Variability in leaf-level CO₂ and water fluxes in *Pinus banksiana* and *Picea mariana* in Saskatchewan

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Received October 21, 1996

Summary  We measured seasonal and canopy-level gas exchange in two stands of jack pine (*Pinus banksiana* Lamb.) and one stand of black spruce (*Picea mariana* (Mill.) B.S.P.) on relatively clear days from late May until mid-September 1994. Field measurements were made with a portable infrared gas analyzer, and laboratory measurements included photosynthetic oxygen evolution and needle chemical composition. Seasonally averaged light-saturated assimilation rates in the field were 4.0 µmol m⁻² s⁻¹ in jack pine and 2.7 µmol m⁻² s⁻¹ in black spruce. Rates of assimilation and transpiration were highest in midsummer. The seasonal pattern was especially pronounced for black spruce, probably because cold soil temperatures limited early season gas exchange rates in this species. Among stands, instantaneous water-use efficiency was highest in a young jack pine stand early in the season and higher in the upper canopy foliage than in the lower canopy foliage at all sites at the end of the season. Needles of young jack pine exhibited higher photosynthetic capacity, dark respiration and needle N concentrations than needles of trees at the old site. In both species, slight acclimation to shading was manifested by reductions in photosynthetic capacity in the lower canopy foliage. In both species, first-year needles had greater photosynthetic capacity than older needles but in situ rates of CO₂ assimilation in the field showed little difference among needle age classes. In both species, there was a strong correlation between assimilation and stomatal conductance, indicating that assimilation was highly stomatal limited and that environmental factors that alter conductance (e.g., VPD) have a strong influence on CO₂ and water fluxes, especially after early season thawing concludes.

Keywords: black spruce, boreal forest, BOREAS, canopy position, jack pine, photosynthesis, shade acclimation.

Introduction

Boreal forests of the northern hemisphere comprise the second largest terrestrial biome in the world and the largest biome in North America (Larsen 1980). In North America, these forests, which are dominated by coniferous species, cover approximately 28% of the continent north of Mexico (Johnson et al. 1995). Low species diversity and frequent disturbance by fire, and more recently by logging, has led to the formation of a patchy mosaic of nearly even-aged stands that tend to be dominated by single species (Elliot-Fiske 1987).

The dominant conifers of the region are jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) B.S.P.) with white spruce (*P. glauca* (Moench) Voss) also dominant in some areas. Jack pine dominates the upland regions along with quaking aspen (*Populus tremuloides* Michx.), whereas black spruce frequently dominates low lying or poorly drained areas. Other mixed wood stands may contain the above species along with balsam fir (*Abies balsamea* (L.) Mill., tamarack (*Larix laricina* (Du Roi) K. Koch), balsam poplar (*Populus balsamifera* L.) and others.

Variations in soil water content, soil type, elevation, and other environmental factors along with disturbance history determine which species will dominate a given site (Dix and Swan 1971). For example, jack pine and quaking aspen stands tend to segregate along soil type and moisture gradients with aspen generally favoring sites on loamy soil with intermediate soil water contents, whereas jack pine favors drier and more sandy sites (Mugasha 1986).

Boreal forests may contribute significantly to global carbon and water fluxes (Tans et al. 1990). Moreover, they may also be particularly sensitive to alterations in temperature and water availability that could arise from changes in atmospheric trace gases (Harrington 1987, Schlesinger and Mitchell 1987). Increases in atmospheric trace gases such as carbon dioxide, chlorofluorocarbons, methane, nitrous oxides and tropospheric ozone have been well documented and may produce global effects on Earth’s ozone layer and climate (WMO 1986, Hansen et al. 1988). Therefore, the Boreal Ecosystem–Atmosphere Study (BOREAS) was initiated to improve our understanding of the exchange of radiative energy, sensible heat, water and trace gases between the boreal forest and the lower atmosphere (Sellers et al. 1995). An important objective of the BOREAS investigation is to obtain sufficient data to improve computer simulation models of the processes controlling gas exchanges between the atmosphere and the biota, and to assess how these might be altered by global climate change (e.g.,
Sellers et al. 1995). To achieve this goal, substantial descriptive and process-level data on key plant species are required.

One may hypothesize that the role each community type plays in regional CO\(_2\) or H\(_2\)O flux is variable because of the variation in site characteristics and species composition. However, few in situ studies have been conducted to test this hypothesis. It is also not well known whether intrinsic differences among species or environmental conditions are primarily responsible for the regulation of gas fluxes. Therefore, understanding the seasonal and interspecific variation in leaf-level fluxes of CO\(_2\) and H\(_2\)O and the controls exerted by the environment is an important component of the BOREAS program. The objectives of this study were to determine whether seasonal leaf-level gas exchange characteristics differed among the Pinus banksiana and Picea mariana sites and to assess the factors that control intraspecific variability of gas exchange at these sites.

