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

QING-LAI DANG,[1–3] HANK A. MARGOLIS,[1,2] MARIE R. COYEA,[1] MIKAILOU SY[1,4] and G. JAMES COLLATZ[2]

[1] *Centre de recherche en biologie forestière, Pavillon Abitibi-Price, Université Laval, Sainte-Foy, Québec G1K 7P4, Canada*

[2] *Biospheric Sciences Branch, Code 923, Building 22, NASA Goddard Space Flight Center, Greenbelt, MD 20771, USA*

[3] *Present address: Lakehead University, Faculty of Forestry, 955 Oliver Road, Thunder Bay, Ontario P7B 5E1, Canada*

[4] *Present address: Institute of Biology, Biology Department, Carleton University, Ottawa, Ontario K1S 5B6, Canada*

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 (A_n) and mesophyll conductance (g_m) of jack pine and g_m 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 (g_s) of black spruce decreased continuously with decreasing Ψ, whereas g_s of jack pine showed a threshold response. Mesophyll limitations were primarily responsible for the decline in A_n 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 A_n 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 g_s 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 A_n of aspen than on A_n of the conifers as a result of aspen's greater stomatal sensitivity to VPD and greater slope of the relationship between A_n and intercellular CO_2 concentration (C_i). During the 1994 growing season, VPD averaged 1.0 kPa, corresponding to ratios of C_i to ambient CO_2 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 CO_2 and H_2O 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 CO_2 in the atmosphere suggest that photosynthetic activity of the boreal forest may be responsible for a significant portion of the "missing sink" of anthropogenic CO_2, i.e., the portion of the CO_2 emitted by fossil fuel burning and deforestation that does not accumulate in the atmosphere (Tans et al. 1990, Slegenthaler and Sarmiento 1993, Ciais et al. 1995, Denning et al. 1995). However, general circulation model (GCM) simulations suggest that increasing atmospheric CO_2 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 (Ψ). Low Ψ can induce stomatal closure, thus shutting down the dominant pathway for the exchange of CO_2 and H_2O between a leaf and the atmosphere (Ludlow 1980, Osonubi and Davies 1980). Low Ψ can also reduce or halt the photosynthetic activity of the mesophyll (Teskey et al. 1986, Ni and Pallardy 1992). Although the effects of Ψ 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 Ψ in controlling the exchange of H_2O 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, Kawamitsu 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 (Losch 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, Warrit 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 (Ψ) 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 feathermoss (*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 gleysols.

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 *Cornus 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 (Ψ) 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 were 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_2O 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_2O became stable.

For the measurement of Ψ response at high (less negative) Ψ, water was supplied to the branch as described above. To decrease Ψ, 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 Ψ. 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 Ψ 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 Ψ was measured on a nearby branch.

The BOREAS staff monitored predawn Ψ 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: $VPD_i \times PAR_i / \Sigma(PAR_i)$, where subscript i denotes the ith 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 Ψ), 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 Ψ value at the intersection of the two lines defined the threshold or critical Ψ.

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

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

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 ($g_{s,wv}$). For an equation with a single independent variable, this is equivalent to the nonlinear regression R^2 value calculated by [1 − (Error Sum of Squares/ Corrected Sum of Squares)] for Equation 1. The first derivative of Equation 1 describes the sensitivity of g_s to a change in VPD.

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

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 (Ψ); i.e., they were relatively constant over the range of Ψ values above the threshold, but decreased linearly as Ψ decreased below the threshold (Figures 1a–c, Table 1). In IFC-2, the threshold Ψ of jack pine was −1.2 MPa for A_n and g_m, and −1.1 MPa for $g_{s,CO2}$. The threshold Ψ 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 Ψs 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 Ψ 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_a), 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 Ψ somewhat differently in IFC-2 than in IFC-3. In IFC-2, C_i/C_a was relatively stable with decreasing Ψ, reflecting similar rates of decrease of g_m and $g_{s,CO2}$ with decreasing Ψ (Figure 1d), whereas in IFC-3 C_i/C_a decreased with decreasing Ψ (Figure 1d), reflecting a greater rate of decrease for $g_{s,CO2}$ than for g_m with decreasing Ψ as the tissue hardened late in the growing season. The C_i/C_a ratio was higher in IFC-2 than in IFC-3 for high values of Ψ, reflecting the combined effects of higher g_m and lower $g_{s,CO2}$ in IFC-3 than in IFC-2 (Figures 1b–d).

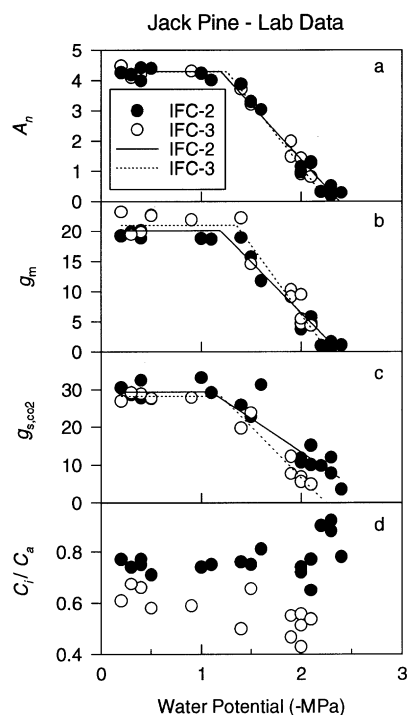Figure 1. Relationships between shoot water potential and: (a) net photosynthesis (A_n, µmol m^{-2} s^{-1}); (b) mesophyll conductance (g_m, mmol m^{-2} s^{-1}); (c) stomatal conductance to CO_2 ($g_{s,CO2}$, mmol m^{-2} s^{-1}); and (d) the ratio of intercellular to ambient CO_2 concentrations (C_i/C_a) of jack pine. Measurements were taken under controlled laboratory conditions (20 °C, 360 µmol mol^{-1} CO_2, 1100 µmol m^{-2} s^{-1} PAR, and 0.6 to 0.8 kPa VPD) on cut branches during the middle (IFC-2) and end (IFC-3) of the growing season. Symbols are data points and lines are regressions. Regression parameters are shown in Table 1.
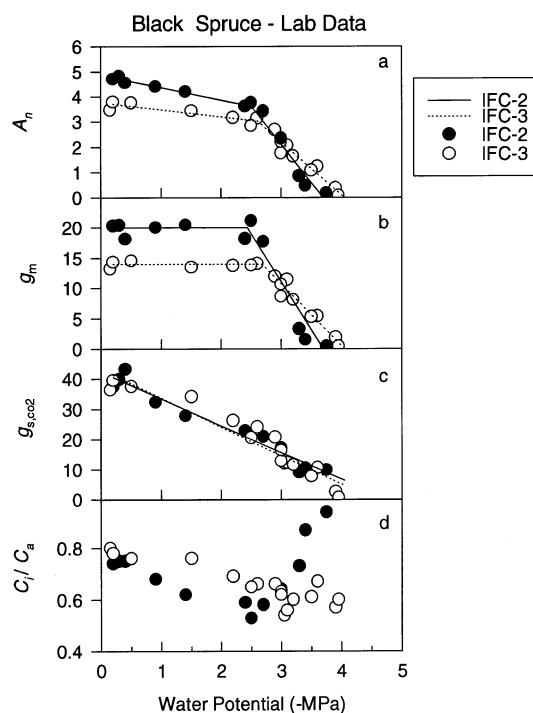
Figure 2. Relationships between shoot water potential and A_n, g_m, $g_{s,CO2}$ and C_i/C_a of black spruce. See caption to Figure 1 for measurement conditions. Regression parameters are shown in Table 2.

