Regulation of branch-level gas exchange of boreal trees: roles of shoot water potential and vapor pressure difference

QING-LAI DANG, HANK A. MARGOLIS, MARIE R. COYEA, MIKAILOU SY, and G. JAMES COLLATZ

Summary  Effects of shoot water potential (Ψ) and leaf-to-atmosphere vapor pressure difference (VPD) on gas exchange of jack pine (Pinus banksiana Lamb.), black spruce (Picea mariana (Mill.) B.S.P.), and aspen (Populus tremuloides Michx.) were investigated at the northern edge of the boreal forest in Manitoba, Canada. Laboratory measurements on cut branches showed that net photosynthesis (Aₙ) and mesophyll conductance (gₘ) of jack pine and gₘ of black spruce did not respond to Ψ until a threshold Ψ was reached below which they decreased linearly. Photosynthesis of black spruce decreased slowly with decreasing Ψ above the threshold and declined more rapidly thereafter. The threshold Ψ was lower in black spruce than in jack pine. However, stomatal conductance (gₛ) of black spruce decreased continuously with decreasing Ψ, whereas gₛ of jack pine showed a threshold response. Mesophyll limitations were primarily responsible for the decline in Aₙ at low Ψ for jack pine and black spruce in the middle of the growing season, but stomatal limitations became more important later in the season. Field measurements on in situ branches on warm sunny days showed that both conifer species maintained Ψ above the corresponding threshold and there was no evidence of Ψ limitation on Aₙ of jack pine, black spruce or aspen.

Vapor pressure difference was important in regulating gas exchange in all three species. An empirical model was used to quantify the gₛ response to VPD. When parameterized with laboratory data for the conifers, the model also fit the corresponding field data. When parameterized with field data, the model showed that stomata of aspen were the most sensitive of the three species to VPD, and stomata of black spruce were the least sensitive. For jack pine and aspen, stomata of foliage in the upper canopy were significantly more sensitive than stomata of foliage in the lower canopy. Vapor pressure difference had a greater impact on Aₙ of aspen than on Aₙ of the conifers as a result of aspen’s greater stomatal sensitivity to VPD and greater slope of the relationship between Aₙ and intercellular CO₂ concentration (Cᵢ). During the 1994 growing season, VPD averaged 1.0 kPa, corresponding to ratios of Cᵢ to ambient CO₂ of 0.77, 0.71 and 0.81 for jack pine, black spruce and aspen, respectively. We conclude that increases in VPD at the leaf surface in response to climate change should affect the absolute CO₂ and H₂O fluxes per unit leaf area of the aspen component of a boreal forest landscape more than those of the conifer component.

Keywords: aspen, black spruce, jack pine, photosynthesis, stomatal conductance.

Introduction

Analyses of the temporal and spatial distribution of CO₂ in the atmosphere suggest that photosynthetic activity of the boreal forest may be responsible for a significant portion of the “missing sink” of anthropogenic CO₂, i.e., the portion of the CO₂ emitted by fossil fuel burning and deforestation that does not accumulate in the atmosphere (Tans et al. 1990, Slegenhuis and Sarmiento 1993, Ciais et al. 1995, Denning et al. 1995). However, general circulation model (GCM) simulations suggest that increasing atmospheric CO₂ concentrations should result in significant changes to the climate of the boreal forest region (e.g., Mitchell 1983, Sellers et al. 1996a). These climatic changes are expected to modify the physiological and ecological functioning of the forest (Davies and Botkin 1985, Solomon and Webb 1985), which in turn, could feedback on the physical climate system (Sato et al. 1989). A major challenge in global change research is to link the top-down models typified by global atmospheric tracer models with bottom-up models that scale physiological and ecological processes from leaf or canopy up to the region (Ehleringer and Field 1993). Accomplishing this for the boreal forest biome requires a detailed knowledge of factors controlling carbon and water fluxes between leaves of boreal forest species and the atmosphere.

Soil water supply and evaporative demand of the atmosphere are important environmental factors influencing gas exchange between plants and the atmosphere. Soil water con-
ditions directly affect the water potential of the plant ($\Psi$). Low $\Psi$ can induce stomatal closure, thus shutting down the dominant pathway for the exchange of CO$_2$ and H$_2$O between a leaf and the atmosphere (Ludlow 1980, Osonubi and Davies 1980). Low $\Psi$ can also reduce or halt the photosynthetic activity of the mesophyll (Teskey et al. 1986, Ni and Pallardy 1992). Although the effects of $\Psi$ on net photosynthesis ($A_n$) and stomatal conductance ($g_s$) have been studied extensively (e.g., Jarvis 1980, Ludlow 1980, Melzack et al. 1985, Schulze 1986, Abrams and Mostoller 1995), the role of $\Psi$ in controlling the exchange of H$_2$O and CO$_2$ between mature boreal forest trees and the atmosphere is not well understood.

There has been increasing interest in the influence of the vapor pressure difference (VPD) between the intercellular space of a leaf and the atmosphere on $g_s$ (Farquhar et al. 1980, Ludlow 1980, Osonubi and Davies 1980, Johnson and Ferrell 1983, Sandford and Jarvis 1986, Schulze 1986, Dai et al. 1992, Kawaminato et al. 1993, Meinzer et al. 1993). In part, this reflects recognition of the potential for strong feedbacks between the dynamics of the planetary boundary layer and stomatal function (e.g., McNaughton and Jarvis 1991, Raupach 1991, Pielke et al. 1993). In 1981, it was reported that at least 70 species showed decreased $g_s$ in response to decreasing atmospheric humidity (Losche and Tenhunen 1981). However, VPD does not directly affect photosynthetic activity in the mesophyll, rather a reduction in $g_s$ decreases the intercellular CO$_2$ concentration which in turn reduces the CO$_2$-limited rate of photosynthesis. The responsiveness of stomata to VPD, however, can vary with species, genotype, physiological conditions, and developmental stage of the foliage (Ludlow 1980, Osonubi and Davies 1980, Warril et al. 1980, Meinzer 1982, Johnson and Ferrell 1983, Sandford and Jarvis 1986).