Materials and methods

Study sites

Our study sites were located within the area defined by BOREAS as the southern study area (SSA), an area of approximately 11,170 km\(^2\), located about 40 km north of Prince Albert, Saskatchewan, centered at approximately 54° N latitude and 105° W longitude. The study was conducted at one Picea mariana and two Pinus banksiana sites.

The Picea mariana (old black spruce or OBS) site, located at 53.85° N and 105.12° W, consists primarily of a Picea mariana overstory (up to 12 m tall and 155 years of age) with some tamarack and Pinus banksiana present. Stem densities in the upper and lower strata are approximately 4330 and 3710 live stems ha\(^{-1}\), respectively, with basal areas of 30 and 10 m\(^2\) ha\(^{-1}\) (Sellers et al. 1995). Mid-season leaf area index (LAI) is 4.0 (optical estimation) or 6.3 (allometric estimation) (Chen et al. 1997). Brooks et al. (1997) concluded that the large difference between LAI values was associated with the clustered nature of the foliage. The site is characterized by poorly drained soil and an organic layer of from 5 to over 100 cm in the low peatland areas.

The Pinus banksiana sites, which were designated as Young Jack Pine (YJP) and Old Jack Pine (OJP), are located at 53.875° N, 104.65° W and 53.916° N, 104.69° W, respectively. Both sites are on sandy well-drained soils with poor water holding capacity and organic layers of from 5 to over 100 cm. Tree age is approximately 60 to 75 years at the OJP site and 11 to 16 years at the YJP site with canopy heights of up to 15 and 4 m at the OJP and YJP sites, respectively. Stem densities are approximately 1330 and 4056 live stems ha\(^{-1}\) at the OJP and YJP sites, respectively. Mid-season LAI is 2.6 or 2.5 (optical and allometric estimations, respectively) at the OJP site, and the corresponding values at the YJP site are 3.1 or 2.8 (Chen et al. 1997). The shrub understory consists primarily of green alder (Alnus crispa Ait. Pursh) at the OJP site and is essentially lacking at the YJP site. Both sites contain ground cover of bearberry, feather mosses and lichens with the later being particularly well developed at the OJP site.

Field measurements

Measurements were made from platform canopy access towers constructed on site by the BOREAS staff at the OBS and OJP sites and from the ground at the YJP site. Data were obtained during three discrete measurement periods (1 to 2 measurement days each period) designated by BOREAS as Intensive Field Campaigns (IFCs). These IFCs were selected to measure parameters at bud break (IFC-1 = May 24 to June 12), midsummer or peak growing season (IFC-2 = July 26 to August 8) and at the onset of dormancy in autumn (IFC-3 = August 30 to September 15).

In situ gas exchange rates were measured at each site during each IFC with an ADC-IV Portable Photosynthesis System (Analytical Development Corporation, Hoddesdon, U.K.). Fluxes of CO\(_2\) and H\(_2\)O were measured and CO\(_2\) assimilation rate (A), transpiration rate (E) and stomatal conductance of water vapor (g\(_s\)) were calculated, according to the equations of von Caemmerer and Farquhar (1981). Measurements were made on intact branches from both the upper and lower canopy sections of the trees adjacent to the canopy access towers at the OJP and OBS sites and on the young trees present near the flux tower site at the YJP site. For Pinus banksiana, measurements were made on each needle age class present. For Picea mariana, the newest age class (1994 needles) was measured alone, whereas the 2- and 3-year-old needles (1992 and 1993 needles) were combined in one measurement, as were the 4- and 5-year-old needles (1990 and 1991 needles). At least eight replicate measurements per IFC, canopy location and age group were made for each species. Measurements were made on trees that were accessible from the canopy access towers (approximately four trees with two upper and two lower branches measured per tree) at the OBS and OJP sites and on the same number of trees for each IFC at the YJP site.

Measurements were made on relatively clear days between 0900 and 1300 h local time. Sampling was stratified across needle age and position to minimize variation due to time of day. All branch tips had been exposed to sunlight for several hours to insure that photosynthetic activation had occurred before the measurements began. Measurements were made at ambient temperature, relative humidity and photosynthetic photon flux density (PPF) when possible. Artificial lighting (12-V quartz halogen lamp) was provided when ambient irradiance was below 1500 \(\mu\)mol m\(^{-2}\) s\(^{-1}\). Therefore, our values represent ambient light-saturated gas exchange rates. Instantaneous water-use efficiency (WUE) was calculated as A/E. Gas exchange rates were expressed on a half or hemi-surface leaf area basis standardized for the BOREAS project and obtained by the volume displacement method (cf. Sullivan and Terman 1989).

