# Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired $CO_2$ within boreal forest canopies

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**Summary** We compared vertical gradients in leaf gas exchange, $CO_2$ concentrations, and refixation of respired $CO_2$ in stands of *Populus tremuloides* Michx., *Pinus banksiana* Lamb. and *Picea mariana* (Mill.) B.S.P. at the northern and southern boundaries of the central Canadian boreal forest. Midsummer gas exchange rates in *Populus tremuloides* were over twice those of the two conifer species, and *Pinus banksiana* rates were greater than *Picea mariana* rates. Gas exchange differences among the species were attributed to variation in leaf nitrogen concentration. Despite these differences, ratios of intercellular $CO_2$ to ambient $CO_2$ ($c_i/c_a$) were similar among species, indicating a common balance between photosynthesis and stomatal conductance in boreal trees.

At night, $CO_2$ concentrations were high and vertically stratified within the canopy, with maximum concentrations near the soil surface. Daytime $CO_2$ gradients were reduced and concentrations throughout the canopy were similar to the $CO_2$ concentration in the well-mixed atmosphere above the canopy space. Photosynthesis had a diurnal pattern opposite to the $CO_2$ profile, with the highest rates of photosynthesis occurring when $CO_2$ concentrations and gradients were lowest. After accounting for this diurnal interaction, we determined that photosynthesizing leaves in the understory experienced greater daily $CO_2$ concentrations than leaves at the top of the canopy. These elevated $CO_2$ concentrations were the result of plant and soil respiration. We estimated that understory leaves in the *Picea mariana* and *Pinus banksiana* stands gained approximately 5 to 6% of their carbon from respired $CO_2$.

*Keywords: boreal forest, BOREAS, carbon dioxide gradients, carbon isotope discrimination, carbon refixation, photosynthesis.*

## Introduction

Boreal forests are among the largest biomes on earth and are believed to exert a significant influence on global water and carbon fluxes. Tans et al. (1990) presented evidence that terrestrial ecosystems in the northern and temperate latitudes are large carbon sinks that influence atmospheric carbon dynamics. The Boreal Ecosystem–Atmosphere Study (BOREAS) was established to investigate internal carbon and water dynamics of the boreal forest biome and to provide information to estimate the boreal forests' impact on global environmental change (Sellers et al. 1995).

Three main factors govern dynamics of $CO_2$ within a forest canopy: turbulent mixing with the atmosphere above the canopy, photosynthesis and respiration. Carbon dioxide released by respiration is either lost from the forest through turbulent mixing or refixed by photosynthesis within the canopy. Sternberg (1989) defined $CO_2$ recycling as the percentage of respired carbon refixed by the entire canopy. Past estimates for tropical rainforests have ranged between 3 and 26% (Sternberg 1989, Broadmeadow and Griffiths 1993, Buchmann et al. 1996). In this study, we determined the amount of carbon from respired sources that was refixed by foliage at different canopy levels. Calculating leaf $CO_2$ refixation requires detailed information on the spatial and temporal patterns of the $\delta^{13}C$ of leaves and source $CO_2$ within the canopy, gas exchange and $CO_2$ concentrations ($[CO_2]$). Fluctuations in $[CO_2]$ will affect the $\delta^{13}C$ of source $CO_2$ for the leaves because a relationship exists between $\delta^{13}C$ and $[CO_2]$ (Keeling 1961). As a result, the source $CO_2$ for photosynthesis will change both diurnally and spatially within the canopy. How $[CO_2]$ patterns vary with forest species and canopy structure, and how they interact with the patterns of gas exchange, will determine the extent of $CO_2$ refixation within forests.

The temporal and spatial dynamics of foliage gas exchange are influenced by environmental factors. Vertical gradients in photosynthesis ($A$) are driven by light availability (Schulze et al. 1977, Reich et al. 1990, Brooks et al. 1996). Patterns of variation in stomatal conductance ($g$) and transpiration ($E$) are complex because they change with light, boundary layer conductance, and the vapor pressure deficit of the air (Leverenz et al. 1982, Beadle et al. 1985, McNaughton and Jarvis 1991). The interplay of photosynthesis and stomatal conductance ($A/g$) can be inferred by $c_i/c_a$, which is defined as the ratio of intercellular $[CO_2]$ to ambient $[CO_2]$ (Farquhar et al. 1989). Gradients of $c_i/c_a$ can be used to describe the balance between

carbon and water exchange within the canopy. In addition, $c_i/c_a$ is the physiological parameter driving carbon isotope discrimination (Farquhar et al. 1989). The patterns of gas exchange and $[CO_2]$ vary with the structure and species composition of the canopy. In central Canada, the boreal forest is largely composed of monodominant and mixed stands of *Populus tremuloides* Michx.*, Pinus banksiana* Lamb. and *Picea mariana* (Mill.) B.S.P. These species differ in canopy structure and productivity rate. The characteristics of these forests also change between the southern and northern boreal boundaries. Stands in the northern part of the range are generally less productive and smaller in stature than stands in the southern part of the range (Sellers et al. 1995). Our goal was to understand how forest structure and species composition affect gas exchange characteristics and $CO_2$ dynamics within the canopy. We examined these processes in each of three forest ecosystems at their northern and southern boundaries. We also estimated the extent that leaves in the understory refix respired $CO_2$ based on the $\delta^{13}C$ of the foliage and the interplay of gas exchange and $CO_2$ dynamics.

## Materials and methods

### Site description

This study was conducted in association with the Boreal Ecosystem–Atmosphere Study (BOREAS). Two study areas were located at the northern and southern limits of the boreal forest in central Canada. The Southern Study Area (SSA) was located 40 km north of Prince Albert, Saskatchewan and extended a further 90 km north and 130 km east–west. The Northern Study Area (NSA) was 100 km east–west and 80 km north–south and included the town of Thompson, Manitoba. In both the SSA and the NSA, we studied stands dominated by each of the target species: *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides*.

In the Southern Study Area, the *Picea mariana* site (BOREAS site: SSA-OBS, 53.985° N and 105.12° W) was located on poorly drained, sandy-clay soil. The stand was approximately 150 years old with 4300 stems per hectare. Tree heights ranged up to 12 m, with a leaf area index (LAI) of 2.3 (Rich et al. 1995, hemispherical photograph estimates) or 6.2 (S.T. Gower, unpublished allometry data). The large difference between LAI estimates resulted from the clustered nature of *Picea mariana* foliage. Ground cover was an almost continuous layer of *Pleurozium schreberi* (Willd. ex Brid) Mitt with patches of *Sphagnum* spp. The *Pinus banksiana* site (BOREAS site: SSA-OJP, 53.916° N and 104.69° W) was located in a well drained, sandy area. Stand age was 60–75 years and stand density was about 1300 trees per hectare. Tree heights ranged from 11 to 15 m, with a leaf area index of 1.4 (S.T. Gower, unpublished data) or 2.5 (Rich et al. 1995). *Alnus crispa* (Ait.) Pursh was the dominant shrub in the understory, and the ground cover was comprised predominantly of lichens, with patches of feather moss. The *Populus tremuloides* site (BOREAS site: SSA-OA, 53.629° N, and 106.20° S) was located on a well-drained clay-loam soil. Stand age was approximately 60 years and stand density was about 900 trees per

hectare. Tree heights ranged from 12 to 20 m with a leaf area index of 3.0 (Rich et al. 1995, S.T. Gower, unpublished data). The understory was dominated by *Corylus cornuta* Marsh. and *Rosa woodsii* Lindl.

