Transpiration of a boreal pine forest measured by branch bag, sap flow and micrometeorological methods

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Summary Three independent methods were used to evaluate transpiration of a boreal forest: the branch bag, sap flow and eddy covariance methods. The branch bag method encloses several thousand needles and gives a continuous record of branch transpiration. The sap flow method provides a continuous record of sap velocity and an estimate of tree transpiration. The eddy covariance method typically measures evaporation rates between a forest and the atmosphere. We deployed an extra eddy covariance system below the forest to estimate canopy transpiration by difference.

The three systems detected small water vapor fluxes despite a plentiful supply of energy to drive evaporation. We also observed that transpiration rates were low even when the soil was well supplied with water. Low rates of transpiration were attributed to the canopy’s low leaf area index and the marked reduction in stomatal conductance as vapor pressure deficits increased. Water vapor fluxes, derived from the sap flow method, lagged behind those derived by the branch bag method by 1 to 2 h. The sap flow method also suffered from sampling errors caused by the non-uniformity of flow across the sapwood and the spatial variability of sapwood cross section throughout the forest. Despite technical difficulties associated with hourly measurements, daily totals of transpiration agreed well with values derived from micrometeorological systems.

Keywords: canopy transpiration, eddy covariance method, jack pine, Pinus banksiana, transpiration rate, water loss, water vapor flux.

Materials and methods

Site characteristics

This work was conducted under the auspices of the BOREAS experiment (Sellers et al. 1995), an international study of the energy and matter exchanges of the boreal forest on a large area in Canada. Our research took place in the Southern Study Area. The region is covered with pure and mixed stands of black spruce (Picea mariana (Mill.) BSP) and white spruce (Picea glauca (Moench) Voss), aspen (Populus tremuloides Michx.) and jack pine (Pinus banksiana). Spruce stands occupy wet sites with limited drainage, whereas jack pine stands are established on sandy soils that are well drained and nutrient-poor.
Field measurements were conducted on a jack pine stand on relatively flat land near Nipawin, Saskatchewan, Canada (53°54′59″ N, 104°41′31″ W; elevation 579 m).

Stand characteristics were determined by various BOREAS investigators. The stand was between 75 and 90 years old. Stand density was 1875 stems ha\(^{-1}\), mean diameter at breast height was 0.117 m, and basal area was 21.9 m\(^2\) ha\(^{-1}\). Canopy height varied between 12 and 15 m with a mean of 13.5 m. Some seasonal variation in canopy structure was observed. A flush of needles and male cones occurred in early June and needle yellowing, with appreciable loss of 2-, 3- and 4-year-old needles, occurred in September. Chen (1996) estimated leaf area index (LAI, one-half of total surface area of needles per unit ground area) of the site to be 1.89, 2.27 and 2.22 on Days 146, 210 and 253, respectively.

The understory was sparse, with isolated groups of alder (Alnus crispa (Ait.) Pursh). Ground cover consisted of bearberry (Arctostaphylos uva-ursi (L.) K. Spreng.), bog cranberry (Vaccinium vitis-idea L.), and lichens (Cladina and Cladonia spp.) that formed a nearly continuous cover.

The soil was a coarse-textured sand and was classified as a degraded Eutric Brunisol/Orthic Eutric Brunisol. Volumetric soil water measurements were made with a neutron probe by a team led by Dr. R. Cuenca (Oregon State University, Corvallis, OR). Total soil water content in the 0–170 cm layer decreased from 211 to 125 mm from May to September.

Sap flow measurements were started in spring (May 1, 1994) and continued until September 16. Branch bag measurements were limited to a 2.5-week-period between July 28 and August 16. Micrometeorological measurements were performed from May 21 to September 13.

**Branch bags**

Two translucent bags were installed on branches of two jack pine trees. The measurement system was supported by a scaffold tower. The branch bag gas exchange system has been described in detail by Dufrêne et al. (1993). Briefly, an acrylic fold tower. The branch bag gas exchange system has been described in detail by Dufrêne et al. (1993). Briefly, an acrylic

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The bag to stir the air.

