rye, New York, USA), air was drawn for 20 min at a flow rate of 10 ml/s through a pre-evacuated 2-l glass flask (with two high-vacuum stopcocks) before both stopcocks were closed. Up to four flasks were collected at the same time using separate lines. Canopy air was collected during 3- to 7-day periods three to four times during the 1993 growing season, and four times during April to July 1994 (until canopy closure). Continuous CO_2 concentrations ($[CO_2]_{\mathrm{canopy}}$) were measured simultaneously as described in Buchmann et al. (1996). These $[CO_2]$ measurements were averaged over the 20-min collection period, thus providing the corresponding $[CO_2]$ for a

Table 1 Site characteristics (*LAI* leaf area index measured after full overstory canopy development)

	Uinta Mountains		Red Butte Canyon
	Pinus contorta	*Populus tremuloides*	*Acer* spp.
Latitude	40°39′N	40°34′N	40°47′N
Longitude	110°54′E	111°2′E	111°46′E
Elevation	2800m	2400m	1700m
Canopy height	13–15m	9–13m	13–15m
LAI	1.5–2.2	1.5–2.9	2.1–4.5

given flask sample. During the 1993 growing season, 440 flask samples were collected between 0145 and 2210 hours; during the 1994 growing season, 122 flask samples were collected between 0725 and 2150 hours.

Soil respiration rates and soil moisture

Soil respiration rates were measured during the 1994 growing season using a soil respiration chamber (LI 6000-09S; LiCor, Lincoln, Neb., USA) connected to a portable photosynthesis system (LI-6200). Three PVC tubes (25 cm long, 10 cm inside diameter) to which the chamber could be attached, were inserted into the soil, 24 h prior to measurement. The protocol recommended by LiCor (LiCor 6000-09S manual) was changed to five observations of 5 ppm change per measurement (J. Norman, personal communication). CO_2 concentrations within the system were scrubbed with soda lime in an open configuration until the CO_2 level was 50 ppm below ambient. After closing the system, CO_2 was allowed to increase by 20 ppm before measurements were taken. Three to four measurements were taken for each site and sampling time.

Gravimetric soil water content was determined during the 1993 and 1994 growing seasons. Five replicates were taken per measurement, and sampling containers were sealed in the field with Parafilm. The wet soil samples were weighed, then dried until weight constancy, and weighed again. Soil moisture is expressed as per cent dry weight (% dw).

Sampling and isotope analyses

Foliage samples for carbon isotope analyses ($\delta^{13}C_{leaf}$) were collected from three positions in the canopy: upper canopy (> 6 m, 3 dominant trees of different species), lower canopy (3–6 m) and understory (< 3 m, 5 tree saplings and herbaceous plants of different species). During the 1993 growing season, samples were taken in July for *Acer* spp. and in August for *Pinus contorta* (current and 1-year-old needles) and *Populus tremuloides.* In 1994, foliage samples were taken four times between April and July. Old litter and soil samples (0–5 cm, 10–15 cm) were collected at each site in August 1993 and four times during the 1994 growing season (3 replicates per site and depth). Fresh litter was collected during a 1-week period in October 1993. Plant and litter samples were dried for 48 h at 70°C and then ground with mortar and pestle to a fine powder. Soil materials were acid-washed and then sieved (mesh size 1 mm). A 2-mg subsample was combusted and analyzed for $^{13}C/^{12}C$ using an isotope ratio mass spectrometer (delta S, Finnigan MAT, Bremen, Germany).

CO_2 of the flask samples was extracted cryogenically using a three-trap vacuum line (each trap with a double loop) and transferred into a sampling tube within 12 h after flask collection. Due to possible interferences at mass 44, CO_2 was separated from N_2O by combusting the sample with copper oxide wire (1993 data) or by using a gas chromatograph (1994 data; GC-14A; 3-M Poraplot Q column, Shimadzu Corporation, Kyoto, Japan) prior to isotope analysis. The CO_2 gas was introduced manually into the mass spectrometer, and carbon isotope ratios of canopy air ($\delta^{13}C_{canopy}$) were analyzed from the same sample.

The isotope ratio (δX) was calculated as

$$\delta X = (R_{sample}/R_{standard} - 1) \times 1000‰ \tag{1}$$

where R_{sample} and $R_{standard}$ are the $^{13}C/^{12}C$ ratios of the sample and the standard (PDB for carbon), respectively (Farquhar et al. 1989). The overall precision of the carbon isotope measurements was ± 0.11‰ for organic carbon, and 0.03‰ for carbon isotopes in gas samples.

Carbon isotope discrimination of a leaf (Δ_{leaf}) was calculated as

$$\Delta_{leaf} = (\delta^{13}C_{air} - \delta^{13}C_{leaf})/(1 + \delta^{13}C_{leaf}) \tag{2}$$

where $\delta^{13}C$ is expressed in absolute units (e.g., 0.026 instead of 26), not in the per mil notation used in Eq. 1. The $\delta^{13}C_{air}$ was calculated for each height where foliage was collected by applying the linear regression equations ($\delta^{13}C_{canopy}$) as a function of $1/[CO_2]_{canopy}$, see below) to the average $[CO_2]$ between 0800 and 1800 hours.

Modelling of $\delta^{13}C_{canopy}$ and estimates of Δ_e

Carbon isotope ratios of canopy air ($\delta^{13}C_{canopy}$) are the result of turbulent mixing of two major CO_2 sources with different $\delta^{13}C$ (tropospheric and respired CO_2), and of a photosynthetic effect due to discrimination during carbon assimilation (Keeling 1958; Sternberg 1989). Thus, $\delta^{13}C_{canopy}$ are linearly related to the inverse of the corresponding $[CO_2]_{canopy}$.