Laboratory measurements

Following the gas exchange measurements in the field, the branch tips were excised, sealed in plastic bags with moist towels and placed on ice for transport to the laboratory at Paddockwood, SK, (approximately 60 km from the research sites) for further analysis. Each sample was divided into two components; one portion was used for measurement of oxygen...
evolution and photosynthetic pigments and the remaining material was used for analysis of leaf optical properties (Middleton et al. 1997) and N concentration. To assess potential photosynthetic capacity ($A_{\text{max}}$) and apparent quantum yield (AQY), photosynthetic oxygen evolution was measured on each needle age class collected (generally 3 years for *Pinus banksiana* and 5 years for *Picea mariana*) within 24 h after branch samples were excised. Our studies indicated that $A_{\text{max}}$ of the branches was maintained for at least 24 h under the experimental conditions. Photosynthetic oxygen evolution was measured at saturating CO$_{2}$ concentrations (100 mmol mol$^{-1}$ CO$_{2}$) with an oxygen electrode (Hansatech Corp., King’s Lynn, U.K.). The temperature of the electrode was maintained by a circulating water bath set at temperatures to approximate maximum air temperature for each IFC (26 °C for IFC-1 and IFC-3 and 28 °C for IFC-2), and maximum PPF was 2175 µmol m$^{-2}$ s$^{-1}$ supplied by an LED light source (Hansatech Model LH36 Ultrabright, Hansatech Corp., King’s Lynn, U.K.). To generate the light response curves, PPF was reduced to zero in eight steps, and AQY was computed between 0 and 84 µmol m$^{-2}$ s$^{-1}$. Measurements made in the dark were used as estimates of dark respiration rates. Because of instrumentation problems during IFC-1, data are only reported for IFC-2 and IFC-3.

Photosynthetic pigments were extracted with dimethyl sulfoxide (DMSO) from the needles used in the above measurements. Absorbances were measured at 470, 640, 648 and 750 nm with a dual beam spectrophotometer (Beckman DU-600 or Perkin-Elmer Lambda 3) and used to calculate chlorophyll and carotenoid concentrations by the equations of Lichtenthaler (1987) as modified for DMSO by Chappelle and Kim (1992). Chemical analysis of tissue was conducted by the Maryland Soil Testing Laboratory, University of Maryland, with a CHN-600 Elemental Analyzer System (LECO Corp., St. Joseph, MO).

Data were subjected to analysis of variance (ANOVA) to test for main effects of species, site (*Pinus banksiana* only), IFC, canopy position, needle age and their interactions. Significantly different means were separated using the Student-Newman-Keouls means separation procedure for multiple means and t-tests for paired measurements using the SAS software package (SAS Institute, Cary, NC, 1985).

**Results**

**Seasonal trends in CO$_{2}$ and H$_{2}$O fluxes**

Seasonally averaged assimilation rates ($A$) were 4.0 and 3.7 µmol m$^{-2}$ s$^{-1}$ at the young (YJP) and old (OJP) *Pinus banksiana* sites, respectively, and 2.7 µmol m$^{-2}$ s$^{-1}$ at the *Picea mariana* (OBS) site. Assimilation rate was consistently highest in the upper canopy at the YJP site and was lowest during IFC-1 at the OBS site (Figure 1A). Only marginal increases in $A$ were observed during the peak growing season (IFC-2), but transpiration rate ($E$) of OBS showed a distinct peak at that time (Figure 1B). Transpiration rates differed between species only during IFC-1 when it was highest at the OJP site, followed by the YJP site and then the OBS site.

Transpiration rate and stomatal conductance (Tables 1–3) were lower during IFC-3 than during IFC-2 and this led to increases in WUE at the final measurement period in all measurement groups, with the exception of the lower canopy foliage of young *Pinus banksiana*, where WUE decreased throughout the season (Figure 1C). At all three sites, instantaneous WUE was higher in the upper canopy foliage than in the lower canopy foliage.

