Seasonal variation of energy and water vapor exchange rates above and below a boreal jack pine forest canopy

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Abstract. Fluxes of energy and water vapor over boreal forest stands are expected to vary during the growing season due to temporal variations in solar energy, soil and air temperature, soil moisture, photosynthetic capacity, and leaf area. To investigate this hypothesis, we measured fluxes of energy balance components (solar, latent and sensible heat, and soil and canopy heat storage) over and under a boreal jack pine forest in central Canada during the 1994 growing season. Temporal trends of daily-integrated energy fluxes were significant during a 117 day period between spring and autumn. Mean fluxes of net radiation and latent heat peaked near the summer solstice. By the autumnal equinox their magnitudes were half of their peak values. On a day-to-day basis the presence or absence of clouds modulated solar energy fluxes, while evaporation rates were dependent on whether the canopy was dry or wet. When the canopy was dry, daily evaporation was generally less than 2.5 mm d^{-1} . This amount was less than one-half the rate of equilibrium evaporation and was low compared to evaporation from vegetation in temperate zones. When the canopy was wet, daily evaporation approached 3 mm d⁻¹ and exceeded predicted rates of equilibrium evaporation. Evaporation from the dry forest was weakly coupled to available energy and was restricted by the canopy AEs low-surface conductance. Biotic factors limiting the forest AEs surface conductance include the forest AEs low-leaf area index and partial stomatal closure. Abiotic and physiological factors restricting stomatal opening included a scarce supply of soil moisture, limiting vapor pressure deficits and the low photosynthetic capacity of the needles. The fluxes of solar energy and latent and sensible heat at the floor of the forest were a significant portion of energy exchange between the forest and the atmosphere. Typically, 20 to 40% of the total energy exchange by the jack pine stand originated at the understory. Since a substantial amount of energy occurs under the forest, two-layer, not a big-leaf AE, evaporation models are recommended as a tool for estimating water vapor fluxes from this open forest stand.

Introduction

... forests tremble under the axe—millions of trees are lost, animals and birds have to flee, rivers dry out, beautiful landscapes are lost forever... waters are polluted, wildlife disappears, the climate is harsher...

Anton Chekhov (from Uncle Vanya, 1899)

Links between climate and forests have long been recognized by foresters and playwrights. Quantitatively, state variables that describe climate, such as air temperature, humidity, convective precipitation, and net radiation, are influenced by the rates at which solar energy, water vapor, and heat are exchanged between land and atmosphere control. Moreover, the amount of energy absorbed by a forest canopy and the amount converted into heating the air and evaporating water is governed by the biophysical properties of the surface (albedo, aerodynamic roughness, and surface conductance) and driving potentials, established by the gradient between the surface and the atmosphere's temperature and humidity.

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The boreal forest is the major biome occupying the circumpolar region between 50° and 70° north. Climate models predict that the boreal forest is poised to experience a significant change in climate [Manabe and Stouffer, 1980], and ecosystem models predict that potential climate change may cause a shift in the composition and structure of the boreal forest [Smith et al., 1992; Sykes and Prentice, 1995; Hogg and Hurdle, 1995]. The boreal forest's potential to impact the Earth's climate arises from its great areal extent (it covers 11% of the terrestrial surface [Bonan and Shugart, 1989]) and its unique biophysical properties. With regard to its structure, evergreen conifer forests are the most profuse vegetation class in this region [Oechel and Lawrence, 1985; Bonan and Shugart, 1989]. In general, conifer forests have a greater ability to exchange mass and energy with the atmosphere than other vegetation types. For example, they are optically darker than broadleaved forests and short vegetation [Monteith, 1972; Jarvis et al., 1976; Shuttleworth, 1989; Sellers et al., 1995]. This attribute allows them to absorb more solar radiation and gives them a greater potential to evaporate water and heat the air and soil. Conifer forests are also aerodynamically rougher than broadleaved forests, shrubs, and herbaceous vegetation. This characteristic enhances their ability to transfer mass and energy with the atmosphere [Jarvis et al., 1976; Shuttleworth, 1989; Kelliher et al., 1993].

We expect fluxes of energy and water vapor over boreal forest stands to vary during the growing season due to temporal variations in solar energy, soil and air temperature, soil moisture, photosynthetic capacity, and leaf area. However, we have little information on (1) when mass and energy fluxes of a boreal forest are significant; (2) how much energy fluxes will change during the growing season; (3) how much energy fluxes vary across the boreal landscape; or (4) how darker and rougher boreal forests will use available solar energy and an enhanced turbulent exchange capacity to evaporate water, to heat the air and soil, and to drive primary productivity. Longterm measurements of energy and water vapor exchange over boreal forests are needed to address these questions. Longterm flux experiments can also reveal responses that are never uncovered during short-term and summertime field campaigns. In pioneering Swedish studies, for example, it was observed that transpiration rates of boreal forest stands were relatively low in the spring during clear days with high evaporative demand. Low evaporation rates occurred because cold soils restricted root uptake of soil moisture [Halldin et al., 1980]. Field data on mass and energy fluxes can also be used to verify, improve, and parameterize algorithms used to simulate the lower boundary condition of climate and ecosystem models.

In central Canada the boreal forest landscape consists of deciduous broad-leaved (aspen, *Populus*, birch, *Betula*) and evergreen conifer (black spruce, *Picea mariana*; jack pine, *Pinus banksiana*; and larch, *Larix*) forests, fens, and lakes. Mature jack pine stands are distinct from the other vegetation classes growing on the region. Jack pine grow on well-drained and nutrient-poor sites, whereas black spruce occupy cold and poorly drained sites [*Bonan and Shugart*, 1989]. Hence, jack pine may experience stress from soil moisture deficits when other vegetation classes in the region are not. Jack pine stands may also experience a longer growing season since their drier soils can warm faster than wetter sites.

The remote location and harsh climate of boreal forests has kept them elusive to most modern micrometeorologists. Only a few teams of European [Perttu et al., 1980; Lindroth, 1985a; Hollinger et al., 1995; Arneth et al., 1996] and North American researchers [Amiro and Wuschke, 1987; Lafleur, 1992; Fitzjarrald and Moore, 1994; den Hartog et al., 1994; Fan et al., 1995; Baldocchi and Vogel, 1996; Black et al., 1996] have attempted field measurements of mass and energy exchange over boreal forests. Logistical infrastructure, provided by international projects such as Boreal Ecosystem-Atmosphere Study (BOREAS) [Sellers et al., 1995], and technological advances place our scientific community at the beginning of an era for investigating seasonal trends in mass and energy fluxes over remote forests. During 1994 we participated in the BOREAS experiment and measured flux densities of water vapor, sensible heat, solar radiation, and CO₂ above and below a jack pine forest (Pinus banksiana) between spring and autumn. The objective of this paper is to report on seasonal variations of climatic variables and mass and energy flux above and below a jack pine forest stand. A discussion on the factors controlling these fluxes is also given. Additional information on the seasonal variation of CO₂ flux measurements and the relationships between environmental variables and mass and energy fluxes are reported by Baldocchi et al. [1997] and Baldocchi and Vogel [1996].