In the Northern Study Area, the *Picea mariana* site (BOREAS site: T6R5S, 55.908° N and 98.519° W) was located in an upland area with poorly drained clay soils. The stand was around 50 years old and was very dense (about 9300 trees ha$^{-1}$), with an LAI of 8.4 (S.T. Gower, unpublished data). Tree heights ranged from 6 to 9 m. The ground was covered with a deep layer of feather moss. The *Pinus banksiana* site (BOREAS site: NSA-OJP, 55.928° N, 98.622° W) was similar to the southern pine site in that the soils were sandy and well drained with an understory of *Alnus crispa* and a lichen ground cover. The stand was 40–60 years old and had a density of 2000–3000 trees per hectare. Trees were shorter (8–11 m) than pines in the Southern Study Area but LAI was similar (1.6, Rich et al. 1995; 2.3, S.T. Gower, unpublished data). The *Populus tremuloides* site (BOREAS site: T2Q6A, 55.888° N, 98.676° W) was approximately 60 years of age and had a dense understory of *Alnus crispa*. Tree heights ranged from 7 to 18 m and stand density was about 2000 trees per hectare. Leaf area index estimates ranged from 2.3 (S.T. Gower, unpublished data) to 3.2 (Rich et al. 1995).

### Field measurements

Field measurements were made in three intensive field campaigns (IFCs) during the 1994 growing season. The IFC-1 was from May 24 through June 12, at the time of bud break for both conifer species and early leaf expansion for *Populus tremuloides*. The IFC-2 was at the peak of the growing season, between July 26 and August 8. The IFC-3 was at the onset of dormancy, from August 30 to September 15. During each IFC, we measured gas exchange of the dominant species, photosynthetic photon flux density (PPFD), air temperature, soil respiration, daily profiles of $[CO_2]$, and the $\delta^{13}C$ of the foliage for the dominant species. During IFC-1, photosynthesis was measured only at the conifer sites. The most extensive data set was collected during IFC-2, when photosynthesis was measured at all six sites. In September (IFC-3), photosynthesis was measured only in the southern conifer sites. All other parameters were measured at all six sites during each field campaign, except $[CO_2]$ profiles, which were not collected at the *Populus tremuloides* site in the SSA during IFC-1.

*Gas exchange*   Foliage gas exchange was measured with a portable photosynthesis system (LI-6200, Li-Cor Inc., Lincoln, NE) equipped with a 250-ml leaf chamber. All measurements were made under ambient conditions unless otherwise stated. For each IFC, 22 foliage samples were selected from four canopy levels: upper sunlit foliage (six samples), middle canopy shaded foliage (lower part of the main dominant canopy, six samples), lower canopy of dominant trees (0.5–1 m from the ground, five samples), and ground-level saplings (0.10–0.25 m, five samples). Because *Populus tremuloides* was not present in the understory of *Populus tremuloides* stands, we measured gas exchange for understory leaves of *Corylus cornuta* in the SSA and of *Alnus crispa* in the NSA. In September,

only upper canopy measurements were taken. For the conifer sites, gas exchange was measured on mature 1-year-old foliage. For the *Populus tremuloides* sites, gas exchange was measured on fully expanded leaves. Gas exchange measurements were taken two to six times for each sample during a day (between 0900 and 2000 h), covering a range of irradiances for each foliage sample. Values of $A_{max}$ (photosynthesis at light saturation) and $g_{max}$ (conductance at light saturation) were calculated by averaging photosynthesis measurements when PPFD was greater than 1000 $\mu$mol m$^{-2}$ s$^{-1}$. Air temperature and PPFD were measured at 9 and 0.5 m above ground and recorded by a data logger (CR-21X, Cambell Scientific, Logan, UT) at 30-min intervals. Photosynthetic photon flux density was measured with either a quantum sensor (LI-190, Li-Cor Inc., Lincoln, NE) or a photodiode (GaAsP 1118, Hamamatsu, Bridgewater, NJ) which was calibrated against a quantum sensor. Air temperature was measured with copper-constantan thermocouples shielded from direct beam radiation but open to air flow. Leaf area for conifers was measured by the volume displacement method. Gas exchange data are presented based on half the total leaf surface area (BOREAS Experimental Plan, J. Norman, personal communication). Projected leaf area was used for *Populus tremuloides*.

To examine directly the effects of light limitation in the lower canopy, an LED light source (QB6200, Quantum Devices Inc., Barnsveld, WI) was used to provide supplemental light for a subset of gas exchange measurements taken at the conifer sites in the SSA. After measuring gas exchange under ambient conditions, the foliage was exposed to supplemental light (1200 mol m$^{-2}$ s$^{-1}$) and the chamber was flushed with ambient air. Once the [CO$_2$] in the chamber returned to ambient values, a measurement of gas exchange in the supplemental light was made.

*Soil respiration*　Soil respiration was measured with a portable photosynthesis system (LI-6200) equipped with a soil respiration chamber (LI-6000-09S, Li-Cor Inc.). Twenty-four hours before measuring respiration, two PVC tubes (9.5 cm in diameter, 24 cm in length), which served as soil collars for the chamber, were inserted into the soil such that 5 cm of each collar remained above the soil surface. Two respiration measurements were made on each collar as described by Li-Cor (Publication No. 9311-69, 1993).

*Carbon dioxide concentrations*　Canopy [CO$_2$] was monitored continuously over a 2–5-day period at each site for each field campaign. Carbon dioxide concentrations were measured at six canopy heights: 9, 3, 1, 0.5, 0.25 and 0.05 m, and monitored every 10 min at the NSA and every 30 min at the SSA. Switching between canopy heights was controlled by a relay driver (A6Rec-12, Campbell Scientific) and a series of solenoid valves. Carbon dioxide was drawn from tubing attached to a rohn mast at the rate of 10 ml s$^{-1}$ and pumped through an infrared gas analyzer (LI-6262, Li-Cor Inc.). The CO$_2$ concentration was recorded by a data logger (CR-21X in the NSA, and CR-10 in the SSA, Campbell Scientific).

*Carbon isotope ratios*　Leaf carbon isotope ratios ($\delta^{13}$C) were measured on the foliage samples used for gas exchange measurements. For the conifers, current-year foliage growing just beyond the photosynthesis sample was also measured in IFC-2 and IFC-3. Because these samples contained carbon fixed in 1994, they were used to calculate $c_i/c_a$. Leaf samples were dried at 70 °C for 24 h and ground to a fine powder with a mortar and pestle. Two-mg samples were combusted and the resulting CO$_2$ was analyzed by isotope mass spectrometry (Delta S, Finnigan Mat, Bremen, Germany) for $\delta^{13}$C, as described by Boutton (1991).

*Data Analysis*

All statistical analysis was conducted with JMP 3.0.2 software (SAS Inc. Cary, NC). Analysis of variance was used to test the overall models, and if the ANOVA was significant, the Tukey-Kramer Honestly Significant Differences test was applied to test all combinations of means. To test for canopy gradients in continuous [CO$_2$] data, we used a split-plot design with time as the main factor and tested for effects of height within time.

The ratio of intercellular CO$_2$ to ambient CO$_2$ ($c_i/c_a$) was estimated both from direct gas exchange measurements and from carbon isotope data. We used $\delta^{13}$C of current-year (1994) leaves to calculate $c_i/c_a$ based on the equations of Farquhar et al. (1989). The $\delta^{13}$C of the source CO$_2$ was calculated from the continuous [CO$_2$] data (see below).

In addition to reporting actual [CO$_2$], we weighted [CO$_2$] by photosynthetic rates to calculate an average [CO$_2$] for carbon assimilated by leaves at the four canopy levels where photosynthesis was measured. Gas exchange data were used to develop a photosynthetic PPFD response curve for each species and canopy level. These curves were fitted with a logarithmic equation, and the photosynthetic weights were calculated using the diurnal PPFD data. When photosynthetic rates were negative (nighttime respiration), the weight was set to zero so that [CO$_2$] at night was not included in the weighted average. Each observation of [CO$_2$] was multiplied by the photosynthetic weight, and daily weighted means were calculated.

