Photosynthesis and respiration of black spruce at three organizational scales: shoot, branch and canopy

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Summary To gain insight into the function of photosynthesis and respiration as processes operating within a global ecosystem, we measured gas exchange of mature black spruce (Picea mariana (Mill.) B.S.P.) trees at three organizational scales: individual shoots, whole branches and a forest canopy. A biochemical model was fitted to these data, and physiological parameters were extracted. Pronounced seasonal variation in the estimated model parameters was found at all three organizational scales, highlighting the need to make physiological measurements throughout the year. For example, it took over 100 days for physiological activity to increase from zero during the springtime thaw to its yearly maximum. Good agreement was found between parameter values estimated for the different organizational scales, suggesting that, in the case of aerodynamically rough, largely mono-specific forest canopies, physiological parameters can be estimated from eddy covariance flux measurements. The small differences between photosynthetic parameters estimated at the different scales suggest that the overall spatial organization of photosynthetic capacity is nearly optimized for carbon uptake at each scale.

Keywords: BOREAS, Picea mariana, scaling.

Introduction

In recent years, considerable effort has been put into large-scale field experiments aimed at improving our understanding of the interactions between the land surface and the lower atmosphere (e.g., FIFE (Sellers et al. 1992), BOREAS (Sellers et al. 1997)). A major objective has been to develop and parameterize simulation models of the processes controlling the exchange of gases and energy between the biosphere and the atmosphere. The parameterized models, together with remote sensing, can then be used to facilitate the integration of these processes over areas larger than the initial study site (e.g., a land surface parameterization for the entire boreal forest from two sites in central Canada). The parameterized models also enable computer simulations of the likely biological effects of possible future climates.

The extraction of physiologically meaningful parameters from measured flux data is an essential part of this modeling procedure because such parameters can help us understand how mass and energy fluxes can be scaled up in space and time. Analysis of physiological parameters may also help us understand the biology of the ecosystem. For example, physiological parameters could be used to determine whether variation in growth rates of branches at different heights in the canopy is a straightforward consequence of different incident photon flux densities (PFD), or whether branches become physiologically acclimated to their differing light environments. Similarly, physiological parameters could be used to determine if part of the seasonality observed in ecosystem behavior is a function of biological changes in the biosphere and not simply a reflection of seasonality in the climate. Physiological parameters also provide a basis for quantitative comparisons of ecosystem function among different ecosystems.

The time constants of most biological control processes vary from minutes to years, and their assessment is essential for predicting the behavior of vegetation canopies. If model parameterizations based on short-term measurements of physiological behavior are inappropriate for the whole season, the biological function must be monitored throughout the year and perhaps over a number of years. A convenient way of acquiring long-term data for foliage in a forest ecosystem is with automated branch bags that measure gas exchange of whole branches by infrared gas analysis (Dufrêne et al. 1993, Saugier et al. 1997). From data collected over a long period, it is possible to derive model parameters from the natural variation in the driving environmental variables.

A complete description of photosynthesis, however, is only possible when the physiology is studied outside the range of normal environmental variation. This is particularly true in the case of the response of photosynthesis to increased concentrations of CO2. Conventional methods used to characterize ecophysiological functions (e.g., stomatal action or photosynthetic capacity) are typically carried out at the tissue or organ scales, and the results scaled up to the whole canopy. In practice, however, the procedures used for scaling between organizational scales are seldom validated. This is primarily because measurements of whole-canopy exchanges made, for example, with the eddy covariance technique, measure the summation of all the ecosystem exchange processes, of which canopy
exchange is but one. Therefore, before whole canopy data can be used to validate scaling methods, the other biotic processes (notably heterotrophic respiration in the soil) need to be accounted for.

It may be possible to scale up measurements made at the leaf or shoot scale to some intermediate scale (e.g., the branch), enabling validation of the procedures against direct measurements at a range of scales. Success in scaling from leaf to branch then gives the confidence to apply these procedures to scaling from leaves to the entire canopy.

This paper describes a study of photosynthesis and respiration of the most extensive Canadian boreal forest tree species, black spruce (*Picea mariana* (Mill.) B.S.P.), based on gas exchange measurements made at three organizational scales: shoot, branch and canopy. Variation in physiological parameters over the course of a year and between organizational scales was investigated. Transpiration and conductance measurements were made at the same time and are described in a companion paper (Rayment et al. 2000).

**Materials and methods**

The study was made at the BOREAS southern study area (SSA) old black spruce (OBS) site in northern Saskatchewan, Canada, during 1996. A full description of the site is given by Jarvis et al. (1997).