Conditions within the bags were recorded every 20 s, air temperature and relative humidity were monitored with Vaisala HMB 30YB probes (Vaisala OY, Helsinki, Finland) protected by a white hood, and photosynthetically active radiation (PAR) was measured with laboratory-made gallium arsenide sensors that were calibrated against an LI-190B sensor (Li-Cor, Inc., Lincoln, NE). A 21X data logger (Campbell Scientific, Logan, UT) was used to drive the system and to log the data.

Branch transpiration rate, \(E\), was computed as:

\[
E = (V/v)(de/dt)/(pS),
\]

where \(V\) is bag volume (m\(^3\)), \(v\) is the volume of one mole of air (m\(^3\) mol\(^{-1}\)), \(S\) is half the total needle area (m\(^2\)), \(de/dt\) is the increase in water vapor pressure (\(e\), hPa) during time \(t\) (s), and \(p\) is atmospheric pressure (hPa).

Relative error in \(E\) was expressed as:

\[
\Delta E/E = \Delta V/V + \Delta (de/dt)/ (de/dt) + \Delta S/S.
\]

Bag volume, \(V\), was estimated from the dimensions of the bag. Because the walls of the bag were flexible, \(V\) changed slightly during the measurement because only part of the air to be sampled was returned to the bag. The relative change in bag volume, \(\Delta V/V\), over a 5-min period was less than 1%. The value of \(S\) was estimated from needle volume. At the end of the measurements, branches were cut and separated into small twigs, whose volumes were measured by displacement of water. Twigs were immersed in a container filled with water and placed on a balance. Their volume was equivalent to the observed weight increase. Needles were assumed to be cylinders with an ellipsoid section, and their average area was computed from their volume and average length. The error associated with the displacement method (\(\Delta S/S\)) was between 5 and 10%. Errors in \(de/dt\) may arise as a result of sensor performance or non-linearities in the increase in water vapor caused by leaks or because of decreases in VPD in the bags caused by \(E\) (see Appendix 1). The Vaisala sensors were calibrated against a dew-point hygrometer both before and after the measurements. The sensors appeared stable, exhibiting a negligible change in calibration during the experiment and an absolute accuracy of ± 2% in RH. Plots of vapor pressure, \(e\), versus time, \(t\), showed that the best interval to compute \(de/dt\) was between 20 and 120 s after closure. Errors in \(de/dt\) were believed to be below 10%. Thus, altogether the relative error in \(E(\Delta E/E)\) was less than 20%, except at low values of \(E\). We systematically recorded negative \(E\) at night, implying uptake of water vapor by the branch. This may have been an artifact caused by dew formation through radiative cooling after bag closure. The large flow rate over the branch between measurements may also have caused a superficial drying out of the bark and of the dry cones, followed by uptake of water vapor when the bag was closed. In relative terms, nocturnal values of \(E\) represented about 6% of maximal \(E\) in Bag 2, which had more cones, and 4% in Bag 1.
Sap flow

Sap flow was monitored with 2-cm long radial sap flowmeters (Granier 1985, 1987). Each sensor had two probes, one was heated continuously at a constant power, the other one was not heated. The temperature difference ($T_{\text{diff}}$) between the two probes was measured every 10 s with a copper-constantan thermocouple connected to a Campbell CR10 data logger and averaged every 30 min. Sap flow density $F \left(10^{-6} \text{ m}^2 \text{ m}^{-3} \text{ s}^{-1} \text{ or } \mu \text{m} \text{s}^{-1}\right)$ was computed as:

$$F = 119 \left(\frac{T_{\text{diff,max}}}{T_{\text{diff}}}\right)^{1.23},$$

where $T_{\text{diff,max}}$ is the maximum value of $T_{\text{diff}}$ recorded at night when transpiration is near zero. The $T_{\text{diff,max}}$ changed slightly from day to day. To determine the extent of this variation, $T_{\text{diff,max}}$ was plotted against time. Local maxima of $T_{\text{diff,max}}$ were then determined and linear interpolations were made between these values. Values of $T_{\text{diff,max}}$ ranged from 10 to 15 $^\circ$C between sensors, and for a given sensor the variation was within 1 $^\circ$C during the entire period.