In this study, we examined the responses of $A_n$, $g_s$, and other related variables to changes in shoot water potential ($\Psi$) and leaf-to-atmosphere VPD in jack pine ($Pinus banksiana$ Lamb.), black spruce ($Picea mariana$ (Mill.) B.S.P.), and aspen ($Populus tremuloides$ Michx.) near the northern boundary of the boreal forest in Manitoba, Canada. Additionally, we used a simple empirical model to quantify the characteristics of stomatal response to VPD of foliage at different canopy positions for the three species. These results supply some of the branch-level information required to interpret the results from the sap flow, flux-tower, flux-aircraft and radiosonde-boundary-layer measurements taken during the Boreal Ecosystem–Atmosphere Study (BOREAS) (Sellers et al. 1995, Margolis and Ryan 1997). The results also provide information for parameterizing various ecosystem and land surface process models to predict carbon, water and energy fluxes for the boreal forest.

Materials and methods

Study area

The study was conducted in the BOREAS Northern Study Area between Nelson House and Thompson, Manitoba, Canada (56°N, 99°W). The forests in this region consist primarily of black spruce and jack pine with smaller patches of aspen. The landscape of the region is a mosaic of low-relief terrain, moderate-size hills and small lakes. The soils are derived predominantly from Glacial Lake Agassiz sediments and consist of clays, organic materials and some sandy deposits. Treed peatlands are common in lowland areas.

The study was conducted in three stands, designated as Old Black Spruce, Old Jack Pine and Old Aspen stands in the BOREAS Experiment Plan (see Sellers et al. 1995 for further information). The Old Black Spruce stand was about 75 years old, averaged 9 to 12 m in height and contained between 600 and 900 stems ha$^{-1}$. It is located on a peatland site with high water-holding capacity but variable drainage. On the better drained microsites, the groundcover consists primarily of feather moss ($Hylocomium$ spp.) and the soils are primarily orthic grey luvisols. On the poorly drained microsites, the groundcover is primarily $Sphagnum$ spp., the organic layer depth is between 20 and 100 cm, and the soils are classified as peaty-phase orthic gley soils.

The Old Jack Pine stand was 58 years old, averaged 9 m in height and contained 1875 to 3100 stems ha$^{-1}$. It is located on a sandy outwash with low water holding capacity. The groundcover is primarily lichen ($Cladina$ spp.), although some wetter spots contain $Alnus$ spp. and $Pleurozium$ spp. There is a shallow organic layer of less than 5 cm and the soils are classified as brunisols.

The Old Aspen stand was 70 to 80 years old, ranged between 16 and 20 m in height, and contained approximately 2000 stems ha$^{-1}$. The understory is primarily $Alnus$ crispa (Ait.) Pursh and $Salix$ spp. whereas the groundcover contains a variety of herbaceous species dominated by $Corrnus canadensis$ L. The soil is a heavy clay.

Measurements were taken during the three Intensive Field Campaigns (IFC-1, -2 and -3) of BOREAS in 1994. IFC-1 ran from May 24 to June 16, IFC-2 from July 19 to August 8, and IFC-3 from August 30 to September 19.

Laboratory measurements

We examined the responses of net photosynthesis ($A_n$), mesophyll conductance ($g_m$) and stomatal conductance ($g_s$) of black spruce and jack pine to shoot water potential ($\Psi$) and leaf-to-atmosphere water vapor pressure difference (VPD) under controlled environmental conditions in the laboratory. We also measured the responses of jack pine, black spruce and aspen to a range of ambient CO$_2$ concentrations. Measurements were taken on branches harvested from the forest.

Cut-branch techniques have been used previously to examine the response of $A_n$ and $g_s$ to environmental factors (e.g., Watts and Neilson 1978, Beadle et al. 1979, 1981). We conducted two tests to establish the limits of the cut-branch technique. First, to examine differences in $A_n$ and $g_s$ between cut branches and in situ branches, we selected 20 uniform branches from the same tree and orientation and cut ten of them. We immediately recut the stem under water, keeping the cut surface submerged while the foliage was kept above the water and then measured the gas exchange of the ten cut branches and the ten in situ branches with a portable gas exchange system (LI-6200, LI-Cor Inc., Lincoln, NE). Measurements proceeded in a sequence that alternated between cut
branches and in situ branches. The cut branches were kept under similar environmental conditions as the branches that remained on the tree. Measurements were taken in the morning when water stress was minimal (Dang et al. 1991) and continued for 2 h. There were no significant differences ($P > 0.35$) in $A_n$ and $g_s$ between the cut and in situ branches in any of the species.

To examine the stability of $A_n$ and $g_s$ of cut branches over the time periods required to obtain the response curves in the laboratory, we measured the gas exchange of cut branches under controlled environmental conditions in the laboratory over a 14-h period. Measurements were taken each hour on two branches per species. There were no significant changes in $A_n$ and $g_s$ in jack pine and black spruce during this time period. Photosynthesis in aspen, however, was stable for the first 10 h and then started to decline. Consequently, all measurements were made well within the 14- and 10-h time limits determined for each species.

To measure the responses of $A_n$ and $g_s$ to VPD and water potential, jack pine and black spruce branches were harvested from the upper canopy with a 12-gauge shotgun. Branches were taken from five individual trees per site between 0530 and 0700 h. The branches were immediately recut under water and the cut surfaces were kept submerged until the time of measurement in the laboratory.

Carbon dioxide and water vapor exchange rates were measured with an open-system infrared gas analyzer (IRGA) (Li-Cor LI-6262) operated in differential mode (see Yue et al. 1992 for details). Measurements were made on shoots with foliage of all age classes. Humidity inside the cuvette was controlled by passing saturated air through a series of temperature-controlled condensers. For low target humidities, we split the air into two streams and passed one of them through a column of desiccant. The flow rate through each column was regulated with flowmeters. Air temperature inside the leaf cuvette was controlled by two radiators located inside the cuvette. The temperature of the radiators was controlled with a temperature-controlled water bath. Precautions were taken to avoid condensation of water on the radiators.

The concentration of CO$_2$ inside the cuvette was regulated by passing split air streams through columns with and without soda lime. The main air source was ambient air taken from 15 m above the ground with an air sampling tower and an air compressor. A 0.5-m$^3$ mixing box as well as the reservoir on the compressor were used as buffers to prevent abrupt changes of CO$_2$ concentration in the input air to the cuvette. The CO$_2$ concentration of the ambient air was maintained at the desired value (usually 360 µmol mol$^{-1}$) by adding small amounts of 10% CO$_2$ in air from a compressed air tank. Photosynthetically active radiation of around 1100 µmol m$^{-2}$ s$^{-1}$ was supplied by two 1000-W high-pressure sodium lamps. The natural orientation of the samples was maintained during the measurement. The light was passed through an 8-cm thick water filter to reduce heating in the cuvette. Environmental conditions inside the leaf cuvettes and leaf temperature were monitored continuously with an MT-1000 data logger (Measurement Technology Inc., Stoughton, MA).