**Gas exchange**

**Shoot measurements** In July and October 1996, measurements were made on shoots in the upper, mid- or lower crown of four black spruce trees. Each measured shoot had a total needle area of about 70 cm$^2$ and comprised four to seven needle age classes (typically, needles were retained for up to 10 years). One intercellular CO$_2$ concentration ($c_i$) and one photosynthetic photon flux density (400 to 700 nm) ($Q$) response curve of net CO$_2$ assimilation rate, transpiration and stomatal conductance was made for each of 14 shoots in July and six shoots in October using an open gas exchange system (Compact Minicuvette System, Walz, Effeltrich, Germany). Shoots were positioned in the cuvette and received bilateral illumination from two fiber-optic illuminators (Walz) comprising 200 parallel optical fibers applied to the glass lid of the cuvette at a distance of 3 cm from the needle surface. The $c_i$ response curves were determined by varying ambient CO$_2$ mole fraction ($c_a$) from 1500 to 0 µmol mol$^{-1}$ in saturating $Q$ (1500 µmol m$^{-2}$ s$^{-1}$ at the needle surface). The $Q$ response curves were determined by varying $Q$ from 1100 to 0 µmol m$^{-2}$ s$^{-1}$, with ambient CO$_2$ concentration ($c_a$) set to 1500 µmol mol$^{-1}$. Air temperature was set at 17.5 °C, and dew point temperature was set at 8 °C. Because illumination was bilateral, gas exchange was calculated on an illuminated needle area basis, i.e., 2.54 times projected area.

In July, temperature responses of gas exchange were determined for five shoots both in the dark and at an irradiance of 1200 µmol m$^{-2}$ s$^{-1}$. These measurements were repeated on six different shoots in October. After several hours acclimation to 20 °C, each shoot was placed in the cuvette at 30 °C. Data were recorded when gas exchange reached a steady state. The temperature response measurements were repeated as the cuvette temperature was decreased from 30 to 5 °C, in 5 °C steps. At each temperature, an equilibration time of about 40 min was required. Based on the assumption that daytime shoot respiration rates are similar to nighttime shoot respiration rates, the temperature response of shoot respiration was determined with the protocol described, but with the cuvette enclosed in aluminum foil.

After completion of the gas exchange measurements, the shoots were excised. The needles of each shoot were dried at 65 °C and weighed according to their age class. Total needle surface area was estimated based on values of specific needle area measured on 30 samples each of five needles. The total surface areas of the 30 samples were calculated from their length and width assuming a rhomboidal cross section with a shape factor (i.e., the ratio of total to projected area) of 2.54. A different specific needle area was applied to each needle age class, but no significant differences in specific needle area were found with respect to needle location in the crown. Total N and P contents of the needles were determined after digestion in hot sulfuric acid by the Kjeldahl method and molybdate ascorbate method, respectively, using an automated analyzer (Autoanalyzer II, Technicon, Dublin, Ireland). In October, subsamples of fresh needles of each shoot were frozen in the field and transported to the laboratory for chlorophyll analysis.

**Branch measurements** We used ventilated closed-system branch bags according to the methodology developed at the Université Paris Sud-Orsay (Dufréne et al. 1993). The branch bags have been described by Rayment and Jarvis (1999a) and Rayment et al. (2000), and are discussed only briefly here. Two branch bags were installed on each of two trees, one bag positioned in the upper canopy (8 m height) and one in the lower canopy (5.3 m height). Modal tree height was about 10.2 m. Water vapor and CO$_2$ exchange were measured on each branch every 20 min, together with air and leaf temperature, incident $Q$ and relative humidity. At the end of the year, the branches were excised and needle area, needle and wood dry mass and chlorophyll and nutrient contents were measured for current-year and all previous years' needles (see Rayment and Jarvis 1999a).

**Canopy measurements** An eddy covariance flux measuring station was installed with the anemometer and gas analyzer intake positioned at 27 m height. The system comprised a closed path infrared gas analyzer (LI-6262, Li-Cor, Lincoln, NE), an ultrasonic anemometer (Solent A1012R, Gill Instruments, Lymington, England) and Edinburgh EdiSol software. The full technical specification is described in detail by Moncrieff et al. (1997). An automatic weather station mounted close to the eddy flux system recorded a full suite of meteorological data. A complete description of the equipment installation is given by Jarvis et al. (1997).