Sap flow was measured on six trees that were selected to represent the diameter distribution of the stand. Circumferences at breast height of these trees ranged from 25.6 to 52.1 cm, and their heights ranged between 10.5 to 14.7 m. For a given tree, sap flow was calculated as the product of sap flux density and sapwood area. Stand sap flow $T$ (per unit ground area) was computed from the formula:

$$T = A_s \sum_i (F_i \cdot p_i),$$

where $A_s$ is stand sapwood area per unit ground area ($\text{m}^2 \text{ ha}^{-1}$), $F_i$ is mean sap flux density of trees in circumference class $i$, $A_i$ is sapwood area of trees in class $i$, and $p_i$ is the $A_i/A_s$ ratio.

The sensor installed on the smallest tree malfunctioned after four weeks, but the remaining five sensors worked properly from May 1, 1994 (Day Of Year 121) to September 16, 1994 (DOY 259). This time span covered most of the growing period. Sapwood thickness was determined on fresh cores taken on a sample of 20 surrounding trees on four perpendicular radii. To identify the sapwood, which is more translucent than heartwood because of its higher water content, cores were observed in front of a light source. A relationship between tree circumference at breast height ($C$ cm) and sapwood area ($A$, cm$^2$) was established:

$$A = 5.8 - 0.46C + 0.0441C^2 \quad (r^2 = 0.89).$$

Estimated stand sapwood area was 12.3 $\text{m}^2 \text{ ha}^{-1}$, i.e., 56% of basal area (21.9 $\text{m}^2 \text{ ha}^{-1}$).

Low temperatures induced xylem freezing in early May. A sequence of four days is presented in Figure 1. When air temperature remained above $-3^\circ$C, sap flow showed diurnal variations that paralleled air temperature (Days 122 and 123 in Figure 1); however, this synchronism ceased when air temperature dropped below $-3^\circ$C (Days 124 and 125). Freezing of the xylem released heat near the cold probe of the sap flowmeter, decreasing the temperature difference between the two probes and producing an apparent increase in sap flow; thawing of the xylem produced the opposite effect.

Micrometeorological fluxes

The eddy covariance method was used to measure evaporation rates. Two systems were employed to measure canopy transpiration. One system was mounted above the forest and the other system was placed 1.8 m aboveground. Details of the equipment and measurement methods are given by Baldocchi et al. (1996). Wind and virtual temperature fluctuations were measured with 3-dimensional sonic anemometers (Applied Technology Inc., Boulder, CO). Carbon dioxide and water vapor fluctuations were measured with an open path, infrared gas analyzer, developed at NOAA/ATDD (Auble and Meyers 1992). Additional measurements were made of: soil heat flux density (flux plates at 1 cm below the soil surface and temperature sensors at depths of 2, 4, 8, 16 and 32 cm), heat storage into the trunks, PAR and net radiation above and below the tree canopy, and profiles of air temperature, humidity and CO$_2$ concentration. Net radiation should be equal to the sum of sensible heat, latent heat, soil heat transfer and canopy heat storage. Baldocchi et al. (1996) were able to close the energy balance within 11% for short-term measurements (30-min averages) and for 24-h periods. A mean bias between net radiation at the forest floor and its energy balance components was only 10 W m$^{-2}$. This reasonable level of energy balance closure provided the rationale for computing the tree canopy evaporation as the difference between water vapor fluxes measured above and below the canopy.

Results

Branch bag measurements

Figure 2 presents 6 days of branch bag measurements of transpiration. Maximum transpiration rates were low, with values slightly above 1 mmol m$^{-2}$ s$^{-1}$. With the same technique, Dufrenê et al. (1993) measured maximum transpiration rates of up to 2.2 mmol m$^{-2}$ s$^{-1}$ on European beech. Because
inertia of the bag was small, the system responded to rapid changes in sunlight, as observed on Day 218, which was a cloudy and partly cloudy day. The method yielded small negative values of evaporation at night.