The intercept of this linear regression is an indicator of the isotopic composition of respired CO_2 and was used to estimate ecosystem discrimination against the heavier ^{13}C during photosynthesis of the entire stand (Δ_e; Buchmann et al. 1997b). Provided no fractionation occurs during respiration, Δ_e can be calculated as

$$\Delta_e = (\delta^{13}C_{trop} - \delta^{13}C_{resp})/(1 + \delta^{13}C_{resp}) \tag{3}$$

where $\delta^{13}C_{trop}$ describes the tropospheric CO_2 and $\delta^{13}C_{resp}$ the respired CO_2. Tropospheric data were collected on a weekly basis during daytime hours at Wendover, Utah (40°03′N 105°38′W; 3749 m above MSL) within the NOAA Cooperative Flask Sampling Network (Conway et al. 1994; Ciais et al. 1995). Monthly mean $[CO_2]_{trop}$ was provided by Thomas Conway (NOAA/CMDL); monthly mean $\delta^{13}C_{trop}$ was provided from Michael Trolier (University of Colorado, INSTAAR). The precision of the NOAA data is < 0.5 ppm for $[CO_2]$, and ± 0.03‰ for $\delta^{13}C$. Natural temporal variability for data, collected at the same station over a 1-month period is < 0.2‰ (M. Trolier, personal communication). Variability between stations at a similar latitude is between 0.5 and 1 ppm and around 0.25‰ (see Conway et al. 1994; Ciais et al. 1995, respectively).

Statistics

The statistical package JMP (Version 3, SAS Institute Inc., Cary, North Carolina, USA) was used for most of the data analyses. Analyses of variance (ANOVA) were done with LAI, season or height as main factors. The Student's *t*-test or Tukey-Kramer honestly significant difference (HSD) test (at the 0.05 level) were used to distinguish among the means of two or more groups, respectively. All linear regressions are stated with $r^2_{adjusted}$. When both x and y variables were associated with an error (such as for $1/[CO_2]$ vs. $\delta^{13}C$), slopes and intercepts were calculated by geometric mean regressions (Sokal and Rohlf 1981). Slopes and intercepts of regressions were tested against each other by introducing indicator variables ("dummy" variables) into a multiple regression model (Neter et al. 1985).

Results

Carbon isotope ratios of foliage

The response of leaf carbon isotope ratios ($\delta^{13}C_{leaf}$) of the dominant understory species to increasing overstory leaf area index (LAI) differed dependent on ecosystem type (Table 2). Understory vegetation in the evergreen Pinus contorta stands showed no effect of increasing overstory LAI on $\delta^{13}C_{leaf}$, whereas understory growing in the deciduous *Populus tremuloides* and *Acer* spp.

Table 2 Leaf carbon isotope ratios (± SE; $n = 3$–5) of understory vegetation (ground cover > 20%) and the dominant tree species in stands with different leaf area index (LAI) in July 1993 (*Acer* spp.) or August 1993 (*Pinus contorta* and *Populus tremuloides*) (*n.a.* not available because plant species was not present. Different *letters* following the means represent significantly different δ^{13}C values within a species, Tukey-Kramer test)

Species	Height (m)	$\delta^{13}C_{leaf}$(‰)				*P*
Pinus contorta		LAI 1.5	LAI 1.7	LAI 2.2		
Grass	0–0.2	−26.9 ± 0.3	−27.4 ± 0.3	−27.8 ± 0.7		0.93
Vaccinium spocarium	0–0.2	−29.3 ± 0.1	−29.2 ± 0.3	−29.0 ± 0.1		0.87
Abies lasiocarpa	0–2	−28.8 ± 0.3	n.a.	−28.5 ± 0.2		0.56
	> 6	n.a.	n.a.	−24.5 ± 0.2		
Picea engelmanii	0–2	−27.1 ± 0.2^{b}	−28.2 ± 0.4^{a}	n.a.		0.0004
	2–3	n.a.	n.a.	−24.4 ± 0.2		
	> 6	n.a.	n.a.	−24.4 ± 0.2		
Pinus contorta	0–2	n.a.	−25.7 ± 0.3	n.a.		
	2–3	−28.6 ± 0.5	−28.3 ± 0.4	n.a.		0.62
	> 6	−27.8 ± 0.3^{a}	−27.7 ± 0.4^{a}	−24.8 ± 0.2^{b}		< 0.0001
Populus tremuloides		LAI 1.5	LAI 2.0	LAI 2.3	LAI 2.9	
Aquilegia spp.	0–1	−27.0 ± 0.2^{c}	−27.2 ± 0.1^{bc}	−27.8 ± 0.3^{b}	−29.3 ± 0.3^{a}	< 0.0001
Rosa nutkana	0–1	−27.5 ± 0.2^{b}	−27.8 ± 0.2^{ab}	−28.4 ± 0.2^{a}	n.a.	0.014
Grass	0–1	−27.1 ± 0.6^{b}	n.a.	n.a.	−31.7 ± 0.2^{a}	< 0.0001
P. tremuloides	1–3	−27.7 ± 0.3^{a}	−26.6 ± 0.2^{b}	n.a.	−27.3 ± 03^{a}	0.025
	3–6	−27.1 ± 0.3	−25.8 ± 0.1	−26.0 ± 0.2	n.a.	0.061
	> 6	−26.2 ± 0.2^{a}	−25.1 ± 0.2^{b}	−25.0 ± 0.2^{b}	−26.0 ± 0.1^{a}	< 0.0001
Acer spp.		LAI 2.1	LAI 3.9	LAI 4.2	LAI 4.5	
Smilacina stellata	0–1	−25.1 ± 0.4^{b}	−29.4 ± 0.1^{a}	−30.1 ± 0.3^{a}	−29.1 ± 0.4^{a}	< 0.0001
Solidago canadensis	0–1	−28.4 ± 0.6	n.a.	n.a.	n.a.	
A. grandidentatum	3–6	n.a.	−28.5 ± 0.3	−29.8 ± 0.4	−30.1 ± 0.5	0.19
	> 6	n.a.	−26.5 ± 2.4	−26.0 ± 0.3	−25.6 ± 0.6	0.86
A. negundo	> 6	−28.7 ± 0.1	−27.6 ± 0.1	−26.6 ± 2.3	−26.5 ± 0.7	0.13

stands exhibited strongly decreasing $\delta^{13}C_{leaf}$ with increasing canopy LAI.

