Carbon dioxide concentrations within forest canopies — variation with time, stand structure, and vegetation type

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Abstract

Vertical CO_2 profiles (between 0.02 and 14.0 m) were studied in forest canopies of *Pinus contorta*, *Populus tremuloides*, and in a riparian forest with *Acer negundo* and *Acer grandidentatum* during two consecutive growing seasons. Profiles, measured continuously during 1- to 13-day periods in four to five stands differing in overstorey canopy area index (CAI < 4.5; including leaves, branches and stems), were well stratified, with highest [CO_2] just above the forest floor. Canopy [CO_2] profiles were influenced by stand structure (CAI, presence of understorey vegetation), and were highly dependent on vegetation type (deciduous and evergreen). A doubling of CAI in *Acer* spp. and *P. tremuloides* stands did not show an effect on upper canopy [CO_2], when turbulent mixing was high. However, increasing understorey biomass in *Acer* spp. stands had a profound effect on lower canopy [CO_2]. In open stands with a vigorous understorey layer, higher soil respiration rates were offset by increased understorey gas exchange, resulting in [CO_2] below those of the convective boundary layer (CBL). Midday depletions up to 20 ppmv below CBL values could be frequently observed in deciduous canopies. In evergreen canopies, [CO_2] stayed generally above the CBL background values, [CO_2] profiles were more uniform, and gradients were smaller than in deciduous stands with similar CAI. Seasonal changes of canopy [CO_2] reflected changes in soil respiration rates as well as plant phenology and gas exchange of both dominant tree and understorey vegetation. Seasonal patterns were less pronounced in evergreen than in deciduous forests.

Keywords: canopy, CO_2, deciduous, evergreen, soil respiration, stand structure, temporal and spatial variation

Received 22 November 1995; revision received 26 March 1996; accepted 10 May 1996

Introduction

Since the development of modern industrial society, global atmospheric carbon dioxide concentrations ([CO_2]) have been steadily increasing as a result of fossil fuel combustion, land use changes and biomass burning (Mook *et al.* 1983; Komhyr *et al.* 1989). This 'inadvertent global experiment' (Ramanthan 1988) revived the interest and the demand for information about internal carbon fluxes within ecosystems and trace gas exchange between the terrestrial biosphere and the atmosphere. Studies about current spatial and temporal variations of [CO_2] in forest canopies provide critical information about how well a forest is coupled to the convective boundary layer (CBL) above the canopy, and therefore how susceptible this ecosystem is to increased atmospheric [CO_2]. Knowing how canopy [CO_2] varies with time, stand structure or vegetation type under current climate conditions will facilitate predictions about the stratification of carbon sinks and sources within different forest ecosystems under climate change.

Since the early sixties, [CO_2] within crop and forest canopies have attracted the attention of plant ecophysiologists. Increased efforts and improved measurement techniques (e.g. eddy-correlation) within the last 25 years, allowed combined measurements of micro-meteorological parameters and atmospheric [CO_2]. Extensive data sets were acquired for a wide variety of ecosystems, including temperate forests (Sparling & Alt 1966; Baumgartner 1969; Eliáš, *et al.* 1989; Bazzaz & Williams

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1991; Wofsy *et al.* 1993; Hollinger *et al.* 1994; Flanagan & Varney 1995). However, none of these studies compared canopy [CO_2] of deciduous and evergreen forests growing in a similar climatic regime, although information about both vegetation types is critical for modelling vegetation responses to climate change on a regional scale. Although stand structure will affect stand functioning by feedback mechanisms such as rain interception, light attenuation and resistance to turbulent mixing with the troposphere, no study known to the authors addresses the question of how [CO_2] profiles change with stand structure characteristics such as foliar biomass distribution, leaf area development or understorey vegetation. Only very limited information is available about seasonal variations of canopy [CO_2] in temperate forests, mainly from a hardwood forest in Massachusetts, USA. Bazzaz & Williams (1991) measured canopy [CO_2] in a mixed oak-maple stand in Harvard Forest, and found a marked seasonal pattern between March and November. In the same forest, Wofsy *et al.* (1993) measured net ecosystem exchange of carbon over two growing seasons, using eddy-correlation techniques. They estimated that temperate forests might be a large carbon sink, provided that the rate of carbon accumulation found in Harvard Forest were representative.

In this study, we address the questions of how attributes of stand structure such as overstorey canopy area index (including leaves, branches and stems; CAI) and the presence of understorey vegetation influences canopy [CO_2] profiles, and how these influences vary during the growing season. Furthermore, we ask if [CO_2] profiles in stands with similar CAI differ between different vegetation types such as deciduous and evergreen.

Material 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), ≈ 80 km east of Salt Lake City, Utah, USA (Table 1). Five individual stands for each species, ranging in overstorey canopy area index (CAI) from 1.5–2.2 for *P. contorta*, and from 1.5–2.9 for *P. tremuloides*, were studied during the 1993 growing season. The understorey vegetation of the *P. contorta* stands was mainly composed of *Vaccinium spocarium* Leiberg (dominant species), and *Trifolium nanum* Torr. Saplings of *Abies lasiocarpa* (Hook.) Nutt., *Picea engelmanii* Parry ex Engelm., and *P. contorta* formed a canopy layer in 1–3 m height. Understorey species in the *P. tremuloides* forest included herbs such as *Actea rubra* (Ait.) Willd.,

Table 1 Site characteristics.

	Uinta Mountains		Red Butte Canyon *Acer* spp.
	Pinus contorta	*Populus tremuloides*	
Latitude	40°39'N	40°34'N	40°47'N
Longitude	110°54'E	111°2'E	111°46'E
Elevation	2800 m	2400 m	1700 m
avg. air temperature[1] [°C]			
April	n.d.	n.d.	7.0 ± 0.22[2]
May	n.d.	10.8 ± 0.23	16.7 ± 0.22[2]
June	n.d.	13.2 ± 0.21	17.9 ± 0.38[2]
July	14.6 ± 0.30	n.d.	19.7 ± 0.12
Sept.	12.8 ± 0.41	17.1 ± 0.63	20.0 ± 0.45
Oct.	n.d.	n.d.	18.3 ± 0.53
Average soil temperature[2] [°C]			
April	n.d.	n.d.	7.3 ± 0.12
May	n.d.	n.d.	12.6 ± 0.10
June	n.d.	n.d.	13.6 ± 0.12
July	n.d.	n.d.	16.7 ± 0.13
Canopy height	13–15 m	9–13 m	13–15 m

n.d., not determined; [1] in 1993 (except *Acer* spp., April – June). Measured in 10.3 m (1993) or 14.0 m (1994) height above the ground; [2] in 1994. Measured in 0.05 m depth.