Materials and Methods

Site Characteristics

The jack pine forest (*Pinus banksiana*) stand under investigation grows near Nipawin, Saskatchewan, Canada (53° 54′ 58.82″ N, 104° 41′ 31.29″ W; elevation 579.3 m). The terrain of the site was relatively flat and well suited for micrometeorological flux measurements. Its mean slope ranged between 2 and 5%. Uniform fetch extended beyond 1000 m in all directions, thereby enveloping the flux footprint (B. Amiro, personal communication, 1996).

Field measurements commenced in the spring (May 23, 1994, day 143). At this date, soil temperatures at 0.32 m were near freezing, snow had fallen recently, and the last hard freeze was on day 141. Data acquisition continued past the first frost and well into the autumn, when deciduous plants and annuals were senescencing and dropping leaves (D259, September 16, 1994).

Details on stand characteristics are reported by Chen [1996] and Baldocchi et al. [1997]. In brief, the mean height of the canopy was about 13.5 m. The leaf area index (one half of total surface area of needles per unit ground area) was estimated to range between 1.9 and 2.2. The understory vegetation was sparse. However, there were isolated groups of alder (Alnus crispa). The ground was covered with an optically bright mat of vegetation that consisted of bearberry (Arctostaphylos uvaursi), bog cranberry (Vaccinium vitisideae), and lichens (Cladina spp).

The soil was a coarse-textured, well-drained sand, containing little carbon and nitrogen; soil properties were characterized by D. Anderson, of the University of Saskatchewan, and are reported by *Baldocchi et al.* [1997]. Soil moisture measurements were made by a team led by R. Cuenca of Oregon State University [see *Cuenca et al.*, this issue]. They used a neutron probe sensor to measure volumetric soil moisture. During the intensive field campaigns, soil moisture was measured every other day.

Flux Measurement Instrumentation

Water vapor and sensible heat fluxes of the jack pine stand were measured using two eddy flux systems. One eddy flux measurement system was mounted above the forest on a 30 m scaffold tower. The sensors were placed on a boom 20 m above the ground and 3 m upwind of the tower; the instrument boom was about 7 m above the mean tree height.

The second eddy flux system was positioned near the floor of the canopy. The instruments were mounted 1.8 m above the ground. This location was in the stem space of the canopy, where little foliage was present between the canopy floor and the measurement height.

Wind velocity and virtual temperature fluctuations were measured with three-dimensional sonic anemometers (Applied Technology Inc., Boulder, Colorado, model SWS-211/3K). Water vapor and CO₂ fluctuations were measured with an open-path, infrared absorption gas analyzer [Auble and Meyers, 1992]. During the experiment the response of the infrared gas analyzer was referenced to a relative humidity sensor (Vaisala model HMP-35A, Helsinki, Finland) and a dew point hygrometer.

Micrometeorological data were digitized, processed, and stored using a microcomputer-controlled system and in-house software. Analog sensor signals were digitized at 10 Hz with a 12 bit analog to digital converter.

Meteorological Instrumentation

Soil heat flux density was measured by averaging the output of four soil heat flux plates (REBS model HFT-3, Seattle, Washington). They were placed under the lichen layer and were buried 0.01 m below the surface of the sand. Plates were randomly placed within a few meters of the flux system. Soil temperature was measured with two multilevel thermocouple probes. Sensors were spaced logarithmically at 0.02, 0.04, 0.08, 0.16, and 0.32 m below the surface.

Photosynthetically active photon flux density and the net radiation balance were measured above the forest with a quantum sensor (LICOR model LI-190S, Lincoln, Nebraska) and a net radiometer (REBS model 6, Seattle), respectively. The sensors were extended 3 m away from the tower to minimize exposure effects. Measurements of solar radiation components under the canopy were made using an instrument package that traversed across a 14.5 m domain [Baldocchi and Vogel, 1996]. The translation velocity and sampling rates were set so a sample was taken every millimeter (0.1 s sample frequency, 1 cm s⁻¹ travel velocity).

Air temperature and relative humidity were measured alongside the flux instrumentation with a humicap sensor (Vaisala HMP-35). Ancillary meteorological and soil physics data were acquired and logged on Campbell 21X data logger (Logan, Utah). Instruments were sampled at 1 s intervals, and half-hour averages were calculated and stored on a computer to coincide with the flux measurements.

Flux Covariance Computations

Vertical flux densities of latent (λE) and sensible heat (H) between the forest and the atmosphere are proportional to the mean covariance between vertical velocity (w') and the respective scalar (c') fluctuations. Positive flux densities represent mass and energy transfer into the atmosphere (and away from the surface), and negative values denote the reverse. Turbulent fluctuations were computed as the difference between instantaneous and mean scalar quantities. Mean scalar values were determined in real time by using a digital recursive filter. In this study, a 400 s time constant was used. Empirical and theoretical calculations indicate that this filter time constant is adequate for flux covariance calculations. Water vapor flux covariances were corrected for density fluctuations arising from variations in temperature and humidity. We numerically rotated the three orthogonal wind axes to align the vertical velocity measurement normal to the mean wind streamlines [see Baldocchi et al., 1988; McMillen, 1988].

During a season-long study, vast amounts of data are acquired. To reduce the data into manageable and digestible bites, we evaluated and will interpret daily sums and averages of water vapor and energy fluxes. To properly evaluate daily integrations of fluxes and climate variable, it is desirable to have nearly continuous data records because the daily patterns are nonlinear. Yet, it is impossible to take perfect and reliable data 24 hours a day, seven days a week, month after month. We calculated daily sums using an approach described by Wofsy et al. [1993], Greco and Baldocchi [1996], and Baldocchi et al. [1997]. First, we screened the data. Data were rejected when sensors were broken or being calibrated. We also rejected data when they were out of range or their absolute value exceeded the mean plus 3 times its standard deviation. Small gaps of missing meteorological data were filled via interpolation between earlier and later measurements. Larger data gaps were filled by assigning the data to the value of the daily ensemble

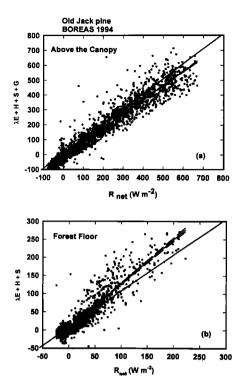


Figure 1. A test for closure of surface energy balance. The independent variable is the net radiation flux density (Rn), and the dependent variable is the sum of λE , H, S, and G (W m⁻²). The data represent hourly averages. Statistics associated with the data in this figure are presented in Table 1. (a) Energy flux densities were measured above the jack pine canopy. (b) Energy flux densities were measure above the forest floor.

mean. Missing mass and energy flux data were treated in a different way. Missing values of net radiation (R_n) , latent (λE) , and sensible heat (H) flux were estimated by using empirical regressions determined from independent field data taken during the 1993 field season [Baldocchi and Vogel, 1996]. The net radiation flux density R_n was estimated as a function of the photosynthetic photon flux density Q_p . The energy flux densities λE and H were estimated as functions of R_n . Overall, the amount of data accepted was high. For example, less than 0.5% of the stand-level and 16% of the forest floor measurements of λE flux densities were corrected with the described procedure.