Sun leaves at the top of the canopy did not follow the same patterns as seen for understory leaves. Although $\delta^{13}C_{leaf}$ of needles in the main canopy of *Pinus contorta* (> 6 m) did not differ among the open stands (LAI 1.5 and 1.7), they were significantly lower than those in the denser stand (LAI 2.2), growing at a nearby but slightly drier site. However, leaves throughout the deciduous canopies of *Populus tremuloides* (1–6 m) and *Acer* spp. (> 3 m) did not show a clear trend with increasing LAI and remained relatively constant within the entire range of canopy LAI (1.5–4.5).

Independent of ecosystem type or LAI, $\delta^{13}C_{leaf}$ decreased with decreasing height above the forest floor ($r^2 = 0.17$, $P < 0.0001$, $F = 46.6$). This depletion was lowest in the open stands (1‰) and greatest in the denser stands (4.5‰). Changes in $\delta^{13}C_{leaf}$ along a vertical canopy profile are the result of two factors: changes in leaf gas exchange as it affects c_i/c_a and thus carbon isotope discrimination (Δ_{leaf}), and changes in the δ^{13}C of source air (see Eq. 2). In general, source air changes were limited and affected $\delta^{13}C_{leaf}$ less than ecophysiological responses. In deciduous stands, the effect of source air was larger in the denser than in the open canopies. Source air accounted for 26% of the gradient observed in $\delta^{13}C_{leaf}$ in the two *Populus tremuloides* stands with LAIs around 2, and 19% in the densest stand (LAI 2.9). While 5–14% of the $\delta^{13}C_{leaf}$ gradient observed in the two open *Pinus contorta* stands resulted from δ^{13}C of canopy air, around 39% was contributed by source air effects in the denser *Acer* spp. stands. Eliminating the source air factor by calculating Δ_{leaf}, we found average Δ_{leaf} to be generally higher in foliage just above the forest floor than in leaves high in the canopy (differences between 0.3‰ and 4‰). However, Δ_{leaf} in the two open *Pinus contorta* stands stayed relatively constant throughout the entire canopy.

Carbon isotope ratios of canopy air

During the course of the day, $\delta^{13}C_{canopy}$ did not remain constant (Fig. 1). The $\delta^{13}C_{canopy}$ values were very low early in the morning before increasing to tropospheric baseline values at midday (Wendover station for comparison). Between 0900 and 1600 hours, $\delta^{13}C_{canopy}$ at all heights in the open *Populus tremuloides* stand (except 0.02 m, immediately above the forest floor) were near to the average daytime baseline δ^{13}C measured at Wendover (−7.8‰). Maximum differences were 0.26‰, well within the natural variability of the baseline values. The $\delta^{13}C_{canopy}$ of CO_2 at 0.02 m never became more enriched than −8.5‰. Late in the afternoon (after 1600 hours), $\delta^{13}C_{canopy}$ of all heights decreased again, with the decrease being steeper for the lower heights compared to the top heights.

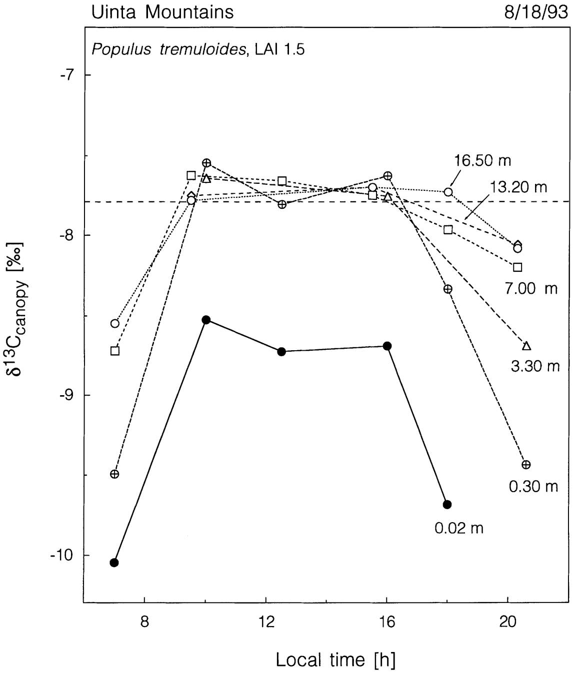

Fig. 1 Diurnal course of $\delta^{13}C_{canopy}$ at different heights within a *Populus tremuloides* canopy. The *dashed line* represents the average daytime tropospheric $\delta^{13}C$ value measured in Wendover during August 1993 (provided by M. Troiler, University of Colorado, INSTAAR)

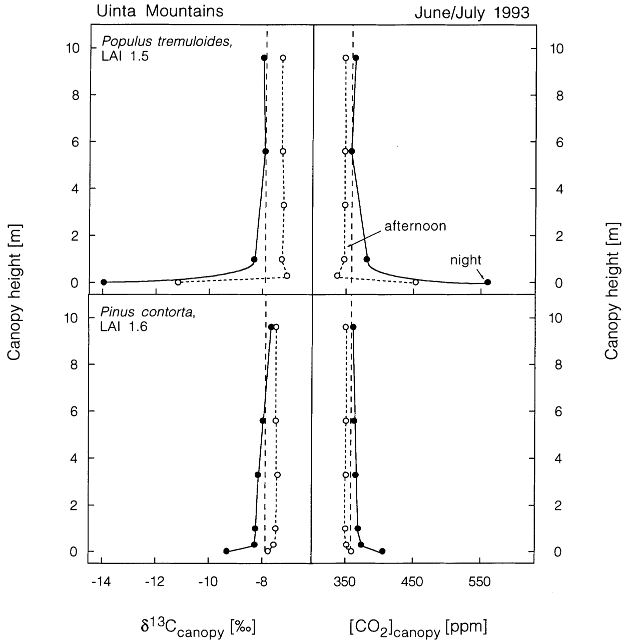

Fig. 2 Height profiles of $\delta^{13}C_{canopy}$ and $[CO_2]_{canopy}$ within two mountain sites, deciduous *Populus tremuloides* and coniferous *Pinus contorta* stands of similar leaf area index (LAI). Night and afternoon values are given. The *dashed line* represents the average daytime tropospheric $\delta^{13}C$ value measured in Wendover during June/July 1993 (provided by M. Trolier, University of Colorado, INSTAAR)