We used two independent techniques to calculate the proportion of carbon in foliage that came from respired CO$_2$. The final step for both techniques involved solving the following mass-balance equation for $x$, the percentage of respired CO$_2$ in air surrounding the foliage:

$$\delta^{13}C_{canopy} = (1 - x)\delta^{13}C_{atm} + (x)\delta^{13}C_{respired}, \qquad (1)$$

where $\delta^{13}C_{atm}$ and $\delta^{13}C_{respired}$ are known values and $\delta^{13}C_{canopy}$, the average $\delta^{13}$C of the CO$_2$ fixed by the leaf, was estimated by the two techniques outlined below. The $\delta^{13}C_{atm}$ was measured at the top of the canopy. This mass-balance approach assumes that the photosynthetic effect on the [CO$_2$] within the canopy was negligible, and that changes in [CO$_2$] were related to turbulent mixing and respiration. If photosynthetic drawdown was a factor, then these calculations provide a minimum estimate of refixation. We assumed that no refixation of respired CO$_2$ took place at the top of the canopy, because our values of [CO$_2$] and $\delta^{13}C_{atm}$ at top of the canopy were similar to the corresponding values for the well-mixed

surface layer above the vegetation ($\approx 350$ ppm and $-8$, respectively). For all sites, $\delta^{13}C_{\text{respired}}$ was approximately $-26$.

*Gas exchange method*    We used the gas exchange method to calculate $\delta^{13}C_{\text{canopy}}$ based on leaf carbon isotope data ($\delta^{13}C_{\text{leaf}}$) and diurnal gas exchange data. From the diurnal gas exchange data, we calculated a daily weighted $c_i/c_a$ value for each canopy level by weighting each $c_i/c_a$ measurement with the corresponding photosynthesis measurement and averaging over the day. We used the equation of Farquhar et al. (1989) to calculate carbon isotope discrimination ($\Delta$) from the weighted $c_i/c_a$:

$$\Delta = a + (b - a)(c_i/c_a). \tag{2}$$

We used the values of $\Delta$ and $\delta^{13}C_{\text{leaf}}$ to calculate $\delta^{13}C_{\text{canopy}}$ for each canopy level (Farquhar et al. 1989):

$$\Delta = (\delta^{13}C_{\text{canopy}} - \delta^{13}C_{\text{leaf}})/(1 + \delta^{13}C_{\text{leaf}}). \tag{3}$$

*Carbon dioxide profile method*    The $CO_2$ profile method used the daily mean $[CO_2]$ weighted by photosynthesis to calculate the average $\delta^{13}C_{\text{canopy}}$ of $CO_2$ fixed by leaves. There is a linear relationship between $1/[CO_2]$ and $\delta^{13}C$ (Keeling 1961), which we calculated for each site for each IFC. Based on these linear relationships, we determined the corresponding $\delta^{13}C_{\text{canopy}}$ for a particular canopy level and used that value in Equation 1 to calculate leaf $CO_2$ refixation. We also used this $\delta^{13}C$ value to calculate $c_i/c_a$ from the leaf carbon isotope data.

## Results

### Comparison between northern and southern limits of the boreal forest

In the SSA, light-saturated photosynthesis ($A_{\text{max}}$) of foliage at the top of the canopy was approximately twice that measured in the NSA for the same species (Figure 1). These intraspecific differences were significant for *Populus tremuloides* and *Pinus banksiana*, but not for *Picea mariana*. Stomatal conductance at light saturation ($g_{\text{max}}$) followed a similar geographical trend, but the magnitude of the difference was greater than for $A_{\text{max}}$: conductances in the SSA were approximately three times higher than those in the NSA. This difference in magnitude between the fluxes also meant that $c_i/c_a$ was lower in the NSA than in the SSA when foliage was light saturated (Figure 2).

Gas exchange also differed significantly among the three species (Figure 1). Stomatal conductance and photosynthetic rate at light saturation in *Populus tremuloides* had values twice those in *Pinus banksiana*, which had values twice those in *Picea mariana* for both northern and southern study sites. All three species had similar $c_i/c_a$ values at light saturation (instantaneous $c_i/c_a$, Figure 2). In the SSA, the mean $c_i/c_a$ for all three species was $0.65 \pm 0.04$, compared with a mean of $0.55 \pm 0.07$ in the NSA. However, $c_i/c_a$ values calculated from carbon isotope data differed from these results because carbon isotope $c_i/c_a$ represents the average $c_i/c_a$ for all carbon fixed by the leaf, not just light-saturated $c_i/c_a$ as represented by the instantaneous data. In the SSA, carbon isotope $c_i/c_a$ was similar for all species
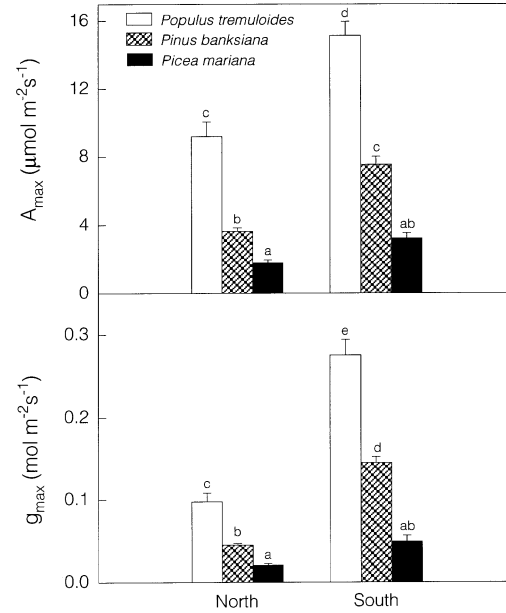


Figure 1. Mean values of photosynthesis ($A_{\text{max}}$) and stomatal conductance ($g_{\text{max}}$) at light saturation at the northern and southern sites. Measurements were taken from fully sunlit foliage (PPFD $> 1000$ µmol $m^{-2} s^{-1}$) at the top of the canopy in July 1994. Error bars represent standard error of the means. Means marked by the same letter are not significantly different ($\alpha = 0.05$, Tukey-Kramer Honestly Significant Difference test comparing all means).
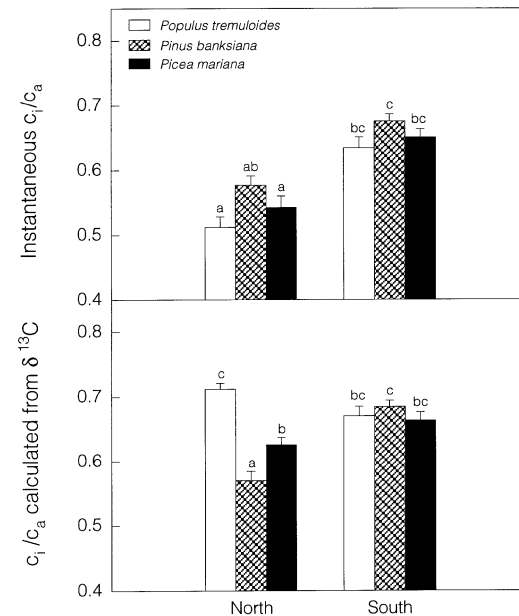


Figure 2. Instantaneous $c_i/c_a$ from light-saturated gas exchange data in Figure 1 and a longer-term integrated $c_i/c_a$ calculated from carbon isotope ratios for the northern and southern study areas. Values of $c_i/c_a$ marked with the same letter are not significantly different ($\alpha = 0.05$, Tukey-Kramer Honestly Significant Difference test comparing all means).

and the average value (0.68 ± 0.03) was comparable to the instantaneous $c_i/c_a$ mean. In the NSA, carbon isotope $c_i/c_a$ differed significantly among species. *Populus tremuloides* had the highest $c_i/c_a$ value and *Pinus banksiana* had the lowest. For *Populus tremuloides* and *Picea mariana*, carbon isotope $c_i/c_a$ values were significantly higher than instantaneous $c_i/c_a$ values (0.71 versus 0.51, $P < 0.001$, and 0.63 versus 0.54, $P < 0.01$, respectively for species, $t$-test).