Laboratory measurements for black spruce Mesophyll conductance (g_m) for black spruce also showed a threshold response to Ψ (Figure 2, Table 2) but the threshold occurred at a more negative Ψ (−2.4 and −2.7 MPa for IFC-2 and IFC-3,

respectively) than for jack pine. Unlike jack pine, $g_{s,CO2}$ of black spruce declined linearly and continuously with decreasing Ψ over the entire range of Ψ examined (Figure 2c). In black spruce, as in jack pine, A_n showed a threshold response to Ψ, 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 Ψ above the threshold Ψ as a consequence of the steady increase in $g_{s,CO2}$ and thus C_i (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 (Ψ; MPa) and: (1) net photosynthesis (A_n; µmol m^{-2} s^{-1}); (2) mesophyll conductance (g_m; mmol m^{-2} s^{-1}); and (3) stomatal conductance to CO_2 ($g_{s,CO2}$; mmol m^{-2} s^{-1}) of jack pine branches measured in the laboratory. IFC = Intensive Field Campaign.

IFC	Variable	Ψ Range	Intercept	Slope	R^2	P
2	A_n	> −1.2	4.3	−0.2	0.13	0.3956
		< −1.2	8.7	−3.6	0.96	0.0000
	g_m	> −1.2	20.1	−0.9	0.10	0.4036
		< −1.2	40.4	−17.3	0.95	0.0000
	$g_{s,CO2}$	> −1.1	29.4	1.6	0.03	0.6639
		< −1.1	51.1	−19.9	0.93	0.0000
3	A_n	> −1.3	4.3	0.0	0.00	0.9399
		< −1.3	9.7	−4.1	0.97	0.0000
	g_m	> −1.4	21.0	0.9	0.07	0.6238
		< −1.4	51.6	−22.6	0.90	0.0003
	$g_{s,CO2}$	> −1.2	28.2	−0.2	0.00	0.9259
		< −1.2	60.4	−26.9	0.89	0.0004

Table 2. Linear regression analysis of the relationships between shoot water potential (Ψ; MPa) and net photosynthesis (A_n; μmol m^{-2} s^{-1}), and mesophyll conductance (g_m; mmol m^{-2} s^{-1}) and stomatal conductance to CO_2 ($g_{s,CO2}$; mmol m^{-2} s^{-1}) of black spruce branches measured in the laboratory. IFC = Intensive Field Campaign.

IFC	Variable	Ψ Range	Intercept	Slope	R^2	P
2	A_n	> -2.5	4.9	-0.5	0.97	0.0000
		< -2.5	11.2	-3.0	0.95	0.0002
	g_m	> -2.4	20.0	-0.3	0.08	0.5196
		< -2.4	60.9	-16.4	0.93	0.0004
	$g_{s,CO2}$	entire range	42.3	-8.9	0.95	0.0000
3	A_n	> -2.6	3.8	-0.3	0.80	0.0069
		< -2.6	8.5	-2.1	0.95	0.0000
	g_m	> -2.7	13.9	-0.1	0.01	0.8027
		< -2.7	41.4	-10.2	0.94	0.0000
	$g_{s,CO2}$	entire range	43.1	-9.5	0.92	0.0000

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_n and g_m of black spruce with decreasing Ψ were faster in IFC-2 than in IFC-3 ($P < 0.05$); however, sensitivity of $g_{s,CO2}$ to Ψ did not differ between IFC-2 and IFC-3 for black spruce ($P > 0.05$, Figure 2c, Table 2).

The C_i/C_a ratio in black spruce showed a different response to Ψ for IFC-2 than for IFC-3. In IFC-2, C_i/C_a 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_m compared to g_s over this range of Ψ values (Figure 2d). In IFC-3, as in IFC-2, C_i/C_a decreased with decreasing Ψ to the threshold Ψ for g_m (-2.7 MPa) as a result of the continuous linear decrease in $g_{s,CO2}$; however, unlike IFC-2, Ψ decreased below the threshold value, and C_i/C_a remained relatively stable because g_m decreased in parallel with $g_{s,CO2}$ (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_n, g_m or $g_{s,CO2}$ in jack pine and no decreases in A_n or g_m in black spruce in response to decreasing Ψ. Both $g_{s,CO2}$ and C_i/C_a 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_n and g_m and a decrease in $g_{s,CO2}$ and C_i/C_a 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_n and g_m 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
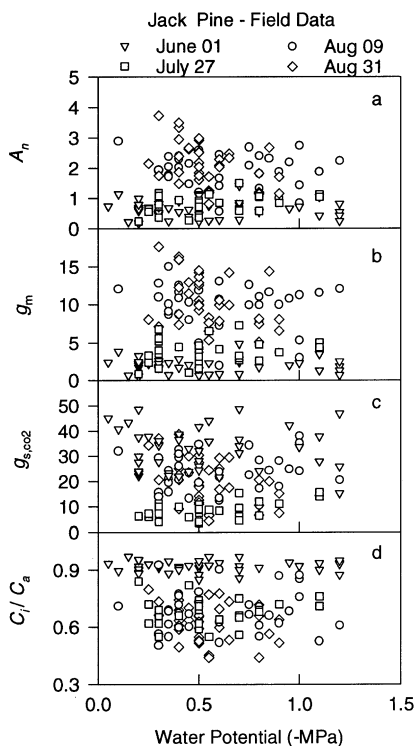