Tree canopy CO$_2$ exchange data were extracted from the net ecosystem flux data by correcting for the simultaneous fluxes of CO$_2$ from soil respiration and moss photosynthesis. The measurement and spatial integration methods used to deter-
mine soil respiration are described by Rayment and Jarvis (1997) and Rayment and Jarvis (1999b), respectively. Moss photosynthetic rates were predicted from data provided by L.B. Flanagan (Carleton University, Ottawa, ON, Canada). The fluxes measured at the canopy scale differed from measurements made at the shoot and branch scales in that the data represented a 30-min mean rather than measurements over shorter periods.

Model parameterization: photosynthesis

**Shoot measurements** Net CO₂ assimilation rate ($A; \text{µmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), transpiration ($E; \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$), stomatal conductance for water vapor ($g_c; \text{mmol H}_2\text{O m}^{-2} \text{ s}^{-1}$) and for CO₂ ($g_c; \text{mmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and substomatal intercellular CO₂ mole fraction ($c_i$) were calculated according to von Caemmerer and Farquhar (1981). A full description of the calculation of the boundary layer and stomatal conductances, and the models derived to describe them are given in Rayment et al. (2000). Maximal velocity of carboxylation ($V_{\text{max}}$), observed maximal electron transport rate ($J_{\text{max}}; \text{µmol e}^{-} \text{ m}^{-2} \text{ s}^{-1}$), daytime “dark” respiration ($R_d; \text{µmol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and apparent quantum efficiency of electron transport ($\alpha; \text{µmol e}^{-} \text{ µmol CO}_2^{-1}$) were determined from the response curves obtained with each shoot (assuming that CO₂ mole fractions in chloroplasts ($c_i$) and substomatal intercellular spaces ($c_i$) were equal), based on the photosynthesis model proposed by Farquhar et al. (1980) and modified by subsequent authors (Harley et al. 1992, Lewis et al. 1994, Walcroft et al. 1997).

All model parameters were extracted from the data by least squares analysis using the SAS NLIN or REG procedures.

**Branch measurements** Branch bag data were used only when the regression line through the concentration versus time data points (from which the flux was calculated) fitted the data with an $r^2$ value $> 0.95$. Photosynthetic models were fitted only to data collected in the daytime, defined as the period when incident $Q$ was $> 3 \text{ µmol m}^{-2} \text{ s}^{-1}$.

The von Caemmerer and Farquhar (1981) model of photosynthesis describes carbon assimilation rate as the minimum of two potential limitations: the carboxylation-limited rate ($A_c$) and the RuBP regeneration (electron transport)-limited rate ($A_d$). Parameters $V_{\text{max}}, J_{\text{max}}$, and $\theta$ (the convexity of the light response curve of $J_{\text{max}}$) are typically determined by analysis of the response of photosynthetic CO₂ uptake to experimental changes in $c_i$. Despite only a limited natural variation in $c_i$ in our study (330 µmol mol$^{-1}$ $< c_i < 400$ µmol mol$^{-1}$ for all branches), it was possible to determine analytically the environmental criteria under which the photosynthetic rate could be guaranteed to be limited by either carboxylation or RuBP regeneration. Figure 1a shows an analysis of a part of the Farquhar model. It is clear that, for the range of $c_i$ experienced, photosynthesis proceeds at the carboxylation-limited rate ($A_c$) when needle temperature is below 25 °C and $Q$ is above 500 µmol m$^{-2}$ s$^{-1}$. Similarly, Figure 1b illustrates that photosynthesis proceeds at the RuBP regeneration-limited rate ($A_d$) when $c_i$ is between 330 and 400 µmol mol$^{-1}$, $Q$ is less than 170 µmol m$^{-2}$ s$^{-1}$ and needle temperature is above 15 °C.

These criteria were obtained by iteratively setting criteria under which photosynthesis was limited by carboxylation in order to determine $V_{\text{max}}$, then prescribing this parameter and $\theta$ (0.677) and fitting the full Farquhar model to all daytime data to determine $J_{\text{max}}$. Parameters $R_d$ and $\alpha$ were estimated from the $A-Q$ response function at $Q < 50$ µmol m$^{-2}$ s$^{-1}$.