The $\delta^{13}C$ of foliage at the top of the canopy showed some seasonal variation among species and location, but leaf $\delta^{13}C$ was more constant than expected (Table 1). In the early season (May–June), $\delta^{13}C$ values were similar among species in both the NSA and the SSA (overall May–June mean: $-27.2 \pm 0.8$). Because we measured 1-year-old foliage for conifers and newly flushed leaves for *Populus tremuloides*, which are usually formed from carbohydrates stored from the previous year, the early season values represented $\delta^{13}C$ of carbon fixed in 1993. As the season progressed, $\delta^{13}C$ in the SSA remained stable for all species, with a mean of $-26.9 \pm 0.5$, whereas $\delta^{13}C$ values in the NSA were more variable. During midsummer, new foliage of *Pinus banksiana* in the NSA had significantly less negative $\delta^{13}C$ values than those of the other species, but by September these differences were less apparent. Throughout the season, for both the NSA and SSA, $\delta^{13}C$ in *Populus tremuloides* ($-27.7 \pm 0.8$) was significantly more negative than $\delta^{13}C$ for the conifers (Tukey-Kramer HSD, $P < 0.05$, *Pinus banksiana* $-26.3 \pm 1.1$, *Picea mariana* $-26.6 \pm 0.8$), and this difference was most evident in September.

### Gas exchange gradients within NSA forest canopies

Rates of photosynthesis decreased as light was attenuated, but the magnitude of the reduction varied among species (Figure 3). Photosynthetic rates in the middle canopy (lower part of the main canopy) of *Populus tremuloides* were approximately 25% of the rates measured at the top of the canopy. Neither of the coniferous species showed such a large reduction, and in *Picea mariana*, in which rates were low at the top of the canopy, there was no significant difference between the top and middle canopy. Differences in photosynthetic rates
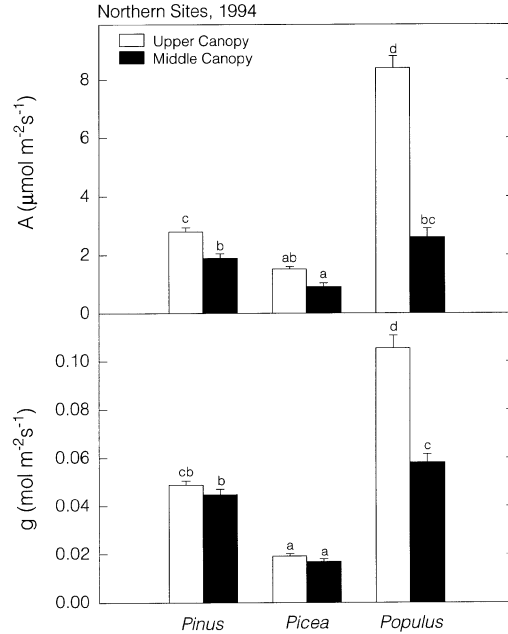
Figure 3. Mean photosynthesis ($A$) and stomatal conductance ($g$) from gas exchange measurements taken between 0900 and 1900 h for the upper and middle positions within the canopy (the upper and lower positions of the dominant canopy). Measurements were taken in July 1994. Values marked by the same letter are not significantly different ($\alpha = 0.05$, Tukey-Kramer Honestly Significant Difference test comparing all means).

among species were related to the degree of light attenuation in the canopies. Light attenuation was greatest in *Populus tremuloides* and *Picea mariana* canopies (about 80%) and least in the *Pinus banksiana* canopy (about 55%). Stomatal conductance was similar in the upper and middle canopies of the conifers, but conductance values were decreased by half in the middle canopy of *Populus tremuloides* compared to the upper canopy. The lack of stomatal response to light in conifers was also indicated by photosynthetic measurements made in the presence of supplemental light in the lower canopy (Ta-

Table 1. Mean $\delta^{13}C \pm SE$ of ($n$) measurements at the top of the canopy for foliage of the three dominant species at the NSA and the SSA through the 1994 growing season. May–June values for the conifers were for foliage formed in 1993, because 1994 foliage had not emerged. Means within an IFC followed by the same letter are not significantly different ($\alpha = 0.05$, Tukey Kramer Honestly Significant Difference test of all combinations within an IFC).

|  | *Pinus banksiana* | *Picea mariana* | *Populus tremuloides* |
|---|---|---|---|
| **May–June** | | | |
| NSA | $-27.0 \pm 0.29$ a (6) | $-26.4 \pm 0.17$ a (6) | $-27.7 \pm 0.47$ a (5) |
| SSA | $-27.0 \pm 0.11$ a (5) | $-27.6 \pm 0.22$ a (5) | $-27.6 \pm 0.48$ a (2) |
| **July** | | | |
| NSA | $-24.7 \pm 0.30$ a (6) | $-25.9 \pm 0.24$ b (6) | $-27.7 \pm 0.20$ d (9) |
| SSA | $-27.1 \pm 0.22$ cd (5) | $-26.7 \pm 0.28$ bc (5) | $-26.2 \pm 0.32$ bcd (4) |
| **September** | | | |
| NSA | $-25.6 \pm 0.22$ a (5) | $-26.6 \pm 0.32$ ab (5) | $-28.4 \pm 0.43$ c (5) |
| SSA | $-26.6 \pm 0.20$ ab (5) | $-26.5 \pm 0.30$ ab (5) | $-27.8 \pm 0.21$ bc (4) |

Table 2. Changes in gas exchange parameters of lower canopy foliage in response to supplemental light. Initial measurements were made under ambient conditions, and then measurements were repeated using supplemental light. Data were collected in July 1994 at the SSA. Asterisks indicate significant differences between ambient and supplemental light values using a paired $t$-test (* $P > 0.05$, ** $P > 0.01$, and *** $P > 0.001$, SAS).

| | *Pinus banksiana* | | *Picea mariana* | |
| --- | --- | --- | --- | --- |
| | Ambient light | Supplemental light | Ambient light | Supplemental light |
| PPFD ($\mu$mol m$^{-2}$ s$^{-1}$) | $40 \pm 15$ | 1200 | $420 \pm 540$ | 1200 |
| Temperature (°C) | $19.3 \pm 2.7$ | $18.5 \pm 0.7$ | $27.2 \pm 1.2$ | $27.5 \pm 1.3$ ** |
| $A$ ($\mu$mol m$^{-2}$ s$^{-1}$) | $0.51 \pm 0.27$ | $3.74 \pm 0.69$ ** | $1.7 \pm 1.0$ | $2.7 \pm 1.0$ *** |
| $g$ (mol m$^{-2}$ s$^{-1}$) | $0.07 \pm 0.01$ | $0.08 \pm 0.01$ | $0.03 \pm 0.01$ | $0.03 \pm 0.01$ |
| $c_i/c_a$ | $0.95 \pm 0.03$ | $0.77 \pm 0.03$ ** | $0.67 \pm 0.17$ | $0.54 \pm 0.11$ *** |

ble 2). Increasing light availability for understory foliage increased photosynthesis but did not significantly affect stomatal conductance.

Because photosynthesis decreased more than stomatal conductance from the top to the bottom of the canopy, $c_i/c_a$ increased from the upper to middle canopy. In the middle canopy, all three species had similar values of instantaneous $c_i/c_a$ ($0.75 \pm 0.13$). In the upper canopy, $c_i/c_a$ values were similar between *Populus tremuloides* and *Picea mariana*, but significantly higher for *Pinus banksiana*. Estimates of long-term integrated $c_i/c_a$ based on carbon isotopes revealed species differences as well as canopy gradients in $c_i/c_a$ (Figure 4).
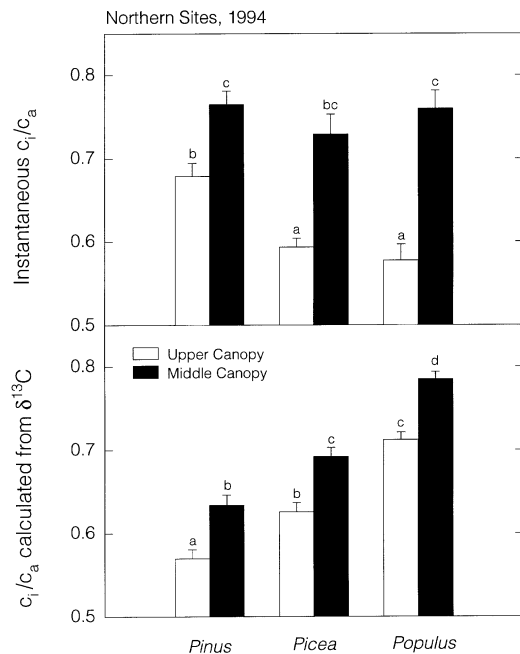


Figure 4. Instantaneous $c_i/c_a$ from the gas exchange measurements presented in Figure 3 and long-term integrated values of $c_i/c_a$ calculated from carbon isotope ratios for the upper and middle positions within the canopy. Values marked by the same letter are not significantly different ($\alpha = 0.05$, Tukey-Kramer Honestly Significant Difference test comparing all means).