For the measurement of VPD responses, all branches were kept in darkness with the cut surface of the stem submerged in water. Branches were exposed to light for 2 h before measurement to induce photosynthetic activity and stomatal opening. Two branches were used for each VPD at each temperature. To maintain an adequate water supply to foliage during measurements, the cut end of the stem was connected to a water reservoir. Changes in the difference between the input and output CO$_2$ and H$_2$O partial pressures in the cuvette were monitored continuously with the IRGA. Measurements were taken at air temperatures of 15, 25 and 35 °C in IFC-1, at 25 and 35 °C in IFC-2, but only at 25 °C in IFC-3. A measurement was taken when the exchange rates of CO$_2$ and H$_2$O became stable.

For the measurement of $\Psi$ response at high (less negative) $\Psi$, water was supplied to the branch as described above. To decrease $\Psi$, the branches were taken out of water and the cut surface of the stem was dried and sealed with silicone grease. The branches were then exposed to light and permitted to transpire freely in an open space where the air was stirred continuously by an electric fan. A pair of branches was chosen randomly at various times for gas exchange measurement at 20 °C. Transpiration rate of the branch being measured was kept low by maintaining a high humidity in the cuvette (VPD < 0.8 kPa). It took from 3 to 6 h for branches to reach their minimum $\Psi$. Immediately after the gas exchange measurement, the stem of the branch was cut and water potential was measured with a pressure chamber (Model 610, PMS Instruments Inc., Corvallis, OR). By controlling the time interval between measurements, a range of shoot water potentials was achieved for black spruce and jack pine during both IFC-2 and IFC-3. Although we attempted a similar protocol with aspen branches, we were not successful because the rates of gas exchange declined so rapidly when the continuous supply of water to the branch was halted that it was not possible to get a stable reading.

The response of $A_n$ to intercellular CO$_2$ concentration ($C_i$) was measured in the laboratory for jack pine, black spruce and aspen. Branches were harvested as described previously. The ambient CO$_2$ concentration in the cuvette was varied from 50 to 900 µmol mol$^{-1}$. The CO$_2$ concentration was measured with the IRGA in differential mode using standard gases that had been calibrated by gas chromatography against the primary BOREAS standard gas as the reference. Two branches were measured at each CO$_2$ concentration but any given branch was measured at only one CO$_2$ concentration.

Field measurements

The responses of $A_n$ and $g_s$ to VPD and $\Psi$ in the field were examined by following the diurnal patterns of these variables on clear or partly cloudy days. Gas exchange was measured with a Li-Cor LI-6200 portable gas exchange system. Shoot water potential was measured with a pressure chamber (Model 610, PMS Instruments Inc.). Measurements were taken at two canopy levels (i.e., upper and lower) for all three species and during all three IFCs with the exception of aspen during IFC-1 because of equipment failure. The upper and lower canopies
were accessed by scaffolding towers. Five trees were chosen per site and the gas exchange of one branch section per tree per canopy level was measured. Ambient environmental conditions were also measured with the cuvette open. The same branches were measured repeatedly at approximately 1 h intervals throughout the day. At the end of the day, the branches were harvested and stored in a freezer for leaf area determination. Immediately following each gas exchange measurement, shoot \( \Psi \) was measured on a nearby branch.

The BOREAS staff monitored predawn \( \Psi \) at the three sites when conditions were dry. Five samples were taken from the general area of the scaffolding towers for each sampling date at each site. The jack pine site was sampled eleven times (June 18, 19, 25 and 26; July 3, 5, 10, 12, 24 and 30, and August 14). The black spruce site was sampled five times (June 21 and 27; July 9, 16 and 24) and the aspen stand was sampled six times (June 18 and 27; July 2, 10, 25 and 30). The BOREAS staff also collected meteorological data from the Old Jack Pine site every 15 min throughout 1994. We calculated daily maximum and photosynthetically active radiation (PAR)-weighted daily mean VPD from this data set for the growing season. The PAR-weighted daily mean VPD was calculated as: \( \text{VPD}_i \times \text{PAR}_i / \Sigma \text{PAR}_i \), where subscript \( i \) denotes the \( i^{th} \) measurement.

**Leaf area measurements**

Aspen leaf area was measured with an optical image analysis system (Decagon Devices, Inc., Pullman, WA). The total hemi-surface area of the foliage for black spruce and jack pine was determined by the volume displacement technique (Brand 1987). The shape factors used for calculating leaf area were determined to be 4.00 and 4.59 for black spruce and jack pine, respectively. The foliage was then oven-dried and specific leaf area was calculated on a hemi-surface basis. The large number of branches used for the laboratory gas exchange measurements made it impractical to count the needles and measure the needle lengths of all the branches. Therefore, specific leaf areas of randomly selected branches (25% of the total samples) were obtained by the volume displacement method, and the hemi-surface area for all the other branches was calculated by multiplying the average specific leaf area from the first 25% of the branches by the foliage dry mass of each of the remaining branches.

**Data calculation and analyses**

For the laboratory measurements, \( A_n, g_s \) and \( C_i \) were calculated according to von Caemmerer and Farquhar (1981). For the field measurements, these variables were calculated by the Li-Cor LI-6200 gas exchange system. Mesophyll conductance \( (g_m) \) was estimated by dividing \( A_n \) by \( C_i \) (Fites and Teskey 1988). Photosynthesis, \( g_s \), and \( g_m \) are expressed on the basis of hemi-surface leaf area.

For data that showed a threshold response (e.g., \( A_n \) versus \( \Psi \)), the response was described by two linear regressions, one for the insensitive part and another for the sensitive part of the response curve (Figures 1 and 2). The \( \Psi \) value at the intersection of the two lines defined the threshold or critical \( \Psi \).