Aquilegia spp., *Galium boreale* L., *Smilacina stellata* (L.) DC., and shrubs such as *Ribes montigenum* McClathie and *Rosa nutkana* Presl. Single individuals of *Alnus incana* (L.). Moench, and sparse regeneration of *P. contorta*, and *P. tremuloides* were also present (nomenclature after Welsh *et al.* 1987).

Mature stands of a riparian community comprised of *Acer negundo* L. (boxelder) and *Acer grandidentatum* Nutt. (bigtooth maple) were chosen in Red Butte Canyon Research Natural Area (Parley's Fork), east of Salt Lake City, Utah, USA (Table 1; Ehleringer *et al.* 1992). Four stands with CAI ranging from 1.5 to 4.5 were studied during the 1993 growing season; two of these stands (CAI 1.9 and 3.6 after full canopy development) were used in 1994 (Table 1). The understorey layer was formed by annual and perennial plants such as *Smilacina stellata* (L.) DC. (the dominant species in dense stands), *Solidago canadensis* L. (the dominant species in the open stand), *Smilacina racemosa* (L.) Desf., and *Geranium richardsonii* Fisch. & Trautv. Regeneration of *A. grandidentatum*, *A. negundo*, *Cornus sericea* var. *sericea* L. were interspersed, and formed a canopy layer in 2–3 m height (nomenclature after Welsh *et al.* 1987).

Leaf area index and biomass measurements

Overstorey canopy area index (projected area of leaves, branches and stems per unit ground area, CAI) was measured in September 1993, prior to leaf senescence

Table 2 Above-ground biomass of the understorey vegetation [g m^{-2}, without tree saplings] in forest stands with different canopy area index (including stems, branches and leaves; CAI). Means and standard errors ($N = 5$) are given. Different letters following the means represent significantly different biomass within one forest type (Tukey-Kramer test, 0.05-level)

P. contorta		P. tremuloides		A. negundo/A. grandidentatum			
8/1993		8/1993		8/1993		6/1994	
CAI	biomass	CAI	biomass	CAI	biomass	CAI	biomass
1.5	45 ± 12[a]	1.5	235 ± 32[ab]	2.1	700 ± 46[a]	1.9	552 ± 133[a]
1.6	32 ± 12[a]	1.5	182 ± 32[ab]	3.9	97 ± 46[b]		
1.7	69 ± 14[a]	2.0	293 ± 32[a]	4.2	95 ± 41[b]		
1.7	34 ± 12[a]	2.3	120 ± 29[b]	4.5	78 ± 53[b]	3.6	110 ± 17[b]
2.2	58 ± 16[a]	2.9	270 ± 32[ab]				

and litterfall. Measurements were taken four times during the 1994 growing season with two plant canopy analysers (LAI-2000; LiCor, Lincoln, Nebraska, USA). Two sensors were used simultaneously to record above and below readings. Fifteen to 20 readings were taken for each replicate CAI measurement. Sampson & Allen (1995) showed that this technique tends to overestimate the leaf area index (LAI) in relatively open pine stands compared to allometric estimates due to the effects of stems and branches (LAI < 2.2), while this technique underestimated the LAI in denser pine stands due to foliage self-shading (2.2 < LAI < 4.2). We measured CAI of 0.8 and 1.2 before leaves emerged in the open and dense riparian stands, respectively, suggesting a branch and stem area index of 0.8 or 1.2. The term CAI describes the overstorey leaf, branch and stem area index, but does not include understorey leaf area (Parker 1995). It is further used to characterize stand openness to turbulent mixing with the convective boundary layer when comparing stands of the same vegetation type.

Understorey biomass was determined by harvesting five 0.25 m × 0.25 m squares. Tree regeneration was sparse and therefore not included. Plant material was dried for 48 h at 70 °C and weighed. Biomass varied greatly among the three forest types (Table 2), with highest above-ground biomass in the riparian stands, lowest in the pine and intermediate in the aspen stands. No significant differences in understorey biomass were found among the five pine stands ($F = 1.39$, $P = 0.2788$). Due to the open nature and therefore variable light conditions in the aspen forest, no clear trend with CAI was observed in these stands ($F = 5.23$, $P = 0.0069$). Understorey biomass in the open riparian stand was five to seven times higher than that in stands with higher overstorey CAI ($F = 43.48$, $P < 0.001$).

Soil analyses

Gravimetric soil water content was determined with five replicates per measurement during the 1993 and 1994

growing seasons. 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 percentage dry weight (%dw).

Soil respiration rates were measured in 1994 using a closed gas-exchange system that consisted of a soil-surface enclosure chamber (LI-6000–09S; LiCor, Lincoln, Nebraska, 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 without leaks to the atmosphere, were inserted into the soil at each site, 24 h prior to measurement. The protocol recommended by LiCor (1993) was changed; instead we used 5 observations per measurement with a 5 ppmv increase in CO$_2$ concentration between each observation (J. Norman, personal communication). CO$_2$ concentrations were decreased by passage over soda lime in an open configuration until [CO$_2$] level were 50 ppmv below ambient. After closing the system, [CO$_2$] was allowed to rise 20 ppmv by respiration before a stedy rate of increase was achieved and measurements were taken. Three to four measurements were taken per site and sampling time.

Continuous CO$_2$ and temperature measurements

Canopy air was sampled from different heights within the canopy (0.02, 0.30, 1.00, 3.30, 5.60 & 9.60 m in 1993; 0.02, 0.30, 1.00, 5.90, 9.60 & 14.0 m in 1994). Air was dried over magnesium perchlorate, and was then drawn through tubing (Dekoron 1300, 0.625 cm outer diameter, non-buffering ethylene copolymer coating; Aurora, Ohio, USA) which was attached to portable masts, at a flow rate of 10 mL s^{-1} using a battery-operated 12 V pump (Spectrex, Redwood City, CA, USA). A relay driver switched between 2 manifolds with 4 solenoids each (A6Rec-12; Campbell Scientific, Logan, Utah, USA) to sample air from 6 heights and two standards (one CO$_2$-free air source and a calibrated CO$_2$ source). The CO$_2$

standards were calibrated in the lab against a primary, certified CO_2 standard (Matheson Gas Products, USA; 357 ppmv). A datalogger (21X or CR10; Campbell Scientific, Logan, Utah, USA) controlled the opening and closing of these solenoids, and allowed measurements of the air from each height for 90 s. A run of the entire profile with six heights was completed within 10 min. The CO_2 concentrations were measured each second with an infrared CO_2 gas analyser (LI-6262; LiCor, Lincoln, Nebraska, USA). The last 15 of the 90 readings of each height were averaged and stored. Every three hours, both calibration gases were measured. Air and soil temperatures were measured in 1.00 and 9.60 m (14.0 m) height, and 0.05 m soil depth by using copper-constantan thermocouples. Thermocouples for air temperature were shielded against direct sunlight, but installation allowed free air movement. Canopy CO_2 was measured continuously during 1- to 13-day periods simultaneously in all stands per forest type three to five times during the 1993 growing season. Measurements were taken four times between April and July 1994 in two *Acer* spp. stands until canopy closure.