Estimates of $c_i/c_a$ at both canopy levels were lowest in *Pinus banksiana*, followed by *Picea mariana*, and then *P. tremuloides*. Carbon isotope estimated $c_i/c_a$ values increased consistently from the upper to middle canopy and this increase was of the same magnitude (mean $c_i/c_a$ difference of 0.07 between upper and middle canopy) for all three species.

## $CO_2$ Profiles within forest canopies

Daily variation in [$CO_2$] within the canopy was similar for the three ecosystems in both the NSA and the SSA (Figure 5). At night, [$CO_2$] reached a daily maximum and was stratified within the canopy. From 0300 to 0600 h, [$CO_2$] was highest at the soil surface, sometimes exceeding 1000 ppm, although average values were closer to 550 ppm. At 9 m above the soil surface, nighttime [$CO_2$] was only slightly greater than [$CO_2$] in the well-mixed surface layer. Between 0600 and 0900 h, [$CO_2$] rapidly decreased in the lower canopy, thereby reducing the magnitude of the canopy gradient. This reduction occurred earliest in the *Pinus banksiana* canopies and latest in the *Picea mariana* canopies. Between 0900 and 1800 h, [$CO_2$] throughout the canopy remained stable. In both the *Picea mariana* and *Populus tremuloides* stands, the $CO_2$ concentration at the top of the canopy was less than the concentration in the well-mixed layer above the canopy. Between 1800 and 2100 h, canopy $CO_2$ gradients began to build again. Even though daytime concentrations were considerably lower than those at night, significant $CO_2$ gradients existed during daylight hours when plants were actively photosynthesizing (Figures 6 and 7). In the *Populus tremuloides* canopies, the greatest differences occurred between 0.05 and 0.5 m above ground in both the SSA and NSA, and in the SSA, soil surface [$CO_2$] always remained above 400 ppm. *Pinus banksiana* stands maintained only a small $CO_2$ concentration gradient during the day; concentrations near the soil surface were only a few ppm higher than at the top of the canopy. *Picea mariana* canopies maintained a larger gradient within the canopy during the day, when the $CO_2$ concentration close to the soil surface was near 370 ppm in both the NSA and SSA sites, approximately 10 ppm higher than $CO_2$ concentration at the top of the canopy.

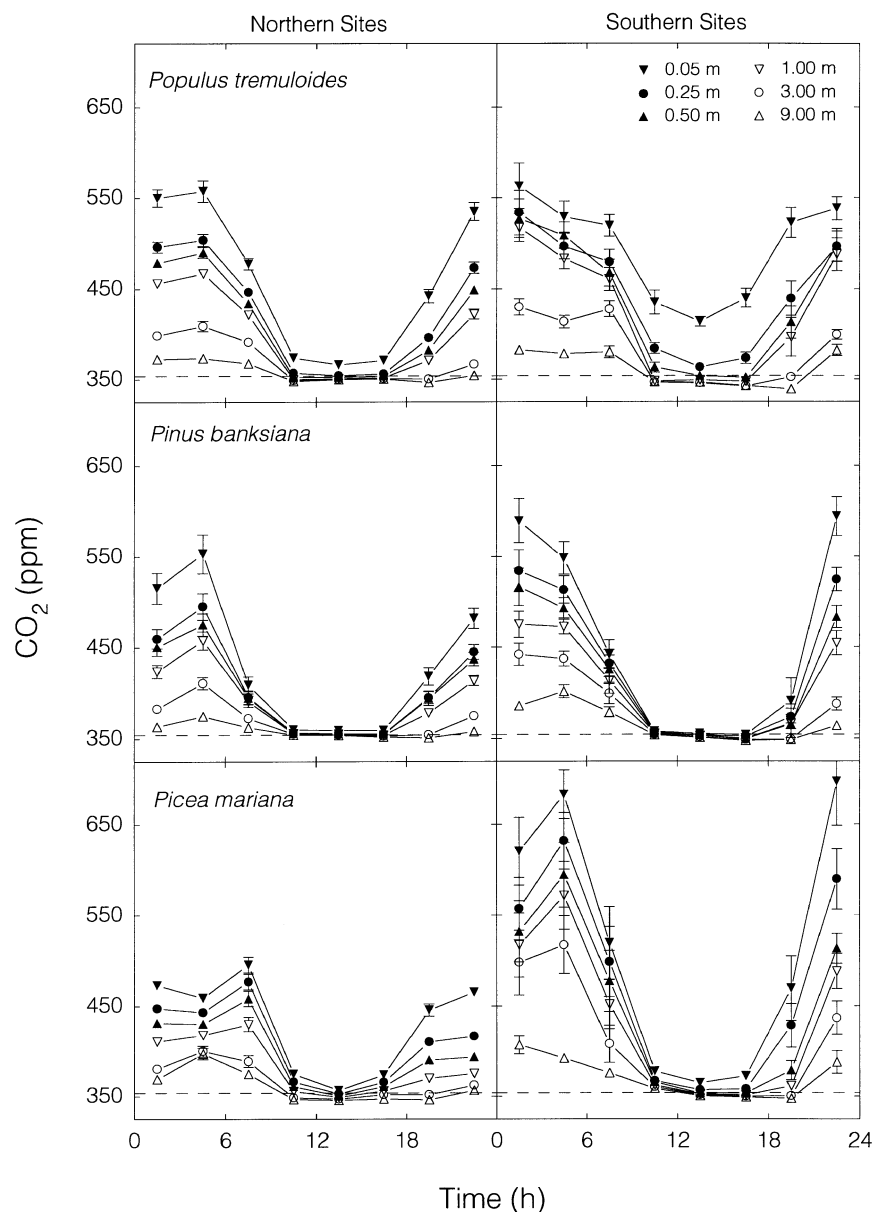To determine the average daytime [$CO_2$] for photosynthesis at different heights in the canopy, we weighted the observed

Figure 5. Daily patterns of [$CO_2$] at six heights in the canopy for all stands in the NSA and SSA. Means of values over 2–5 days ± SE are presented. The dashed line represents tropospheric $CO_2$ concentration in Mould Bay, Canada (354 ppm, July 1994, provided by T. Conway, NOAA/CMDL). Split-plot ANOVAs were calculated for each stand with time as the main factor and height within time as the split-plot factor. For *Populus*, the $r^2$ of the ANOVA model was 0.80 ($F = 243$, $P < 0.0001$) in the NSA and 0.72 ($F = 31$, $P < 0.0001$) in the SSA. For *Pinus*, $r^2 = 0.50$ ($F = 55$, $P < 0.0001$) in the NSA and 0.76 ($F = 33$, $P < 0.0001$) in the SSA. For *Picea*, $r^2 = 0.71$ ($F = 140$, $P < 0.0001$) in the NSA and 0.59 ($F = 16.5$, $P < 0.0001$) in the SSA.

diurnal changes in [$CO_2$] by observed changes in photosynthetic rates for each canopy height (Table 3). Early in the growing season (May–June), $CO_2$ gradients within the canopies were small and not statistically significant, with the exception of the *Picea mariana* canopy in the NSA, where understory foliage was exposed to a [$CO_2$] 18 ppm higher than foliage at the top of the canopy. In the middle of the growing season (July), almost all of the stands had significantly higher understory [$CO_2$] compared to the top of the canopy. In September, the gradients were generally smaller, although still significant for most sites. Throughout the growing season, gradients were smaller in *Pinus banksiana* stands than in *Picea mariana* stands. The *Populus tremuloides* stand in the SSA and the *Picea mariana* stand in the NSA had consistently larger gradients than the other stands; the [$CO_2$] in the understory of

these two stands was 10–30 ppm greater than the concentration in the upper canopy. At the other sites, the canopy gradient rarely exceeded 10 ppm. Throughout the season, changes in [$CO_2$] at the top of the canopy reflected the annual cycle of [$CO_2$] in the well-mixed surface layer (surface layer concentrations: 363 ppm May–June, 354 ppm July, 349 ppm September, for Mould Bay, Canada, provided by T. Conway NOAA/CMDL).