Figure 3. Relationships between shoot water potential and: (a) A_n; (b) g_m; (c) $g_{s,CO2}$; and (d) C_i/C_a of jack pine. Data are from diurnal measurements on *in situ* branches in the upper canopy. See caption to Figure 1 for measurement units.

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 ($g_{s,wv}$) for cut branches of jack pine and black spruce measured

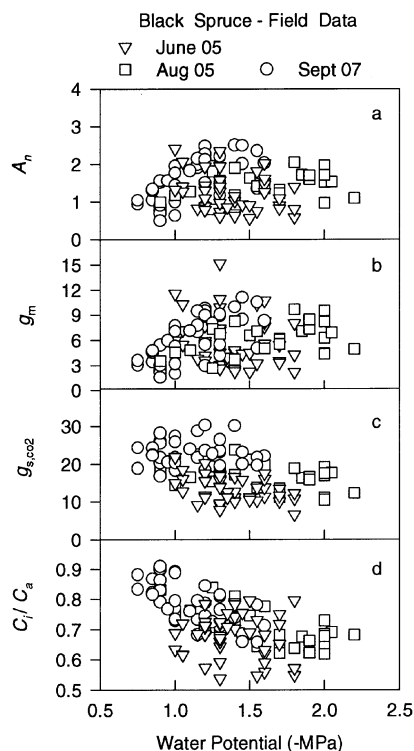Figure 4. Relationships between shoot water potential and: (a) A_n; (b) g_m; (c) $g_{s,CO2}$; and (d) C_i/C_a of black spruce. Data are from diurnal measurements on *in situ* branches in the upper canopy. See caption to Figure 1 for measurement units.

Figure 5. Relationships between shoot water potential and: (a) A_n; (b) g_m; (c) $g_{s,CO2}$; and (d) C_i/C_a for aspen. Data are from diurnal measurements on *in situ* branches in the upper canopy. See caption to Figure 1 for measurement units.

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 °C data and some of the lower VPD data at 25 °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
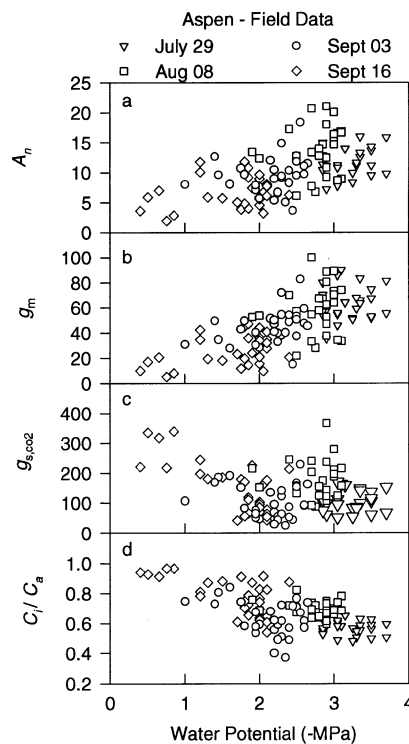
different between the two canopy layers for jack pine and aspen ($P < 0.05$, Table 3, Figures 7d–f). These differences arose from the estimation of parameter c; the curvature and lower asymptote parameters (a and b, respectively) were not significantly different between the two canopy levels (Table 3). Similarly, estimates of the maximum g_s, i.e., g_s 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., $dg_s/dVPD$ 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
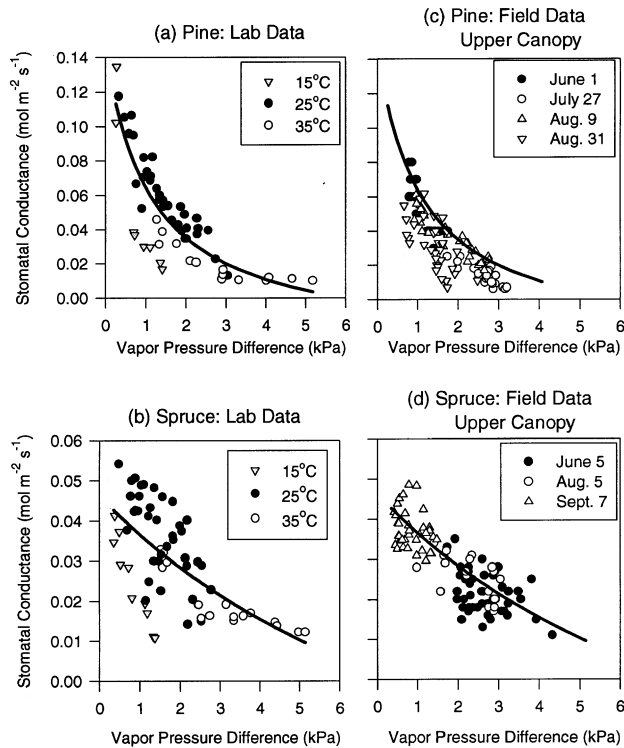
Figure 6. Relationship between vapor pressure difference and stomatal conductance to H_2O ($g_{s,wv}$) for jack pine and black spruce. Data were taken on cut branches of (a) jack pine and (b) black spruce under controlled laboratory conditions (360 μmol mol^{-1} CO_2, 1100 μmol m^{-2} s^{-1} PAR) at 15 (in IFC-1 only), 25 (in all IFCs) and 35 °C (in IFC-2 and -3) air temperature. 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.