The relationship between \( g_s \) and VPD has been described as a negative asymptotic function in the form (Lindroth and Halldin 1986):

\[
g_s = [c/(1 + a \text{VPD})] + b,
\]

where parameter \( a \) defines the degree of curvature and \( b \) defines the lower asymptote. Parameter \( c \) is related to maximum \( g_s \) because \( g_s = (b + c) \) when VPD is zero. The goodness of fit of Equation 1 is expressed using the coefficient of determination of the linear regression between measured and predicted \( g_s \), to water vapor \( (g_{swv}) \). For an equation with a single independent variable, this is equivalent to the nonlinear regression \( R^2 \) value calculated by \( [1 - (\text{Error Sum of Squares}/\Sigma \text{Corrected Sum of Squares})] \) for Equation 1. The first derivative of Equation 1 describes the sensitivity of \( g_s \) to a change in VPD.

\[
d(g_s)/d(\text{VPD}) = (-ac)/[(1 + a \text{VPD})^2].
\]

The parameters in Equation 1 were estimated using the Marquardt-Levenberg algorithm for nonlinear regression and then determining a best fit value for parameters \( a, b \) and \( c \). To facilitate comparisons between species, \( g_s \), calculated by Equation 1, was also expressed as a percentage of \( g_s \) at the seasonal average VPD of 1.0 kPa.

**Results**

**Responses to water potential**

**Laboratory results for jack pine**

Net photosynthesis \( (A_n) \), mesophyll conductance \( (g_m) \) and stomatal conductance to CO\(_2\) \( (g_{s,CO2}) \) of jack pine all showed a threshold response to shoot water potential \( (\Psi) \); i.e., they were relatively constant over the range of \( \Psi \) values above the threshold, but decreased linearly as \( \Psi \) decreased below the threshold (Figures 1a-c, Table 1). In IFC-2, the threshold \( \Psi \) of jack pine was -1.2 MPa for \( A_n \) and \( g_m \), and -1.1 MPa for \( g_{s,CO2} \). The threshold \( \Psi \) values were slightly more negative in IFC-3 than in IFC-2 \( (P < 0.05) \); i.e., -1.3, -1.4, and -1.2 MPa for \( A_n, g_m \) and \( g_{s,CO2} \), respectively. The rate of photosynthesis reached zero at \( \Psi \) of -2.4 and -2.3 MPa in IFC-2 and IFC-3, respectively. The declines in \( g_m \) and \( g_{s,CO2} \) with decreasing \( \Psi \) were steeper in IFC-3 than in IFC-2 \( (P < 0.05) \); Figures 1b and 1c, Table 1).

In jack pine, the ratio of intercellular to ambient CO\(_2\) concentration \( (C_i/C_2) \), which is a measure of the capacity for CO\(_2\) diffusion through the stomata into the leaf \( (g_{s,CO2}) \) relative to the mesophyll capacity to fix CO\(_2\) \( (g_m) \), responded to \( \Psi \) somewhat differently in IFC-2 than in IFC-3. In IFC-2, \( C_i/C_2 \) was relatively stable with decreasing \( \Psi \), reflecting similar rates of decrease of \( g_m \) and \( g_{s,CO2} \) with decreasing \( \Psi \) (Figure 1d), whereas in IFC-3 \( C_i/C_2 \) decreased with decreasing \( \Psi \) (Figure 1d), reflecting a greater rate of decrease for \( g_{s,CO2} \) than for \( g_m \) with decreasing \( \Psi \) as the tissue hardened late in the growing season. The \( C_i/C_2 \) ratio was higher in IFC-2 than in IFC-3 for high values of \( \Psi \), reflecting the combined effects of higher \( g_m \) and lower \( g_{s,CO2} \) in IFC-3 than in IFC-2 (Figures 1b–d).
Laboratory measurements for black spruce  Mesophyll conductance \((g_m)\) for black spruce also showed a threshold response to \(\Psi\) (Figure 2, Table 2) but the threshold occurred at a more negative \(\Psi\) \((-2.4\) and \(-2.7\) MPa for IFC-2 and IFC-3, respectively) than for jack pine. Unlike jack pine, \(g_{s,CO_2}\) of black spruce declined linearly and continuously with decreasing \(\Psi\) over the entire range of \(\Psi\) examined (Figure 2c). In black spruce, as in jack pine, \(A_n\) showed a threshold response to \(\Psi\), but with more negative threshold values than in jack pine, i.e., \(-2.5\) and \(-2.6\) MPa in IFC-2 and IFC-3, respectively (Figures 1a and 2a). However, unlike \(A_n\) of jack pine, \(A_n\) of black spruce increased slowly with increasing \(\Psi\) above the threshold \(\Psi\) as a consequence of the steady increase in \(g_{s,CO_2}\) and thus \(C_i/C_a\) (Figure 2d). Because of the rapid drop in \(g_m\), \(A_n\) decreased rapidly

**Table 1.** Linear regression analysis of the relationships between shoot water potential \((\Psi;\text{MPa})\) and: (1) net photosynthesis \((A_n;\text{µmol m}^{-2}\text{s}^{-1})\); (2) mesophyll conductance \((g_m;\text{mmol m}^{-2}\text{s}^{-1})\); and (3) stomatal conductance to \(CO_2\) \((g_{s,CO_2};\text{mmol m}^{-2}\text{s}^{-1})\) of jack pine branches measured in the laboratory. IFC = Intensive Field Campaign.

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<th>Slope</th>
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Table 2. Linear regression analysis of the relationships between shoot water potential (Ψ; MPa) and net photosynthesis (A<sub>n</sub>; µmol m<sup>−2</sup> s<sup>−1</sup>), and mesophyll conductance (g<sub>m</sub>; mmol m<sup>−2</sup> s<sup>−1</sup>) and stomatal conductance to CO<sub>2</sub> (g<sub>s,CO2</sub>; mmol m<sup>−2</sup> s<sup>−1</sup>) of black spruce branches measured in the laboratory. IFC = Intensive Field Campaign.

<table>
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<th>IFC</th>
<th>Variable</th>
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with decreasing Ψ below 2.5 MPa (Figure 2, Table 2), and reached zero at Ψ values of −3.7 and −4.0 MPa in IFC-2 and IFC-3, respectively. In contrast to jack pine, the declines in A<sub>n</sub> and g<sub>m</sub> of black spruce with decreasing Ψ were faster in IFC-2 than in IFC-3 (P < 0.05); however, sensitivity of g<sub>s,CO2</sub> to Ψ did not differ between IFC-2 and IFC-3 for black spruce (P > 0.05, Figure 2c, Table 2).