These conditions provided enough data points for accurate determination of $V_{\text{max}}$ by nonlinear regression. The more severely restricting conditions imposed to ensure limitation by RuBP regeneration (high temperature plus low light) resulted in fewer data being available to estimate the parameters describing this limitation. In addition, when environmental conditions were such that photosynthesis was limited by $A_d$ (i.e., high temperature plus low light), the actual electron transport rate was much less than $J_{\text{max}}$ (see Figure 1a), so $J_{\text{max}}$ could be estimated only by extrapolation. Consequently, the confidence intervals for $J_{\text{max}}$ and $\theta$ were broad. Moreover, parameters $J_{\text{max}}$ and $\theta$ are highly correlated when obtained by fitting the model to measurements made in normal environmental conditions. Therefore, $\theta$ was fixed at the value found at the shoot scale (0.677) and $J_{\text{max}}$ was determined by first estimating $V_{\text{max}}$ (based on the low temperature plus high light criteria), then prescribing this parameter in a procedure to fit the full Farquhar model to all the daytime data. The temperature response parameters for $V_{\text{max}}, J_{\text{max}}$, and $R_d$ were set equal to the values determined at the shoot level. To investigate changes in these parameters over time, the data were grouped into consecutive 20-day periods.

**Canopy measurements** Effects of changes in CO₂ concentration of the air column below the eddy covariance sensor (the so-called storage flux) were added to the eddy covariance data to yield the biotic flux, i.e., biotic flux = eddy flux + storage flux. From this biotic flux, the forest floor CO₂ flux (Rayment and Jarvis 1999b) was subtracted, resulting in a measure of gas exchange of the aboveground parts of the canopy. Parameters for the Farquhar model of photosynthesis were extracted from the canopy data by the same iterative process as for the branch data. Likewise, the canopy data were also grouped into consecutive 20-day periods. The temperature response parameters for $V_{\text{max}}, J_{\text{max}}$, and $R_d$ were set equal to the values determined at the shoot level, and $R_d$ and $\alpha$ were estimated from the $A-Q$ response function at $Q < 50$ µmol m$^{-2}$ s$^{-1}$.

**Model parameterization: respiration**

An Arrhenius “activation energy” temperature response (e.g., Lloyd and Taylor 1994) was fitted to the shoot, branch and canopy data collected when $Q = 0$ µmol m$^{-2}$ s$^{-1}$. The model was of the form:

$$R_T = R_{20} \cdot \exp \left( \frac{E_o}{293.15} \left( 1 - \frac{293.15}{T} \right) \right),$$

where $R_T$ is CO₂ efflux rate (µmol CO₂ m$^{-2}$ s$^{-1}$) at needle temperature $T$ (K), $R_{20}$ is efflux rate at 20 °C, $R$ is the gas constant (8.314 J mol$^{-1}$ K$^{-1}$) and $E_o$ is the activation energy (56,734 J mol$^{-1}$ K$^{-1}$) determined from shoot measurements.
Although for needle-leaf plants $R_t$ and $T$ are usually well coupled, needle temperature was used as the driving variable for the shoot and branch flux measurements, but air temperature was used for the canopy measurements. For both the branch- and canopy-scale measurements, the data were grouped into consecutive 20-day periods, and the respiration models were fitted to the data when incident $Q = 0$. The canopy data were further screened to exclude periods when turbulence was considered too low for the eddy covariance technique to produce reliable data, thus the models were fitted to data collected when the friction velocity ($U_z$) was above 0.35 m s$^{-1}$ (Jarvis et al. 1997). Because the majority of nighttime respiration derives from soil efflux (M.B. Rayment, poster presentation at the XXth EGS Conference, Hamburg, Germany, 1995), and the estimate for the spatially integrated rate of soil efflux was itself derived from a model in which the main driving variable was temperature (Rayment and Jarvis 1999b), net ecosystem flux data were not corrected for soil CO$_2$ efflux to avoid the circularity of fitting a model to model-derived data.

### Results

#### Shoot photosynthesis

Table 1 shows the values of $V_{\text{max}}$, $J_{\text{max}}$, $\theta$, $R_d$ and $\alpha$ in shoots in July and October. There was no relationship between $V_{\text{max}}$ and the position of the shoot in the canopy; however, there was a significant difference ($P < 0.05$) in $J_{\text{max}}$ between the upper and lower canopy. Between July and October, $V_{\text{max}}$ tended to decrease in shoots in the middle of the canopy, whereas $J_{\text{max}}$, $\theta$ and $\alpha$ measured in the same shoots decreased significantly ($P < 0.05$) over the same period. Estimated mean values of $V_{\text{max}}$, $J_{\text{max}}$, $R_d$ and $\alpha$ for shoots are superimposed on the estimates of these parameters for branches and the canopy in Figure 2.
Neither nitrogen (N) nor phosphorus (P) concentration of the needles used for gas exchange measurements differed significantly between crown levels (Table 2). In contrast, there was a significant effect ($P < 0.05$) of needle age class on needle P concentration, with the highest concentration in the youngest needles. This effect was almost significant ($P = 0.078$) for N concentration. Specific needle area did not differ between crown levels but was significantly higher ($P < 0.05$) in the current-year needles, i.e., age class 1996, than in older needles. The patterns of distribution of N and P were still significant when N and P concentrations were expressed on a surface area basis, i.e., when age differences were not accounted for by the differences in specific needle area.