Photosynthetic capacity ($A_{\text{max}}$) did not differ between the first and second measurement periods or between *Pinus banksiana* and *Picea mariana* (Figure 2A). However, chlorophyll concentration showed a marked increase in OJP during IFC-2 (Figure 2B) but otherwise remained rather constant at each measurement period within a species or canopy stratum. Foliar N concentrations were similar at each IFC for any given measurement group (Figure 2C), but were higher in the young jack pine stand than in the old jack pine stand (11.1 versus 9.5 µmol mol$^{-1}$ CO$_{2}$ m$^{-2}$ s$^{-1}$ for young jack pine and old jack pine, respectively).
Table 1. Parameters measured for *Picea mariana* at each field campaign (IFC) of the BOREAS program. Data for $A$, $E$, $g_s$ and WUE are from field measurements, whereas the remaining data are from laboratory analyses. Values are means $\pm$ SE of all needles (all ages combined) measured in the upper and lower canopy at each IFC ($n = 24$ to $40$). An asterisk (*) indicates that one member of a pair of measurements for each IFC differs significantly ($P < 0.05$) from the other according to $t$-tests; NA = data not available.

<table>
<thead>
<tr>
<th></th>
<th>IFC-1</th>
<th>IFC-2</th>
<th>IFC-3</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A$ (µmol CO$_2$ m$^{-2}$ s$^{-1}$)</td>
<td>1.6 ± 0.4</td>
<td>3.1 ± 0.5</td>
<td>3.5 ± 0.4</td>
</tr>
<tr>
<td>$E$ (mmol H$_2$O m$^{-2}$ s$^{-1}$)</td>
<td>0.5 ± 0.1</td>
<td>1.2 ± 0.2</td>
<td>0.6 ± 0.4</td>
</tr>
<tr>
<td>$g_s$ (mmol H$_2$O m$^{-2}$ s$^{-1}$)</td>
<td>27.5 ± 4.7</td>
<td>38.2 ± 4.9</td>
<td>24.1 ± 2.5</td>
</tr>
<tr>
<td>WUE ($A/E$)</td>
<td>2.8 ± 0.4</td>
<td>2.7 ± 0.2</td>
<td>5.6 ± 0.2</td>
</tr>
<tr>
<td>$A_{\text{max}}$ (µmol O$_2$ m$^{-2}$ s$^{-1}$)</td>
<td>NA</td>
<td>19.8 ± 1.4</td>
<td>19.8 ± 1.6</td>
</tr>
<tr>
<td>$R_d$ (µmol O$_2$ m$^{-2}$ s$^{-1}$)</td>
<td>NA</td>
<td>−3.7 ± 0.3</td>
<td>−3.2 ± 0.2</td>
</tr>
<tr>
<td>AQY (µmol CO$_2$ mmol$^{-1}$)</td>
<td>NA</td>
<td>0.041 ± 0.003</td>
<td>0.033 ± 0.004</td>
</tr>
<tr>
<td>N (mg g$^{-1}$)</td>
<td>7.70 ± 0.2</td>
<td>8.23 ± 0.2</td>
<td>7.71 ± 0.4</td>
</tr>
</tbody>
</table>

Table 2. Parameters measured for *Pinus banksiana* (Young Jack Pine stand) at each field campaign (IFC) of the BOREAS program. Data for $A$, $E$, $g_s$ and WUE are from field measurements, whereas the remaining data are from laboratory analyses. Values are means $\pm$ SE of all needles (all ages combined) measured in the upper and lower canopy at each IFC ($n = 24$ to $40$). An asterisk (*) indicates that one member of a pair of measurements for each IFC differs significantly ($P < 0.05$) from the other according to $t$-tests; NA = data not available.

<table>
<thead>
<tr>
<th></th>
<th>IFC-1</th>
<th>IFC-2</th>
<th>IFC-3</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A$ (µmol CO$_2$ m$^{-2}$ s$^{-1}$)</td>
<td>4.3 ± 0.4</td>
<td>5.2 ± 0.2</td>
<td>4.7 ± 0.3</td>
</tr>
<tr>
<td>$E$ (mmol H$_2$O m$^{-2}$ s$^{-1}$)</td>
<td>0.9 ± 0.1</td>
<td>1.2 ± 0.05</td>
<td>0.9 ± 0.07</td>
</tr>
<tr>
<td>$g_s$ (mmol H$_2$O m$^{-2}$ s$^{-1}$)</td>
<td>63.3 ± 5.1</td>
<td>56.3 ± 3.0</td>
<td>41.2 ± 3.0</td>
</tr>
<tr>
<td>WUE ($A/E$)</td>
<td>4.6 ± 0.3</td>
<td>4.6 ± 0.2</td>
<td>5.2 ± 0.3</td>
</tr>
<tr>
<td>$A_{\text{max}}$ (µmol O$_2$ m$^{-2}$ s$^{-1}$)</td>
<td>NA</td>
<td>19.9 ± 1.3</td>
<td>21.78 ± 1.6</td>
</tr>
<tr>
<td>$R_d$ (µmol O$_2$ m$^{-2}$ s$^{-1}$)</td>
<td>NA</td>
<td>−3.3 ± 0.3</td>
<td>−3.2 ± 0.2</td>
</tr>
<tr>
<td>AQY (µmol CO$_2$ mmol$^{-1}$)</td>
<td>NA</td>
<td>0.030 ± 0.003</td>
<td>0.034 ± 0.002</td>
</tr>
<tr>
<td>N (mg g$^{-1}$)</td>
<td>11.2 ± 0.1</td>
<td>11.9 ± 0.2</td>
<td>9.9 ± 0.4</td>
</tr>
</tbody>
</table>