Influence of vegetation type on $\delta^{13}C_{canopy}$

Vertical height profiles of $\delta^{13}C_{canopy}$ and $[CO_2]_{canopy}$ showed profound differences between deciduous and evergreen stands with a similar LAI (1.5 and 1.6; Fig. 2). While the deciduous *Populus tremuloides* stand exhibited large canopy gradients even during the afternoon (afternoon: 3.6‰, 100 ppm; night: 6‰, 200 ppm), vertical gradients within the evergreen *P. contorta* canopy were much smaller (afternoon: 0.3‰, 10 ppm; night: 1.6‰, 21 ppm). Both vegetation types exhibited a significant draw-down in $[CO_2]$ within the main canopy during photosynthetic periods of more than 10 ppm below average baseline concentration (358 ± 0.5 ppm; for errors see Methods). As a result, $\delta^{13}C_{canopy}$ in both canopies were about 0.5‰ more enriched than that of the troposphere (−7.9 ± 0.25‰), with the difference to the average baseline values being slightly larger in the deciduous forest. Using all flask data for these two stands in linear regression analyses ($\delta^{13}C_{canopy}$ as a function of $1/[CO_2]_{canopy}$) revealed that both slopes and intercepts were similar ($r^2 = 0.98$, $P > 0.9$, $F < 0.002$). Thus, the photosynthetic effect on canopy CO_2 and the carbon isotope ratio of respired CO_2 were similar for these two stands.

We found little seasonal variability of the relationships $\delta^{13}C_{canopy}$ versus $1/[CO_2]_{canopy}$ within the *Populus tremuloides* and *Pinus contorta* canopies during the 1993 growing season (Table 3). Thus, combining all sampling times resulted in an intercept of −24.83 ± 0.38‰ for all *Populus tremuloides* stands ($r^2 = 0.93$, $P < 0.0001$, $F = 1787$), and in −26.25 ± 0.57‰ for all *Pinus contorta* stands ($r^2 = 0.90$, $P < 0.0001$, $F = 911$), indicating very similar $\delta^{13}C$ of respired CO_2. Using the intercepts of the regressions given in Table 3 to estimate ecosystem discrimination (Δ_e, see Eq. 3) resulted in quite similar Δ_e of 18.0 ± 0.65‰ ($n = 8$) for *Populus tremuloides* and in Δ_e of 18.3 ± 0.93‰ ($n = 6$) for *Pinus contorta* in this very wet and cool year of 1993. Compared to the long-term average precipitation, rainfall during spring 1993 (March–May) was 15% higher, and rainfall during summer 1993 (June–August) was 80% higher than average (Utah Climate Center). Springtime air temperatures were similar to the long-term average, but about 3.5°C lower during summertime.

Influence of overstory LAI on $\delta^{13}C_{canopy}$

Comparing $\delta^{13}C_{canopy}$ and $[CO_2]_{canopy}$ of two *Acer* spp. stands with different LAIs (2.1 and 4.5) showed subtle differences between these stands (Fig. 3). Although the shape of the vertical profiles was very similar, canopy gradients were always greater in the dense stand (morning: 3.1‰, 94 ppm; afternoon: 2‰, 58 ppm; night: 2.8‰, 84 ppm) than those in the open stand (morning: 2.1‰, 48 ppm; afternoon: 0.3‰, 7 ppm; night; 1.9‰, 50 ppm). However, the enrichment above and the photosynthetic draw-down of $[CO_2]_{canopy}$ below average Wendover baseline values (−7.8 ± 0.25‰, 356 ± 0.5

Table 3 Linear regressions between $\delta^{13}C_{canopy}$ and $1/[CO_2]_{canopy}$ for *Pinus contorta* and *Populus tremuloides* stands with different leaf area index (LAI) throughout the 1993 growing season. Equations are given with 1 SE in *parentheses*. P was < 0.0001 for all equations. Different *letters* following the equations represent significantly different regressions within a LAI (F-test at the 0.05 level)

LAI	Time^{+}	Regression	r^2	n	F
Pinus contorta					
1.5	July	$y = 5409\ (\pm\ 302) \times x - 23.24\ (\pm\ 0.81)$	0.97	12	311
1.6	July	$y = 7998\ (\pm\ 498) \times x - 29.94\ (\pm\ 1.39)^{a}$	0.93	21	239
	August	$y = 6117\ (\pm\ 261) \times x - 24.82\ (\pm\ 0.71)^{b}$	0.97	18	534
1.7	July	$y = 6052\ (\pm\ 386) \times x - 24.66\ (\pm\ 1.04)$	0.92	21	227
2.2	August	$y = 7374\ (\pm\ 549) \times x - 28.48\ (\pm\ 1.49)^{a}$	0.90	20	163
	September	$y = 5212\ (\pm\ 502) \times x - 22.43\ (\pm\ 1.43)^{a}$	0.95	7	103
Populus tremuloides					
1.5	May	$y = 8170\ (\pm\ 1157) \times x - 30.29\ (\pm\ 3.13)^{a}$	0.80	12	40
	June	$y = 6025\ (\pm\ 194) \times x - 24.49\ (\pm\ 0.52)^{a}$	0.98	18	949
	August	$y = 5717\ (\pm\ 350) \times x - 23.75\ (\pm\ 0.95)^{a}$	0.94	17	252
	September	$y = 6248\ (\pm\ 284) \times x - 25.06\ (\pm\ 0.78)^{a}$	0.97	16	469
2.0	August	$y = 5104\ (\pm\ 402) \times x - 21.96\ (\pm\ 1.08)$	0.91	16	147
2.3	August	$y = 4559\ (\pm\ 465) \times x - 20.46\ (\pm\ 1.26)$	0.92	18	183
2.9	May	$y = 8264\ (\pm\ 1459) \times x - 30.86\ (\pm\ 4.0)^{a}$	0.63	14	20
	June	$y = 6653\ (\pm\ 575) \times x - 26.23\ (\pm\ 1.53)^{a}$	0.90	16	120