**Branch photosynthesis**

Figure 2 shows the values of $V_{\text{max}}$, $J_{\text{max}}$, $R_d$ and $\alpha$ derived for the branches for successive 20-day periods. There was pronounced seasonality in both $V_{\text{max}}$ and $J_{\text{max}}$ for successive 20-day periods. There was no evidence of photosynthetic acclimation to seasonal temperature change (D. Loustau et al., unpublished data). Between the springtime thaw and Day 140, there was a gradual decrease in temperature sensitivity. Between Day 140 and Day 300, $E_0$ varied little. After Day 300, temperature sensitivity increased rapidly. There were no consistent significant differences among the respiration parameters for the different branches, although differences between individual 20-day periods were significant.

**Canopy respiration**

The seasonal time courses of the parameters for the net ecosystem response of respiration to temperature are given in Figure 3. After an initial decline, $R_{20}$ increased until the middle of the year, then decreased to nearly zero by the end of the measurement period. Nighttime respiration rates measured at the start and end of the measurement period were similar. There was considerable variation in $E_0$ throughout the year, although the 95% confidence limits were large.

**Discussion**

**Temporal variation**

Large variation in photosynthesis and respiration parameters over time is an important characteristic of this boreal forest. There was a marked ramping up of the parameters describing biochemical activity ($V_{\text{max}}$, $J_{\text{max}}$, and $\alpha$) from the time that air temperature first rose above zero at the start of the season (Day 98; see Figure 2). This steady rise in activity continued even after air temperature had reached a seasonal maximum and daily incident $Q$ had started to decrease. Parameter $V_{\text{max}}$ continued to increase until a severe drop in air temperature occurred around Day 250, whereupon it started to decline. Despite the large seasonal variation in $V_{\text{max}}$ and $J_{\text{max}}$, the temperature responses of these parameters changed little between summer and winter, i.e., activation energies were constant and there was no evidence of photosynthetic acclimation to seasonal temperature change (D. Loustau et al., unpublished data). For the branches and the canopy, a large part of the annual variation in $V_{\text{max}}$ was closely correlated with changes in

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<table>
<thead>
<tr>
<th>Period</th>
<th>Shoot position</th>
<th>$V_{\text{max}}$ ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$)</th>
<th>$J_{\text{max}}$ ($\mu$mol e$^{-}$ m$^{-2}$ s$^{-1}$)</th>
<th>$\theta$</th>
<th>$R_d$ ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$)</th>
<th>$\alpha$ (mol e$^{-}$ mol$^{-1}$ quanta)</th>
</tr>
</thead>
<tbody>
<tr>
<td>July</td>
<td>Upper (6)</td>
<td>16.0 ± 5.5</td>
<td>64.1 ± 15.6</td>
<td>0.64 ± 0.10</td>
<td>0.72 ± 0.27</td>
<td>0.24 ± 0.07</td>
</tr>
<tr>
<td>July</td>
<td>Mid (5)</td>
<td>15.8 ± 4.1</td>
<td>47.1 ± 6.5</td>
<td>0.73 ± 0.09</td>
<td>0.53 ± 0.55</td>
<td>0.21 ± 0.03</td>
</tr>
<tr>
<td>July</td>
<td>Lower (3)</td>
<td>23.7 ± 9.5</td>
<td>46.6 ± 10.9</td>
<td>0.66 ± 0.13</td>
<td>0.75 ± 0.92</td>
<td>0.24 ± 0.08</td>
</tr>
<tr>
<td>Oct</td>
<td>Mid (6)</td>
<td>13.5 ± 2.6</td>
<td>26.9 ± 12.8</td>
<td>0.43 ± 0.28</td>
<td>0.45 ± 0.21</td>
<td>0.06 ± 0.04</td>
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</tbody>
</table>