Figure 7. Stomatal conductance to water vapor ($g_{s,wv}$) versus vapor pressure difference for the upper and lower canopies of the (a) jack pine, (b) black spruce and (c) aspen stands. Values are *in situ* field data collected from canopy access towers. The jack pine data were collected on June 1, July 27, August 9 and August 31, 1994. The black spruce data were collected on June 5, August 5 and September 7. The aspen data were collected on July 29, August 8, September 3 and September 16. Nonlinear regressions were derived from the field data for the lower canopy, upper canopy and both canopy layers combined for (d) jack pine, (e) black spruce and (f) aspen. Refer to Table 3 for regression model and parameters.

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.

Maximum values of daily maximum and PAR-weighted daily mean VPD were 3.8 and 2.8 kPa, respectively, for the 1994 growing season (Figure 11). The seasonal averages were 1.7 and 1.0 kPa for the daily maximum VPD and PAR-weighted daily mean VPD, respectively. The seasonal C_i/C_a ratios corresponding to a seasonal average VPD of 1.0 kPa were 0.77, 0.71 and 0.81 for jack pine, black spruce and aspen, respectively.

Because aspen has a higher photosynthetic capacity than the conifers, its CO_2-limited rate of photosynthesis was more sensitive to changes in C_i. Carbon dioxide-limited photosynthesis was slightly more sensitive to changes in C_i in jack pine than in black spruce (Figure 12). For both jack pine and black spruce, data points fell on the same line independently of whether the changes in C_i were achieved by varying VPD or
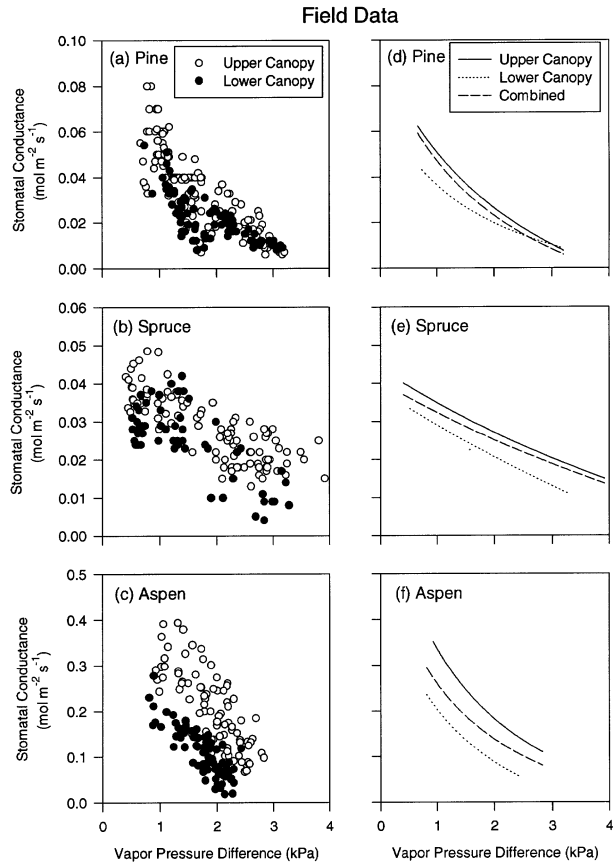
ambient CO_2 (Figure 12). No VPD response data were collected for cut branches of aspen.

Discussion

Water potential

When a cut-branch technique is used to determine the effect of shoot water potential (Ψ) on gas exchange, it is primarily the short-term, direct hydraulic effect of Ψ 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-

Table 3. Nonlinear regression parameters for the relationship between vapor pressure difference (kPa) and stomatal conductance to water vapor ($g_{s,wv}$; 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.

Parameters	Upper canopy	Lower canopy	Combined
Jack pine			
a	0.355 a	0.604 a	0.476 a
b	−0.068 a	−0.025 a	−0.052 a
c	0.161 a	0.099 b	0.147 a
g_{max}[1]	0.093	0.074	0.095
R^2 value[2]	0.71	0.61	0.67
Black spruce			
a	0.086 a	0.052 a	0.070 a
b	−0.072 a	−0.150 a	−0.084 a
c	0.116 a	0.188 a	0.124 a
g_{max}	0.044	0.038	0.040
R^2 value	0.68	0.52	0.52
Aspen			
a	0.693 a	0.702 a	0.729 a
b	−0.193 a	−0.194 a	−0.153 a
c	0.895 a	0.675 b	0.713 a,b
g_{max}	0.702	0.481	0.560
R^2 value	0.56	0.68	0.32

[1] Maximum stomatal conductance, g_{max}, was calculated as $b + c$, i.e., g_s when VPD = 0.

[2] The R^2 values are the coefficients of determination for the relationship between predicted $g_{s,wv}$ and measured $g_{s,wv}$. The slope of the relationship between predicted and measured $g_{s,wv}$ did not differ significantly from 1.0 at $P < 0.05$.

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 Ψ 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 Ψ was −2.6 MPa for A_n.
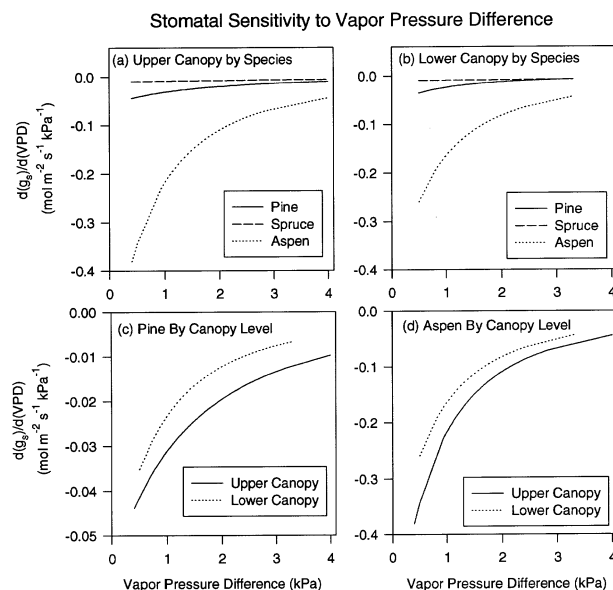