$^{+}$ *Pinus contorta*: 6–14 July; 3–19 August; 8–9 September; *Populus tremuloides*: 24–28 May; 23 June–1 July; 23–26 August; 8–9 September

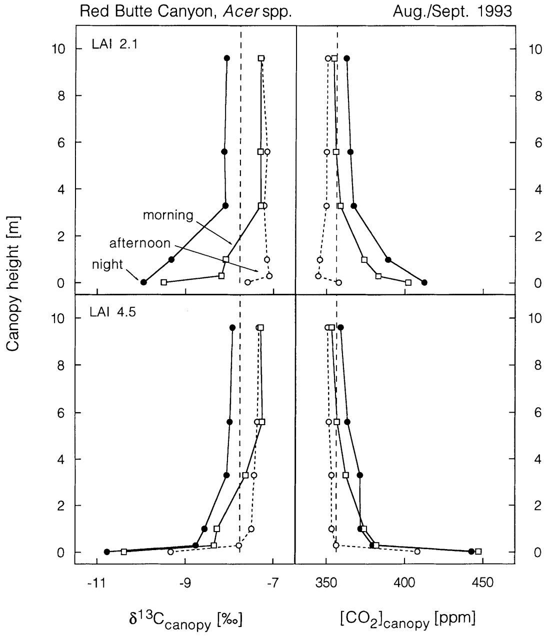

Fig. 3 Height profiles of $\delta^{13}C_{canopy}$ and $[CO_2]_{canopy}$ within two *Acer* spp. stands of differing LAI. Three different times during the day are given. The *dashed line* represents the average daytime tropospheric $\delta^{13}C$ value measured in Wendover during Aug./Sept. 1993 (provided by M. Trolier, University of Colorado, INSTAAR)

ppm) were larger in the open stand (approx. 0.6‰ and 10 ppm), especially in the lower part of the canopy (< 4 m). As pointed out in Buchmann et al. (1996), this might be due to the presence of a very vigorously growing understory vegetation with biomass 9 times larger in the open than in the dense stand (700 g m^{-2} vs. 78 g m^{-2}).

Seasonal variability of $\delta^{13}C_{canopy}$

This very synchronous pattern of $\delta^{13}C_{canopy}$ and $[CO_2]_{canopy}$ was reflected in high r^2 of the linear regressions (1993 growing season: $r^2 > 0.94$; Table 4). Furthermore, seasonal variations were different between *Acer* spp. stands differing in overstory LAI. For the open stand (LAI 2.1), slopes and intercepts of the June and August/September relationships were lower than those in July ($r^2 = 0.98$, $P < 0.001$, $F > 7$). This means that $\delta^{13}C$ of respired CO_2 was more depleted, and ecosystem discrimination was higher in the beginning (June) and the end of summer (August/September) than those during mid summer (July), reflecting the interaction of phenology and gas exchange of this open stand. Seasonal patterns were more pronounced in the dense stand (LAI 4.5), where steadily increasing intercepts during the summertime represented changing $\delta^{13}C$ of respired CO_2 and indicated a decreasing Δ_e between mid to late summer (1993 growing season: $r^2 = 0.98$, $P < 0.001$, $F > 6$). However, following canopy development of the two *Acer* spp. stands in the pattern was different (Table 5). The slopes and intercepts of the regressions in these two stands did not differ significantly. What was different in 1994 compared to the previous year? Neither year was "average", and 1994 was the fourth driest summer on record according to the Utah Climate Center (precipitation during June and August was 60% below long-term average). Spring temperatures were 0.5°C higher, but summer temperatures were on average 2°C higher than normal, and as a result, the 1994 summer was the warmest on record. Combined with the below average rainfall, these above average temperatures strongly increased water stress for plants in 1994, thus shortening the growing season and accelerating leaf se-

Table 4 Linear regressions between $\delta^{13}C_{canopy}$ and $1/[CO_2]_{canopy}$ for three riparian *Acer* spp. stands with different leaf area index (LAI) throughout the 1993 growing season. Equations are given with 1 SE in *parentheses*. P was < 0.0001 for all equations. Different *letters* following the equations represent significantly different regressions within a LAI (*top panel*) or across all combinations (*lower panel*; F-test at the 0.05 level)

LAI	Time$^+$	Regression	r^2	n	F
2.1	June	$y = 6102 (\pm 245) \times x - 25.06 (\pm 0.64)^a$	0.98	12	610
	July	$y = 5741 (\pm 133) \times x - 23.76 (\pm 0.35)^b$	0.99	22	1832
	Aug./Sept.	$y = 6441 (\pm 347) \times x - 25.61 (\pm 0.96)^a$	0.96	16	331
3.9	Aug./Sept.	$y = 5433 (\pm 324) \times x - 22.83 (\pm 0.89)$	0.94	17	275
4.5	June	$y = 6555 (\pm 368) \times x - 25.59 (\pm 0.90)^a$	0.98	8	312
	July	$y = 5461 (\pm 195) \times x - 23.17 (\pm 0.52)^b$	0.98	14	771
	Aug./Sept.	$y = 5529 (\pm 270) \times x - 23.27 (\pm 0.73)^c$	0.96	18	391
2.1, 4.5	June	$y = 6088 (\pm 210) \times x - 24.80 (\pm 0.76)^a$	0.95	20	395
2.1, 4.5	July	$y = 5669 (\pm 116) \times x - 23.63 (\pm 0.31)^b$	0.99	36	2325
2.1	Aug./Sept.	$y = 6441 (\pm 347) \times x - 25.61 (\pm 0.96)^a$	0.96	16	331
3.9, 4.5	Aug./Sept.	$y = 5394 (\pm 215) \times x - 22.80 (\pm 0.59)^c$	0.95	35	593

$^+$ 2–14 June; 19–27 July; 30 August 3 September

Table 5 Linear regressions between $\delta^{13}C_{canopy}$ and $1/[CO_2]_{canopy}$ for two riparian *Acer* spp. stands with different leaf area index (LAI) throughout the 1994 growing season. Equations are given with 1 SE in *parentheses*. P was < 0.0001 for all equations. Different *letters* following the equations represent significantly different regressions within a stand (F-test at the 0.05 level)