The degree to which the surface energy balance can be closed is one measure of data quality. During the 1994 field study, the sum of energy balance components ($\lambda E + H + G + S$, where G is soil heat flux and S is canopy heat storage), measured above the canopy, was closely related to and highly correlated (r^2) with net radiation ($R_{\rm net}$) (Figure 1). The regression of the sum of the energy balance components on net radiation yielded a slope equal to 0.94, an intercept equal to 0.94 (Table 1). Using these regression statistics, we calculate that the energy closure imbalance at a typical value of net radiation (e.g., 350 W m⁻²) was 8%. This small imbalance of surface energy balance closure is consistent with the results from our 1993 pilot study [Baldocchi and Vogel, 1996] and other field studies [e.g., Baldocchi, 1994; Black et al., 1996].

Eddy covariance flux measurements will be in error if they are not made within a fully adjusted internal boundary layer,

Table 1a. Statistics on Energy Balance Closure Above and Below a Jack Pine Forest

Variable	R_n	$\lambda E + H + S + G$	
Mean, W m ⁻² std. error, W m ⁻²	Above Canopy 126.3 110.6 3.98 3.6		
	R_n	$\lambda E + H + S$	
Mean, W m ⁻² std. error, W m ⁻²	Below Canopy 21.8 1.28	31.3 1.68	

 R_n is net radiation flux density, λE is latent heat flux density, H is sensible heat flux density, S is the soil heat flux density, and G is the canopy heat storage. Hourly averages were used for the comparisons.

the so-called "constant flux" layer. To test this condition, we measured sensible heat transfer at two levels above the canopy (at 16.9 and 20.4 m). Our statistical analysis reveals that the energy fluxes agreed within 2% of one another; the regression coefficients were H (16.9 m) = 0.013 + 1.02 H (20.4 m), r^2 equaled 0.98. From these results we conclude that it is valid to use a one-dimensional framework for interpreting eddy covariance flux measurements in this study. We also investigated transfer functions for imperfect sensor response time and separation distance [Moore, 1986]. These corrections were less than 3% for our experimental configuration, so they were not applied.

Near the forest floor, the regression of the sum of the energy balance components on net radiation yielded a slope equal to 1.22, an intercept equal to 4.7 W m⁻², and a coefficient of determination (r^2) equal to 0.87 (Figure 1b). These results are comparable to observations we have made previously under a broad-leaved forest [Baldocchi and Meyers, 1991].

The bias difference between the dependent and the independent variables was greatest under sunny periods, when R_{net} exceeded 50 W m⁻². Under sunny skies we observed that the coefficient of variation of net radiation measurements (the ratio between the standard deviation and the mean) over the 15 m domain of the tram ranged between 50 and 100% during 30 min sampling periods. Another source of sampling error can be introduced by fluctuations in wind speed and wind direction, which will cause the footprint sampled by the eddy covariance system to differ from the one sampled by the radiation system. Considering the heterogeneous nature of the subcanopy, the difficulty of measuring a net radiation field representative of the flux footprint and the large r^2 between the independent and the dependent variables, we conclude that this degree of energy balance closure is acceptable for understanding processes and examining the relative differences between energy fluxes occurring above and below the canopy.

Results

Seasonal variation in surface energy fluxes will be modulated by a concurrent seasonality in canopy architecture and physiological and environmental variables. To understand if and how mass and energy fluxes may vary, we first report how selected plant, climate, and soil variables varied during the 1994 growing season.

Canopy Architecture

Some seasonal variation in canopy structure was observed during the 1994 experimental season. In early June there was a new flush of needles, and male cones emerged. During September there was needle yellowing and appreciable loss of 2, 3, and 4 year old needles. *Chen* [1996] evaluated the plant and leaf area indices of the site on days 146, 210, and 253 using an indirect method based on remote sensing of light transfer through the canopy. The plant area index was 2.78, 3.34, and 3.26 on these three respective study days; this variable represented the sum of one-half the surface area of needles and the woody biomass.

Aerial and Soil Climate

Air and soil temperature. The onset and cessation of biological activity in the boreal region is strongly influenced by duration of air and soil temperatures above freezing. Temperature also influences evaporation rates through its impact on relative humidity and stomatal mechanics. Figure 2 shows the seasonal pattern of daily-averaged air temperatures (Figure 2a) at 20 m. Also presented are the mean differences between air and bole temperatures (Figure 2b) and air and soil (4 cm deep) temperatures (Figure 2c). Between days 140 and 260 the majority of daily-averaged air temperatures ranged between 10° and 20°C. Exceptions include three relatively warm periods (when mean air temperature exceeded 20°C) and one cold period (when mean air temperature dropped to near 5°C).

Bole temperatures either equaled or were up to 2°C warmer than air temperature during most of the growing season. Only early in the spring (around day 140) and into the autumn (after day 240) were bole temperatures consistently cooler than air temperature. The mean temperature of the boles generally remained above air temperature because, being optically dark, they are very capable of absorbing a substantial amount of sunlight that is transmitted through the sparse crown (see below).

At the start of the experiment, the mean soil temperature of the fine root layer (at 4 cm) was 4°C, or about 8°C cooler than the mean air temperature. The temperature of the soil at 32 cm was even colder and was slightly above freezing (1.8°C). Throughout most of the growing season, the mean daily difference air and shallow soil temperature ranged between 0° and 5°C.

Using meteorological data, taken at this field site by the BOREAS project, we report that a hard freeze occurred as late as day 141. The last day with a mean air temperature below 0°C was day 117, and soil temperature at 0.50 m exceeded freezing after day 127.

Table 1b. Regression Statistic for the Sum of Energy Balance Components ($\lambda E + H + S + G$) on Net Radiation (R_n)

Variable	Above Canopy	Near-Forest Floor	
n	2448	1273	
<i>b</i> 0	-8.62	4.66	
b0 b1 r ²	0.945	1.22	
r^2	0.944	0.87	

The value of n is the number of samples, b0 is the zero intercept, b1 is the slope, and r^2 is the coefficient of determination. Hourly averages were used for the comparisons.

Soil moisture and precipitation. The experimental season started with a relatively full profile of soil moisture (Figure 3); the volumetric soil moisture content in the zone inhabited by fine roots (the upper 0.15 m) was above 10%, while deep in the soil profile (at 1.25 m), the volumetric soil moisture content was 16%. Referring to soil moisture retention curves for sandy soil, the initial soil moisture content approached values that characterize the soil moisture matrix potential at field capacity (-0.033 M Pa) (D. Anderson, University of Saskatchewan, BORIS database [Baver et al., 1972]). As the growing season progressed, moisture was removed from the soil column, between precipitation events, by evaporation and drainage (Figure 4). Through the experimental period, the volumetric soil moisture (m³ m⁻³) in the top 0.15 m layer of the soil ranged between 11 and 3%. The volumetric soil moisture content at 1.25 m below the surface was more conservative, ranging between 15 and 8%.

Modest precipitation events (less than 20 mm) occurred frequently throughout the growing season (Figure 4). The most notable rain event occurred on day 198, when over 100 mm of precipitation fell on the region. This event is noteworthy because it initiated a chronological sequence when the soil moisture profile was replenished and, subsequently, depleted by canopy evaporation. We will explore the consequence of this event on latent and sensible heat exchange later.