Exact $[CO_2]$ of the convective boundary layer (CBL) are not known for the area of our study sites. However, within the NOAA Cooperative Flask Sampling Network (data provided by Thomas Conway and Michael Trolier, NOAA/CMDL), two locations were potentially suitable for comparisons, Wendover, Utah (40°44'N 114°02'W; 1398 m above MSL), and Niwot Ridge, Colorado (40°03'N 105°38'W; 3749 m above MSL). Although Wendover is a remote desert site, its weather patterns and elevation correspond better with our study sites than Niwot Ridge, a site at upper montane elevation. Therefore, the station at Wendover was used for comparison in this study.

Statistics

In general, continuous $[CO_2]$ data are presented as the 10-min records. Data in Figs 1–3 were smoothed with moving-averages (intervals of seven data points) by using Microsoft Excel Version 4.0. 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 performed with multiple main factors such as date, site, height, etc., or with a nested design, e.g. height within date. If the interaction terms were not significant ($P > 0.05$), data were pooled and one-way ANOVA calculated. The Student's *t*-test or Tukey–Kramer HSD (honestly significant difference) test (at the 0.05 level) were used to distinguish among the means of two or more groups, respectively. Regression models were analysed also with Microsoft Excel Version 4.0. All linear regressions are stated with $r^2_{adjusted}$.
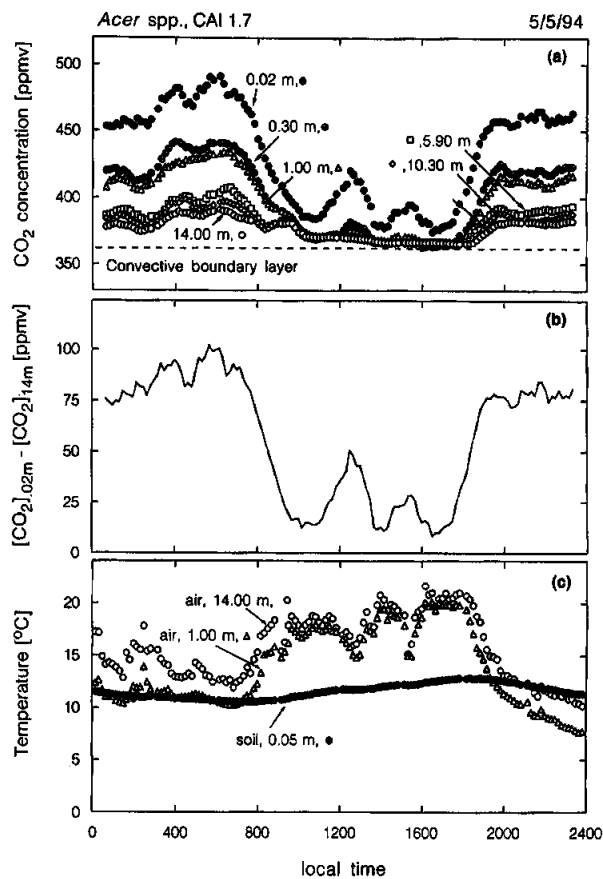

Fig. 1 Daily pattern of CO_2 concentrations (a) within a riparian *Acer* spp. canopy, canopy CO_2 gradient (b) as well as soil and air temperatures (c) (CAI 1.7 in May 1994). The canopy gradient was calculated as the difference between upper canopy (14 m) and soil surface (0.02 m) concentrations. All CO_2 concentrations (recorded each 10 min) are smoothed by moving-averages. The CO_2 concentration of the CBL was provided by T. Conway, NOAA/CMDL.

Results

Daily variability of canopy CO_2 concentrations

Canopy $[CO_2]$ followed a distinct daily course (Fig. 1), with high $[CO_2]$ during times with low turbulent mixing but large respiratory fluxes, and low concentrations during times with high turbulent mixing and net photosynthesis. $[CO_2]$ throughout the *Acer* spp. canopy were well stratified ($F > 226$, $P < 0.001$), and increased with decreasing height above the forest floor. $[CO_2]$ at any position in the canopy was generally higher early in the morning (e.g. 04.00 hours) than late at night (e.g. 24.00 hours). This 'lagtime effect' resulted from a continuous buildup of respiratory CO_2 throughout the night when turbulent mixing with the CBL is low. During this representative spring day, $[CO_2]$ within the *Acer* spp. canopy remained usually near CBL background values,

except for sudden CO_2 bursts. While soil temperature stayed almost constant, air temperatures dropped, and $[CO_2]$ just above the forest floor (0.02 m) showed large increases. At the same time, the CO_2 bursts were seen in the understorey layer (0.30 and 1.00 m), but with smaller amplitude. $[CO_2]$ gradients between the forest floor and the top of the canopy ranged between 75 and 100 ppmv at night, compared to 10–50 ppmv during the day. Both ranges represented spring conditions when canopy leaf area development had not been completed.

How do abiotic factors influence these daily fluctuations in canopy $[CO_2]$? Daily patterns of soil respiration were strongly influenced by soil temperature (ranging from 16 to 22 °C) that explained about one third of the variance in soil respiration rates ($r^2 = 0.34$, $P = 0.04$). Rates measured four times during a day in mid July (between 11.00 hours and 17.00 hours) ranged between 3.6 µmol m⁻² s⁻¹ and 5.0 µmol m⁻² s⁻¹. The influence of another major factor influencing canopy $[CO_2]$ in forest ecosystems, turbulent mixing, became evident when we observed typical daily courses of $[CO_2]$ in the *Acer* spp. canopy before leaf emergence (CAI 1.2), early in the growing season (mid-April 1994; Fig. 2). Despite the lack of tree foliage and understorey vegetation, we found a 5 ppmv canopy gradient during the day, but an average 23 ppmv gradient at night. During most of the day, canopy $[CO_2]$ stayed very close to the CBL background level. We also measured $[CO_2]$ profiles in a more open *Acer* spp. stand (CAI 0.8; data not shown), and only found a 0.4 ppmv $[CO_2]$ gradient during the day, but a similar mean nocturnal gradient of 23 ppmv. Furthermore, air temperatures, a driving variable for turbulent mixing, were highly negatively correlated with canopy $[CO_2]$ ($r < -0.78$; Fig. 1). Thus, even very early in the growing season, canopy $[CO_2]$ profiles differ among stands with different CAI.