The C<sub>i</sub>/C<sub>a</sub> ratio in black spruce showed a different response to Ψ for IFC-2 than for IFC-3. In IFC-2, C<sub>i</sub>/C<sub>a</sub> decreased with decreasing Ψ between −0.2 and −2.5 MPa and then increased with further decreases in Ψ because of greater sensitivity of g<sub>m</sub> compared to g<sub>s</sub> over this range of Ψ values (Figure 2d). In IFC-3, as in IFC-2, C<sub>i</sub>/C<sub>a</sub> decreased with decreasing Ψ to the threshold Ψ for g<sub>m</sub>(−2.7 MPa) as a result of the continuous linear decrease in g<sub>s,CO2</sub>; however, unlike IFC-2, Ψ decreased below the threshold value, and C<sub>i</sub>/C<sub>a</sub> remained relatively stable because g<sub>m</sub> decreased in parallel with g<sub>s,CO2</sub> (Figure 2c and 2d, Table 2).

Field results Field measurements of Ψ were all at or above the threshold values identified in the laboratory for both jack pine and black spruce. For all three IFCs, the minimum field Ψs were −1.2 and −2.2 MPa for jack pine and black spruce, respectively (Figures 3 and 4). There were no significant decreases in A<sub>n</sub>, g<sub>m</sub> or g<sub>s,CO2</sub> in jack pine and no decreases in A<sub>n</sub> or g<sub>m</sub> in black spruce in response to decreasing Ψ. Both g<sub>s,CO2</sub> and C<sub>i</sub>/C<sub>a</sub> of black spruce showed a decline (P < 0.01) with decreasing Ψ when the three dates of measurement were combined (Figure 4c).

In aspen, there was an increase in A<sub>n</sub> and g<sub>m</sub> and a decrease in g<sub>s,CO2</sub> and C<sub>i</sub>/C<sub>a</sub> as Ψ decreased (P < 0.01) when data from the four dates were pooled; however, these trends were not apparent when values for each date were examined individually (Figure 5). Because A<sub>n</sub> and g<sub>m</sub> increased over the entire range of Ψ values measured in the field, it appears that the threshold Ψ for aspen must be below −3.8 MPa.

Predawn Ψ measurements indicated that Ψ remained fairly stable over the summer at all three sites. Predawn Ψ measured for the jack pine stand ranged from −0.46 to −0.88 MPa, and it ranged from −0.72 to −1.16 MPa and −0.47 to −0.67 MPa, for the black spruce and aspen stands, respectively.

Responses to VPD  
Vapor pressure difference (VPD) and its interaction with temperature strongly affected stomatal conductance to water vapor (g<sub>s,wv</sub>) for cut branches of jack pine and black spruce measured...
in the laboratory (Figures 6a and 6b). When all temperatures and VPDs were taken together, however, the relationship formed a reasonably well-defined negative asymptotic curve that can be described empirically by Equation 1. The fit of Equation 1 to the cut branches of jack pine was better than for black spruce based on the linear regression of measured versus predicted $g_{s, wv}$ ($R^2 = 0.80$ and $0.52$ for jack pine and black spruce, respectively, and slope = 1.0 at $P < 0.05$). The poorer fit for black spruce than for jack pine was caused largely by the failure of the model to fit correctly the $15^\circ C$ data and some of the lower VPD data at $25^\circ C$ (Figure 6b). The same curves developed from the cut-branch data for these two species also fit the field data (Figures 6c and 6d). The curve defined from the jack pine cut-branch data slightly overestimated $g_{s, wv}$ of the jack pine field data (Figures 6a and 6c); however, a more physiologically based conductance model that accounts for the effect of other environmental factors (e.g., light) on $g_{s, wv}$ may correct this discrepancy. On the other hand, the curve used to define the black spruce cut-branch data fit the black spruce field data without apparent bias (Figures 6b and 6d).

Field data collected from the upper and lower canopies of the jack pine, black spruce and aspen stands all showed a strong relationship between $g_{s, wv}$ and VPD (Figures 7a–c). However, $g_{s, wv}$ tended to be lower for the lower canopy than for the upper canopy at the same VPD. Nonlinear regression procedures used to fit Equation 1 to both the upper and lower canopy data showed that the relationship was significantly different between the two canopy layers for jack pine and aspen ($P < 0.05$, Table 3, Figures 7d–f). These differences arose from the estimation of parameter $c$; the curvature and lower asymptote parameters ($a$ and $b$, respectively) were not significantly different between the two canopy levels (Table 3). Similarly, estimates of the maximum $g_s$, i.e., $g$, when VPD equals zero, were greater for the upper canopy than for the lower canopy (Table 3). For jack pine and black spruce, the $R^2$ values for measured versus predicted $g_{s, wv}$ were higher for the upper canopy than for the lower canopy (Table 3). Furthermore, the $R^2$ values for both canopy layers combined fell between the $R^2$ values calculated for the upper and lower canopies separately. On the other hand, for aspen, the fit was better for the lower canopy than for the upper canopy, whereas the fit for the combined data was worse (Table 3).

For both the upper and lower canopies, the sensitivity of $g_{s, wv}$ to VPD was greatest for aspen (i.e., $d g_{s, wv} / d VPD$ was the most negative), followed by jack pine and then black spruce (Figures 8a and 8b). The sensitivity of $g_{s, wv}$ in the upper canopy was greater than in the lower canopy for jack pine and aspen (Figures 8c and 8d), whereas there were no significant differences between canopy levels for black spruce (Table 3). For relative $g_s$, aspen and jack pine showed similar sensitivities to changes in VPD, whereas black spruce was less sensitive (Figure 9).

Both laboratory and field data showed that VPD strongly affected $C_i$ (Figure 10). The ranges of $C_i$ were similar for all
species, i.e., 150 to 350 ppm. The $C_i$ of black spruce appeared to decline at a slower rate than that of both jack pine and aspen with increasing VPD. The laboratory data followed a similar pattern to the field data for jack pine and black spruce. The curves were calculated from Equation 1. Field data from the upper canopy were from diurnal measurements of gas exchange on in situ branches of (c) jack pine and (d) black spruce. The curves were developed from laboratory data for the corresponding species. Regression parameters are $a = 6.518$, $b = 0.004$ and $c = 0.311$ for jack pine and $a = 0.249$, $b = -0.012$ and $c = 0.050$ for spruce.