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Table 3. Parameters measured for *Pinus banksiana* (Old Jack Pine stand) at each field campaign (IFC) of the BOREAS program. Data for $A$, $E$, $g_s$ and WUE are from field measurements, whereas the remaining data are from laboratory analyses. Values are means ± SE of all needles (all ages combined) measured in the upper and lower canopy at each IFC ($n = 24$ to 40). An asterisk (*) indicates that one member of a pair of measurements for each IFC differs significantly ($P < 0.05$) from the other according to $t$-tests; NA = data not available.

<table>
<thead>
<tr>
<th></th>
<th>Upper canopy</th>
<th>Lower canopy</th>
<th>Upper canopy</th>
<th>Lower canopy</th>
<th>Upper canopy</th>
<th>Lower canopy</th>
</tr>
</thead>
<tbody>
<tr>
<td>$A$ ($\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$)</td>
<td>3.5 ± 0.2</td>
<td>3.8 ± 0.2</td>
<td>4.3 ± 0.3</td>
<td>3.8 ± 0.3</td>
<td>3.0 ± 0.2</td>
<td>3.9 ± 0.2*</td>
</tr>
<tr>
<td>$E$ (mmol H$_2$O m$^{-2}$ s$^{-1}$)</td>
<td>1.1 ± 0.1</td>
<td>1.1 ± 0.1</td>
<td>1.3 ± 0.2</td>
<td>1.4 ± 0.2</td>
<td>0.7 ± 0.05</td>
<td>1.0 ± 0.05*</td>
</tr>
<tr>
<td>$g_s$ (mmol H$_2$O m$^{-2}$ s$^{-1}$)</td>
<td>47.5 ± 2.8</td>
<td>42.0 ± 2.8</td>
<td>53.9 ± 3.6</td>
<td>52.1 ± 3.6</td>
<td>23.1 ± 1.6</td>
<td>31.3 ± 1.6*</td>
</tr>
<tr>
<td>WUE ($A/E$)</td>
<td>3.4 ± 0.1</td>
<td>3.4 ± 0.1</td>
<td>3.6 ± 0.2</td>
<td>2.8 ± 0.2*</td>
<td>4.7 ± 0.2</td>
<td>3.9 ± 0.2*</td>
</tr>
<tr>
<td>$A_{max}$ ($\mu$mol O$_2$ m$^{-2}$ s$^{-1}$)</td>
<td>NA</td>
<td>NA</td>
<td>17.8 ± 0.9</td>
<td>16.9 ± 1.0</td>
<td>18.8 ± 0.8</td>
<td>18.2 ± 1.3</td>
</tr>
<tr>
<td>$R_d$ ($\mu$mol O$_2$ m$^{-2}$ s$^{-1}$)</td>
<td>NA</td>
<td>NA</td>
<td>−2.9 ± 0.3</td>
<td>−2.6 ± 0.3</td>
<td>−2.8 ± 0.3</td>
<td>−2.6 ± 0.2</td>
</tr>
<tr>
<td>AQY ($\mu$mol CO$_2$ mmol$^{-1}$)</td>
<td>NA</td>
<td>NA</td>
<td>0.028 ± 0.002</td>
<td>0.034 ± 0.003</td>
<td>0.027 ± 0.002</td>
<td>0.032 ±0.002</td>
</tr>
<tr>
<td>$N$ (mg g$^{-1}$)</td>
<td>9.0 ± 0.3</td>
<td>7.4 ± 0.2*</td>
<td>10.6 ± 0.2</td>
<td>10.4 ± 0.2</td>
<td>10.1 ± 0.2</td>
<td>9.3 ± 0.2*</td>
</tr>
</tbody>
</table>

mg g$^{-1}$, respectively). Both of these values were higher than in the Old Black Spruce stand (8.2 mg g$^{-1}$). Photosynthetic capacity was also higher in the Young Jack Pine stand than in the Old Jack Pine stand (19.4 versus 17.9 $\mu$mol m$^{-2}$ s$^{-1}$, respectively).