Seasonal variability

Absolute values and amplitude of canopy $[CO_2]$ profiles, measured in the same *Acer* spp. stand over two years, varied substantially within a growing season (Table 3; $70.63 < F < 628.23$, $P < 0.001$). Mean daytime $[CO_2]$ at the top of the *Acer* spp. canopy (9.60 or 14.0 m height) were close to CBL background $[CO_2]$, and followed a very similar seasonal pattern. Daytime $[CO_2]$ in the upper canopy (6.00–14.0 m) were highest before bud break (April), and decreased during the early growing season. During June and July, $[CO_2]$ in the upper and lower canopy (3.30–14.0 m) dropped below those of the CBL, depleting canopy air by 1–2 ppmv in June, and by 4–11 ppmv in July. Lowest canopy $[CO_2]$ were reached in July, before they increased again in fall. However, daytime $[CO_2]$ immediately above the forest floor (0.02 m) showed
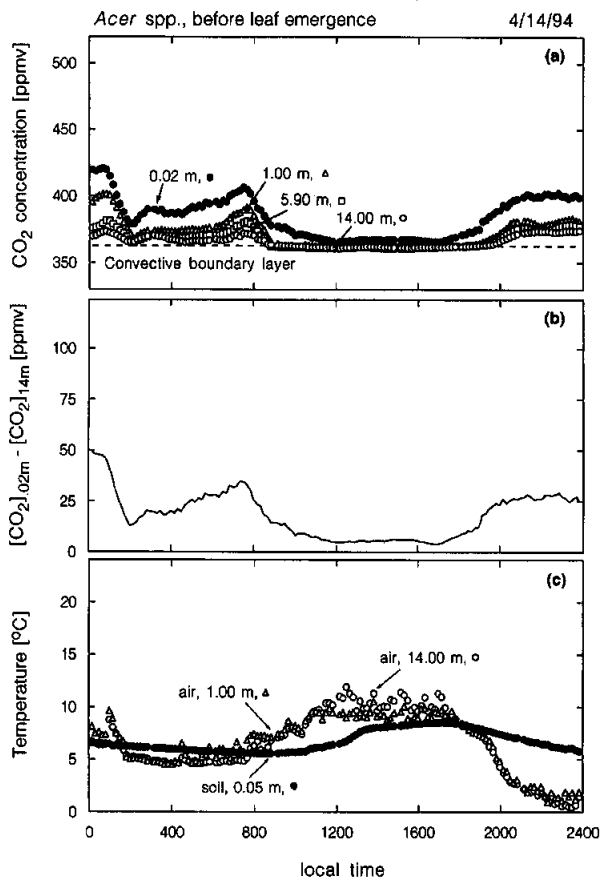

Fig. 2 CO_2 concentrations (a) within a riparian *Acer* spp. canopy, canopy CO_2 gradient (b) as well as soil and air temperatures (c) before leaf emergence (CAI 1.2 in April 1994). The canopy gradient was calculated as the difference between upper canopy (14 m) and soil surface (0.02 m) concentrations. All CO_2 concentrations (recorded each 10 min) are smoothed by moving-averages. The CO_2 concentration of the CBL was provided by T. Conway, NOAA/CMDL.

a very different pattern, more similar to the one found at night. The typical night-time pattern in deciduous stands showed increasing $[CO_2]$ between April and June, and then decreasing values until October. Thus, canopy $[CO_2]$ gradients (between 0.02 m and 14.0 m) also exhibited strong seasonality. Daytime gradients started out low in April (6 ± 0.6 ppmv), increased until June (104 ± 10 ppmv), then decreased again until October (between 36 and 83 ppmv). These seasonal variations in canopy $[CO_2]$ profiles were also seen in the second deciduous forest, a montane *P. tremuloides* forest, but with a smaller amplitude in canopy $[CO_2]$ (data not shown).

Canopy $[CO_2]$ exhibited very similar seasonal patterns within open and dense riparian *Acer* spp. canopies (Fig. 3). Night-time canopy $[CO_2]$ were always higher in the open stand than in the dense stand, at any given canopy CAI ($36.13 < F < 414.56$, $P < 0.0001$), reflecting higher
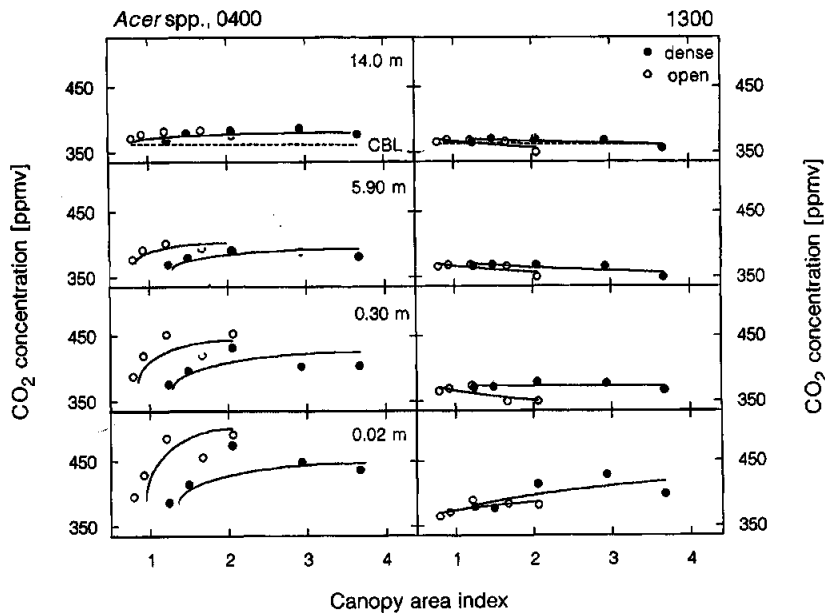
Fig. 3 CO_2 concentrations at selected canopy heights as a function of CAI development of two riparian *Acer* spp. stands during the growing season in 1994. Mean concentrations from two selected times are presented (04.00 hours in the morning and 13.00 hours midday, ± 30 min). If standard error bars are absent, bars are smaller than symbol size. CO_2 concentrations of the CBL were provided by T. Conway, NOAA/CMDL.

Table 3 Fluctuation of vertical CO_2 profiles (at midday and night) in a dense riparian *Acer* spp. stand during the growing season. CAI increased from 1.4 at the beginning of the season to around 4 at canopy closure. CO_2 concentrations at 04.00 and 13.00 hours (± 30 min.) were averaged for 1- to 13-days periods during two consecutive growing seasons (1993: mid-June, July – Oct, 1994: April – beg. June, beg. July). CO_2 concentrations of the convective boundary layer (CBL; Wendover, UT) were provided by T. Conway, NOAA/CMDL