Discussion

Water potential

When a cut-branch technique is used to determine the effect of shoot water potential ($\Psi$) on gas exchange, it is primarily the short-term, direct hydraulic effect of $\Psi$ on the foliage and its subsequent physiological consequences that are measured. Recently, there has been considerable interest in the communication between roots and shoots in response to environmental stress (e.g., Johnson and Ferrell 1982, Davies and Jeffcoat 1990, Davies and Zhang 1991, Correia and Pereira 1995, Jackson et al. 1995). Increased abscisic acid flux and decreased cytokinin flux from roots to foliage have been pro-
posed as possible mechanisms for this communication (Jones 1990, Jackson et al. 1995), but evidence is controversial. In our study, the branches would have been affected by whatever root to shoot signals were active at the time of branch harvest, but not subsequently. Thus, the cut-branch technique would only partially account for these root signals if they exist. Additionally, the physiological performance of a given branch may also be influenced by the environmental conditions and physiological behavior of other branches on the same tree (Whitehead et al. 1996). Therefore, caution should be taken when cut-branch data are scaled to the whole tree, especially when environmental conditions differ among different branches.

We observed threshold responses of $A_n$ and $g_m$ to $\Psi$ in both black spruce and jack pine (Figures 1 and 2). Similar responses have been reported in other species (e.g., Collatz et al. 1976, Collatz 1977, Ludlow 1980, Waring et al. 1981, Armitage et al. 1983, Melzack et al. 1985). Our threshold values are within the $−2.5$ to $−0.8$ MPa range reported for other conifers (Brix 1962, Turner and Waggoner 1968, Jarvis 1980, Beadle et al. 1981, Melzack et al. 1985), except for black spruce later in the growing season where the threshold $\Psi$ was $−2.6$ MPa for $A_n$.

**Table 3. Nonlinear regression parameters for the relationship between vapor pressure difference (kPa) and stomatal conductance to water vapor ($g_{swv}$; mol m$^{-2}$ s$^{-1}$) for the upper and lower canopy of jack pine, black spruce and aspen. Parameters were calculated with Equation 1 and parameterized with field data shown in Figure 7. Within the same row, values followed by different letters are significantly different at $P < 0.05$ as determined from the asymptotic 95% confidence interval estimate for each parameter.**

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Upper canopy</th>
<th>Lower canopy</th>
<th>Combined</th>
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<tr>
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<td></td>
<td></td>
</tr>
<tr>
<td>$a$</td>
<td>0.355 a</td>
<td>0.604 a</td>
<td>0.476 a</td>
</tr>
<tr>
<td>$b$</td>
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<td>$−0.025$ a</td>
<td>$−0.052$ a</td>
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<td>$c$</td>
<td>0.161 a</td>
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<td>$R^2$ value</td>
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1 Maximum stomatal conductance, $g_{max}$, was calculated as $b + c$, i.e., $g_m$ when VPD = 0.
2 The $R^2$ values are the coefficients of determination for the relationship between predicted $g_{swv}$ and measured $g_{swv}$. The slope of the relationship between predicted and measured $g_{swv}$ did not differ significantly from 1.0 at $P < 0.05$.

Jarvis (1980) reported threshold $\Psi$ values for $A_n$ of $−0.8$ and $−2.0$ MPa for Sitka spruce and Scots pine, respectively.

The response pattern of stomatal conductance ($g_{CO2}$) to $\Psi$ varied between the two conifers. The $g_{CO2}$ of jack pine showed a threshold response, but the threshold $\Psi$ was less negative than that for $A_n$ and $g_m$ (Figure 1). The $g_{CO2}$ of black spruce, on the other hand, decreased continuously with decreasing $\Psi$ over the entire range examined (Figure 2).
threshold (e.g., Brix 1962, Turner and Waggoner 1968, Puritoh 1973, Running 1976, Watts and Neilson 1978, Ludlow 1980, Johnson and Ferrell 1983) and continuous (e.g., Dykstra 1974, Davenport et al. 1977, Schulze and Kupper 1979) stomatal responses to $\Psi$ have been reported for other species. Consistent with our results, Stewart et al. (1995) report that $g_m$ of black spruce seedlings subjected to repeated cycles of drought was unaffected by $\Psi$ as low as $-1.5$ MPa, whereas $g_s$ decreased significantly with decreasing $\Psi$. Our data also support the modeling approach taken by Sellers et al. (1996) and others whereby low $\Psi$ brought on by low soil water potential is assumed to impact $g_m$ directly by diminishing the maximum catalytic capacity of Rubisco (Wong et al. 1985, Figures 1 and 2).

Stomatal conductance had a higher threshold $\Psi$ than $A_n$ and $g_m$ for both jack pine and black spruce (Figures 1 and 2). Similar phenomena have been reported for other species (e.g., Melzack et al. 1985). This type of response has ecological implications for species growing at high latitudes. A relatively high $g_{s,CO_2}$ combined with a high $g_m$ allows a tree to maintain high $A_n$ when water conditions are favorable. However, when the rate of transpiration exceeds the rate of water delivery to leaves as a result of cold soil, low soil water or high evaporative demand, $\Psi$ declines. Before $\Psi$ falls below the threshold for $g_{so}$, $g_{s,CO_2}$ begins to decrease, reducing the transpiration rate and maintaining a favorable $\Psi$ for photosynthetic activity in the mesophyll. Field measurements on warm, sunny days showed that both jack pine and black spruce maintained their $\Psi$ above the corresponding threshold and that $A_n$ was unaffected by fluctuations in $\Psi$ (Figures 3 and 4). Tower flux measurements in the Old Jack pine stand in the BOREAS Southern Study Area (54° N, 105° W) have shown no effects of volumetric soil water content on CO$_2$ flux even though the water content varied widely (approximately 4.8 to 12.4%) (Baldocchi and Vogel 1996). Although we were unable to determine a threshold $\Psi$ for aspen in the laboratory, field data showed no evi-

Figure 10. Intercellular CO$_2$ concentration ($C_i$) versus vapor pressure difference (VPD) for field and laboratory data of (a) jack pine, (b) black spruce, and (c) aspen for IFC-1, -2 and -3. Open circles = field data. Solid circles = lab data. Solid lines = models. No laboratory data are available for aspen. The models are as follows: $C_i = 178.6/(1 + 1.362 \text{ VPD}) + 176.3, R^2 = 0.53$, for black spruce; $C_i = 634.6/(1 + 0.1338 \text{ VPD}) - 293.2, R^2 = 0.62$, for jack pine; and $C_i = 519.5/(1 + 0.2207 \text{ VPD}) - 139.5, R^2 = 0.62$, for aspen.

Figure 11. Cumulative frequency of daily maximum and PAR-weighted daily mean vapor pressure deficit (VPD) for the growing season (May to September) of 1994. Data were collected from the Old Jack Pine site by BOREAS staff.

