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Energy and CO_2 flux densities above and below a temperate broad-leaved forest and a boreal pine forest

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Summary Fluxes of carbon dioxide, water vapor and energy were measured above and below a temperate broad-leaved forest and a boreal jack pine (*Pinus banksiania* Lamb.) forest by the eddy covariance method. The aim of the work was to examine differences between the biological and physical processes that control the fluxes of mass and energy over these disparate forest stand types.

Carbon and latent heat flux (LE) densities over the temperate broad-leaved forest were about three times larger than those observed over the boreal forest. Available energy was the key variable modulating LE over the temperate broad-leaved forest, whereas LE over the boreal jack pine stand was sensitive to variations in water vapor pressure deficits (VPDs) and available energy. It was also noted that VPDs had different impacts on transpiration rates of the two forest stands. Increasing VPDs forced a negative feedback on jack pine transpiration, whereas transpiration rates of the well-watered broad-leaved forest responded favorably to increasing VPDs.

Carbon dioxide flux densities over the broad-leaved forest stand were more sensitive to changes in absorbed photosynthetic photon flux density than those over the boreal forest. The efficiency of CO_2 uptake over the jack pine stand was reduced, in part, because the low leaf area of the stand caused a sizable fraction of available quanta to be absorbed by nonphotosynthetic organs, such as limbs and trunks. Over both forest stands, variations in photosynthetic photon flux density of photosynthetically active radiation (Q_P) explained only 50 to 60% of the variance of CO_2 exchange rates. Consequently, caution should be exercised when scaling carbon fluxes to regional scales based on unmodified, satellite-derived indices.

The more open nature of the boreal jack pine forest caused water vapor, CO_2 and heat fluxes at the forest floor to be a significant component of whole canopy mass and energy exchange rates. About 20 to 30% of net canopy mass and energy exchange occurred at the forest floor. Much smaller rates of mass and energy exchange occurred under the temperate broad-leaved forest.

Keywords: boreal forests, carbon balance, ecophysiology, evaporation, micrometeorology, temperate forests.

Introduction

The rates at which trace gases are exchanged between the atmosphere and biosphere is central to many contemporary environmental issues. For example, we must know the rates at which carbon dioxide, water vapor, heat, greenhouse gases and pollutants enter and leave the atmosphere if we aim to understand the processes that control the chemistry of our atmosphere and its climate. The presence of forests on the earth's surface profoundly influence how the surface interacts with the overlying atmosphere. For instance, forests are optically darker and aerodynamically rougher than crops, grasslands and deserts (Shuttleworth 1989, Kelliher et al. 1993). Because they are darker, forests absorb more solar radiation than short vegetation. In turn, more solar energy is available to evaporate water, to heat the air and soil, and to drive primary productivity. Because they are aerodynamically rougher than short vegetation, forests have a greater capacity to transfer material between the earth and atmosphere and show tighter coupling between physiological processes and their environmental drivers (Jarvis and McNaughton 1986).

Forests are important sources and sinks of trace gases that participate in the radiative balance and chemistry of the atmosphere. As a major store of mobilizable carbon, they influence planetary carbon balance and climate through the rates at which they take up and lose carbon (Musselman and Fox 1991). They contribute to the oxidizing capacity of the atmosphere by emitting isoprene and monoterpenes. These compounds are oxidized by hydroxyl radicals to form products that react with nitrogen oxides, in the presence of light, to form ozone.

Together, temperate broad-leaved forests and boreal conifer forests comprise a large portion of the terrestrial biosphere and in sum constitute almost 50% of the world's forests. Temperate forests occupy regions with large human populations, and are thus directly affected by human activity (CO_2 fertilization, harvesting, reforestation, and nitrogen deposition). Boreal forests, although remote from major centers of human habitation, are of interest because they are thought to be a major site of global carbon sequestration (Tans et al. 1990).

The rates at which temperate broad-leaved and boreal conifer forests exchange energy and trace gases with the atmosphere are intrinsically different because of differences in both the climate of the zones they inhabit, and the physiology and morphology of the species of which they are composed. In the boreal zone, the decomposition and mineralization of biomass is relatively slow (Bonan and Shugart 1989, McGuire et al. 1992). This climate-imposed nutritional restraint lowers rates of carbon dioxide uptake (McGuire et al. 1992) and causes lower stomatal conductances, lower rates of evaporation, and higher rates of sensible and soil heat exchange (see Schulze et al. 1994, Baldocchi and Harley 1995).

Alterations in sensible heat flux impact the dynamics of the climate system because high rates of sensible heat exchange perturb the rate of growth of the planetary boundary layer (PBL) (McNaughton and Spriggs 1986, Culf 1992). Consequently, high water vapor pressure deficits (VPDs) are maintained near the surface, and reinforce a negative feedback on stomatal opening and transpiration and a positive feedback on sensible heat exchange. Eventually, this linkage of sequences is broken if parcels of upward moving air reach the lifting condensation level (LCL), condense, form clouds and restrict the amount of solar radiation that subsequently reaches the surface.

In this paper we report on measurements of mass and energy exchange over a temperate broad-leaved forest and a boreal pine forest. We draw conclusions about both similarities and differences between the two forests in the way that they exchange mass and energy with the atmosphere.

Material and methods

Temperate broad-leaved forest

Micrometeorological flux measurements were made above and beneath a temperate broad-leaved forest between July 15 (Day 196) and August 6 (Day 218), 1992. The field site was located on the United States Department of Energy reservation near Oak Ridge, TN (35°57′30″ N, 84°17′15″ W, 365 m asl). The annual average temperature is 13.9 °C, and the annual precipitation is 1350 mm. During August, mean maximum and minimum temperatures are 30 and 18 °C, respectively, and mean monthly precipitation is 95 mm.