	April N = 28	May N = 21	beg. June N = 53	mid-June N = 25	beg. July N = 8	July N = 40	Sept. N = 18	Oct. N = 7
CBL	362.5	361.9	360.4	360.4	360.4	359.1	356.4	358.3
Daytime								
14.0 m	368.4 ± 0.9	368.1 ± 0.4	363.9 ± 0.9		357.8 ± 0.9			
10.0 m	368.5 ± 0.9	366.8 ± 1.2	356.8 ± 0.8	356.9 ± 0.9	356.9 ± 0.3	346.9 ± 0.9	356.8 ± 0.9	358.8 ± 0.3
6.00 m	368.2 ± 0.9	368.2 ± 1.0	361.4 ± 1.1	358.2 ± 1.0	359.5 ± 0.5	352.0 ± 1.3	358.0 ± 1.3	359.7 ± 0.7
3.30 m				365.2 ± 2.1		350.6 ± 1.3	358.4 ± 1.3	361.9 ± 1.1
1.00 m	368.8 ± 0.9	369.4 ± 1.2	360.2 ± 1.0	360.7 ± 1.4	358.2 ± 0.6	352.8 ± 1.8	360.9 ± 1.8	364.2 ± 1.5
0.30 m	370.3 ± 0.9	370.3 ± 1.6	364.4 ± 1.4	366.4 ± 1.8	365.6 ± 1.1	363.6 ± 2.6	368.9 ± 2.6	372.1 ± 1.6
0.02 m	374.3 ± 0.8	387.5 ± 6.4	431.8 ± 4.3	460.2 ± 9.6	411.2 ± 9.1	411.2 ± 9.1	440.0 ± 9.1	397.5 ± 3.0
Night-time								
14.0 m	373.4 ± 0.8	384.8 ± 1.5	386.4 ± 1.4		375.5 ± 0.4			
10.0 m	374.1 ± 0.7	389.8 ± 2.9	378.7 ± 2.0	385.3 ± 2.0	375.1 ± 0.7	373.5 ± 2.2	373.2 ± 1.0	371.0 ± 2.1
6.00 m	375.7 ± 0.9	392.4 ± 2.8	386.8 ± 2.4	384.1 ± 1.8	382.4 ± 1.5	377.7 ± 2.0	376.0 ± 0.8	374.6 ± 2.4
3.30 m				392.7 ± 1.4		382.3 ± 2.9	377.8 ± 0.9	379.0 ± 2.0
1.00 m	384.1 ± 1.5	414.2 ± 3.8	386.7 ± 2.6	393.6 ± 2.8	393.3 ± 1.4	393.4 ± 3.4	381.0 ± 0.8	387.0 ± 2.3
0.30 m	387.2 ± 1.8	425.2 ± 4.6	395.9 ± 2.7	401.4 ± 3.4	399.8 ± 2.0	393.7 ± 3.0	390.7 ± 1.1	398.8 ± 1.8
0.02 m	400.5 ± 2.5	456.0 ± 7.3	459.1 ± 4.7	478.0 ± 8.6	448.4 ± 7.5	448.4 ± 7.5	455.8 ± 3.0	408.6 ± 3.6

soil respiration rates (6.88 ± 0.30 µmol m^{-2} s^{-1} vs. 3.09 ± 0.13 µmol m^{-2} s^{-1}) and higher understorey biomass (Table 2) of the open stand. However, despite the steady decrease in daytime canopy [CO_2], concentrations in the upper canopy (5.90 m and 14.0 m) were similar for both stands when corresponding sampling times were compared. [CO_2] at 0.30 m and 0.02 m were lower in the open stand than in the dense stand (148.52 < F < 190.69, P < 0.0001), although soil respiration rates and understorey biomass were higher in the open stand.
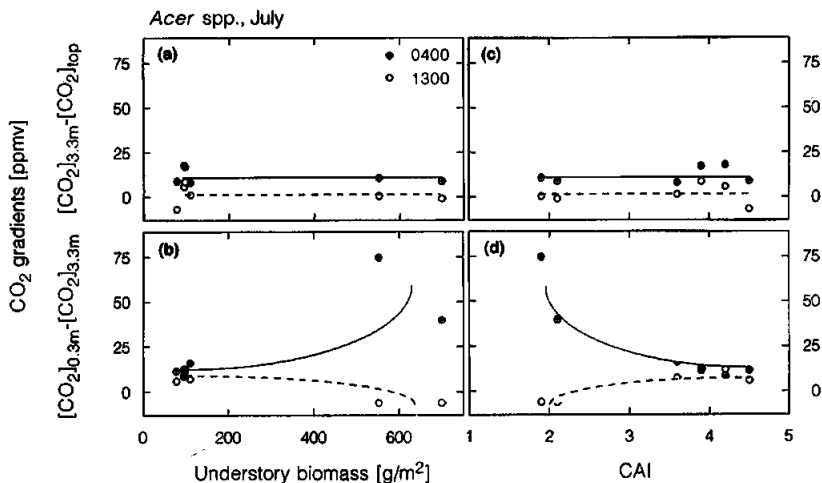
Acer spp., July

Fig. 4 Relationship between understorey biomass or CAI and CO$_2$ gradients within upper canopy (a & c; between 3.3 m and 14.0 or 9.6 m) and lower canopy (b & d; between 0.30 m and 3.3 m) at two selected times (04.00 hours in the morning and at 13.00 hours midday). Gradients were calculated by subtraction, using July measurements of both growing seasons. Lines are fitted by eye.

Seasonal changes in soil respiration rates, which varied between 2.9 ± 0.2 and 9.1 ± 0.4 μmol m^{-2} s^{-1} in these *Acer* spp. stands, were highly dependent on soil temperature and soil moisture. Soil temperature was the driving factor, and explained 53% of the total variance ($y = 0.30 + 0.37$ °C, $P = 0.010$, $n = 11$). Adding soil moisture as a second variable, increased the overall r^2 to 0.60 ($y = -7.28 + 0.72$ °C $+ 0.17$ %dw, $P = 0.017$, $N = 11$). As a result, soil respiration rates in the riparian *Acer* spp. stands did not increase steadily with time because soil moisture dropped to very low values in mid-summer (17 %dw in the top 10 cm). Instead, soil CO$_2$ efflux decreased in July. This was reflected in decreased night-time [CO$_2$] at 0.02 m in July compared to the values in mid-June and September (Table 3). Immediately above the forest floor, the influence of soil respiration on daytime [CO$_2$] did not show a clear trend due to the counteracting effect of understorey gas exchange.

Variation associated with stand structure

Understorey vegetation. The stratification of canopy [CO$_2$] profiles of six *Acer* spp. stands during the mid-growing season (July 1993 & 1994) was used to examine the influence of understorey vegetation on canopy [CO$_2$] (Fig. 4). Because changes in [CO$_2$] occurred predominantly in the lower canopy and not within the upper canopy, [CO$_2$] profiles were divided into lower canopy (0.30–3.30 m) and upper canopy (3.30–9.60 or 14.0 m). Regardless of understorey biomass or changes in overstorey CAI, [CO$_2$] gradients within the upper canopy were unaffected and stayed very stable over the entire range, both during night and day (Fig. 4 a, c). However, in the lower canopy daytime [CO$_2$] gradients were positive in

the stands with lowest understorey biomass, but were negative in the stand with highest biomass (Fig. 4b, d), indicating the large draw-down of [CO$_2$] associated with understorey photosynthesis. Consistent with this result, night-time gradients increased with increasing understorey biomass, probably due to higher plant respiration. Furthermore, daytime [CO$_2$] depletions within the lower canopy could last for 7–9 h, and were more pronounced for the open *Acer* spp. stands (26 ppmv) than for the dense stands (17 ppmv). This confirmed results shown in Fig. 3, indicating that understorey photosynthesis was able to offset the effects of increased soil respiration on elevating [CO$_2$], resulting in low [CO$_2$] at 0.02 m in a open *Acer* spp. stand with vigorous understorey vegetation.