*Intraspecific variation in CO$_2$ and H$_2$O fluxes*

Both species showed differences in photosynthetic characteristics that were related to needle age and the position of branches (needles) within the canopy. Photosynthetic capacity was higher in the upper canopy foliage in *Picea mariana* and young *Pinus banksiana* at IFC-3 but there was no significant difference in $A_{max}$ associated with needle position in the canopy at the old *Pinus banksiana* site (Figure 2A, Tables 1–3). Chlorophyll concentrations did not differ between canopy strata until IFC-3 when chlorophyll concentrations were higher in the lower foliage than in the upper foliage in OBS and OJP (Figure 2B). Nitrogen concentrations were higher during IFC-1 in the upper foliage of *Pinus banksiana* but not of *Picea mariana* (Figure 2C). Dark respiration was higher in the young jack pine stand than in the old jack pine stand (−3.2 versus −2.6 $\mu$mol m$^{-2}$ s$^{-1}$) but AQY did not differ between species or by location of foliage in the canopy (Tables 1–3).

Current-year needles had a higher $A_{max}$ and higher rates of oxygen evolution at irradiances down to approximately 500 $\mu$mol m$^{-2}$ s$^{-1}$ than older foliage; however, this effect of needle age was only significant in the lower canopy foliage. Neither dark respiration nor AQY was significantly affected by needle age (Figure 3). Older needles of both species had similar dark respiration rates and AQY values. Assimilation rates measured in the field were only affected by needle age at the old *Pinus banksiana* site (Figure 4), and there was also a significant interaction between needle age and IFC at that site (Figure 4B).

Assimilation rates were high in 3-year-old needles early in the season (IFC-1) before the new needles had emerged; however, by late season (IFC-3) as senescence approached, $A$ was reduced in the 3-year-old needles (Figure 4B). In general, values of $E$ and $g_s$ did not differ across the age classes of needles sampled and no other needle age by time of year interactions were observed.

Tissue N concentrations did not account for much of the intraspecific variability observed in $A$ (data not shown) or $A_{max}$ (Figure 5). This was particularly true for *Picea mariana* where no statistically significant relationship was detected (Figure 5A); however, the relationship was more defined in *Pinus banksiana*, especially at the OJP site (Figure 5B).

A close correlation was observed between assimilation rate and stomatal conductance in both species. This relationship was consistent among sites, canopy positions and needle age classes, although the slope of the response was slightly greater for *Picea mariana* than for *Pinus banksiana* (Figures 6A and 6B). The calculated stomatal limitation to photosynthesis ($A_{max} - A/A_{max}$) was 82 to 85% across season, canopy position and needle ages measured in *Picea mariana* and 76 to 85% in *Pinus banksiana*. There were no differences between species or between the two *Pinus banksiana* sites for this parameter.
Discussion

Our gas exchange data are consistent with reported values for jack pine and black spruce (e.g., Ceulemans and Sangier 1991, Johnsen et al. 1996) and for similar studies conducted as part of BOREAS (e.g., Brooks et al. 1997). They provide an indication of interspecific, seasonal, temporal (needle age) and positional variability in gas exchange rates and photosynthetic characteristics of these species.

Although $A_{\text{max}}$ was similar in *Picea mariana* and *Pinus banksiana*, $A$ was generally higher in *Pinus banksiana*. Higher values of $A$ have been reported previously in *Pinus* species compared to *Picea* species (e.g., Ceulemans and Sangier 1991) and in these species in particular (Brooks et al. 1997). Foliar N concentrations were highest at the YJP site and lowest at the OBS site (cf. Dang et al. 1997a), and these differences were consistent with differences in $A$ and $A_{\text{max}}$ measured at these sites. Nitrogen concentrations have been correlated with net photosynthesis in a variety of species (e.g., Field and Mooney 1986, Evans 1989). Tan and Hogan (1995a, 1995b) also demonstrated that nitrogen deficiency results in reduced net photosynthesis, perhaps as a result of decreased biochemical and carboxylation capacity and reduced dry matter production.