Soil surface concentrations of $CO_2$ were always higher than $CO_2$ concentrations at any other canopy level (Figure 5). Soil respiration in the three forest ecosystems had distinct temperature response curves (Figure 8), and soil temperatures were also variable among sites. In July, mean soil temperatures at a depth of 10 cm in the NSA and SSA, respectively, were 6.7 and 9.9 °C for *Picea mariana* stands, 12.1 and 13.2 °C for *Populus*
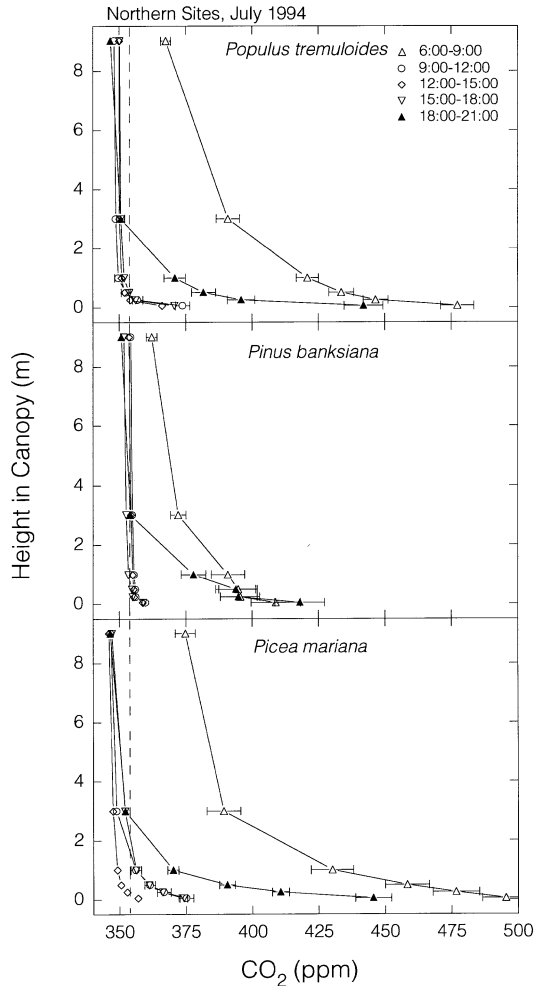
Figure 6. Daytime canopy profiles of [$CO_2$] for sites in the NSA. Data are a subset of the data presented in Figure 5.



Figure 7. Daytime canopy profiles of [$CO_2$] for sites in the SSA. Data are a subset of the data presented in Figure 5.

*tremuloides* stands, and 13.2 and 15.6 °C for *Pinus banksiana* stands. As a result, soil respiration rates only varied by 4 to 6 $\mu$mol m$^{-2}$ s$^{-1}$ among sites.

*Refixation of respired CO₂*

We used two methods to estimate the amount of $CO_2$ refixed within the canopy (Table 4). We excluded *Populus tremuloides* stands from these estimates because our sampling masts were below the top of the canopy in these stands and because *P. tremuloides* was not present in the understory. Refixation at the top of the canopy was assumed to be zero. Refixation of respired $CO_2$ increased in lower canopy positions (Table 4). Leaves in the middle canopy generally fixed less than 1% of the carbon from respired sources. The highest rates of refixation were found in seedlings 0.10–0.25 m above the forest floor. Estimated rates ranged from 0 to 15% refixation, with an average of 6% at 0.25 m. Estimates varied as much between methods as between forest ecosystems and locations. In general, the $CO_2$ profile method predicted lower rates of refixation than the gas exchange method. Within a method, *Picea mari-*
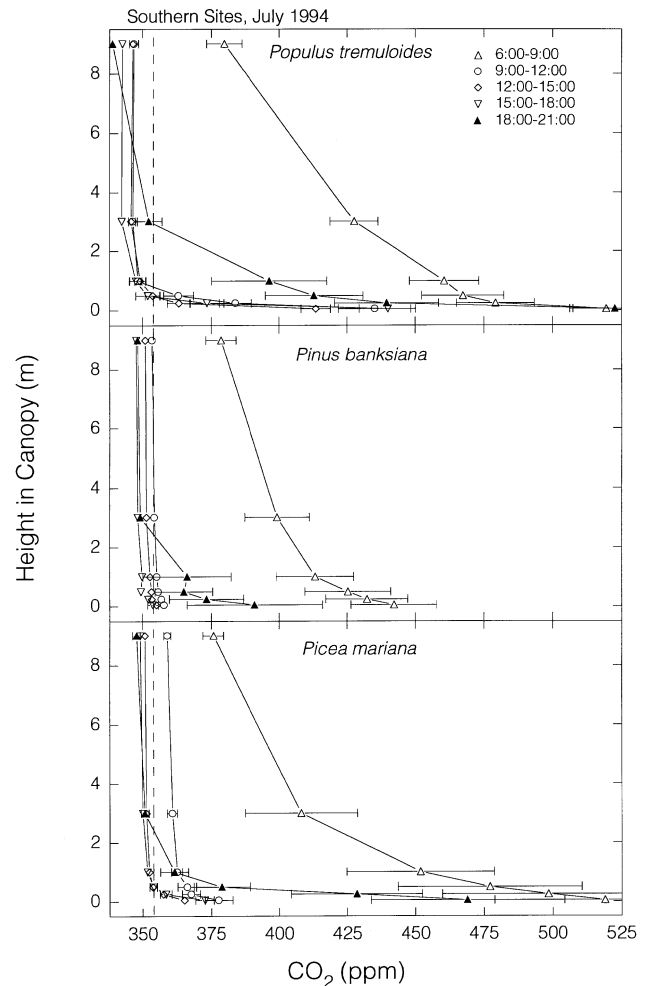
*ana* stands had higher refixation rates (7.5% average) than *Pinus banksiana* stands (4.5% average), with no apparent difference between northern and southern sites.

**Discussion**

The gas exchange rates reported here for boreal tree species are similar to previously published values (Lawrence and Oechel 1983, Ceulemans et al. 1987 for *Populus*; Stewart and Hoddinott 1993 for *Pinus banksiana*; Hom and Oechel 1983 for *Picea mariana*). Although differences in $A_{max}$ existed among species, these were largely explained by variation in leaf nitrogen concentrations. Foliage nitrogen concentrations (per dry weight) in the NSA were 2.0 ± 0.03% in *Populus tremuloides*, 1.1 ± 0.1% in *Pinus banksiana*, and 0.7 ± 0.09% in *Picea mariana* (H. Margolis and Q. Dang, unpublished data). For *Pinus banksiana* and *Picea mariana*, values of $A_{max}$ were lower in the NSA than in the SSA, but nitrogen differences between locations did not sufficiently explain this photosynthetic difference (M. Ryan and M. Lavigne, unpublished data). Lower

Table 3. Concentration of $CO_2$ weighted by photosynthesis to represent the average $[CO_2]$ for photosynthesizing leaves at different canopy levels. Each mean ($\pm$ SE) represents the weighted average of two to five $CO_2$ diurnals. Weighted averages within each gradient followed by the same letter are not significantly different ($\alpha = 0.05$, Tukey-Kramer Honestly Significant Differences Test). Asterisks denote significantly different canopy $[CO_2]$ gradients (* $P > 0.05$, ** $P > 0.01$, and *** $P > 0.001$); ND indicates no data available.