Figure 12. Photosynthesis versus intercellular CO$_2$ concentration ($C_i$) for jack pine, black spruce and aspen for IFC-2. Data are from laboratory measurements of cut branches. For all above species, the range of $C_i$ was obtained by varying ambient CO$_2$ at approximately 0.8 kPa vapor pressure difference (VPD) and 20 °C air temperature. For jack pine and black spruce, $C_i$ was also changed between 150 and 350 $\mu$mol mol$^{-1}$ by varying VPD from 0.7 to 2.8 kPa at 360 $\mu$mol mol$^{-1}$ ambient CO$_2$ and 25 °C air temperature.
dence of $\Psi$ limitation on $A_n$, suggesting that aspen also maintained a favorable $\Psi$ for photosynthetic activity (Figure 5). It has been suggested that trees normally approach but do not exceed the $\Psi$ limit for catastrophic xylem embolism on warm sunny days when transpiration rates are near maximum (Meinzer and Grantz 1991, Sperry and Pockman 1993, Saliendra et al. 1995, Sperry 1995). Our results suggest that this idea might be extended to $A_n$ as well, because $\Psi$ approached but did not go below the threshold value for photosynthesis (Figures 3 and 4), even though the 1994 growing season was the driest on record in the area. If this is true, then the threshold $\Psi$ for $A_n$ must be similar to the threshold $\Psi$ for catastrophic xylem embolism.

Black spruce can tolerate much lower $\Psi$ than jack pine before either $g_m$ or $A_n$ is substantially affected, indicating that black spruce, which often grows on wet, organic soils, is able to exert a much stronger force for extracting water from its substrate and moving it to foliage before its photosynthetic activity is disturbed than jack pine, which typically grows on coarse, sandy soils with low water-holding capacity. This adaptation of black spruce can be explained in several ways. For example, the low hydraulic conductivity and low matrix potentials of organic soils compared with sandy soils make water uptake by roots more difficult (Mitsch and Gosselink 1993). Furthermore, the low thermal conductivity of the moss cover on a typical black spruce site results in a much colder root environment with lower oxygen concentration than sandy soils with a thin lichen cover. The viscosity of water increases and the permeability of membranes decreases at low temperatures (Mannerkoski 1985). Root systems of black spruce are usually much less developed than those of jack pine (Lieffers and Rothwell 1986, 1987). Additionally, there are differences in the hydraulic conductance of the xylem among tree species (Pothier et al. 1989a, 1989b). Some or all of the above factors likely interact to explain the greater stress resistance of the mesophyll in black spruce compared to jack pine.

The photosynthetic activity of aspen leaves appears to be more resistant to low $\Psi$ than that of black spruce. Field data showed no decrease in $A_n$ or $g_m$ at $\Psi$ values as low as $-3.0$ MPa (Figure 5). The larger size and possibly greater boundary layer resistance of aspen leaves compared with conifer needles may require the maintenance of active transpiration and carbon assimilation at low $\Psi$ to avoid overheating (Waring and Schlesinger 1985).

The relative drought resistances of stomata and mesophyll changed over the season in both jack pine and black spruce. In IFC-2, the $C_i/C_a$ ratio for jack pine and black spruce increased with decreasing $\Psi$ below $-2.0$ and $-3.0$ MPa, respectively, indicating that the mesophyll was more sensitive than the stomata to low $\Psi$. In contrast, this ratio decreased at low $\Psi$ in IFC-3, indicating progressively more stomatal limitation to $A_n$ and that the stomata were relatively more sensitive to $\Psi$ than the mesophyll. The increase in relative drought resistance of the mesophyll may be related to increases in cold hardiness later in the growing season.

### Vapor pressure difference

Stomatal conductance ($g_{s,wv}$) of all three species decreased in response to increased leaf-to-air vapor pressure difference (VPD) (Figures 6 and 7). This stomatal response to VPD is necessary to maximize carbon gain relative to transpirational water loss as described in the optimization theory proposed by Cowan and Farquhar (1977). The influence of VPD on $g_{s,wv}$ was strong in both the laboratory and the field data. For the laboratory data, the impact of VPD was apparent at all test temperatures (15, 25 and 35 °C), but $g_{s,wv}$ declined faster with increasing VPD at 15 than at 25 and 35 °C (cf. Jarvis 1980). Sap flow data on aspen showed a pronounced VPD effect on transpiration rate, i.e., sap flow increased with increasing VPD up to 1.0 kPa and then remained constant with further increases in VPD (Hogg and Hurdle 1997). Additionally, tower and airborne flux studies in BOREAS have found higher Bowen ratios in these forests on clear days than on cloudy days (Sellers et al. 1995, Baldocchi and Vogel 1996, Baldocchi et al. 1997), suggesting that VPD responses of the vegetation influences the energy budget of the entire ecosystem.

A simple empirical model (Equation 1) was used to quantify certain features of the $g_s$ response to VPD, e.g., maximum conductance and stomatal sensitivity. The model parameters derived from the cut-branch data of jack pine and black spruce also fit the field data reasonably well (Figure 6), indicating that vapor pressure difference and temperature variations explain much of the variation encountered in the field data. The model also supports the validity of using a cut-branch technique for determining the responses of $A_n$ and $g_s$ to different environmental conditions. We did not test whether the cut-branch technique can be applied to highly stressful environmental conditions; however, even the 15 and 35 °C data were consistent with the $g_{s,wv}$ values obtained in our field measurements. The period of measurement for cut branches was 15 to 30 min and thus these measurements do not take into account acclimation of or damage to the foliage that occurs over a longer period of time.

When parameterized with field data, the model accounted for 52 to 68% of the $g_s$ variation for the lower canopy and 56 to 71% for the upper canopy of the three species. Furthermore, slopes of the regression of measured versus predicted $g_s$ did not differ significantly from one ($P > 0.05$). Given that the field data were collected at different times during the growing season and on days having a wide range of weather conditions, it is interesting that so much of the variation can be explained by a simple empirical model. Much of the remaining variation might be explained by light limitations and, for black spruce, varying shoot water potential. A more mechanistic model, such as the coupled photosynthesis-conductance model described by Collatz et al. (1991), might perform better than the Lindroth and Hallidin (1986) model used in this study, because the former model takes into account light limitations and feedbacks between $A_n$ and $g_s$.