Seasonal Trends of Energy Fluxes

Solar radiation. Solar radiation drives energy exchange and photosynthesis. At the high boreal latitudes, the potential flux density of incident sunlight is less than at southerly locales because the Sun is lower in the sky. The daily sums of incident

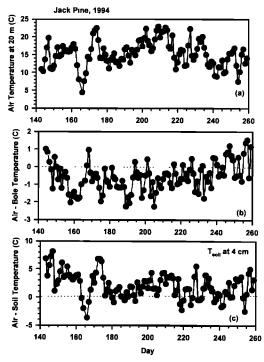


Figure 2. Seasonal variation of mean air, bole, and soil temperatures over a boreal jack pine stand during the 1994 growing season. The data were averaged over 24 hours. (a) Air temperature at 20 m. (b) Difference between air and bole temperature. (c) Difference between air and soil temperature at 4 cm.

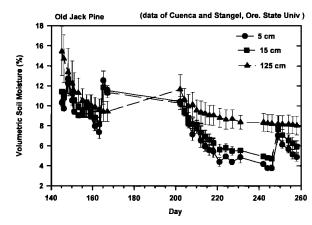


Figure 3. Seasonal variation of the volumetric soil moisture percentage at three depths (5, 15, and 125 cm) from the sandy soil of a jack pine stand. The data were acquired by R. Cuenca and D. Stangel, Oregon State University, with a neutron probe measurement system. The error bars represent one standard deviation from data measured at five access tubes.

sunlight, however, need not be diminished by this effect. Near the summer solstice, compensation for lower Sun angles can occur because daylength at boreal latitudes is longer and because sunlight travels through a cleaner optical path.

How the daily sums of photosynthetic photon flux density (Q_p) varied above the canopy and at the forest floor during the growing season are shown in Figure 5. Over the 117 day experimental period, values of Q_p on clear days (as denoted by the upper bound of the envelope of data) varied between 57 mol m⁻² d⁻¹, near the summer solstice, to about 30 mol m⁻² d⁻¹, before the equinox. The presence or absence of cloud cover had as large, if not greater, an impact on daily Q_p as the seasonal change in the Sun's declination angle. Day-to-day differences in Q_p typically exceeded 30 mol m⁻² d⁻¹.

The magnitude and fraction of Q_p penetrating to the forest floor was relatively large. On clear days, more than 15 mol m⁻² d⁻¹ of quanta was received at forest floor. These values represent 20 to 35% of incident Q_p . The jack pine's low leaf area and its clumped foliage allowed a high proportion of sunlight to reach the forest floor [Chen, 1996; Baldocchi and Vogel, 1996]. Despite its bright appearance, only a modest (<5%)

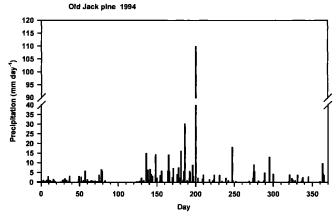


Figure 4. Seasonal variation of daily precipitation at the Boreal Ecosystem-Atmosphere Study (BOREAS) jack pine stand during 1994. The site was near Nipawin, Saskatchewan, Canada.

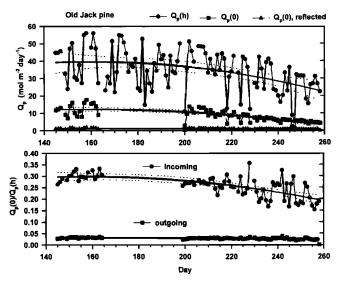


Figure 5. (top) Seasonal variation of photosynthetically active photon flux (Q_p) measured above $(Q_p(h))$ and under $(Q_p(0))$ a jack pine stand. Data represent sums from daylight periods. (bottom) Ratios of Q_p measured below and above the jack pine forest stand. Incoming refers to the photon flux penetrating the foliage space. Outgoing refers to the photon flux reflected from the bright lichen mat on the soil surface. The dashed lines represent the 95% confidence intervals of the regression.

amount of incident Q_p received at the forest floor was reflected by the lichen mat.

Substantial penetration of sunlight through the foliage space seems to be a common characteristic of northern conifer forests. For comparison, 34% of incoming global radiation (300 to 3000 nm waveband) reached the floor of a boreal pine forest (Pinus sylvestris) growing near Jadraas, Sweden [Perttu et al., 1980], and 17 to 26% of visible sunlight (480 to 600 nm waveband) is transmitted through a spruce (Picea sitchensis) stand, whose leaf area index is equal to 2 [Jarvis et al., 1976]. In contrast, less than 5% of incoming Q_p penetrates to the floor of dense temperate and tropical broad-leaved forests, whose leaf area indices exceed 5 [Hutchison and Baldocchi, 1989; Shuttleworth, 1989].

Mean flux densities of net radiation R_n (averaged over 24 hours) experienced discernible seasonality (Figure 6). Peak-averaged values exceeded 200 W m⁻² (17.3 MJ m⁻² d⁻¹) at midsummer and diminished to levels near 100 W m⁻² (8.64 MJ m⁻² d⁻¹) by the end of the experiment (after day 250). Large day-to-day variation of R_n (100 W m⁻²) occurred throughout the experimental period due to the presence or absence of clouds or smoke.

For perspective the daily sums of net radiation fall within the range of measurements observed at other boreal forest sites [Budyko, 1974; Perttu et al., 1980; Amiro and Wuschke, 1987; den Hartog et al., 1994; Fitzjarrald and Moore, 1994]. On the other hand, the peak daily totals of net radiation, reported in Figure 6, exceed values measured over midlatitude broadleaved temperate forests, which are less than 15 MJ m⁻² d⁻¹ [Hutchison and Baldocchi, 1989; Galloux et al., 1981]. Despite the Sun being lower in the boreal sky, the combination of longer days, clearer skies, and a low canopy reflectivity (the albedo of the jack pine stand and a temperate forest are about 10 and 14%, respectively [Shuttleworth, 1989; Hutchison and

Baldocchi, 1989; Sellers et al., 1995]) allows a boreal jack pine forest to absorb more radiation over 24 hours than temperate broad-leaved forests growing at temperate latitudes.

The proportion of net radiation measured at the forest floor $(R_n(0))$, as compared to measurements made over the canopy $(R_n(h))$, varied from 30%, at the start of the experiment, to less than 10%, at the end of the experiment. Lower solar elevation angles, in the autumn, allowed more radiation to be intercepted by boles, thereby reducing the ratio between $R_n(0)$ and $R_n(h)$. As with Q_p , a much smaller proportion of available net radiation is received at the floor of denser temperate broad-leaved forests (<8% [Galloux et al., 1981; Hutchison and Baldocchi, 1989]) and conifer forests (15% [Black and Kelliher, 1989]).

Canopy heat storage (S) and soil heat flux (G). On a 24 hour basis the amount of energy stored by the canopy (S) was small (Figure 7a); the average canopy heat storage (S) revolved about zero with a variation of plus/minus 6 W m⁻². While this component of the surface energy balance can be neglected on a daily basis, its magnitude can approach 100 W m⁻² on an hourly basis.