LAI	Time$^+$	Regression	r^2	n	F
Open stand					
0.8	April	$y = 6250 (\pm 526) \times x - 24.94 (\pm 1.34)^a$	0.89	16	127
1.9	June	$y = 6458 (\pm 513) \times x - 25.35 (\pm 1.33)^a$	0.85	25	135
1.9	July	$y = 6032 (\pm 376) \times x - 24.96 (\pm 1.00)^a$	0.94	17	242
	A, J, J	$y = 6516 (\pm 315) \times x - 25.77 (\pm 0.82)$	0.85	58	335
Dense stand					
1.4	April	$y = 5534 (\pm 435) \times x - 22.99 (\pm 1.15)^a$	0.93	13	151
1.7	May	$y = 5507 (\pm 654) \times x - 23.33 (\pm 1.67)^a$	0.86	11	62
3.2	June	$y = 6762 (\pm 321) \times x - 26.29 (\pm 0.81)^a$	0.95	22	424
3.6	July	$y = 7135 (\pm 434) \times x - 27.65 (\pm 1.18)^a$	0.94	18	252
	A, M, J, J	$y = 6230 (\pm 210) \times x - 25.01 (\pm 0.55)$	0.93	64	901
Overall		$y = 6333 (\pm 196) \times x - 25.28 (\pm 0.52)$	0.88	122	923

$^+$ 14–21 April; 4–5 May; 1–2 June; 30 June–1 July

nescence. Therefore, any potential seasonal differences were effectively reduced, and one regression equation now described both stands adequately (Table 5: overall).

Seasonal variability of Δ_e

We used data for 1993 and 1994 to evaluate the temporal patterns in net ecosystem discrimination (Δ_e) for the two *Acer* spp. stands (Fig. 4). Δ_e is dependent on two parameters (see Eq. 3), the $\delta^{13}C$ of tropospheric ($\delta^{13}C_{trop}$) and respired CO_2 ($\delta^{13}C_{resp}$). While seasonal changes in average $\delta^{13}C_{trop}$ values for the Wendover station were relatively small (0.24‰ between April and October 1993; 0.21‰ between April and October 1994), changes in $\delta^{13}C_{resp}$ could be considerable (Tables 3–5). Hence, Δ_e varied seasonally, although this difference was not always statistically significant. Fluctuations were smaller for the open stand (2‰) than for the dense stand (5‰). Average Δ_e for the *Acer* spp. stands was 16.8 ± 0.5‰ ($n = 7$) in 1993 and 17.4 ± 0.7‰ ($n = 7$) in 1994.

Influence of stand structure on soil respiration and soil $\delta^{13}C$

Soil respiration rates, measured in June 1994, did not differ between the two montane sites (*Populus tremuloides* and *Pinus contorta*; Table 6), and were close to the

Table 6 Soil respiration rates (μmol m^{-2} s^{-1}; means ± SE; $n = 3$–4) during the 1994 growing season. Different *letters* following the means represent significantly different soil respiration rates within a month (Tukey-Kramer test at the 0.05-level). Leaf area index (LAI) is given for full canopy development

	Uinta Mountains		Red Butte Canyon	
	Pinus contorta	*Populus tremuloides*	*Acer spp.*	
	LAI 1.6	LAI 2.3	LAI 1.9	LAI 3.6
April	n.d.	n.d.	4.3 ± 0.1^a	3.7 ± 0.1^b
May	n.d.	n.d.	7.3 ± 0.1^a	3.8 ± 0.1^b
June	3.5 ± 0.2^b	3.3 ± 0.2^b	6.9 ± 0.3^a	3.1 ± 0.1^b
July	n.d.	n.d.	4.4 ± 0.4	n.d.

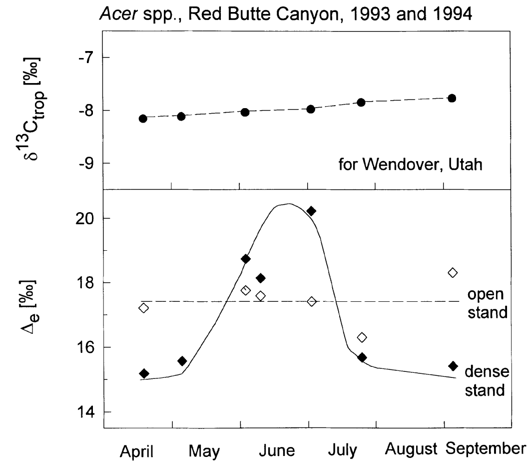

Fig. 4 Seasonal course of the carbon isotope ratio of the troposphere ($\delta^{13}C_{trop}$) and estimates of ecosystem discrimination (Δ_e) for two *Acer* spp. stands of different LAI. $\delta^{13}C_{trop}$ are given as monthly averages for the station in Wendover (data provided by M. Trolier, University of Colorado, INSTAAR)

rates measured in the dense riparian *Acer* spp. stand. However, soil CO_2 efflux in the open *Acer* spp. stand was significantly higher. As described in Buchmann et al. (1996), soil temperature was more important in explaining the variance of soil respiration rates (53% of total variance) than soil moisture (an additional 7%) during 1994, an exceptionally dry year.

In order to test the influence of stand structure on $\delta^{13}C_{SOC}$, we also included sites with an overstory LAI of 0 in this analysis. These were sites with only very sparse understory vegetation, but no trees or shrubs in the overstory, located near the other stands. Stands in the riparian habitat were not included in this analysis because the disturbance regime with frequent spring floods tends to redistribute litter, thus homogenizing the surface litter layer. $\delta^{13}C_{SOC}$ increased by about 1‰ with increasing LAI in both *Populus tremuloides* and *Pinus contorta* ecosystems (Fig. 5). At the same time, soil moisture in 5 cm depth also increased with increasing LAI, i.e., denser stands had more water in the top soil horizon than open stands. A similar pattern of increasing soil moisture with increasing LAI (in the little layer and 5 cm solid depth) was observed during the 1994 growing season in the *Acer* spp. stands (not shown). However, during this very hot and dry year, soil moisture in deeper soil depths (30 and 50 cm) stayed constant at very low values (6% dw) during canopy LAI development.