The stomata of foliage in the upper canopy were more sensitive to VPD than those in the lower canopy in both jack pine and aspen (Figures 8c and 8d), suggesting that $A_n$ of foliage in the upper canopy is more likely to be limited by
$g_{s, CO_2}$ than foliage in the lower canopy. This conclusion is supported by the lower $C_i/C_a$ ratios in the upper canopy than in the lower canopy measured by Brooks et al. (1997). Stomatal sensitivity to VPD can also vary during the growing season (e.g., Meinzer 1982, Meinzer et al. 1993), but we were unable to examine the seasonal variation from the field data because different ranges of VPD tended to occur on the different measurement days (Figure 6). Laboratory measurements on cut branches at 25 °C during the three IFC periods showed no seasonal changes in stomatal sensitivity to VPD (data not shown). Given the strong interaction between temperature and VPD (Figure 6), data taken over a range of temperatures are probably necessary to detect seasonal variation in sensitivity.

The magnitude of the VPD limitation on gas exchange varied with species. Aspen stomata were the most sensitive to VPD of the three species (Figure 8), probably because maximum $g_s$ of aspen was an order of magnitude greater than those of the conifers and thus had further to fall (Table 3). This difference in stomatal sensitivity to VPD between aspen and conifers was further enhanced in the case of photosynthesis by the greater slope of the $A_n$ versus $C_i$ relationship for aspen than for the conifers (Figure 12). As VPD increased, $g_s$ decreased, restricting the diffusion of CO$_2$ into the leaf, reducing $C_i$ (Figure 10) and thus decreasing $A_n$ (Figure 12). However, when we normalized the $g_s$ of each species to the $g_s$ for the seasonal average VPD of 1.0 kPa, the rate of decrease in relative $g_s$ with increasing VPD for jack pine was about the same as that for aspen (Figure 9). Furthermore, the relative reduction in $A_n$ in response to a decrease in $C_i$ from 300 to 200 μmol mol$^{-1}$ was smaller for aspen (26%) than for jack pine (34%) and black spruce (35%).

Differences among species in the magnitude of the gas exchange response to VPD could have significant implications for understanding feedbacks between the land surface and the atmosphere under different climate change scenarios. For instance, a given increase in VPD at the leaf surface over the growing season would be expected to decrease absolute water flux to the atmosphere more from leaves of aspen than from jack pine and black spruce (Figures 6–8). However, the relative decreases in water flux for a given increase in VPD should not differ greatly between aspen and jack pine. Because aspen stands tend to support higher leaf areas than jack pine or black spruce stands, the effect of VPD on the absolute fluxes should be even more pronounced for aspen than for the conifers at the canopy level. Such decreases in water flux could further dry out the planetary boundary layer, thereby further increasing VPD while decreasing $g_s$ and $A_n$ (Field et al. 1995). In addition to altering energy and water fluxes, such a feedback could change the balance between photosynthetic CO$_2$ assimilation and respiratory CO$_2$ release, particularly because higher temperatures associated with elevated VPD increase carbon fluxes from the soil and nonphotosynthetic components of living vegetation. Possible increases in the surface area occupied by aspen as a result of increased wildfires associated with warmer and drier conditions could extend this effect to the entire landscape.

The PAR-weighted average VPD was only 1.0 kPa during the growing season (Figure 11), even though 1994 was the driest year on record for the region and the daily maximum VPD reached 3.8 kPa on hot days (Figure 11). The seasonal average $C_i/C_a$ ratios corresponding to this 1 kPa VPD were 0.77, 0.71 and 0.81, respectively, for jack pine, black spruce and aspen (Figure 10). The $C_i/C_a$ ratios calculated from $^{13}$C/$^{12}$C isotope data collected from trees in the same area as our study were in agreement with our $C_i/C_a$ ratio for jack pine (0.77), within 14% for black spruce (0.82), and within 10% for aspen (0.90) (Flanagan et al. 1997). Although these $C_i/C_a$ ratios suggest that, on average, there was no strong stomatal limitation to $A_n$ they should not be interpreted to mean that there was no VPD limitation on $A_n$ over the growing season. For example, our data indicate that $A_n$ was about 18, 27 and 20% lower at 2 kPa VPD than at 1 kPa for black spruce, jack pine and aspen, respectively (Figure 12). Furthermore, daily average VPD was greater than 1 kPa for 50% of the growing season and greater than 2 kPa for 8% of the days during the 1994 growing season (Figure 11). However, because photosynthetic capacities of jack pine and black spruce were relatively low, absolute decreases in $A_n$ per unit leaf area basis (μmol CO$_2$ m$^{-2}$ s$^{-1}$) resulting from an increase in VPD from 1.0 to 2.0 kPa would be small (Figure 12).

**Conclusion**

Laboratory measurements on jack pine and black spruce showed a threshold response of net photosynthesis ($A_n$) and mesophyll conductance ($g_m$) to shoot water potential ($Ψ$). The threshold was lower for black spruce than for jack pine. In situ field data from mature stands suggest that both black spruce and jack pine maintained their $Ψ$ above the corresponding threshold and that there was no evidence of $Ψ$ limitations on $A_n$ in these mature jack pine, black spruce or aspen, even though the study was conducted during the driest year on record in the area. Stomatal conductance to CO$_2$ ($g_{s, CO_2}$) of jack pine also showed a threshold response, but $g_{s, CO_2}$ of black spruce declined continuously with decreasing $Ψ$. Mesophyll limitations appeared to be primarily responsible for the decline in $A_n$ at low $Ψ$ for jack pine and black spruce in the middle of the growing season, whereas stomatal limitations became more important later in the season.

Vapor pressure difference (VPD) and its interaction with temperature were important in regulating the gas exchange of these species. Stomatal sensitivity to VPD was greater for aspen than for jack pine and greater for jack pine than for black spruce. It was also greater for foliage in the upper than in the lower canopy for jack pine and aspen. A simple empirical model of $g_s$ versus VPD explained 50 to 70% of the variation in $g_s$ observed in the field measurements.

Vapor pressure difference had a much greater absolute impact on $A_n$ of aspen than on $A_n$ of jack pine or black spruce because of the greater stomatal sensitivity to VPD and steeper slope of the $A_n-C_i$ relationship in aspen. We conclude that a given increase in VPD at the leaf surface in response to climate change will affect the absolute fluxes of CO$_2$ and water vapor...
per unit leaf area more from the aspen component of a boreal forest landscape than from the conifer component.

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