Trees at the young *Pinus banksiana* site exhibited higher physiological activity in terms of gas exchange rates (both photosynthetic uptake and respiratory release) than trees of the older stand. Higher productivity was also observed at the Young Jack Pine site compared with the Old Jack Pine site (Sellers et al. 1995, Middleton et al. 1997); therefore, the increased respiration rate of the younger trees appears to be more than offset by increased photosynthetic activity. Yoder et al. (1994) found lower photosynthetic rates in 1-year-old foliage of old compared to young *Pinus contorta* Dougl. ex Loud. and *P. ponderosa* Dougl. ex Laws. and they attributed the reduction to a greater stomatal limitation to photosynthesis. They suggested that the reduced assimilation was a result of reduced hydraulic conductivity, as opposed to reduced photosynthetic capacity in older trees. In our study, the stomatal limitation to photosynthesis did not vary between the young and old stands of *Pinus banksiana*. We cannot determine from
our data whether differences in water fluxes, \( A_{\text{max}} \) or foliar N concentrations are due to tree age itself or to possible differences in water or N availability between the two sites. As data from the entire BOREAS project are compiled, it will be important to partition differences in gas fluxes between stand age and site quality as part of scaling efforts.

Variation in gas flux rates was observed during the season for both \textit{Pinus banksiana} and \textit{Picea mariana}. The low initial \( A \) in \textit{Picea mariana} may have been associated with low soil temperatures. DeLucia (1987), Day et al. (1991) and others have demonstrated that, in some conifers, photosynthesis and stomatal conductance are regulated by root temperatures and subsequent stomatal opening. In contrast to the wet and frozen soil at the \textit{Picea mariana} site during IFC-1, we observed that the soil at both \textit{Pinus banksiana} sites had already thawed and bud break was initiated earlier at these sites than at the OBS site. Therefore, it was not surprising that net photosynthesis was higher at the jack pine sites than at the black spruce sites, especially during the early season. Higher atmospheric flux rates were also observed at the \textit{Pinus banksiana} sites than at the \textit{Picea mariana} site during IFC-1 (Sellers et al. 1995).

Figure 4. Carbon dioxide assimilation rates in \textit{Picea mariana} (A) and \textit{Pinus banksiana} at the OJP site (B) and YJP site (C), measured at three times during the summer of 1994. Each column is the mean ± SE (vertical bars) of approximately 10 measurements. Different letters above a column within a panel indicate that the means are significantly different (\( P < 0.05 \)).

Figure 5. Relationship between foliar nitrogen content and photosynthetic capacity (\( A_{\text{max}} \)) in \textit{Picea mariana} (A) and two sites (OJP—dotted regression line and YJP—solid regression line) of \textit{Pinus banksiana} (B) measured during the summer of 1994. Each point is the mean (± SE) of approximately eight measurements for each position in the canopy and needle age class measured. Coefficients of variation for linear regression analysis are shown within the plots.

Figure 6. The relationship between CO\(_2\) assimilation and stomatal conductance in \textit{Picea mariana} (A) and two sites (OJP and YJP) of \textit{Pinus banksiana} (B) measured at three times during the summer of 1994. A single regression equation is shown for all points in each panel because no differences were detected between \textit{Pinus banksiana} sites or from needles from upper or lower canopy positions. The linear regression equation and coefficient of variation are shown in the plot.
Stomatal conductance and $E$ were lower at IFC-3 compared to IFC-2, perhaps because of cooler soils and lower leaf-to-air vapor pressure deficits (VPD). Dang et al. (1997b) have demonstrated a strong response of stomata to VPD in these species. In contrast to $E$ and $g_s$, $A$ remained rather constant especially in the upper canopy foliage in IFC-3 compared to IFC-2. There was some evidence that the lower canopy foliage was responding to shading at the end of the season, and this could have contributed to the reductions in $A$ and $A_{\text{max}}$ observed in the lower canopy and to the difference in WUE of the upper and lower canopy foliage observed at IFC-3. In the upper canopy, reduced $E$ and $g_s$ were not accompanied by a concurrent reduction in $A$ and this led to an apparent increase in WUE for the well-lit upper canopy needles.

Chen et al. (1997) found that LAI did not increase between IFC-2 and IFC-3 and so it is possible that increased shading may have occurred in the lower canopy as a result of the increased solar angle at that time of the year. Further pieces of evidence for some late-season shade acclimation are the increase in total chlorophyll observed in the lower canopy needles and the observed trend ($P < 0.10$) of a reduction of the ratio of chlorophyll a to b at IFC-3. Also, the extent of the shade-response was consistent with the LAI of each site, because LAI was highest at OBS and lowest at OJP, where no shade responses were observed.