Figure 8. Stomatal sensitivity to vapor pressure difference, [d($g_{s,wv}$)/d(VPD)], as a function of vapor pressure difference (kPa) (a) for the upper canopy of each species, (b) for the lower canopy of each species, (c) for jack pine by canopy level and (d) for aspen by canopy level. Sensitivity was calculated using Equation 2 and the parameters are shown in Table 3. Black spruce did not have significant differences in stomatal sensitivity between the upper and lower canopy.
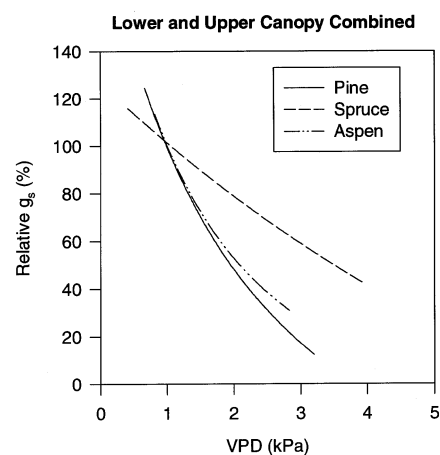

Figure 9. Relationship between relative stomatal conductance (g_s) and vapor pressure difference (VPD) for jack pine, black spruce and aspen. The curves were obtained by dividing Equation 1 by the stomatal conductance to water vapor ($g_{s,wv}$) of the seasonal average VPD of 1.0 kPa for each species.

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

The response pattern of stomatal conductance ($g_{s,CO2}$) to Ψ varied between the two conifers. The $g_{s,CO2}$ of jack pine showed a threshold response, but the threshold Ψ was less negative than that for A_n and g_m (Figure 1). The $g_{s,CO2}$ of black spruce, on the other hand, decreased continuously with decreasing Ψ over the entire range examined (Figure 2). Both
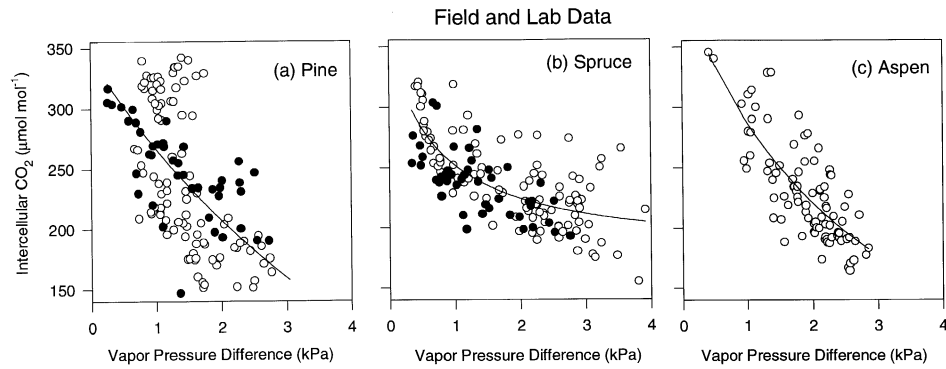
Field and Lab Data

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: $C_i = 178.6/(1 + 1.362$ VPD$) + 176.3$, $R^2 = 0.53$, for black spruce; $C_i = 634.6/(1 + 0.1338$ VPD$) - 293.2$, $R^2 = 0.62$, for jack pine; and $C_i = 519.5/(1 + 0.2207$ VPD$) - 139.5$, $R^2 = 0.62$, for aspen.
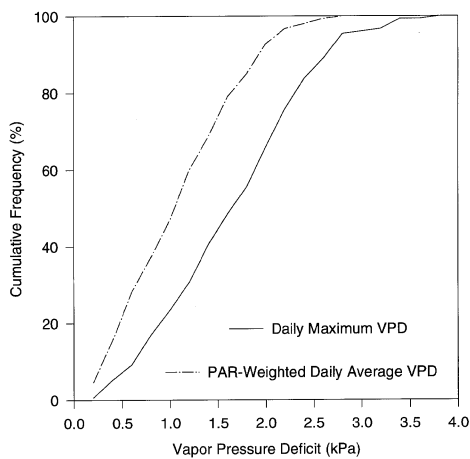

Figure 11. Cumulative frequency of daily maximum and PAR-weighted daily mean vapor pressure deficit (VPD) for the growing season (May to September) of 1994. Data were collected from the Old Jack Pine site by BOREAS staff.

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 μmol mol^{-1} by varying VPD from 0.7 to 2.8 kPa at 360 μmol mol^{-1} ambient CO_2 and 25 °C air temperature.

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 Ψ 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 Ψ as low as -1.5 MPa, whereas g_s decreased significantly with decreasing Ψ. Our data also support the modeling approach taken by Sellers et al. (1996b) and others whereby low Ψ 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 Ψ 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 $g_{s,CO2}$ combined with a high g_m allows a tree to maintain
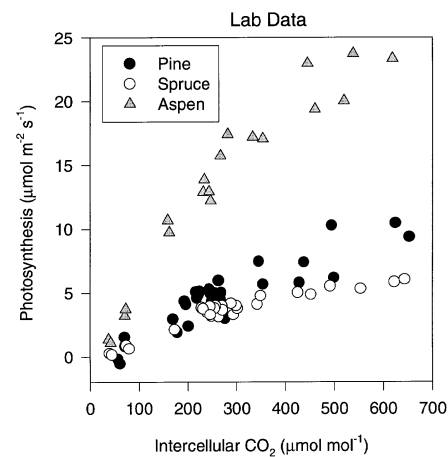
high A_n when water conditions are favorable. However, when the rate of transpiration exceeds the rate of water delivery to leaves as a result of cold soil, low soil water or high evaporative demand, Ψ declines. Before Ψ falls below the threshold for g_m, $g_{s,CO2}$ begins to decrease, reducing the transpiration rate and maintaining a favorable Ψ for photosynthetic activity in the mesophyll. Field measurements on warm, sunny days showed that both jack pine and black spruce maintained their Ψ above the corresponding threshold and that A_n was unaffected by fluctuations in Ψ (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 Ψ for aspen in the laboratory, field data showed no evi-

dence of Ψ limitation on A_n, suggesting that aspen also maintained a favorable Ψ for photosynthetic activity (Figure 5).