Following the $\delta^{13}C$ of foliage during leaf senescence, litterfall, litter decay and soil organic matter formation revealed a very distinct course of ^{13}C enrichment independent of vegetation type (Fig. 6). The increase of $\delta^{13}C$ from green foliage to soil organic carbon in 15 cm depth was about 2.4‰ for *Pinus contorta* needles, about 1.7‰ for *Populus tremuloides*, and about 2.9‰ for *Acer* spp. leaves. This pattern was found independent of vegetation type or overstory LAI in all forest stands.

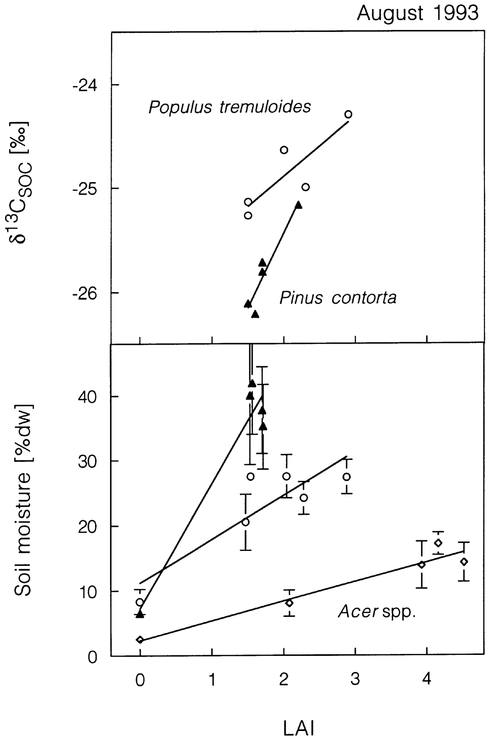

Fig. 5 Relationship of LAI and $\delta^{13}C_{SOC}$ (*top panel*) and soil moisture (*bottom panel*) for an evergreen ecosystem (*Pinus contorta*) and a deciduous ecosystem (*Populus tremuloides*). Soil samples were taken at 5 cm soil depth

Discussion

Vertical profiles of leaf $\delta^{13}C$ in deciduous canopies showed the typical pattern of increasing $\delta^{13}C_{leaf}$ and decreasing Δ_{leaf} with increasing height above the forest floor (Vogel 1978; Schleser and Jayasekera 1985; Ehleringer et al. 1987; Medina et al. 1991). In agreement with other studies analyzing both $\delta^{13}C_{leaf}$ and $\delta^{13}C_{canopy}$, the changes in $\delta^{13}C_{leaf}$ are due primarily to changes in c_i/c_a and to a much lesser extent to changes in source air (Brooks et al. 1996; Buchmann et al. 1997a). The contribution of source air to the vertical gradient of $\delta^{13}C_{leaf}$ increased with increasing LAI. While source air contributed 5–14% to the vertical gradient of $\delta^{13}C_{leaf}$ in the *Pinus conorta* stands (LAI 1.5–2.2), its contribution ranged between 20 and 30% in the *Acer* spp. stands (LAI $\approx$ 4). However, the main factor influencing changes in $\delta^{13}C_{leaf}$ with height was factors contributing to changes in c_i/c_a. In the densest stands, c_i/c_a decreased with increasing height above the forest floor from 0.81 to 0.64 in the *Populus tremuloides* canopy, from 0.73 to 0.64 in the *Populus tremuloides* canopy, from 0.73 to 0.64 in the *Acer* spp. and from 0.70 to 0.58 in the *Pinus contorta* canopy. Decreasing c_i/c_a with increasing canopy height might have been the result of photosynthetic rates that increased faster than stomatal conductance rates with increasing height, as observed in boreal forests (Brooks et al. 1996).

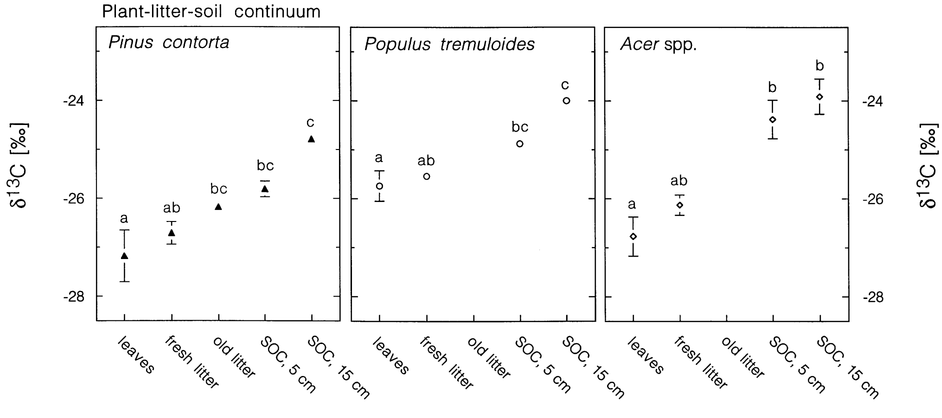

Fig. 6 Carbon isotope ratios of foliage, litter and soil organic carbon (SOC) during fall 1993. Means and standard errors are given ($n = 3$–5). Different *letters* above the means represent significantly different $\delta^{13}C$ within an ecosystem (Tukey-Kramer test)

The increase in Δ_{leaf} of understory vegetation with height above the ground was more pronounced in dense than in open *Populus tremuloides* and *Acer* spp. canopies (Table 2). The difference in Δ_{leaf} between understory and upper canopy leaves in *Populus tremuloides* stands increased from 0.3‰ (LAI 1.5) to 4‰ (LAI 2.9) and in *Acer* spp. stands from −3‰ (LAI 2.1) to 1.9‰ (LAI 4.5). This implies that c_i/c_a of foliage in a dense stand increased more with decreasing height than the c_i/c_a of foliage in open stands, where light conditions were more favorable in the understory. A similar trend was observed by Gutiérrez and Meinzer (1994) where Δ_{leaf} of coffee leaves in the lower canopy increased from −0.3‰ to 2.3‰ as light and assimilation rates decreased when coffee hedgerows grew older and denser (LAI 0.7 – −7.5). Δ_{leaf} in *Pinus radiata* seedlots increased by about 1.5‰ with increasing stocking density (100–600 stems ha^{-1}; Walcroft et al. 1996) and was also attributed to changing light conditions. However, the canopy LAI effect in our study was only evident in the understory, but not in the upper canopy, implying that environmental conditions such as light, relative humidity, and water supply for sun leaves at the top of the canopy were similar among these stands.