| | Pinus banksiana | | Picea mariana | | Populus tremuloides | |
|---|---|---|---|---|---|---|
| | NSA | SSA | NSA | SSA | NSA | SSA |
| *May–June* | | | | | | |
| 9 m | $362.2 \pm 0.6$ a | $353.1 \pm 0.5$ a | $360.3 \pm 1.9$ a | $364.2 \pm 0.8$ a | $357.6 \pm 0.9$ a | ND |
| 3 m | $362.6 \pm 0.7$ a | $352.8 \pm 0.5$ a | $355.7 \pm 1.1$ a | $363.4 \pm 0.5$ a | $356.1 \pm 0.8$ a | ND |
| 0.5 m | $362.9 \pm 0.7$ a | $354.9 \pm 1.4$ a | $375.1 \pm 2.5$ b | $364.8 \pm 0.8$ a | $358.7 \pm 1.1$ a | ND |
| 0.25 m | $363.2 \pm 0.7$ a | $355.7 \pm 1.6$ a | $378.2 \pm 2.4$ b | $365.9 \pm 1.0$ a | $358.3 \pm 1.3$ a | ND |
| Gradient | 1.0 | 2.6 | 17.9 *** | 1.7 | 0.7 | |
| *July* | | | | | | |
| 9 m | $353.1 \pm 0.5$ a | $354.1 \pm 0.6$ a | $349.0 \pm 0.6$ a | $356.3 \pm 1.7$ a | $351.5 \pm 0.6$ a | $352.3 \pm 2.4$ a |
| 3 m | $354.0 \pm 0.5$ a | $356.7 \pm 0.6$ a | $350.3 \pm 0.5$ a | $357.4 \pm 2.9$ a | $351.1 \pm 0.6$ a | $354.7 \pm 4.1$ a |
| 0.5 m | $357.9 \pm 1.1$ a | $352.9 \pm 2.9$ a | $362.2 \pm 1.3$ b | $371.2 \pm 6.6$ ab | $353.6 \pm 0.8$ b | $365.7 \pm 4.8$ ab |
| 0.25 m | $358.1 \pm 1.1$ b | $354.1 \pm 1.7$ a | $368.0 \pm 1.6$ c | $380.6 \pm 8.2$ b | $356.8 \pm 0.9$ c | $380.4 \pm 5.2$ b |
| Gradient | 5.0 *** | 0.0 | 19.0 *** | 24.3 *** | 5.3 *** | 28.1 *** |
| *September* | | | | | | |
| 9 m | $349.7 \pm 0.4$ a | $352.3 \pm 1.2$ a | $349.1 \pm 0.3$ a | $356.5 \pm 0.9$ a | $357.6 \pm 0.5$ a | $358.9 \pm 0.9$ a |
| 3 m | $351.8 \pm 0.6$ b | $358.1 \pm 2.1$ ab | $349.1 \pm 0.3$ a | $352.2 \pm 0.7$ a | $358.0 \pm 0.5$ a | $359.4 \pm 0.9$ a |
| 0.5 m | $353.0 \pm 0.8$ b | $363.8 \pm 3.2$ ab | $353.7 \pm 0.7$ b | $355.0 \pm 0.6$ a | $362.8 \pm 0.7$ b | $369.8 \pm 2.1$ b |
| 0.25 m | $352.8 \pm 0.5$ b | $365.5 \pm 3.6$ b | $356.9 \pm 1.0$ c | $357.7 \pm 1.7$ a | $365.4 \pm 1.0$ b | $377.1 \pm 4.1$ b |
| Gradient | 1.9 ** | 13.2 * | 7.8 *** | 1.2 | 7.8 *** | 18.2 *** |
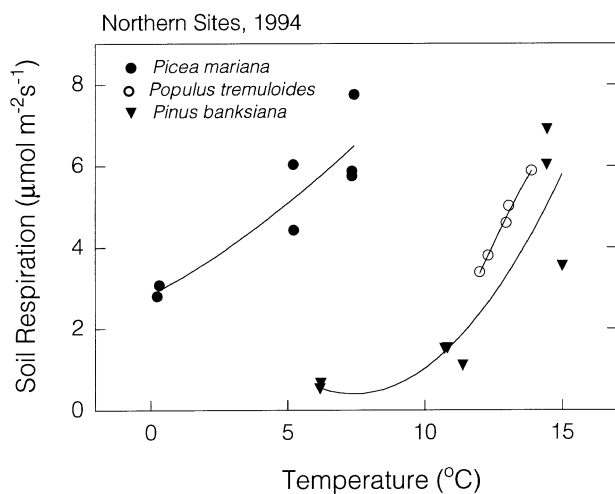


Figure 8. Soil respiration rates as a function of soil temperature (10-cm depth) for the three stands in the NSA. Data from all three field campaigns are combined.

gas exchange rates in the NSA may have been the result of differences in precipitation as well as differences in nitrogen content. In 1994, the northern sites were drier than the average summer (200 mm in 1994 versus 270 mm mean precipitation from May through August for Thompson, Manitoba, Atmospheric Environment Service, Canada), whereas the southern sites were wetter than average (255 mm for 1994 versus 220 mm mean precipitation for Prince Albert, Saskatchewan, Atmospheric Environment Service, Canada). Consistent with

water availability differences, stomatal conductances were significantly lower in the NSA. Intraspecific differences in stomatal conductance between the NSA and the SSA were greater than $A_{max}$ differences, supporting the idea that water was limiting in the NSA.

Instantaneous measures of $c_i/c_a$, which are related to intrinsic water-use efficiency, also support the idea that photosynthesis in the NSA was limited by water stress during midsummer (Figure 2). However, long-term integrated measures of $c_i/c_a$ indicated that water availability was low for a sufficient period of time to influence leaf $\delta^{13}C$ values only in midsummer in the NSA *Pinus banksiana* canopy. This finding is consistent with the observation that *Pinus banksiana* grows on sandy sites with limited capacity to retain water (Stangel et al. 1995).

We found minimal differences in sunlit foliage $\delta^{13}C$ values among the dominant boreal tree species; in contrast, previous studies from other ecosystems at lower latitudes have demonstrated large variation among dominant species (Farquhar et al. 1989, Ehleringer et al. 1992). In May–June, all three species had similar $\delta^{13}C$, but in September, *Populus tremuloides* had more negative $\delta^{13}C$ values than the conifers. Because the $\delta^{13}C$ of foliage can be related to the internal balance of water and carbon fluxes or intrinsic water-use efficiency (WUE) (Farquhar et al. 1989), we speculate that *Populus tremuloides* had lower WUE compared to the conifers. Similar differences in WUE between deciduous and coniferous trees have been reported by others (Garten and Taylor 1992, Valentini et al. 1992, Marshall and Zhang 1994). Bonan (1993) noted that differences between evergreen and deciduous trees were more important than species differences in regulating carbon balances

Table 4. Recycling in boreal coniferous forests at northern (NSA) and southern boundaries (SSA) estimated by two independent methods. Recycling is defnded as the amount of carbon in leaves that is derived from respired $CO_2$. The data were collected in July 1994.

| Canopy level | NSA $CO_2$ recycling (%) | | SSA $CO_2$ recycling (%) | |
|---|---|---|---|---|
| | $CO_2$ profile method | Gas exchange method | $CO_2$ profile method | Gas exchange method |
| *Pinus banksiana* | | | | |
| Upper | 0.0 | 0.0 | 0.0 | 0.0 |
| Middle | 0.3 | 0.4 | 0.7 | ND |
| Lower | 1.3 | 4.7 | 0.0 | 5.8 |
| Ground | 1.4 | 7.3 | 0.0 | 9.2 |
| *Picea mariana* | | | | |
| Upper | 0.0 | 0.0 | 0.0 | 0.0 |
| Middle | 0.4 | 2.1 | 0.3 | ND |
| Lower | 3.7 | 2.5 | 4.0 | 7.1 |
| Ground | 5.1 | 3.8 | 6.4 | 15.0 |

in boreal forest ecosystems. The coniferous species had similar $\delta^{13}C$ and WUE values, despite differences in habitat. *Picea mariana* inhabits the very wet nutrient-poor sites, whereas *Pinus banksiana* occupies the dry sandy sites. Marshall and Zhang (1994) also noted minimal differences between *Pinus* and *Picea* species growing over a range of environments. The similarity in $\delta^{13}C$ among species across a wide geographical area implies that these boreal trees balance water and carbon fluxes in a similar manner throughout their range.