Overstorey canopy area. In order to test the influence of CAI on canopy [CO$_2$] profiles without changes in the understorey vegetation, we compared three *P. tremuloides* stands (CAI from 1.5 to 2.9) at the same day in August (Fig. 5). No differences were found for day- and night-time [CO$_2$] in the upper canopy (9.60 m), independent of overstorey CAI. Although night-time [CO$_2$] in the lower canopy (3.30 m) were higher in the densest stand (CAI 2.9), daytime [CO$_2$] were again almost identical for all three stands, and dropped about 7 ppmv below the CBL background concentration. A doubling of CAI in these *P. tremuloides* canopies did not have a strong effect on canopy [CO$_2$] when turbulent mixing was high, confirming results from the *Acer* spp. stands growing in a very different habitat.

Variation due to vegetation type

Canopy [CO$_2$] profiles in stands of similar CAI showed characteristic features for the dominant tree life form
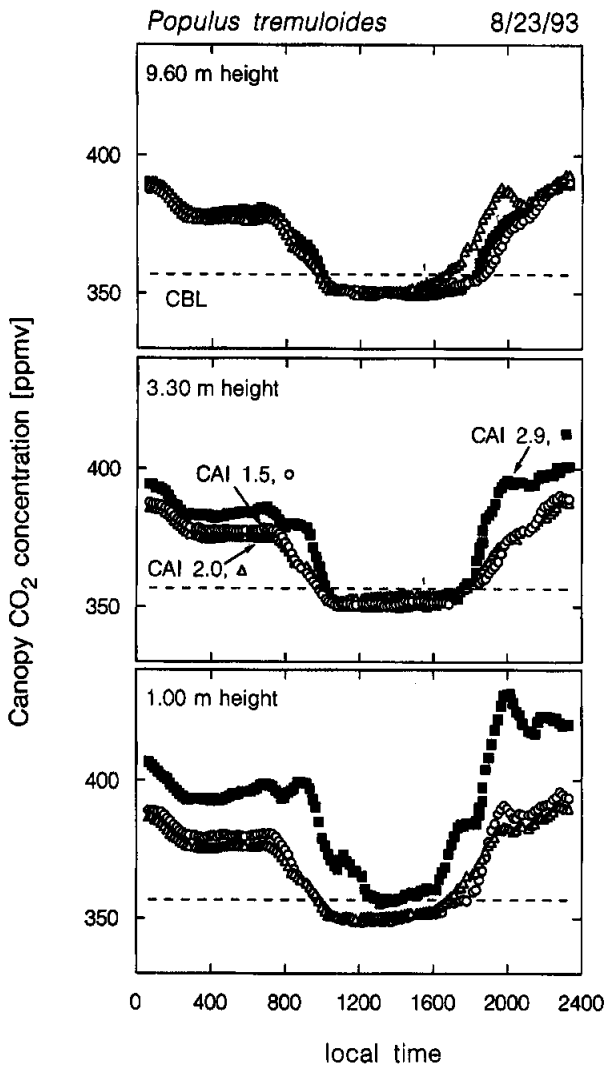
Fig. 5 Daily variation of CO_2 concentrations at three selected canopy heights in three montane *Populus tremuloides* stands with differing CAI. Data are smoothed by using moving-averages. CO_2 concentration of the CBL was 356.7 ppmv (Wendover, UT; provided by T. Conway, NOAA/CMDL).

(Table 4). Daytime canopy $[CO_2]$ in the evergreen *P. contorta* were very uniform, and showed only small gradients between 0.30 and 9.60 m. In contrast, the deciduous canopy of *P. tremuloides* showed very dynamic $[CO_2]$ profiles, with significant depletions at 0.30 m below CBL background concentrations, reflecting high photosynthetic activity of the larger understorey vegetation in the deciduous stand (Table 2). Thus, higher $[CO_2]$ immediately above the forest floor in the *P. tremuloides* than in the *P. contorta* stand, resulted in seven times larger $[CO_2]$ gradients between 0.02 and 0.30 m height in the deciduous than in the evergreen stand, in spite of similar CAI values.

Moreover, seasonal fluctuations of canopy $[CO_2]$ pro-

Table 4 Daytime CO_2 concentrations and canopy gradients [ppmv] during July 1993 among montane deciduous and evergreen stands with similar leaf area index (CAI measured at full canopy development). Means and standard errors are presented ($N = 35$ for *P. contorta*, $N = 50$ for *P. tremuloides*). Different letters following the means represent significantly different CO_2 concentrations or gradients within one stand (Tukey–Kramer test at the 0.05 level)

	Evergreen *P. contorta* CAI 1.6	Deciduous *P. tremuloides* CAI 1.5
CBL[1]		
Niwot Ridge, CO	354.4	354.4
Wendover, UT	357.7	357.7
Canopy[2]		
upper (9.60 m)	353.2 ± 0.4^a	351.7 ± 0.4^b
middle (5.60 m)	353.2 ± 0.3^a	351.3 ± 0.3^b
lower (1.00 m)	354.1 ± 0.3^a	348.8 ± 0.4^b
understorey (0.30 m)	354.5 ± 0.3^a	341.9 ± 0.8^a
Floor (0.02 m)[2]	367.7 ± 1.7^b	440.9 ± 3.3^c
Gradient between[2]		
1.00–9.60 m	0.95 ± 0.1^a	-2.8 ± 0.4^a
0.30–1.00 m	0.41 ± 0.12^a	-6.6 ± 0.8^a
0.02–0.30 m	13.2 ± 1.6^b	95.0 ± 4.2^b

[1]July; data provided by T. Conway, NOAA/CMDL [2]during 13.00 hours (± 30 min, local time), July 7–14 for *P. contorta*, June 24 – July 3 for *P. tremuloides*.

files were lower in the evergreen canopy of *P. contorta* than in either deciduous *Acer* spp. or *Populus tremuloides* forests (data not shown). Night-time $[CO_2]$ were lowest early in the growing season (July, at this montane site), and increased steadily until September ($9.14 < F < 47.82$, $P < 0.0001$). In contrast to the two deciduous canopies, no decrease in nocturnal $[CO_2]$ was observed in fall. Mean daytime $[CO_2]$ in the upper and lower canopy (3.30–14.0 m) did not vary during the growing season ($0.86 < F < 13.14$, $0.1369 < P < 0.4281$). Similar to the pattern in deciduous stands, $[CO_2]$ above the forest floor (0.02 m, 0.30 m), showed the typical 'night-time' pattern, with lowest $[CO_2]$ in July, and highest in September ($5.39 < F < 9.23$, $0.0002 < P < 0.0061$). Thus, seasonal changes in $[CO_2]_{canopy}$ showed significant differences between different vegetation types.