The average rate that heat was conducted into or out of the soil (G), on the other hand, experienced a distinct seasonal pattern (Figure 7b). Springtime warming of the soil caused it to gain energy at an average rate of 10 W m⁻² (0.86 MJ m⁻² d⁻¹) at the beginning of the experiment. With time, the magnitude of the daily-average soil heat flux trended downward until day 220. Afterward, heat was lost from the soil on a daily basis. By the end of the experiment, the soil was losing heat at a daily-averaged rate equal to 5 W m⁻². Heat lost from the soil, late in the growing season, is an additional energy source for heating the air and evaporating water and partially offsets the effect of the seasonal diminution of net radiation (Figure 6).

Latent heat flux (\lambda E). Figure 8a shows the seasonal pattern of daily-averaged λE measured above and below the canopy. Throughout the experimental period, the daily-averaged value of λE was less than 100 W m⁻². Typical values of daily-

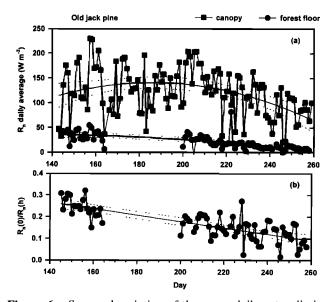


Figure 6. Seasonal variation of the mean daily net radiation flux density measured (a) above and (b) below a jack pine stand. The data were averaged over 24 hours and were obtained during the 1994 growing season. The dashed lines represent the 95% confidence intervals of the regression.

averaged λE ranged between 30 and 80 W m⁻² (2.59 to 6.91 MJ m⁻² d⁻¹) until day 220. Afterward, there was a gradual downtrend in daily λE . By the end of the experiment (day 260), the daily average evaporative flux was between 15 and 30 W m⁻² (1.29 to 2.59 MJ m⁻² d⁻¹).

The highest λE values were associated with clear days, after a period of significant rainfall (e.g., days 200, 201, and 202), because available energy was plentiful and evaporation rates from a wet canopy approach and exceed potential rates of evaporation [Jarvis et al., 1976; Lindroth, 1985a; Shuttleworth, 1989]. With regard to the seasonality of λE , modest and typical rates of evaporation were already occurring at the beginning of the experiment (and growing season) despite the fact that soil water, deep in the soil profile, was nearly frozen.

Evaporation from the canopy floor was significant throughout the growing season (Figure 8b). It ranged between 5 and 25 W m⁻² (0.43 to 2.16 MJ m⁻² d⁻¹) and generally accounted for 10 to 40% of the moisture evaporated from the canopy, as a whole. The importance of forest floor under a jack pine stand is comparable to values measured under temperate conifer forests [Black and Kelliher, 1989; Kelliher et al., 1990]. On the other hand, the ratio between forest floor and total canopy evaporation is much larger than that measured over a sparser, subarctic woodland at the northern extreme of the boreal forest. Lafleur [1992] estimated that 70% of the water lost from an open subarctic forest originated from the forest floor. Evaporation rates from the floor of a temperate deciduous forest, in contrast, are less than 5% of peak canopy evaporation fluxes [Baldocchi and Vogel, 1996].

Figure 9 translates the daily-averaged rates of λE into daily totals of water usage to facilitate comparison with data in the literature. Daily evaporation from the jack pine stand typically ranged between 0.5 and 2.5 mm d⁻¹. Higher values, approaching 3.5 mm d⁻¹ only occurred after significant rainfall events. For comparison, *Kelliher et al.* [1993] report that peak values of daily evaporation from conifers range between 4.5 and 4.8 mm d⁻¹; they compiled data from studies on the *Pseudotsuga men*-

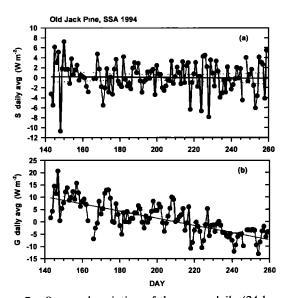


Figure 7. Seasonal variation of the mean daily (24 hour average) canopy heat storage (G) and soil heat flux (S) measured at the jack pine stand during the 1994 growing season. The dashed lines represent the 95% confidence intervals of the regression.

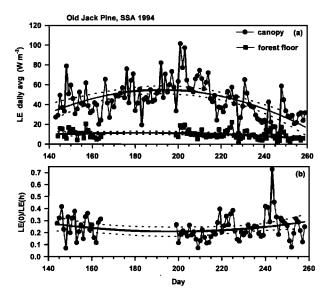


Figure 8. Seasonal variation of the mean latent heat flux density measured (a) above and (b) below a jack pine stand. The data were averaged over 24 hours and were obtained during the 1994 growing season. The dashed lines represent the 95% confidence intervals of the regression.

ziesii in the Pacific Northwest, Pinus pinaster growing in the Les Landes forest of France and Pinus sylvestris growing in Sweden, among others. At another extreme the daily totals of jack pine evaporation were less than one fifth of maximum evaporation totals measured over an actively transpiring alfalfa field, which approach 12 mm d⁻¹ [Rosenberg, 1969]. The low daily totals of evaporation (less than 3 mm per day) have also been observed over a jack pine stand growing in central Canada [Amiro and Wuschke, 1987] and from a spruce/lichen woodland growing in the boreal region of eastern Canada [Fitzjarrald and Moore, 1994].

With regard to seasonality of daily evaporation, our observation of appreciable springtime evaporation and a modest seasonal trend of daily evaporation are consistent with evaporation data from a Swedish *Pinus sylvestris* stand and other northern European conifer forests [*Lindroth*, 1985a], a Canadian jack pine stand in Manitoba [*Amiro and Wuschke*, 1987],

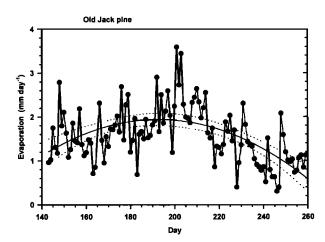


Figure 9. Seasonal variation of daily evaporation above the jack pine stand. The units are expressed in millimeter per day. The dashed lines represent the 95% confidence intervals of the regression.

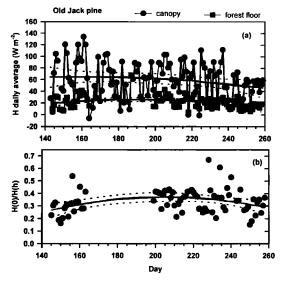


Figure 10. Seasonal variation of mean sensible heat flux density measured (a) above and (b) below a jack pine stand. The data were averaged over 24 hours. The dashed lines represent the 95% confidence intervals of the regression.

and the nearby aspen stand [Black et al., 1996]. We were unable to assess when evaporation started and stopped, but Black et al. [1996] report significant rates of evaporation between days 60 and 310 over an aspen stand near Prince Albert, Saskatchewan. Hence evaporation from boreal forests is not confined to the frost-free growing season.