In general, photosynthetic photon flux density (the only component of radiation that was measured inside the bags), varied in parallel with most variations in transpiration (Figure 3). This correlation was not expected because, in forests, and especially in coniferous forests that are closely coupled to the atmosphere, transpiration is usually determined by the vapor pressure deficit of the air (VPD) and stomatal conductance. To determine how stomata controlled transpiration, average stomatal conductance was computed for the whole branch, assuming needle temperature was equal to air temperature measured inside the bag. Because needle temperature was slightly above air temperature during daytime, this procedure underestimated stomatal conductance, but the error was small because air inside the bags was well stirred by the two inner fans. Stomatal conductance ranged from 40 to 80 mmol m$^{-2}$ s$^{-1}$. Stomata are known to respond to light and to VPD. To separate the effects of these factors, we plotted stomatal conductance, $g_s$, against PAR at low values of VPD (< 15 hPa, Figure 4) and against VPD at high PAR values (> 700 $\mu$mol m$^{-2}$ s$^{-1}$, Figure 5). Figure 4 shows the usual hyperbolic increase in $g_s$ with increasing PAR, with half the maximum value being reached at about 250 $\mu$mol m$^{-2}$ s$^{-1}$. Figure 5 shows a decrease in $g_s$ from 80 to 40 mmol m$^{-2}$ s$^{-1}$ when VPD increases from 10 to 30 hPa, indicating that as VPD increased from 10 to 30 hPa, transpiration rate, $E$ (= $g_s$VPD), increased slightly from 0.8 to 1.2 mmol m$^{-2}$ s$^{-1}$.

Sap flow versus branch bag measurements

Although the branch bag technique provided accurate measurements of transpiration and of its dependence on climatic factors, measurements only covered a 2.5-week period. Furthermore, they could not give a true average of transpiration under fluctuating conditions because measurements lasted

![Figure 2](image2.png)

Figure 2. Variations in transpiration rate of a branch over a 6-day period at the beginning of August 1994.

![Figure 3](image3.png)

Figure 3. Branch transpiration rate as a function of incident PAR over a 2.5 week measurement period in August 1994.

![Figure 4](image4.png)

Figure 4. Average stomatal conductance of a branch versus incident PAR, for VPD values below 15 hPa. Data from two branch bags.

![Figure 5](image5.png)

Figure 5. Average stomatal conductance of a branch versus VPD inside the branch bag, for PAR values above 700 $\mu$mol m$^{-2}$ s$^{-1}$. Data from two branch bags.
only 100 s every half-hour. Because sap flow measurements were performed at the stand level from May to mid-September, this method provided an estimate of transpiration over the entire season. A direct comparison between measurements of sap flow and transpiration for a clear day indicated that sap flow lagged behind transpiration (Figure 6). Even with a 1-h time lag, the curves differed: sap flow started later and more abruptly than transpiration. Sap flow also reached a maximum sooner and decreased more slowly than transpiration in the afternoon and evening.

The explanation for this time lag is complex. It is at least partly a result of changes in water storage in the wood and needles above sap flow sensors (at 1.3 m height). To obtain an empirical estimate of the time lag, sap flow was plotted against branch transpiration for three time lag periods (Figure 7). A half-hour time lag clearly gave a hysteresis loop, whereas there was a better fit for the 1 h and 1.5 h time lags. Values of the square of the correlation coefficient ($r^2$) between the sap flow and transpiration were 0.855, 0.906 and 0.902 for time lags of 0.5, 1 and 1.5 h, respectively ($n = 673$). A 1-h lag was finally retained for subsequent analysis. It was a compromise, because the time lag is not constant (e.g., Loustau et al. 1996). For instance, a comparison of two sets of data on a cloudy day with two peaks of solar radiation (Day 208 of Figure 2, data not shown) indicated that the time lag was in excess of 2 h. This longer time lag occurred because transpiration rate was low and it took more time to change the amount of water stored above the sap flow sensors.

**Sap flow versus micrometeorological measurements**

We compared daily values of stand sap flow and canopy evaporation, computed as the difference between water vapor fluxes above ($E_c$ for canopy evaporation) and below the tree canopy ($E_s$ for soil evaporation). Because $E_s$ was not available for the whole period of measurement, $E_c - E_s$ was regressed against $E_c$ for the period of common measurements. On average $E_c - E_s$ equalled 0.76$E_c$. We then compared sap flow with this parameterized estimate of tree evaporation (Figure 8). There was a good overall agreement between the two data sets. Discrepancies arose mainly during wet days or immediately after a rainy period. When there was rain, the eddy flux system measured evaporation from the wet canopy that was not recorded by sap flow sensors. Also, when the soil was wet, $E_c$ increased significantly. Once the tree canopy had dried, 0.76$E_c$

![Figure 6](image1.png)

**Figure 6.** Latent heat fluxes of transpiration measured by the branch bag and sap flow methods. Sap flow measured at time $t$ is plotted at time $t-1$ hour (time lag of 1 h). To provide a better graphical comparison, values of branch bag transpiration were multiplied by 2 (which is close to the LAI value of 2.3 recorded at that time). Data are from branch Bag 1 on August 5, 1994.