Our field data represent maximum assimilation rates for the lower canopy foliage because measurements were made under conditions of saturating PPF. Brooks et al. (1997) found very low assimilation rates and conductance in lower canopy foliage under shaded conditions. Similar to our findings, they also observed that, in response to supplemental lighting, $A$ increased to rates close to those observed in upper canopy foliage; however, they also found that conductance responded more slowly and did not reach the values found in the upper canopy. Therefore, the potential contribution that lower foliage may make at any given time to overall atmospheric fluxes of CO$_2$ and H$_2$O is similar to that of the upper canopy, but the extent to which this potential is realized will vary with light availability and probably other factors.

Subtle differences in gas fluxes were observed between needle age groups. Variation due to needle age was detected primarily as changes in $A_{\text{max}}$, rather than in actual field rates of $A$ or $E$, so that the relative contribution to CO$_2$ and H$_2$O fluxes by each age class that we measured was similar. Among sites, the only differences in gas fluxes found in the field were at the OJP site. There was a steady increase in the photosynthetic contribution of first-year foliage as the season progressed and this was accompanied by a gradual decrease in the contribution of older foliage. However, the contribution to CO$_2$ and H$_2$O fluxes by the five newest needle age classes of Picea mariana and the 1- to 3-year-old foliage of Pinus banksiana, young site, was similar. There were more 4-year-old needles present at the YJP site than at the OJP site and Picea mariana retains needles for approximately 15 years. This greater needle longevity may have contributed to the reduced needle age effects at the YJP and OBS sites.

In addition to evaluating inter- and intraspecific variations in gas exchange characteristics of these species, our objective was to increase our understanding of the mechanisms by which environmental factors regulate gas exchange in these species. Irradiance appears to play a key role as do N concentrations and stomatal regulation. Although tissue N concentrations were related to interspecific and between-site variation in photosynthesis, short-term and intraspecific changes in photosynthesis were not well correlated with tissue N concentration. This may be because N concentrations were rather constant within a given species and location or because other factors imposed stronger limitations on photosynthesis. Also, variation in N concentration on a dry weight basis, as our data are expressed, may not be as tightly coupled to photosynthesis as data expressed on a leaf area basis. Changes in the amount of starch, for example, could alter nitrogen concentration on a dry weight basis but not on an area basis.

In addition to light and N concentration, stomatal regulation may also exert a high degree of control over gas fluxes in these species. The calculated stomatal limitation to photosynthesis was high in both species, 83% in Picea mariana versus 79% in Pinus banksiana. Although these calculations probably represent an overestimate of the stomatal limitation because our ambient rates of assimilation included stem respiration, which may have reduced our measured rates of net assimilation, they are indicative of the strong stomatal control over assimilation found in these species.

The response of $A$ to $g_s$ also suggests the importance of water conservation in these species. Although Picea mariana grows in wetter habitats than Pinus banksiana, because the rooting depth of Picea mariana is shallow the species could be more susceptible to seasonal drought than the deeper-rooted Pinus banksiana. Sellers et al. (1995) found that evapotranspiration was quite low from all of the BOREAS study areas, especially the Picea mariana sites. However, although these sites are presumed to be “wet,” Sellers et al. (1995) found that the Picea mariana sites were effectively functioning as arid sites with respect to sensible versus latent heat loss and Bowen ratios. Our physiological data on stomatal activity and H$_2$O flux rates are consistent with these observations.

In conclusion, these data provide information about both inter- and intraspecific variations in CO$_2$ and H$_2$O fluxes from two dominant species in the boreal region. They are in agreement with flux measurements made from the BOREAS flux towers and from aircraft (Sellers et al. 1995). However, at a finer scale, our results suggest that seasonal and daily variations in environmental factors may moderate gas fluxes in the short-term. For example, cold soil early in the season may limit CO$_2$ uptake and water release into the atmosphere. However, on a daily basis during the major portion of the growing season, factors such as air temperature, soil water and VPD may regulate net exchange until cold nights and cooling soil temperatures again predominate at the conclusion of the growing season. Compiling data from all BOREAS investigators will undoubtedly result in a more complete picture of gas fluxes at varying spatial and temporal scales. The addition of measurements made during critical periods of initiation of
photosynthetic activity in the spring and down-regulation of such activity in the fall will also aid in understanding seasonal changes in gas fluxes.

Acknowledgments

The authors thank the BOREAS program for partial funding of this research and the BOREAS program staff for providing important logistical support to the project. We also thank Mr. Stephen Chan, Ms. Andrea Duluca and Ms. Takisha Cannon for assistance in the field and laboratory with data collection and analysis.

References