Sensible heat transfer (H). Figure 10a shows the seasonal pattern of daily-averaged sensible heat flux measured above and below the forest stand. On a day-to-day basis the average sensible heat flux ranged between 0 and 140 W m⁻² (0 to 12.1 MJ m⁻² d⁻¹). A second-order regression, fit through the data, indicates a weak seasonal change in H. At the start of the experiment the mean daily value of H was about 60 W m⁻² (5.18 MJ m⁻² d⁻¹), and by the end of the growing season the regression mean decreased to about 45 W m⁻² (3.89 MJ m⁻² d⁻¹). The peak sums of sensible heat transfer resemble data from a jack pine stand growing in Manitoba, Canada; *Amiro and Wuschke* [1987] reported that daily totals of H approached and exceeded 10 MJ m⁻² d⁻¹.

Sensible heat fluxes measured above the forest floor were a significant portion of the sensible heat flux measured above the canopy (Figure 10b). There, the magnitude of H ranged between 0 and 40 W m⁻², on a daily basis, and it accounted for 25 to 40% of H measured over the canopy (Figure 10b). In contrast, sensible heat fluxes measured near the floor of a temperate forest are almost nil during the summer [Baldocchi and Vogel, 1996].

Discussion: Constraints on Latent and Sensible Heat Exchange, Role of Some Environmental and Biological Factors

Inspection of the Penman-Monteith equation identifies the key factors that control canopy evaporation [see *Monteuth*, 1972; *Jarvis and McNaughton*, 1986]. The most prominent variables are available energy, canopy surface and aerodynamic conductances, and the atmosphere's humidity deficit.

Equilibrium evaporation is one limit of Penman-Monteith evaporation theory. Equilibrium evaporation is defined as

$$\lambda E_{eq} = \frac{s}{s + \gamma} \left(R_n - S - G \right) \tag{1}$$

where s is the slope of the relation between saturation vapor pressure and temperature, and γ is the psychrometric constant. Descriptively, λE_{eq} is the evaporation rate attained by a freely evaporating surface after it saturates the atmosphere [Jarvis and McNaughton, 1986]. This value is approached when the Jarvis-McNaughton coupling factor (omega) approaches 1, as over smooth vegetation with a low aerodynamic conductance or well-watered vegetation with a high surface conductance. Though this condition is rarely met in the field, comparing measured evaporation to predicted rates of equilibrium evaporation helps diagnose which factors control daily jack pine evaporation most.

On the average, λE was about one half of λE_{eq} when the canopy was dry (Figure 11a) and approached and exceeded 1 when the canopy was wet or damp (Figure 11b). The $\lambda E/\lambda E_{eq}$ values of the dry jack pine canopy were low compared to values measured over vegetation that forms a closed canopy and has ample soil moisture; these canopies tend to evaporate at rates proportional to 1.26 times equilibrium evaporation [de Bruin, 1983; Jarvis and McNaughton, 1986; Baldocchi, 1994]. Our observation of low equilibrium evaporation ratios over the jack pine forest is consistent with theory and observations made over a variety of conifer forests [Jarvis et al., 1976; Jarvis and McNaughton, 1986; Jarvis, 1993; Kelliher et al., 1993] and agree with results inferred from Lindroth [1985a] and Amiro and Wuschke [1987], for morphologically and genetically similar stands of boreal conifers. Both authors report that an analogous index, the evaporation ratio $(\lambda E/R_n)$, ranged between 0.40 and 0.60, which is equivalent to $\lambda E/\lambda E_{eq}$ values between 0.24 and 0.36.

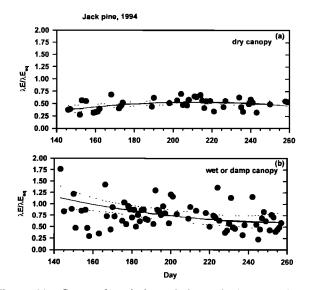


Figure 11. Seasonal variation of the ratio between latent heat flux and equilibrium evaporation. The data were obtained over a jack pine stand during the 1994 growing season and are averaged over 24 hours. (a) Days when the canopy was dry. (b) Days when wetness, by precipitation or dew, was detected on the canopy. The dashed lines represent the 95% confidence intervals of the regression.

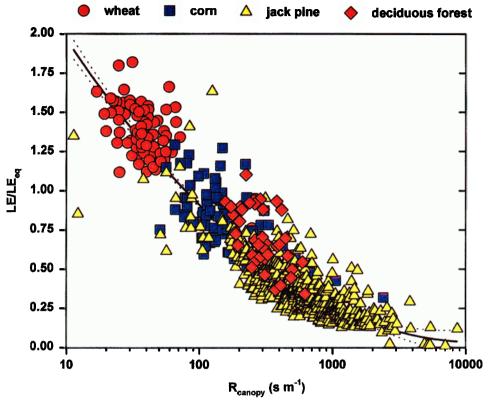


Plate 1. Relationship between the ratio of latent heat transfer and its equilibrium rate versus canopy surface resistance (the inverse of the canopy surface conductance). The canopy resistance was calculated by inverting the Penman-Monteith equation for canopy evaporation. Data are shown for four contrasting canopies, a well-watered and closed wheat crop (a C3 species), a well-watered and partially closed corn crop (a C4 species), a well-watered broad-leaved forest, and the jack pine forest. The wheat and corn data are from Baldocchi [1994]. The deciduous forest data were obtained during the 1995 growing season. The site and experiment are described by Baldocchi and Vogel [1996].

Why were the equilibrium evaporation ratios of the dry jack pine forest so low? Jarvis and McNaughton [1986] show that the coupling of λE to available energy decreases as the canopy's surface resistance (R_c) increases, and its aerodynamic resistance decreases. Consequently, λE becomes increasingly dependent on and limited by surface resistance under such conditions. Indeed, Plate 1 shows that a reduction in $\lambda E/\lambda E_{eq}$ values was strongly correlated with R_c of the jack pine stand; albeit, some autocorrelation is expected because the dependent and independent variables are functions of λE . More importantly, this figure shows that $\lambda E/\lambda E_{eq}$ values, measured over the jack pine stand, rank markedly below normalized evaporation values for a wide range of vegetation classes, a closed C₃ crop (wheat) and an open C₄ crop (corn) and a temperate broad-leaved forest, by exerting more resistance to water vapor transfer.

Partial stomatal closure, from a variety of sources, can reduce canopy stomatal conductance (the inverse of resistance) and the ratio between λE and λE_{eq} [Jarvis and McNaughton, 1986; Jarvis, 1993; Kelliher et al., 1993] when λE is poorly coupled to available energy. To investigate the possibility of this occurrence, we evaluated canopy stomatal (Figure 12a) and aerodynamic (Figure 12b) conductances throughout the growing season using micrometeorological theory. Canopy stomatal conductance was computed by modifying the Penman-Monteith equation [see Jarvis and McNaughton, 1986] and by

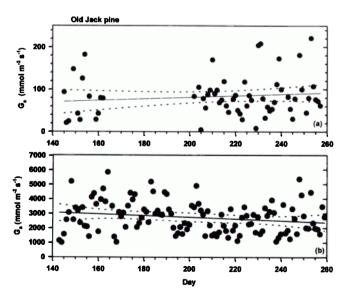


Figure 12. (a) Seasonal variation in the canopy stomatal conductance. This variable was computed using a modified version of the Penman-Monteith equation. The data represent averages of more measurements taken between 0600 and 1900 when inversion of the mathematical relation was stable. (b) Seasonal variation of the canopy aerodynamic conductance. These data were computed as u_*2/u and were averaged over 24 hours.