![Figure 7](image2.png)

**Figure 7.** Comparison of half-hourly values of transpiration rate measured by branch bags and sap flow sensors, with increasing values of the time lag.

![Figure 8](image3.png)

**Figure 8.** Comparison of daily values of stand sap flow and canopy evaporation, computed as the difference between water vapor fluxes above ($E_c$ for canopy evaporation) and below the tree canopy ($E_s$ for soil evaporation). Because $E_s$ was not available for the whole period of measurement, $E_c - E_s$ was regressed against $E_c$ for the period of common measurements. On average $E_c - E_s$ equalled 0.76$E_c$. We then compared sap flow with this parameterized estimate of tree evaporation.
might have been an overestimate of actual tree transpiration because soil evaporation was still substantial. Despite these limitations, the agreement between the two methods was good, especially during cycles of soil drying (Days 233 to 247, and 250 to 258). However, there were also a few days with nearly zero sap flow that had no counterpart in the micrometeorological estimates. Again, these were rainy days for which a significant water vapor flux was not followed by a sap flow of the same magnitude.

Figure 8 also shows that the rates of tree transpiration were low. Daily totals of transpiration did not exceed 1.8 mm per day from sap flow estimates, and were slightly over 2 mm per day from micrometeorological estimates. These rates are low when compared with the available energy (daily net radiation divided by the latent heat of vaporization), which exceeded an equivalent of 6 mm per day on sunny days. Thus, most of the time, less than one-third of net radiation was used for tree transpiration. This reflected the low LAI (maximum of 2.3), the large needle aggregation in this forest, and the low values of stomatal conductance which ranged between 40 and 80 mmol m$^{-2}$ s$^{-1}$. This finding shows that most of the available energy at the land surface warmed the surface and the air.

**Discussion**

We studied the regulation of water loss by a boreal forest stand by three different methods at the branch, tree and stand levels. Branch bag measurements provided strong evidence that trees had low transpiration rates because they had low stomatal conductances. However, although stomatal conductance decreased from 80 to 40 mmol m$^{-2}$ s$^{-1}$ when VPD increased from 10 to 30 hPa, a small increase in transpiration occurred (from 0.8 to 1.2 mmol m$^{-2}$ s$^{-1}$), indicating that stomatal control was not strong enough to prevent a slight increase in $E$ with increasing VPD.

Stomatal response to PAR showed the usual hyperbolic shape, with complete stomatal opening at PAR values above 500 μmol m$^{-2}$ s$^{-1}$. Thus, the increase in $E$ observed at high values of PAR (Figure 3) did not result from stomatal opening but from an increase in VPD that increased the driving force for transpiration (VPD was partly correlated with PAR, $r^2 = 0.515$ for $n = 673$). This slight increase in $E$ at high VPDs conflicts with data obtained at the stand scale by Baldocchi and Vogel (1996) on the same site using the eddy covariance method. They showed a modest reduction in transpiration with increasing atmospheric VPD. This differential response of transpiration to humidity deficits may be a result of scaling. In the branch bag, when stomatal closure was caused by an increase in VPD, leaf temperature increased, heating the bag and causing a further increase in both VPD and transpiration. In the open air, the increase in leaf temperature was smaller, because of strong coupling with the air and high eddy diffusivity. Thus, VPD rarely exceeded 15 hPa in open air (Baldocchi et al. 1996), preventing further increases in transpiration.