It has been suggested that trees normally approach but do not exceed the Ψ 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 Ψ 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 Ψ for A_n must be similar to the threshold Ψ for catastrophic xylem embolism.

Black spruce can tolerate much lower Ψ 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 up-take 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 are 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. 1989*a*, 1989*b*). 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 Ψ than that of black spruce. Field data showed no decrease in A_n or g_m at Ψ 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 Ψ 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 Ψ below −2.0 and −3.0 MPa, respectively, indicating that the mesophyll was more sensitive than the stomata to low Ψ. In contrast, this ratio decreased at low Ψ in IFC-3, indicating progressively more stomatal limitation to A_n and that the stomata were relatively more sensitive to Ψ 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 Halldin (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

$g_{s,CO2}$ 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 ($g_{s,CO2}$) of jack pine also showed a threshold response, but $g_{s,CO2}$ 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.

References

Abrams, M.C. and S.A. Mostoller. 1995. Gas exchange, leaf structure and nitrogen in contrasting successional tree species growing in open and understory sites during a drought. Tree Physiol. 15:361–370.

Armitage, A.M., H.M. Vines, T. Zeng-Ping and C.C. Black. 1983. Water relations and net photosynthesis in hybrid geranium. J. Am. Soc. Hortic. Sci. 108:310–314.

Baldocchi, D.D. and C. Vogel. 1996. Energy and CO_2 flux density above and below a temperate broad-leaved forest and a boreal pine forest. Tree Physiol. 16:5–16.

Baldocchi, D.D., C.A. Vogel and B. Hall. 1997. Seasonal variation of carbon dioxide exchange rates above and below a boreal jack pine forest. Agric. For. Meteorol. 83:147–170.

Beadle, C.L., P.G. Jarvis and R.E. Neilson. 1979. Leaf conductance as related to xylem water potential and carbon dioxide concentration in Sitka spruce. Physiol. Plant. 45:158–166.

Beadle, C.L., R.E. Neilson, P.G. Jarvis and H. Talbot. 1981. Photosynthesis as related to xylem water potential and carbon dioxide concentration in Sitka spruce. Physiol. Plant. 52:391–400.

Brand, D.G. 1987. Estimating the surface area of spruce and pine foliage from displaced volume and length. Can. J. For. Res. 17:1305–1308.

Brix, H. 1962. The effects of water stress on photosynthesis and respiration in tomato plants and loblolly pine seedlings. Physiol. Plant. 15:10–20.

Brooks, J.R., L.B. Flanagan, G.T. Varney and J.R. Ehleringer. 1997. Vertical gradients in photosynthetic gas exchange characteristics and refixation of respired CO_2 within boreal forest canopies. Tree Physiol. 17:1–12.

Ciais, P., P.P. Tans, M. Trolier, J.W.C. White and J.R. Francey. 1995. A large northern hemisphere CO_2 sink indicated by $^{13}C/^{12}C$ of atmospheric CO_2. Science 269:1098–1102.

Collatz, G.J. 1977. Influence of certain environmental factors on photosynthesis and photorespiration in *Simmondsia chinensis*. Planta 134:127–132.

Collatz, G.J., J.T. Ball, C. Grivet and J.A. Berry. 1991. Physiological and environmental regulation of stomatal conductance, photosynthesis and transpiration: a model that includes a laminar boundary layer. Agric. For. Meteorol. 54:107–136.

Collatz, J., P.J. Ferrar and R.O. Slayter. 1976. Effects of water stress and differential hardening treatments on photosynthetic characteristics of a xeromorphic shrub, *Eucalyptus socialis* F. Muell. Oecologia 23:95–105.

Correia, M.J. and J.S. Pereira. 1995. The control of leaf conductance of white lupin by xylem ABA concentration decreases with the severity of water deficits. J. Exp. Bot. 46:101–110.

Cowan, I.R. and G.D. Farquhar. 1977. Stomatal function in relation to leaf metabolism and environment. Symp. Soc. Exp. Biol. 31:471–505.

Dai, Z.Y., G.E. Edwards and M.S.B. Ku. 1992. Control of photosynthesis and stomatal conductance in *Ricinus communis* L. (castor bean) by leaf to air vapor pressure deficit. Plant Physiol. 99:1426–1434.

Dang, Q.L., V.J. Lieffers, R.L. Rothwell and S.E. MacDonald. 1991. Diurnal variation and interrelations of ecophysiological parameters in three peatland woody species under different weather and soil moisture conditions. Oecologia 88:317–324.

Davenport, T.L., W.R. Jordan and P.W. Morgan. 1977. Movement and endogenous levels of abscisic acid during water stress induced abscission in cotton seedlings. Plant Physiol. 59:1165–1168.

Davies, M.B. and D.B. Botkin. 1985. Sensitivity of cool temperature forests and their fossil pollen to rapid climatic change. Quaternary Res. 23:327–340.

Davies, W.J. and J. Zhang. 1991. Root signals and the regulation of growth and development of plants in drying soil. Annu. Rev. Plant Physiol. Plant Mol. Biol. 42:55–76.

Davies, W.J. and B. Jeffcoat. 1990. Importance of root to shoot communication in the responses to environmental stress. Monograph 21. Brit. Soc. Plant Growth Reg., Bristol, U.K., 398 p.

Denning, A.S., I.Y. Fung and D. Randall. 1995. Latitudinal gradient of atmospheric CO_2 due to seasonal exchange with land biota. Nature 376:240–243.

Dykstra, G.F. 1974. Photosynthesis and carbon dioxide transfer resistance of lodgepole pine seedlings in relation to irradiance, temperature, and water potential. Can. J. For. Res. 4:201–206.

Ehleringer, J.R. and C.B. Field. 1993. Scaling physiological processes: leaf to globe. Academic Press, Inc., San Diego, 388 p.