**Branch nighttime respiration**

Figure 3 shows the seasonal time courses of parameters for the temperature response of nighttime respiration for the branches. The $R_{20}$ was significantly higher ($P < 0.05$) around Day 100 and Day 300 than in the middle of the year, although the highest respiration rates were observed in the middle of the year. Between the springtime thaw and Day 140, there was a gradual decrease in temperature sensitivity. Between Day 140 and Day 300, $E_0$ varied little. After Day 300, temperature sensitivity increased rapidly. There were no consistent significant differences among the respiration parameters for the different branches, although differences between individual 20-day periods were significant.
This suggests that the observed seasonality in $V_{\text{max}}$ reflects a seasonal change in photosynthetic activity at the biochemical level rather than at the environmental level, and any direct effects of temperature on $V_{\text{max}}$ must have been mainly limited to short-term (diurnal) temperature variations. Dang et al. (1998) reported that differences between photosynthetic
Table 2. Specific needle area (± 95% confidence intervals) and needle nutrient concentrations averaged with respect to age class and vertical position in the canopy in 1996 at the BOREAS SSA OBS site. In July 1996, needles were sampled on shoots collected at three heights in the canopy (upper, mid- and lower) from five trees with a total sample size of n = 61. In October 1996, 15 shoots were collected from the mid-canopy level only (Oct), and total sample size was n = 59.

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<tbody>
<tr>
<td>N concentration (mg g⁻¹)</td>
<td>Upper</td>
<td>5.2</td>
<td>6.3</td>
<td>7.3</td>
<td>7.2</td>
<td>7.6</td>
<td>7.1</td>
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<tr>
<td></td>
<td>Mid</td>
<td>5.8</td>
<td>6.3</td>
<td>6.8</td>
<td>6.1</td>
<td>11.0</td>
<td>7.5</td>
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<tr>
<td></td>
<td>(Oct)</td>
<td>–</td>
<td>6.4</td>
<td>7.4</td>
<td>7.5</td>
<td>7.8</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>–</td>
<td>6.6</td>
<td>6.8</td>
<td>7.0</td>
<td>6.8</td>
<td>6.8</td>
</tr>
<tr>
<td>P concentration (mg g⁻¹)</td>
<td>Upper</td>
<td>0.47</td>
<td>0.63</td>
<td>0.66</td>
<td>0.64</td>
<td>0.92</td>
<td>0.72</td>
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<td>Mid</td>
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<td>0.51</td>
<td>1.32</td>
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<td>(Oct)</td>
<td>0.49</td>
<td>0.59</td>
<td>0.60</td>
<td>0.62</td>
<td>1.01</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>–</td>
<td>0.56</td>
<td>0.59</td>
<td>0.59</td>
<td>1.03</td>
<td>0.64</td>
</tr>
<tr>
<td>Specific needle area (cm² g⁻¹)</td>
<td>Upper</td>
<td>39.6 ± 0.3</td>
<td>42.6 ± 1.7</td>
<td>38.7 ± 3.6</td>
<td>43.8 ± 2.9</td>
<td>42.2 ± 2.9</td>
<td>48.6 ± 4.1</td>
</tr>
<tr>
<td></td>
<td>Mid</td>
<td>39.7 ± 0.8</td>
<td>42.4 ± 3.7</td>
<td>40.6 ± 1.9</td>
<td>43.7 ± 1.0</td>
<td>44.7 ± 2.9</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Lower</td>
<td>41.2 ± 0.9</td>
<td>40.5 ± 1.8</td>
<td>42.0 ± 0.4</td>
<td>44.8 ± 3.8</td>
<td>48.6 ± 4.1</td>
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parameters estimated for black spruce in each of three intensive field campaigns were small; however, their earliest measurement on black spruce was made on Day 157, at the end of the ramping-up period (see Figure 2a).

Several environmental variables such as the timing of the soil thaw and freeze, the seasonal pattern of soil temperature and soil water availability, the occurrence of spring and autumn frosts, and late summer reduction in atmospheric humidity, co-varied with photosynthetic capacity ($P_{\text{max}}$) at the OBS site in 1996. All of these factors may contribute to the seasonality in $P_{\text{max}}$ in the boreal forest. However, generalizations cannot be drawn from data based on a single year of physiological observations.

The high values of $R_{20}$ around Day 100 coincided with bud burst and subsequent rapid shoot extension. The high values of $R_{20}$ late in the year, around Day 300, followed the first nighttime frosts, and probably resulted from increased demands for repair and biosynthesis. The seasonal change in the response of respiration to temperature contrasts with the assumption made by Ryan et al. (1997) that the sensitivity of black spruce respiration to temperature is constant over the year for trees at this site.

Shoot $P_{\text{max}}$, estimated from shoot $A-Q$ response curves ($4.7 ± 2.1 \mu$mol m⁻² s⁻¹), was slightly higher than the values measured by Middleton et al. (1997) for black spruce at the same site in 1994 ($3.10 ± 0.22 \mu$mol m⁻² s⁻¹). This difference presumably reflects differences between the bilateral illumination system used in the present study and the unilateral system used by Middleton et al. (1997). Bilateral illumination reduces mutual shading within a shoot (Wang and Jarvis 1990). The values of $V_{\text{max}}$ and $J_{\text{max}}$, which were derived from shoot measurements, were broadly typical of published values for other Picea species (Wullschleger 1993).