The values of stomatal conductance determined in this study (40 to 80 mmol m$^{-2}$ s$^{-1}$) are small. Teskey et al. (1994) reported values ranging from 60 to 360 mmol m$^{-2}$ s$^{-1}$ for maximum stomatal conductance, $g_{s,max}$, of various pine species. Thus, $g_{s,max}$ of jack pine appears to be in the lower range of these values. Schulze et al. (1994) examined values of maximum stomatal conductance in the context of leaf nitrogen concentration for various plant species and found that evergreen conifers have a mean $g_{s,max}$ of 5.5 mm s$^{-1}$ or 220 mmol m$^{-2}$ s$^{-1}$ with a mean nitrogen concentration of 11 mg N DM$^{-1}$. At our site, the nitrogen concentration of jack pine needles was 10.3 mg N DM$^{-1}$ (data supplied by Dr. B. Middleton), implying that stomatal conductance of this species is below the average for evergreen conifers. However, with the data for all groups of plant species, Schulze et al. (1994) obtained a linear relationship between maximum stomatal conductance and nitrogen concentration, with a slope of 0.3 mm s$^{-1}$ (or 12 mmol m$^{-2}$ s$^{-1}$).
per mgn gdm$^{-1}$, which would give a $g_{s,max}$ of about 124 mmol m$^{-2}$ s$^{-1}$ for jack pine, a value relatively close to that observed.

Several models have been proposed to explain the variations in stomatal conductance with environmental variables such as VPD and PAR. Some are purely empirical (Jarvis 1976, Lohhammar et al. 1980). Others are partly empirical, based on a relationship between stomatal conductance and CO$_2$ assimilation (Ball et al. 1987, Leuning 1995), with a theoretical interpretation given by Dewar (1995) in terms of guard cell function. Monteith (1995) has proposed several ways of experimentally testing such models. Based on plots of leaf conductance versus transpiration rate or VPD, he distinguished three patterns. The most common pattern involves a linear decrease in stomatal conductance with increasing transpiration; i.e., an increase in VPD leads to a decrease in $g_s$, but this decrease is not strong enough to cause a decrease in transpiration. This was the pattern observed for our branch bag measurements. The equation of Monteith (1995) may be written in the form of a linear regression of stomatal resistance (1/$g_s$) versus VPD (cf. Hall and Kaufmann 1975):

$$1/g_s = 1/g_{s,max} + VPD/E_{max},$$

where $g_{s,max}$ and $E_{max}$ are the maxima of $g_s$ and $E$, respectively. We applied this linear model to our branch bag data and obtained values of 200 mmol m$^{-2}$ s$^{-1}$ and 1.3 mmol m$^{-2}$ s$^{-1}$ for $g_{s,max}$ and $E_{max}$, respectively. Although uncertainty is relatively large on the intercept that gives $g_{s,max}$, it is small on the slope that gives $E_{max}$. This value of $E_{max}$ represents the maximum transpiration under any condition and was close to the highest values that we recorded for transpiration (see Figure 2). Our $E_{max}$ value is low compared with reported values of 3 to 9 mmol m$^{-2}$ s$^{-1}$ for various grasses (Figure 7 in Monteith 1995) and the value of 35 mmol m$^{-2}$ s$^{-1}$ for sunflower (Figure 3 in Monteith 1995).

We believe that $E_{max}$ has greater significance for trees than for herbs because trees have the additional constraint to avoid cavitation in the stem. If trees use stomatal regulation to keep the water potential in the stem above the threshold value causing cavitation, as has been suggested (Cochard 1992), then $E_{max}$ may be determined by the conductivity of the wood to liquid water and the ratio of sapwood area to leaf area, which will impose a limit on transpiration and thus on stomatal conductance and CO$_2$ assimilation. The finding that $E_{max}$ for Pinus banksiana is close to the maximum values that we recorded may mean that the low stomatal conductances and strong response to VPD observed in this species enable it to thrive in environments with high evaporative demand.

Scaling $E_{max}$ to the stand scale for a jack pine stand with an LAI of 2.3 yields a maximum stand transpiration of 1.3 mmol m$^{-2}$ s$^{-1}$ times 2.3, or 3 mmol m$^{-2}$ s$^{-1}$. If this maximum value is maintained for 8 h a day, it leads to a daily transpiration rate of 1.6 mm per day, which is in good agreement with that recorded by the sap flow sensors. Thus, the value of $E_{max}$ is an important component of the water balance and should be a more useful characteristic of a tree species than maximum stomatal conductance.