In contrast to our results, Gutiérrez and Meinzer (1994) found that increasing intrinsic water-use efficiency of upper canopy sun leaves with increasing age and LAI of managed coffee hedgerows (LAI 0.7–7.5) was due to a decreased stomatal conductance (and therefore reduced Δ_{leaf}). Although the hedgerows were irrigated, water supply might not have been adequate to support the high transpirational demand of higher leaf area canopies, thus resulting in more water-conservative strategies of plants at high LAI. Our study indicated no change in intrinsic water-use efficiency among the deciduous stands, perhaps because the LAI range was still fairly small (1.5–4.5) or because the water supply during 1993 was sufficient for all stands independent of LAI. Not only was the year 1993 unusually wet and cool, but *Acer* spp. trees are also capable of using deep (and reliable) groundwater rather than surface water (Dawson and Ehleringer 1991; Phillips and Ehleringer 1995).

Leaf longevity of the dominant tree species and stand structure had profound effects on both [CO$_2$] and $\delta^{13}C$ of canopy air. We used monthly averaged NOAA data from the Wendover station (daytime only) as tropospheric baseline in our study and therefore uncertainties in the tropospheric estimates may arise because of changing air masses. However, natural spatial variability in free tropospheric data is generally smaller than 0.25‰ or 1 ppm (see Methods). Tans et al. (1996) showed that while nighttime variations in [CO$_2$] could be large in the convective boundary layer (between 51 m and 496 m), daytime differences were less than 5 ppm. At higher altitudes (up to 2 km), fluctuations in [CO$_2$] are even smaller (approx. 1 ppm; Tans et al. 1996). In our study, both vegetation types depleted $[CO_2]_{canopy}$ by more than 10 ppm below Wendover baseline values during canopy photosynthesis, thus enriching $\delta^{13}C_{canopy}$ during the day. The observed enrichment of ^{13}C in the main canopy (1–6 m) was larger in deciduous *Populus tremuloides* (0.66‰) than in evergreen *Pinus contorta* stands (0.43‰), well above the 5 ppm and 0.25‰ natural variability. At a given LAI, canopy gradients of $[CO_2]_{canopy}$ and $\delta^{13}C_{canopy}$ were smaller within evergreen canopies than those in deciduous canopies (Fig. 2), although soil respiration rates were similar (Table 6), clearly demonstrating the life form effect on canopy gradients. Life form effects were also shown for carbon flux densities over forest canopies, where fluxes over the temperate broad-leaved forest were three times larger than those above the boreal evergreen forest (Baldocchi and Vogel 1996).

Stand structure affected development of canopy air profiles as seen in more uniform $\delta^{13}C_{canopy}$ and $[CO_2]_{canopy}$ profiles, and smaller gradients in the more open stands (Figs. 2–4). This was most likely due to both a greater turbulent mixing in the open canopies (as in the examples of *Populus tremuloides* and *Pinus contorta*) and to the presence of a vigorous understory vegetation (*Acer* spp.) that overcompensated the effect of higher soil respiration rates in the open stand (Table 6). Among overall climatic conditions such as precipitation and air temperatures (compare Tables 4 and 5), overstory LAI also influenced the extent of seasonal variability of both $\delta^{13}C_{canopy}$ and [CO$_2$] (Table 4). Consequently, the seasonal pattern of Δ_e was more pronounced in dense than in open multi-layered deciduous canopies (Fig. 4).

A number of studies have provided data that can be used to estimate Δ_e (Keeling 1961; Quay et al. 1989; Sternberg et al. 1989; Lancaster 1990; Broadmeadow et al. 1992; Flanagan et al. 1996; Lloyd et al. 1996; Buchmann et al. 1997a). Most of the studies focus on tropical forests. Only one study provided seasonal information (Flanagan et al. 1996; boreal forests). Using tropospheric data from Francey et al. (1995), we calculated Δ_e from the Lancaster (1990) flask data. These Δ_e estimates averaged 17.5‰ for pine stands in California and Montana, and 18.6‰ for deciduous mixed stands of oak, maple and ash in California, Pennsylvania and Vermont, similar to our Δ_e estimates (18.3‰ for pine; between 17.1‰ and 18.0‰ for deciduous forests). However, neither in Lancaster's dataset nor in our study did Δ_e estimates differ between deciduous and evergreen stands growing in the same region under similar climatic conditions. Moreover, Δ_e estimates did not change with overstory LAI, and the seasonal course of Δ_e estimates of our *Acer* spp. stands was very weak (Fig. 4). One might have expected Δ_e to decrease significantly with increasing LAI because the $\delta^{13}C$ values of litter and soil organic carbon increased (Figs. 5 and 6). However, this isotopic shift of about 1‰ was not large enough to be picked up in our Δ_e estimates. Differences of < 1‰ are well within the expected variability of the factors used to calculate Δ_e (Buchmann et al. 1997b).

In conclusion, evergreen versus deciduous differences in leaf longevity appear to have less influence on $\delta^{13}C_{canopy}$ than we had originally expected. Instead, stand structure exhibited large effects on the carbon isotopic composition within terrestrial forest ecosystems. Since soil $\delta^{13}C$ values were influenced by canopy LAI, Δ_e estimates were influenced by both LAI and stand structure. These results suggest the possibility that LAI may be more important than forest type in describing carbon isotope exchange between forests and atmosphere in the Intermountain West of North America.

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