Needle N concentrations were low (Table 2), about half the value typically found in plantation-grown black spruce at similar latitudes (Lamhamedi and Bernier 1994). Needle P concentrations were less than 1 mg g⁻¹, which is considered a sign of P deficiency (Lamhamedi and Bernier 1994) (Table 2), and were found to correlate with differences in branch $P_{\text{max}}$ (Raymont and Jarvis 1999a). This correlation indicates a possible P limitation to photosynthesis. Photosynthesis, however, showed a pronounced sensitivity to ambient oxygen concentration (D. Loustau et al., unpublished observations). This suggests that, despite the low needle P concentration, photosynthesis was not limited by the triose phosphate utilization rate and that most effects of nutrient deficiency on photosynthesis were probably mediated through carboxylation activity and the electron transport rate. This is consistent with studies of the effects of N fertilization on northern latitude forests where the application of additional N significantly increased photosynthetic capacity (Mitchell and Hinckley 1993, Teskey et al. 1994, Roberntz and Stockfors 1998).

Spatial variation
Although branches in the upper canopy received almost twice as much light over the year as branches in the lower canopy (estimated from incident $Q$ multiplied by projected branch area), total carbon uptake of branches in the upper canopy was
only 38% higher than in the lower canopy (Rayment and Jarvis 1999a). There were no significant differences in $V_{\text{max}}$ or $P_{\text{max}}$ of shoots and branches with height. This finding is consistent with the almost uniform vertical distribution of specific needle area and N and P concentrations in the canopy (Table 2). However, it contrasts with the vertical stratification of photosynthetic capacity and N concentrations observed in many vegetation canopies (Field and Mooney 1986, Pearcy and Sims 1994, Hollinger 1996). This apparent lack of photosynthetic acclimation to $Q$ may be the result of the aggregation of needles into tall, narrow, dense tree crowns that do not form a closed canopy. In the study trees, the strongest gradient of light occurs horizontally along the branches, from the needles at the ends of the branches that are nearly always in sunlight, to those in the interior of the crown that are always shaded. Current-year needles growing at the ends of the branches had, on average, 13% higher N and P concentrations than older needles (Table 2), suggesting that there is some degree of optimization of N allocation, but in the horizontal rather than the vertical direction. The branch bag technique, because it integrates photosynthetic rate over the whole of the branch, would tend to obscure differences in photosynthesis resulting from N allocation patterns in the study trees.

Although separate measurements of photosynthetic parameters based on needle age were not made, it is reasonable to assume that current-year needles had higher $P_{\text{max}}$ than older needles because a reduction in photosynthetic activity in needles older than 1 year has been observed in black spruce (Hom...
In view of the theoretical difficulties in determining forest canopy (Table 4). This similarity is particularly striking, values are remarkably similar to the values we found for a boreal (Pseudotsuga menziesii (Mirb.) Franco) (8.2 µmol m\(^{-2}\) s\(^{-1}\); Price and Black 1990) and Sitka spruce (Picea sitchensis (Bong.) Carrière) (5.5 µmol m\(^{-2}\) s\(^{-1}\); Jarvis 1994), but similar to that found in black spruce at a more northerly latitude (about 3.8 µmol m\(^{-2}\) s\(^{-1}\); Goulden et al. 1997). Estimated day respiration was also lower in our study (0.18 ± 0.16 µmol m\(^{-2}\) s\(^{-1}\) than in maritime pine (0.35 µmol m\(^{-2}\) s\(^{-1}\), Douglas-fir (0.71 µmol m\(^{-2}\) s\(^{-1}\) and Sitka spruce (1.27 µmol m\(^{-2}\) s\(^{-1}\)), but slightly higher than in the more northerly black spruce stand (0.126 µmol m\(^{-2}\) s\(^{-1}\) (references as above). The value of α for our stand (0.017 ± 0.014) was similar to the values of 0.018 and 0.02 found in maritime pine (Y. Brunet et al., poster presentation cited in Ruimy et al. 1995) and Douglas-fir (Price and Black 1990), respectively, and lower than the values of 0.04 and 0.051 found in a more northerly black spruce stand (Goulden et al. 1997) and in Sitka spruce (Jarvis 1994), respectively. Compared with other coniferous ecosystems, therefore, this boreal ecosystem has rather low photosynthetic activity.