The decline in photosynthesis from the top to the bottom of the canopy was related to light attenuation within the canopy. In *Populus tremuloides*, photosynthesis decreased by 75% within the canopy and light was attenuated by 80%. Light attenuation was similar in the *Picea mariana* stands, but because photosynthetic rates were low at the top of the canopy, we did not find significant differences in photosynthesis within the canopy. In the *Pinus banksiana* canopy, 55% of the light was attenuated and photosynthesis declined by 35%. Despite differences in light and photosynthetic decline among the species, all three canopies showed a similar increase in $c_i/c_a$ with lower canopy position (Figure 4). Because the canopies differed in light attenuation but not in the pattern of change in $c_i/c_a$, it appears that the integration of gas exchange activities within the canopy was not regulated solely by light attenuation. Light affected $c_i/c_a$ (Table 2), but other factors also seemed to play a role in determining $c_i/c_a$ gradients. Gutiérrez and Meinzer (1994) found a similar change in carbon isotope $c_i/c_a$ within the canopy over a wide range of LAI in coffee hedgerow plants. Doley et al. (1988) noted a strong relationship between stomatal conductance and photosynthesis within a rainforest canopy, but this relationship was only weakly related to irradiance. Ehleringer et al. (1986) found that the change in carbon isotope discrimination from the top to the bottom of the canopy differed for different species in a mixed tropical forest, even though the light attenuation was the same. Discrimination changed the least in the dominant shade-intol-

erant trees (1--2‰), whereas the shade-tolerant species existing lower in the canopy changed discrimination by more than 6‰. In addition to light attenuation, some intrinsic characteristic of the species, such as shade-tolerance, may influence $c_i/c_a$ changes within the canopy.

Three factors cause canopy [$CO_2$] profiles to be dynamic: turbulent mixing with air above the canopy, inputs from respired $CO_2$ and uptake of $CO_2$ by photosynthesis (Wofsy et al. 1988, Sternberg 1989, Fan et al. 1990). At night, soil $CO_2$ effluxes resulted in a build-up of canopy $CO_2$ to a maximum concentration (Figure 5). Nighttime $CO_2$ concentrations were greater in the SSA than in the NSA, reflecting the higher soil temperatures in the southern ecosystems. In the morning, canopy $CO_2$ mixes with $CO_2$ above the nocturnal boundary layer as canopy air heats up (Wofsy et al. 1988, Fan et al. 1990). During the day, turbulent mixing dominated the flux processes, but respiration and photosynthesis also influenced canopy [$CO_2$]. In both the *Populus tremuloides* and *Picea mariana* stands, $CO_2$ at the top of the canopy (346 ppm) was reduced to a concentration below that of the well-mixed layer above the canopy (354 ppm, July 1994 in Mould Bay Canada, provided by T. Conway, NOAA/CMDL; Figure 6). This was a direct result of photosynthesis, because the well-mixed surface layer $CO_2$ concentrations for a location do not vary more than 1 to 2 ppm during a summer month (Conway et al. 1994). The boreal forests studied maintained a small [$CO_2$] gradient during the day because soil respiration rates increased until mid to late afternoon as soil temperatures reached their maximum. These daytime gradients were largest in the densest stands, probably because of stand structure effects on turbulent mixing within the canopy. The open *Pinus banksiana* stands had $CO_2$ concentrations similar to the concentration of the well-mixed surface layer above the canopy and had relatively small daytime $CO_2$ gradients. In the dense *Picea mariana* stands, $CO_2$ concentrations were below surface layer values and had relatively large daytime $CO_2$ gradients. Buchmann et al. (1996) also noted increased daytime canopy $CO_2$ gradients with increased stand LAI.

Photosynthesizing foliage within the canopies experienced $CO_2$ enrichment from respired $CO_2$ (Table 3). This elevated [$CO_2$] can influence understory growth; for example, Bazzaz and Miao (1993) found that shade-tolerant species were responsive to elevated $CO_2$ under low light conditions. This growth response could be the result of increased quantum yield (Ehleringer and Björkman 1977). The greatest understory $CO_2$ enrichment occurred during midsummer when soil temperatures and respiration rates were high and when plant growth rates were high.

The elevated [$CO_2$] within canopies was a direct result of respiration; thus, a certain amount of $CO_2$ that was fixed by the canopy came from respired sources. We calculated that approximately 6% of the carbon in understory foliage originated from respired $CO_2$ (Table 4). Both *Picea mariana* and *Pinus banksiana* stands refixed respired $CO_2$ to a similar extent, even though they differed in [$CO_2$] gradients and gas exchange rates. This similarity occurred because refixation by a leaf is determined by both the photosynthetic rate and the daily pat-

tern of $[CO_2]$ within the canopy. Although $CO_2$ concentration gradients were greater in the *Picea mariana* stands, less light penetrated to the understory than in the *Pinus banksiana* stand, thus limiting photosynthesis and refixation. In the *Pinus banksiana* stand, light penetrated into the canopy for longer periods during the day; therefore, despite lower daytime $[CO_2]$ gradients, understory foliage was fixing carbon during the early morning draw-down and late afternoon build-up of $CO_2$.

Sternberg et al. (1989) estimated that, in a tropical forest on Barro Colorado Island, Panama, leaves in the understory obtain between 13 and 18% of their carbon from respired sources. Vogel (1978) estimated a value of 15% for a mixed deciduous forest in Southern Germany, but did not account for $c_i/c_a$ effects on $\delta^{13}C$ in leaves, so this value should be lower. In our study, much of the vertical gradient in $\delta^{13}C$ of leaves was a result of physiological differences ($c_i/c_a$, Figure 4), but a portion was a result of the $\delta^{13}C$ of source air. For these boreal forests, the isotopic composition of source $CO_2$ accounted for 20% of the gradient in leaf carbon isotope values. A small amount of respired $CO_2$ can make a large difference in leaf isotopic values because above-canopy source $CO_2$ and respired $CO_2$ vary in $\delta^{13}C$ by about 20 (respired $CO_2$ $\delta^{13}C = -26$ to $-27$‰; well-mixed surface layer $CO_2$ $\delta^{13}C = -7.5$ to $-8$‰, M. Trolier, University of Colorado-INSTAAR). Sternberg et al. (1989) estimated that, for a tropical forest, source $CO_2$ could account for roughly 30–70% of the difference in leaf carbon isotope values between the top and bottom of the canopy.

Sternberg (1989) estimated that between 7 and 8% of the respired carbon dioxide in the Barro Colorado Island stand was refixed by the canopy. Lloyd et al. (1996) modeled leaf refixation for entire canopies in both tropical and boreal ecosystems. They estimated that the tropical canopy refixed twice as much $CO_2$ (4% daily average) as the boreal canopy (2% daily average), and related this difference to ecosystem respiration. Both leaf refixation and canopy recycling estimates indicate that most of the carbon fixed by the canopy came from the atmosphere above the canopy, and most carbon respired from the ecosystem was lost to the atmosphere. Thus, the internal cycling of carbon within the stand is a relatively small component of the carbon cycle. Although these canopy-level recycling estimates were similar to the estimates of leaf refixation reported here, they represent different events. Our leaf refixation describes how much of the carbon fixed by a specific leaf came from respired sources, whereas Sternberg (1989) estimated the percentage of respired $CO_2$ refixed by the entire canopy as opposed to being lost to the atmosphere through turbulent mixing.

Although the boreal forest is a diverse mosaic of different ecosystems, the six stands studied were comparable in carbon refixation and in the way they internally balanced water and carbon fluxes. This similarity allows the physiological control over carbon and water fluxes to be considered at the regional scale. For example, it has been found that boreal forests exert strong stomatal control over regional water vapor fluxes and that the boreal vapor fluxes (less than 2 mm day$^{-1}$) are generally lower than those in temperate regions (Sellers et al. 1995). Our results suggest that stomatal closure will also limit carbon

assimilation at these sites. Sellers et al. (1995) found that the photosynthetic capacity of boreal forests was much lower than that of temperate forests. This tight physiological control over water and carbon fluxes and the similarity among forest ecosystems across their range will facilitate linking models that predict net primary production (Melillo et al. 1993) and atmospheric processes on a global scale.

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