Discussion

Vertical profiles of canopy $[CO_2]$ within deciduous and evergreen forests were influenced by stand structure characteristics such as CAI and understorey vegetation, and were highly dependent on vegetation type. Seasonal changes in canopy $[CO_2]$ reflected changes in soil respiration rates, plant phenology and gas exchange of the dominant trees and the understorey vegetation.
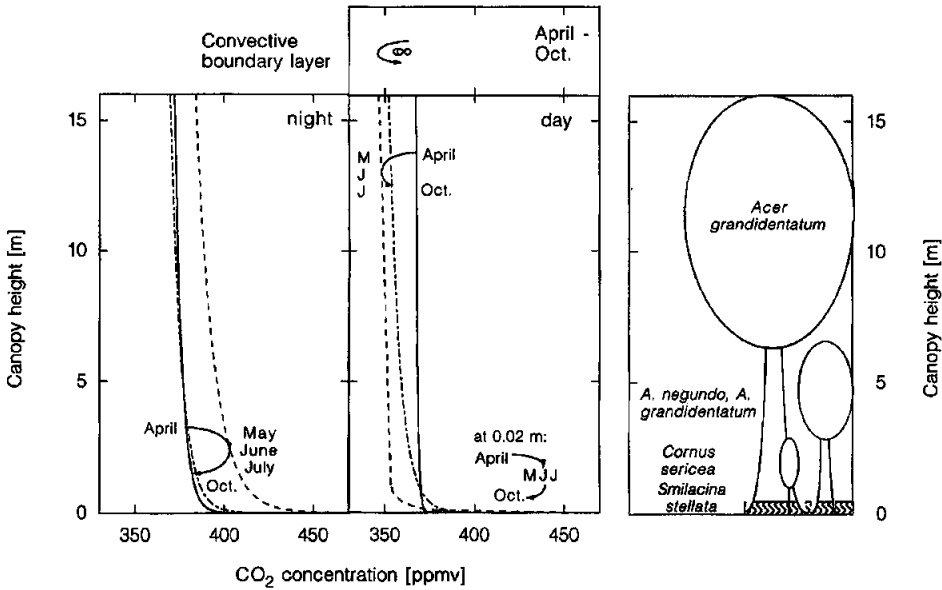
Fig. 6 Conceptual model of seasonal variations of CO_2 concentrations in deciduous forest canopies. Data were collected during two consecutive growing seasons (May–October 1993; April–July 1994) and fitted with a power function. CO_2 concentrations measured at 04.00 hours (± 30 min) were used to represent the night-time patterns; CO_2 at 13.00 hours (± 30 min) represent the daytime patterns. CO_2 concentrations of the CBL (Wendover, UT) were provided by T. Conway (NOAA/CMDL). Canopy structure is generalized from actual measurements; species composition includes dominant species only.

In summarizing the patterns for *Acer* spp. and *P. tremuloides*, we have generalized our results for a multi-layered deciduous forest (Fig. 6; a dense *Acer* spp. forest as an example). During the very early part of the growing season, soil temperatures are still sufficiently cold that soil respiration rates remain low. Understorey plants begin to grow by mid-April, but woody perennials do not leaf out until late April. As air temperatures increased, canopy leaf area development accelerated (e.g. CAI increased by 65% between 14 April and 5 May, and almost tripled by 30 June). Therefore, we expected nocturnal canopy [CO₂] to increase during the growing season and peak in late summer due to increasing plant and soil respiration, until leaf senescence and litterfall prevailed. However, differing life spans of tree and understorey foliage resulted in a different seasonal pattern in these deciduous stands. Annuals and herbaceous plants in this riparian habitat complete growth and reproduction by mid-June, while woody plants remain active until October (Ehleringer *et al.* 1992). Thus, we noticed night-time canopy [CO₂] decreasing by midsummer (Fig. 6), associated with wilting and complete loss of understorey plants. Yet, tree foliage activity and soil respiration rates were still high (and thus [CO₂] were expected to be high). As temperatures decreased in September, leaf senescence and litterfall increased, and canopy [CO₂] decreased, reaching [CO₂] profiles similar to those observed in spring.

Daytime canopy [CO₂] decreased during the early growing season until June/July (Fig. 6), as a result of increasing PAR and photosynthetic rates of a growing canopy (Ehleringer *et al.* 1992; Dawson & Ehleringer 1993). Overstorey canopy development was completed by mid-June. However, as soon as the understorey vegetation started to senesce in mid-summer (July), daytime canopy [CO₂] began to increase again. A different pattern was seen immediately above the forest floor, where a typical 'night-time' response of [CO₂] was evident in the profile associated with the strong influence of soil temperatures on soil respiration (Fig. 6). Similar general characteristics have been observed in a mixed oak–maple stand in Harvard Forest, Massachusetts, USA (Bazzaz & Williams 1991), although seasonal variations were smaller in the hardwood stand.