Farquhar, G.D., E.-D. Schulze, and M. Kuppers. 1980. Responses to humidity by stomata of *Nicotiana glauca* L. and *Corylus avellana* L. are consistent with the optimisation of carbon dioxide uptake with respect to water loss. Aust. J. Plant Physiol. 7:315–327.

Field, C.B., R.B. Jackson and H.A. Mooney. 1995. Stomatal responses to increased CO_2: implications from the plant to global scale. Plant Cell Environ. 18:1214–1225.

Fites, J.A. and R.O. Teskey. 1988. CO_2 and water vapour exchange of *Pinus taeda* in relation to stomatal behaviour: test of an optimization hypothesis. Can. J. For. Res. 18:150–157.

Flanagan, L.B., J.R. Brooks and J.R. Ehleringer. 1997. Photosynthesis and carbon isotope discrimination in boreal forest ecosystems: a comparison of functional characteristics in plants from three mature forest types. J. Geophys. Res. In press.

Hogg, E.H. and P.A. Hurdle. 1997. Sap flow in trembling aspen: implications for stomatal responses to vapor pressure deficit. Tree Physiol. 17:501–509.

Jackson, G.E., J. Irvine, J. Grace and A.A.M. Khalil. 1995. Abscisic acid concentrations and fluxes in droughted conifer saplings. Plant Cell Environ. 18:13–22.

Jarvis, P.G. 1980. Stomatal response to water stress in conifers. *In* Adaptation of Plants to Water and High Temperature Stress. Eds. N.C. Turner and P.J. Kramer. John Wiley and Sons, New York, pp 105–122.

Johnson, J.D. and W.K. Ferrell. 1983. Stomatal response to vapour pressure deficit and the effect of water stress. Plant Cell Environ. 6:451–456.

Johnson, J.D. and W.K. Ferrell. 1982. The relationship of abscisic acid metabolism to stomatal conductance in Douglas-fir during water stress. Physiol. Plant. 55:431–437.

Jones, H.G. 1990. Control of growth and stomatal behaviour at the whole plant level: effects of soil drying. *In* Importance of Root to Shoot Communication in the Responses to Environmental Stress. Monograph 21. Eds. W.J. Davies and B. Jeffcoat. Brit. Soc. Plant Growth Reg., Bristol, U.K., pp 81–93.

Kawamitsu, Y., S. Yoda and W. Agata. 1993. Humidity pre-treatment affects the responses of stomata and CO_2 assimilation to vapor pressure difference in C_3 and C_4 plants. Plant Cell Physiol. 34:113–119.

Lieffers, V.J. and R.L. Rothwell. 1986. Effects of water table and substrate temperature on root and top growth of *Picea mariana* and *Larix laricina* seedlings. Can. J. For. Res. 16:1201–1206.

Lieffers, V.J. and R.L. Rothwell. 1987. Rooting of peatland black spruce and tamarack in relation to depth of water table. Can. J. For. Res. 65:817–821.

Lindroth, A. and S. Halldin. 1986. Numerical analysis of pine forest evaporation and surface resistance. Agric. For. Meteorol. 38:59–79.

Losch, R. and J.D. Tenhunen. 1981. Stomatal responses to humidity-phenomenon and mechanism. *In* Stomatal Physiology. Eds. P.G. Jarvis and T.A. Mansfield. Cambridge University Press, New York, pp 137–161.

Ludlow, M.M. 1980. Adaptive significance of stomatal responses to water stress. *In* Adaptation of Plants to Water and High Temperature Stress. Eds. N.C. Turner and P.J. Kramer. John Wiley and Sons, New York, pp 123–137.

Mannerkoski, H. 1985. Effect of water table fluctuation on the ecology of peat soil. Dept. Peatland Forestry, Univ. Helsinki, Helsinki, Finland.

Margolis, H.A. and M.G. Ryan. 1997. A physiological basis for biosphere–atmosphere interactions in the boreal forest: an overview. Tree Physiol. 17:491–499.

McNaughton, K.G. and P.G. Jarvis. 1991. Effects of spatial scale on stomatal control of transpiration. Agric. For. Meteorol. 54:279–301.

Meinzer, F.C. 1982. The effect of vapour pressure on stomatal control of gas exchange in Douglas-fir *Pseudotsuga menziesii* saplings. Oecologia 54:236–242.

Meinzer, F.C. and D.A. Grantz. 1991. Coordination of stomatal, hydraulic and canopy boundary layer properties: do stomata balance conductances by measuring transpiration? Physiol. Plant. 83:324–329.

Meinzer, F.C., G. Goldstein, N.M. Holbrook, P. Jackson and J. Vaelier. 1993. Stomatal and environmental control of transpiration in lowland tropical forest trees. Plant Cell Environ. 16:429–436.

Melzack, R.N., B. Bravdo and J. Riov. 1985. The effect of water stress on photosynthesis and related parameters in *Pinus halepensis*. Physiol. Plant. 64:295–300.

Mitchell, J.F.B. 1983. The seasonal response of a general circulation model to changes in CO_2 and sea temperature. Q. J. R. Meteorol. Soc. 109:113–152.

Mitsch, W.J. and J.G. Gosselink. 1993. Wetlands. Van Nostrand Reinhold, Inc., New York, 722 p.

Ni, G.-R. and S.G. Pallardy. 1992. Stomatal and non-stomatal limitations to net photosynthesis in seedlings of woody angiosperms. Plant Physiol. 99:1502–1508.

Osonubi, O. and W.J. Davies. 1980. The influence of plant water stress on stomatal control of gas exchange at different levels of atmospheric humidity. Oecologia 46:1–6.

Pielke, R.A., D.S. Schimel, T.J. Lee, T.G.K. Kittel and X. Zeng. 1993. Atmosphere–terrestrial ecosystem interactions: Implications for coupled modeling. Ecol. Model. 67:5–18.

Pothier, D., H.A. Margolis, J. Poliquin and R.H. Waring. 1989*a*. Relation between the permeability and the anatomy of jack pine sapwood with stand development. Can. J. For. Res. 19:1564–1570.