The low transpiration rates of our jack pine stand (Figure 8) represent, on a daily basis, about one-third of the energy available in net radiation. We conclude, therefore, that most of the net radiation warms the air above the forest. This conclusion is also supported by the fact that the ground vegetation is formed mainly of lichens that dry quickly after rain and then act as a mulch, leading to low evaporation rates at the soil level. At the stand level, low transpiration rates were caused by low stomatal conductances and a low leaf area index (maximum of 2.3). The low LAI may be caused by a lack of nitrogen. In boreal ecosystems, low soil temperatures limit decomposition rates and release of mineral nitrogen. For example, Linder (1987) has shown that irrigation and fertilization increased LAI from 1.95 (control, half of total leaf area) to 5.2 in a stand of Pinus sylvestris L. in Sweden. The finding that needle nitrogen concentration was not especially low does not mean nitrogen is not limiting, because trees probably regulate leaf area to avoid excessively low nitrogen concentrations in the needles.

**Conclusion**

Three methods were used to study transpiration at the branch, tree and stand levels. Branch bags gave detailed information on the way that transpiration varied with environmental variables, and have the advantage over classical cuvette systems of being automated, providing a continuous record of a relatively large sample of needles. Sap flow sensors were easy to install, consumed less power than the other two techniques, and also gave a long-term continuous record. On the other hand, their hourly values were less reliable than those of the branch bags. Although micrometeorological measurements are the reference for measuring ecosystem water losses, the estimate of stand transpiration from the two eddy-flux systems was less accurate than values derived from single systems, as a result of errors compounded by taking differences. Nevertheless, they provided a good complement and check to the other methods. This technique is also less intrusive, although it is costly and difficult to implement.

The study was undertaken to determine how boreal forests keep water loss low enough to avoid water stress despite relatively low precipitation and high evaporative demand in summer. We conclude that water loss was minimized as a result of low values of LAI (maximum 2.3 in our stand) and stomatal conductance (40 to 80 mmol m$^{-2}$ s$^{-1}$). Low LAI may result from a lack of nitrogen caused by low decomposition rates of litter and soil organic matter induced by low soil temperatures. Jack pine also appeared to have a low value of maximum stomatal conductance, and limited its maximum transpiration rate to about 1.3 mmol m$^{-2}$ s$^{-1}$ by strong stomatal closure in response to the diurnal increase in VPD. Low transpiration rates also explain why boreal forests are a strong heat source during the daytime.

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References


Appendix 1. Variation in air humidity inside the branch bag after closure

Air vapor pressure inside the bag (e) increases from its value in outside air (e_o) to an equilibrium value (e_l) that is obtained when the loss of water vapor from the bag (due to leaks) is equal to branch transpiration. If V = bag volume, v = molar volume of air, p = atmospheric pressure, E = transpiration rate (per unit area), S = half the total needle area and L = the loss of water vapor due to leaks we may write:

\[(V/v)(de/dt)/p = ES - L. \quad (A1)\]

Transpiration rate is proportional to stomatal conductance g_s and to leaf to air VPD, i.e., E is proportional to \(e_l(T_l) - e_o\) where \(e_l(T_l)\) is the saturation vapor pressure at leaf temperature:

\[E = g(e_l(T_l) - e_o)/p. \quad (A2)\]

The flux of water vapor due to leaks is proportional to the difference in water vapor pressure between the inside and outside of the bag:

\[L = l(e_o - e_l)/p, \quad (A3)\]

where l is leak rate with the dimension of a flux (mmol s\(^{-1}\)).

Substituting the expressions for E (A2) and L (A3) in Equation A1 gives:

\[de/dt = k_1(e_o(T_l) - e_o) - k_2(e_l - e_o), \quad (A4)\]

where \(k_1 = (v/V)g_S\) and \(k_2 = (v/V)l\).

The solution of Equation A4 is:

\[e = e_l + (e_o - e_l)e^{-k_1t/k_2} + \text{leak correction}. \]
with:

$$e_i = \frac{(k_1 e_s(T_i) + k_2 e_a)}{(k_1 + k_2)} = \frac{(gS e_s(T_i) + l e_a)}{(gS + l)}.$$  \hspace{1cm} (A5)

In the branch bags, \(l\) is smaller than \(gS\) and \(e_i\) is closer to \(e_s(T_i)\) than to \(e_a\). The vapor pressure \(e\) increases from \(e_s\) to \(e_i\) in a nonlinear way. The value of \(de/dt\) is maximum at bag closure and decreases with time. Plots of \(e\) versus time showed that the best interval for computing \(de/dt\) was from 20 to 120 s. It was necessary to wait for 20 s for the bag air to reach equilibrium, and a shorter interval would have affected the accuracy of the measurement of \(de\).