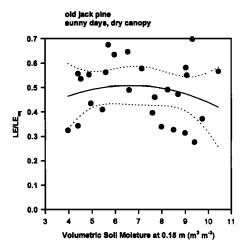


Figure 13. Relation between daily-averaged ratio of latent heat flux and equilibrium evaporation and volumetric soil moisture. The data were obtained during the 1994 growing season at a jack pine stand. The dashed lines represent the 95% confidence intervals of the regression.

applying it to the vegetation component; inputs include measurements of transpiration (E(h) - E(0)) and net radiation absorbed by the canopy $(A = R_n(h) - R_n(0) - S - G)$.

Canopy stomatal conductances were typically less than 150 mmol m⁻² s⁻¹ (Figure 12a). These values are quite low compared to maximum vegetative conductance of conifers. *Kelliher et al.* [1995], for example, report values in the range of 940 \pm 300 mmol m⁻² s⁻¹. However, they are consistent with independent measurements of stomatal conductance made on branches at our site [Saugier et al., 1997].

Daily-averaged values of aerodynamic conductance (u_*^2/u) far exceeded the canopy stomatal conductances (Figure 12b); they ranged between 1000 and 6000 mmol m⁻² s⁻¹ and were centered near 3000 mmol m⁻² s⁻¹. When examined in light of the Jarvis-McNaughton coupling theory, these data reenforce the conclusion that jack pine evaporation is poorly coupled to available energy. Instead, canopy evaporation is more strongly coupled to imposed evaporation, which is proportional to the product of the canopy surface conductance and the atmosphere's humidity deficit. Consequently, ecophysiological factors limiting stomatal conductance will have a disproportionate influence on the evaporation from jack pine.

Why were canopy stomatal conductances of the jack pine stand inherently low? One explanation worth exploring is the impact of the supply of soil moisture on stomatal conductance and evaporation. Physiologically, low soil water potentials cause abscisic acid (ABA) to be released from the roots. When

Table 2. Predawn Water Potential on Jack Pine Needles

Day	Predawn Water Day Potential, MPa		
170	-0.72		
178	-0.51		
187	-0.42		
193	-0.48		
205	-0.59		
214	-0.71		
220	-0.69		

The data were taken by Jason Vogel, BOREAS staff.

ABA is sensed by the stomata, stomatal closure occurs [Gollan et al., 1986]. Consequently, the ratio between λE and available energy, for conifers, has been observed to diminish when the volumetric soil moisture content drops below a threshold [Kelliher et al., 1993]. The cardinal value for the soil moisture threshold, however, is not fixed because soil texture affects the soil moisture retention curve [Baver et al., 1972].

With regard to the jack pine stand, no detectable relation was observed between $\lambda E/\lambda E_{eq}$ and volumetric soil moisture in the top 0.15 m, for sunny days when the canopy was dry (Figure 13). Despite the range of soil moisture experienced in the layer dominated by fine roots, this result was not unexpected, based on the data shown in Figure 11a. There, we saw no discernible relation between $\lambda E/\lambda E_{eq}$ and time during the chronosequence between the 100 mm rainfall event, on day 198, and the subsequent dry period through day 230; during this period, soil moisture in the upper 0.15 m dropped from 10 to 6% (see Figures 3 and 4) as only 14 mm of precipitation fell.

Teskey and Sheriff [1996] argue that a close correlation between soil water content in the upper soil horizon and transpirational water loss indicates that moisture is coming from the soil rather than the groundwater. On the other hand, they state that a poor correlation between these two variables suggests that tree water use is from deeper sources of moisture. On the basis of their premise we hypothesize that the jack pine trees were able to tap deeper sources of soil moisture because soil moisture was more abundant at 1.25 m than in the layer between the surface and the 0.15 m, where fine roots were predominant (Figure 3).

Although $\lambda E/\lambda E_{eq}$ was independent of soil moisture, it is tenuous to conclude that the stomatal opening did not suffer from modest and chronic soil moisture deficits due to the low water holding capacity of the sandy soil. Predawn water potentials ranged between -0.4 and -0.72 M Pa (Table 2), and our porometry data show that stomatal conductance of jack pine needles ranged between 70 and 220 mmol m⁻² s⁻¹ (Table 3). These values are below stomatal conductances for well-watered crops, under ideal conditions (which range between 400 to 500 mmol m⁻² s⁻¹) and below or near maximum stomatal conductances of woody plants (which exceed 200 mmol m⁻² s⁻¹) [Korner, 1994; Kelliher et al., 1995]. We also report in the companion paper [Baldocchi et al., 1997] that the diurnal

Table 3. Stomatal Conductance Measurements (g_s) on Jack Pine Needles

Day-Hour	g_s	Q_p	RH	Tl
2121500	73	621	10.5	29.2
2131100	94	380	41.2	27.5
2131600	192	343	34.8	28.2
2141030	136	755	41.2	26.4
2141200	98	278	23.5	27.2
2161000	213	562	42.3	17.4
2161100	122	1113	23.8	23.7
2161400	78	786	17.4	28.2
2481200	165	1240	43.1	17.6
2481400	132	271	19.3	22.4
2481600	82	370	17.3	22.8
2501000	199	87.5	34.7	12.2

The values are in units of mmol m⁻² s⁻¹ and are on the basis of the hemicylinder surface area. Q_p is quantum flux density, RH is relative humidity, and T_I is leaf temperature. The data are the average of five to six samples, with two needles in each sample. Read 2121500 as day 212, 1500.

pattern of carbon dioxide exchange is characteristic of plants exposed to modest water deficits (with reference to data presented by *Korner* [1994]).

Another body of literature shows that atmospheric humidity deficits impose partial stomatal closure [e.g., Collatz et al., 1991; Saugier et al., 1997]. Figure 14 shows that lower values of daily-averaged canopy stomatal conductances were correlated with lower vapor pressure deficits. This correlation is consistent with branch scale measurements made at this site by our French colleagues [Saugier et al., 1997] and correspond to data reported in key reviews of the conifer evaporation literature [Jarvis et al., 1976; Kelliher et al., 1993].

Claiming that low evaporation rates are a chronic effect of limited soil moisture or humidity deficits on stomatal conductance only accounts for short-term environmental limitations. We argue that long-term biogeochemical factors can also impact the canopy surface conductance and the ability for the jack pine stand to transpire. First, the jack pine forest experiences cold and cool temperatures most of the year, modest precipitation (<500 mm), and a growing season that is short. Together, these factors, plus the well-drained nature of the sandy soil, cause low rates of decomposition, the availability of nutrients to be limited, and growth to be low [McMurtrie et al., 1992]. Consequently, unproductive sites can only sustain canopies with a low leaf area [Waring and Schlesinger, 1985; Woodward, 1987]. Because canopy stomatal conductance scales with leaf area and photosynthetic capacity [Kelliher et al., 1995] and photosynthetic capacity scales with leaf nutrition, a canopy with a low surface conductance is also established. The chronically low productivity of this forest also imparts a hydraulic impact on transpiration. Sapwood cross-sectional area is positively correlated with leaf area index [Waring and Schlesinger, 1985]. Narrow growth rings restrict the hydraulic conductivity of xylem by forcing the permeability and the cross-sectional area of the sapwood to be low.