Lloyd et al. (1995) estimated leaf-area-based values for \(V_{\text{max}}\) (15.5 µmol m\(^{-2}\) s\(^{-1}\), \(J_{\text{max}}\) (29.5 µmol m\(^{-2}\) s\(^{-1}\) and \(R_d\) (0.16 µmol m\(^{-2}\) s\(^{-1}\) for a tropical rainforest canopy. These values are remarkably similar to the values we found for a boreal forest canopy (Table 4). This similarity is particularly striking in view of the theoretical difficulties in determining \(V_{\text{max}}\) and \(J_{\text{max}}\) at higher organizational scales. Notably, the canopy consists of many foliage elements subject to a wide variety of environmental conditions, so that although some elements may be operating under carboxylation limited conditions, photosynthesis in others may be limited by electron transport.

Variation in parameters between organizational scales
Not all the physiological parameters describing the functioning of this boreal forest ecosystem could be extracted at each organizational scale. For instance, canopy daytime respiration rate (\(R_d\)), calculated from the y-axis intercept of the Q response curve of canopy uptake, was particularly sensitive to errors in the corrections applied for the soil and understory CO\(_2\) exchanges, and consequently, reliable estimates of canopy daytime respiration using this method were not possible.

In Table 4, mean model parameter values estimated for each of the three organizational scales for the period Day 180 to Day 200, between 15 and 20 °C, are compared. Estimated canopy parameters that were calculated on a ground area basis have been divided by the estimated leaf area index (4.4; see Chen et al. 1997) so that all parameters are expressed on a leaf area basis. Although this is a crude method to scale between leaf and canopy, because photosynthesis is a nonlinear function of absorbed radiation and absorbed radiation is a nonlinear function of leaf area, it nevertheless provides a means by which the functional differences between organizational scales can be compared.

Most of the estimated parameters were found to vary with organizational scale. Estimated values of \(V_{\text{max}}\) and \(J_{\text{max}}\) decreased with increasing organizational scales, although the differences were not statistically significant. Values reported by Meir (1996) for \(V_{\text{max}}\) (26–59 µmol m\(^{-2}\) s\(^{-1}\) and \(J_{\text{max}}\) (40–105 µmol m\(^{-2}\) s\(^{-1}\)) measured on leaves of tropical rainforest trees were typically three times higher than values of \(V_{\text{max}}\) (15.5 µmol m\(^{-2}\) s\(^{-1}\) expressed on leaf area basis) and \(J_{\text{max}}\) (29.5 µmol m\(^{-2}\) s\(^{-1}\) expressed on leaf area basis) for the whole canopy at the same site (Lloyd et al. 1995). Jarvis (1994) observed an increase in \(P_{\text{max}}\) with scale in a study of needle, shoot and canopy photosynthesis in Sitka spruce, but this may have been largely a consequence of the rates being expressed on total projected needle area, shoot silhouette area and ground area bases, respectively. Similarly, Jarvis (1994) found that respiration increased with organizational scale from needles to shoots to canopy. In contrast, we found that differences between estimates of \(R_d\) for the different scales were not significantly different. The difficulties in estimating daytime respiration of the canopy alone have been discussed above.

There was a significant reduction in \(\alpha\) in branches compared with shoots, and in the canopy compared with branches, presumably because of more mutual shading of needles in branches than in shoots and more mutual shading in the canopy than in the branches—an effect that was not observed in Sitka spruce (Jarvis 1994).

Nighttime respiration increased significantly (\(P < 0.05\)) between branches and shoots and between the canopy and branches, reflecting the increased costs of supporting an increasing amount of biomass. The temperature sensitivity of respiration was not significantly different at any scale, even though, in the canopy, an increased proportion of autotrophic respiration takes place in the woody stem, which is relatively less well coupled to changes in air temperature.

Conclusion
The order of magnitude agreement among parameter values at the three organizational scales suggests that, at least for aerodynamically rough, largely mono-specific forest canopies, physiological parameters may be estimated from eddy covariance flux measurements with reasonable accuracy. The small differences between \(V_{\text{max}}\) and \(J_{\text{max}}\) at the different scales also suggest that the overall spatial organization of photosyn-
thetic capacity is more or less optimized for carbon uptake at each of the scales, and contrasts strongly with the threefold reduction in photosynthetic capacity found for tropical rainforests. We note that, despite the different spatial organizations of boreal and tropical forests, there is a remarkable similarity between the estimates of $V_{\text{max}}$ and $J_{\text{max}}$ for the whole canopy.

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