Pothier, D., H.A. Margolis, J. Poliquin and R.H. Waring. 1989*b*. Patterns of change of saturated permeability and sapwood conductance with stand development. Can. J. For. Res. 19:432–439.

Puritoh, G.A. 1973. Effect of water stress on photosynthesis, respiration and transpiration of four *Abies* species. Can. J. For. Res. 3:293–298.

Raupach, M.R. 1991. Vegetation–atmosphere interaction in homogenous and heterogeneous terrain and some implications of mixed-layer dynamics. Vegetatio 91:105–120.

Running, S.W. 1976. Environmental control of leaf water conductance in conifers. Can. J. For. Res. 6:104–112.

Saliendra, N.Z., J.S. Sperry and J.P. Comstock. 1995. Influence of leaf water status on stomatal response to humidity, hydraulic conductance, and soil drought in *Betula occidentalis*. Planta 82:1220–1229.

Sandford, A.P. and P.G. Jarvis. 1986. Stomatal response to humidity in selected conifers. Tree Physiol. 2:89–103.

Sato, N., S.J. Sellers, D.A. Randall, E.K. Schneider, J. Shukla, J.L. Kinter III, Y.T. Hou and E. Albertazzi. 1989. Effects of implementing the Simple Biosphere Model (SiB) in a general circulation model. J. Atmos. Sci. 46:2757–2782.

Schulze, E.-D. 1986. Carbon dioxide and water vapour exchange in response to drought in the atmosphere and in the soil. Annu. Rev. Plant Physiol. 37:247–274.

Schulze, E.-D. and M. Kupper. 1979. Short-term and long-term effects of plant water deficits on stomatal responses to humidity in *Corylus avellana* L. Planta 146:319–326.

Sellers, P.J., F.G. Hall, H.A. Margolis, R. Kelly, D. Baldocchi, G.D. Hartog, J. Cihlar, M.G. Ryan, B. Goodison, P. Crill, K.J. Ranson, D. Lettenmaier and D.E. Wickland. 1995. The Boreal Ecosystem-Atmosphere Study (BOREAS): an overview and early results from the 1994 field year. Bull. Am. Meteorol. Soc. 76:1549–1577.

Sellers, P.J., L. Bounoua, G.J. Collatz, D.A. Randall, D.A. Dazlich, S. Los, J.A. Berry, I. Fung, C.J. Tucker., C.B. Field and T.G. Jensen. 1996*a*. A comparison of the radioactive and physiological effects of doubled CO_2 on the global climate. Science 271:1402–1406.

Sellers, P.J., D.A. Randall, G.J. Collatz, J.A. Berry, C.B. Field, D.A. Dazlich, C. Zhang and G.D. Collelo. 1996*b*. A revised land surface parameterization (SiB2) for atmospheric GCMs. Part 1. Model formulation. J. Climat. 9:676–705.

Slegenthaler, U. and J.L. Sarmiento. 1993. Atmospheric carbon dioxide and the ocean. Nature 365:119–125.

Solomon, A.M. and T. Webb, III. 1985. Computer-aided reconstruction's of late-Quaternary landscape dynamics. Annu. Rev. Ecol. Syst. 16:63–84.

Sperry, J.S. 1995. Limitations on stem water transport and their consequences. *In* Plant Stems: Physiology and Functional Morphology. Ed. B.L. Gartner. Academic Press, San Diego, pp 105–124.

Sperry, J.S. and W.T. Pockman. 1993. Limitation of transpiration by hydraulic conductance and xylem cavitation in *Betula occidentalis*. Plant Cell Environ. 16:279–287.

Stewart, J.D., A. Zine El Abidine and P.Y. Bernier. 1995. Stomatal and mesophyll limitations of photosynthesis in black spruce seedlings during multiple cycles of drought. Tree Physiol. 15:57–64.

Tans, P.P., I.Y. Fung and T. Takahashi. 1990. Observational constraints on the global atmospheric CO_2 budget. Science 247:1431–1438.

Teskey, R.O., J.A. Fites, L.J. Samuelson and B.C. Bongarten. 1986. Stomatal and non-stomatal limitations to net photosynthesis in *Pinus taeda* L. under different environmental conditions. Tree Physiol. 2:131–142.

Turner, N.C. and P.E. Waggoner. 1968. Effects of changing stomatal width in a red pine forest on soil water content, leaf water potential, bole diameter and growth. Plant Physiol. 43:973–978.

von Caemmerer, S. and G.D. Farquhar. 1981. Some relationships between biochemistry of photosynthesis and the gas exchange of leaves. Planta 153:376–387.

Waring, R.H. and W.H. Schlesinger. 1985. Forest ecosystems: concepts and management. Academic Press, Inc., San Diego, 340 p.

Waring, R.H., J.J. Rogers and T.W. Swank. 1981. Water relations and hydrologic cycles. *In* Dynamic Properties of Forest Ecosystems. Ed. D.E. Reichle. Intl. Biol. Prog. Publ. No. 23, Cambridge Univ. Press, London, U.K., pp 205–264.

Warrit, B., J.J. Landsberg and M.R. Thorpe. 1980. Response of apple leaf stomata to environmental factors. Plant Cell Environ. 3:13–22.

Watts, W.R. and R. Neilson. 1978. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Car.). VIII. Measurements of stomatal conductance and $^{14}CO_2$ uptake in controlled environments. J. Appl. Ecol. 15:245–255.

Whitehead, D., N.J. Livingston, F.M. Kelliher, K.P. Hogan, S. Pepin, T.M. McSeveney and J.N. Byers. 1996. Response of transpiration and photosynthesis to a transient change in illuminated foliage area for a *Pinus radiata* D. Don tree. Plant Cell Environ. 19:949–957.

Wong, S.C., I.R. Cowan and G.D. Farquhar. 1985. Leaf conductance in relation to rate of CO_2 assimilation. III. Influences of water stress and photoinhibition. Plant Physiol. 78:830–834.

Yue, D., Y. Desjardins, M. Lamarre and A. Gosselin. 1992. Photosynthesis and transpiration of *in vitro* cultured asparagus plantlets. Sci. Hortic. 49:9–14.