The influence of stand structure on canopy [CO₂] profiles showed distinct differences depending on whether or not [CO₂] in the overstorey or the understorey was considered. [CO₂] and gradients within the overstorey canopy of *Acer* spp. and *P. tremuloides* stands stayed fairly constant, even when CAI doubled (Figs 3 and 4). Although tree foliage influenced upper canopy [CO₂] (Table 3, Fig. 6), when stands with different CAI were compared at the same sampling time, an increase in upper canopy biomass did not result in lower daytime or higher night-time [CO₂]. Instead, we found higher [CO₂] at night in an open compared to a dense *Acer* spp. stand (Fig. 3) and similar [CO₂] in both stands during the day. Thus, the distinct seasonal pattern in overstorey
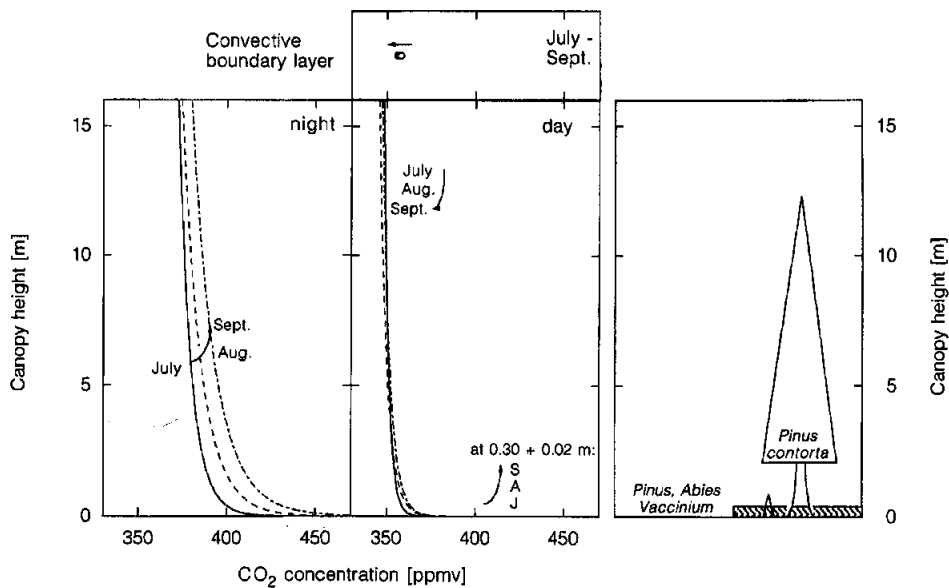
Fig. 7 Conceptual model of seasonal variations of CO_2 concentrations in coniferous forest canopies. Data were collected during the 1993 growing season (July–September) and fitted with a power function. CO_2 concentrations measured at 04.00 hours ($\pm$ 30 min) were used to represent the night-time patterns; CO_2 at 13.00 hours ($\pm$ 30 min) represent the daytime patterns. CO_2 concentrations of the CBL (Wendover, UT) were provided by T. Conway (NOAA/CMDL). Canopy structure is generalized from actual measurements; species composition includes dominant species only.

[CO_2] throughout the two growing seasons was most likely a combined effect of increasing leaf area and increasing assimilation rates (Ehleringer *et al.* 1992; Dawson & Ehleringer 1993) rather than simply a foliage biomass effect. A similar observation was made in three *P. tremuloides* stands (Fig. 5), even though the montane habitat was quite different from the more buffered riparian sites. Thus, turbulent mixing, which is highest during the day, seemed to have counteracted the effect of increased foliage biomass in the denser, but still fairly open stands (CAI < 4.5).

However, we found significant differences with CAI in the understorey [CO_2]. Daytime understorey [CO_2] were lowest or most depleted compared to CBL background values in the most open *Acer* spp. stands that had the highest understorey biomass (Fig. 4). In denser stands, where light conditions were less favourable in the understorey, biomass of the understorey vegetation was lower by a factor of five to seven than in the open stands (Table 2). In addition, soil respiration rates were higher in the more open stands compared to the dense stands, probably due to lower light attenuation and therefore higher soil temperatures. In agreement with other studies (Baldocchi *et al.* 1986; Toland & Zak 1994; Raich & Potter 1995), about one third of the variance in soil respiration rates was explained by soil temperatures, while the influence of soil moisture was secondary to that of temperature. As a result of these environmental conditions, soil CO_2 efflux was overcompensated by

assimilation of a vigorous understorey layer in the most open *Acer* spp. stand (Fig. 3), thus resulting in very low [CO_2] at 0.02 and 0.3 m height. Furthermore, the influence of overstorey CAI on soil temperatures and therefore soil respiration (Results, Seasonal Variability) was illustrated in the 'night-time' seasonal pattern of daytime [CO_2] immediately above the forest floor, which was characterized by increasing [CO_2] at 0.02 m until mid-summer enen though [CO_2] in the overstorey were decreasing (Table 3).

Unexpected interactions among stand structure, turbulent mixing and soil CO_2 efflux became further evident when we observed typical daily courses of canopy [CO_2] in *Acer* spp. stands before leaf emergence in mid April (Fig. 2). Although Bazzaz & Williams (1991) did not see any daily fluctuations during the dormant season (March, November) in a mixed oak-maple stand (Harvard Forest Massachusetts, USA), we found canopy [CO_2] in two riparian stands to be 4–9 ppmv above CBL values at night, but close to the background [CO_2] during the day. Although differences in CAI were small (0.8 compared to 1.2), the open stand seemed to allow more turbulent mixing during the day than the dense stand, reducing the [CO_2] gradient during the day to zero, whereas the dense stand still showed a 5 ppmv difference between 0.02 and 14.0 m.

Vertical [CO_2] profiles were highly dependent on the vegetation type of the dominant tree species, and differed between montane evergreen and deciduous

forests. Canopy [CO$_2$] in *P. contorta* stands were more uniform, and [CO$_2$] gradients smaller than those in *P. tremuloides* (Table 4), reflecting the uniform leaf area distribution in the *P. contorta* stand. In contrast to the deciduous stands, overall photosynthetic rates were low enough that we did not observe significant canopy [CO$_2$] below CBL values in the evergreen canopies (Table 4), probably due to a slow growing understorey vegetation with low biomass accumulation (Table 2). Furthermore, the increase of [CO$_2$] at 0.02 m was smaller in the evergreen than in the deciduous stand, indicating low soil respiration and decomposition rates, maybe related to litter quality. Higher canopy roughness of the evergreen canopy and therefore higher turbulent mixing with the CBL might explain the differences in canopy [CO$_2$] profiles between the two vegetation types. However, overstorey CAI values and stand density were very similar and, as mentioned before, our CAI measurements are more likely to underestimate the actual LAI in coniferous stands compared to deciduous forests due to the effects of needle clusters. Thus, ecophysiological differences between vegetation types might also be represented in the different seasonal fluctuations of canopy [CO$_2$]. Throughout the short growing season, night-time [CO$_2$] in the *P. contorta* stand increased and daytime [CO$_2$] decreased steadily, but did not come back to springtime values (Fig. 7). Foliage life span is much higher in *P. contorta* than in deciduous species. Late in the growing season, evergreen trees are still physiologically active while deciduous trees have gone dormant (Waring & Franklin 1979). Thus, differences in foliage longevity seem to be responsible for high night-time and low daytime [CO$_2$] late in the season in evergreen canopies, whereas both canopy roughness and ecophysiology contribute to the overall seasonal pattern.

In conclusion, static [CO$_2$] profile measurements clearly reflected the influences of life form and stand structure on canopy CO$_2$ fluxes. The potential to spatially distinguish among canopy layers can supplement the interpretation of eddy-correlation measurements, which integrate CO$_2$ fluxes over the entire canopy height below the plane of instrumentation (Fan *et al.* 1990; Wofsy *et al.* 1993; Hollinger *et al.* 1994). The influence of overstorey CAI on canopy [CO$_2$] profiles reflected differences in turbulent mixing, but also changes in light attenuation and soil temperatures. We found that soil respiration and understorey vegetation, both affected by light and temperature among stands with different CAI, were important parameters shaping [CO$_2$] profiles. Large differences in canopy [CO$_2$] between evergreen and deciduous forests, and differences in their seasonal variability provide important information about mechanisms that influence CO$_2$ fluxes in forest ecosystems.

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