We proffer to refute counterarguments that aspen/hazel stands exist in the boreal region are subject to the same biogeochemical pressures described above, yet maintain leaf area indices reaching 5 [Chen, 1996; Black et al., 1996]. The aspen tend to exist in regions where precipitation and potential evap-

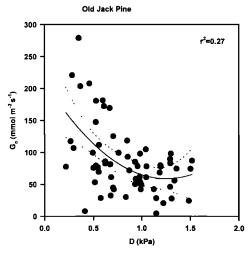


Figure 14. Relationship between daily-averaged canopy stomatal conductance and atmospheric humidity deficit. The dashed lines represent the 95% confidence intervals of the regression.

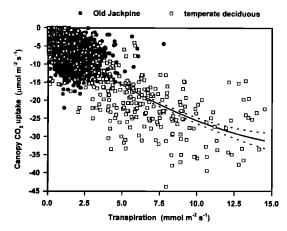


Figure 15. Relation between canopy photosynthesis and transpiration of a sparse jack pine stand and a temperate broad-leaved forest. The temperate forest data were obtained from *Baldocchi and Vogel* [1996]. The dashed lines represent the 95% confidence intervals of the regression.

oration are in balance, while the conifers exist where precipitation far exceeds potential evaporation [Hogg and Hurdle, 1995].

Another illustration of the links between the carbon, water, and nutrient cycles on regulating carbon dioxide and water vapor fluxes is shown by comparing rates of canopy photosynthesis and transpiration rates of the sparse jack pine stand and a more productive temperate broad-leaved forest (Figure 15). These data show that photosynthesis and transpiration of aerodynamically rough forests scale with one another. The leaf area and rates of transpiration and photosynthesis over the jack pine are one third to one half of the rates experienced by the broad-leaved forest.

The decline of λE late in the growing season (Figure 9) may have resulted from a variety of factors. One plausible explanation is the covariance with available energy, which decreases after the summer solstice. However, as shown above, this explanation does not completely account for the diminution of λE , because evaporation rates from pine forests are only weakly coupled to net radiation and available energy [Lindroth, 1985a; Jarvis and McNaughton, 1986]. The occurrence of autumn frost may play a partial role, through its links to photosynthesis and stomatal conductance. We reported in the companion paper [Baldocchi et al., 1997] that photosynthetic capacity of the forest declined after a killing frost. Since stomatal conductance is correlated with photosynthetic capacity [Collatz et al., 1991] and frost reduces photosynthetic capacity [Schulze et al., 1977; Beadle et al., 1985], we hypothesize that frost events may have reduced stomatal conductance and transpiration too.

Comparing H data in Figure 10a with λE data in Figure 8a reveals that the magnitude of sensible heat flux was generally greater than latent heat flux. Bowen ratios $(H/\lambda E)$ exceeding 1 are commonly observed over conifer forests [Jarvis et al., 1976; Lindroth, 1985b; Kelliher et al., 1993; Fitzjarrald and Moore, 1994; Sellers et al., 1995]. Diagnostically, the Penman-Monteith equation indicates that Bowen ratios exceed 1 when the surface conductance is small relative to the aerodynamic conductance [Jarvis et al., 1976; Jarvis, 1993]. Such conditions were easily met over the aerodynamically rough jack pine forest that has low leaf area and a low canopy surface conduc-

tance; in this case, G_a was of the order of magnitude larger than G_s (Figure 12). In contrast, λE often exceeds H over nonstressed and short vegetation [e.g., Jarvis and McNaughton, 1986; Baldocchi, 1994].

Conclusion

... the forest teaches us to appreciate beauty, it softens the harshness of the climate, ...

Anton Chekhov (from *Uncle Vanya*, 1899)

A jack pine stand may not soften the harshness of the boreal climate, but it does have an impact on the weather and climate of the boreal region. The biophysical attributes of the jack pine stand caused a large fraction of available energy to be converted into sensible heat and evaporation rates to be relatively low

Daily totals of incident and net solar radiation were affected by changes in the Sun's declination angle and whether clouds or smoke were present. Consequently, the seasonal trends of solar energy and latent and sensible heat exchange over a boreal jack pine forest were significant, though modest.

Our measurements can give some guidance to modelers of mass and energy exchange processes over the boreal landscape. We found that a jack pine stand does not evaporate at a rate predicted by the Priestley-Taylor equation (1.26 times equilibrium evaporation) when the canopy was dry. Hence climate and hydrological models cannot rely on simple radiation-driven models to estimate its evaporation [see Vogel et al., 1995]. Instead, they must predict the canopy surface conductance correctly if they expect to model evaporation from jack pine correctly. We also observed that fluxes of solar energy and latent and sensible heat at the floor of the forest are a significant portion of energy exchange between the forest and the atmosphere. Reliance on a simple one-dimensional big-leaf models to predict evaporation may be inappropriate in this circumstance, as has been learned from studies over the subarctic woodland [Lafleur, 1992].

Why were evaporation rates from a dry jack pine forest relatively low? We argue that short-term physiological factors and long-term biogeochemical processes interacted to reduce rates of evaporation by lowering the maximum canopy stomatal conductance. On the short term, humidity deficits may have restricted stomatal opening. On the long term, growth is restricted in the boreal region due to climate and low rates of decomposition and nutrient cycling. These factors limit leaf area index, photosynthetic capacity, xylem hydraulic conductance, and canopy stomatal conductance. Hence low rates of evaporation over jack pine are inevitable.

Our observations lead us to contend that constraints imposed on the jack pine by linkages between carbon, water, and nutrients cycles allow jack pine to exist in this region. Although the annual precipitation is low (400 mm), a favorable water balance, is maintained by the ecosystem. Its establishment of a canopy with low leaf area and a low transpiration potential prevents the canopy for evaporating more than 2 mm of water on most days. These factors prevent the canopy from evaporating more than the 400 mm of water that is supplied over the course of a year by precipitation, even if the hydroactive season lasts 180 days. On the basis of these observations we encourage modelers to implement biogeochemical cycling principles to parameterize global and regional-scale climate and ecosystem models, where site-specific parameterization data are scarce.

Finally, the rates of energy exchange over the jack pine stand

share many similarities with vegetation growing on a desert steppe [Doran et al., 1992] or a savannah woodland during the dry period [Culf et al., 1993]. This resemblance of energy partitioning to deserts and savannah woodlands may have an impact on how the climate will respond to potential change in the composition and structure of the boreal forest. Smith et al. [1992] used two climate warming projections and predict that jack pine will decline in the boreal region over a 50- to 75-year period. Since interactions between jack pine and the atmosphere are already like those with scarce vegetation, which may replace it, the effect of a new vegetation type on the climate where jack pines exist may be minimal. We suggest and encourage climate modelers to test this hypothesis.

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