The surrounding area is vegetated with a mixed stand of oak (*Quercus alba* L., *Q. prinus* L.), maple (*Acer rubrum* L.), hickory (*Carya* spp.) and loblolly pine (*Pinus taeda* L.). The mean canopy height was about 24 m, and its leaf area index was about 4.9 (Hutchison et al. 1986). The stand was about 50 years old having regenerated on farm land abandoned during the second World War. The upwind fetch of the forest extends several kilometers in all directions. Detailed information on leaf area profiles, leaf angle distributions, species composition and forest stocking densities are provided by Hutchison et al. (1986) and Johnson and van Hook (1989).

Physiological variables of the forest, such as leaf photosynthesis and stomatal conductance, were measured during the canopy flux experiment. These data, which are reported in Harley and Baldocchi (1995), indicate that no physiological water stress occurred during the experimental period.

The soil is classified as a typic Paleudult, which encompasses clayey and kaolinitic soils. Soil water was measured gravimetrically each day on 0.15-m deep soil cores. Throughout the duration of the experiment soil water content ranged between 0.27 and 0.53 $m^3\ m^{-3}$.

Although the local terrain is moderately complex, our past work indicates that our micrometeorological measurements are adequate for making flux measurements in the internal boundary layer of a plant canopy (see Verma et al. 1986, Baldocchi and Harley 1995).

Boreal pine forest

We measured flux densities of CO_2, water vapor, sensible heat and solar radiation above and below a jack pine (*Pinus banksiana* Lamb.) forest during the 1993 BOREAS campaign (Sellers et al. 1995). The stand was located near Nipawin, Saskatchewan, Canada (53°92′ N, 104°69′ W). The mean annual temperature is 0.8 °C, and the annual precipitation is 403 mm. Here, we report on data obtained between August 24 (Day 236) and September 8 (Day 251), 1993. The data are representative of late-summer growing conditions (mean maximum and minimum temperatures for August are 23.9 and 10.6 °C, respectively, and mean monthly precipitation for August is 56 mm).

Stand characteristics were determined by us and other BOREAS investigators. The stand age ranged between 75 and 90 years old. Stand density was 1875 stems ha^{-1}, the mean diameter at breast height was 0.117 m, and basal area was 21.9 $m^2\ ha^{-1}$. The height of the canopy ranged between 12 and 15 m, with a mean of 13.5 m.

Chen (1995) evaluated the plant and leaf area indices of the jack pine stand by an indirect and remotely sensed method, obtaining values between 2.78 and 3.34 over the growing season; this variable represented the sum of one-half the surface area of needles and woody biomass. Chen (1995) also reported that leaf area index (excluding branches and trunk) ranged between 1.89 and 2.27, needle to shoot area ratio ranged between 1.28 and 1.51, and the element clumping index was 0.71.

The understory was sparse with isolated groups of alder (*Alnus crispa* (Ait.) Pursh) and ground cover of bearberry (*Arctostaphylos uva-ursi*), bog cranberry (*Vaccinium vitisideae*) and lichens (*Cladina* spp.).

The soil was a coarse-textured sand and was classified as a degraded Eutric Brunisol/Orthic Eutric Brunisol. The terrain was nearly flat, with a mean slope between 2 and 5%. The mature jack pine forest extended for over a kilometer in all directions.

Soil water measurements were unavailable at our site during the 1993 experiment. However, regional precipitation data and soil water measurements taken by colleagues allow us to argue that mass and energy exchanges measured during this experiment are representative of a wet soil. Local precipitation was above normal over the 1993 growing season and during the experiment. At the nearby Prince Albert airport, the August 1993 precipitation was 38.5 cm, compared to a mean of 32 cm. Between April 1 and September 8, 1993, precipitation at Prince Albert and Nipawin meteorological stations was 117 and 141%, respectively, above average. Soil water was measured at a young jack pine stand, a site about 5 km away (David Stannard and Dean Anderson, USGS, Denver, CO, personal communication). Between September 2 and 6 (Days 245 and

249), volumetric soil water in the upper 10 cm ranged between 10 and 18%. These values are near the upper limit for soil water content of this porous sandy soil (Baldocchi et al., unpublished observations).

Instrumentation

During the temperate forest experiment, one set of micrometeorological instruments was placed 36 m above ground. The instrument boom was supported on a 44-m tall scaffold tower and extended 3 m in front of the tower. Another eddy flux system was operated 2 m above the forest floor. Previous work at this site (Baldocchi and Meyers 1991) validates the execution of eddy flux measurements at the forest floor.

During the boreal forest experiment, one eddy flux measurement system was mounted on a scaffold tower provided by the BOREAS project. The sensors were placed on a boom located 20 m above ground and extending 3 m upwind of the tower to minimize flow distortion. The instrument boom was 7 m above tree height, and subsequent measurements have demonstrated that it was positioned in the constant flux layer (Vogel and Baldocchi, unpublished data). The azimuth angle of the boom was altered periodically to place the instrument array into the predominant wind direction. A second eddy flux system was positioned near the canopy floor, 1.8 m above ground.

An identical suite of instruments was used during the temperate and boreal forest experiments. Wind velocity and virtual temperature fluctuations were measured with three-dimensional sonic anemometers (Model SWS-211/3K, Applied Technology, Inc. Boulder, CO.). Carbon dioxide and water vapor fluctuations were measured with an open-path, infrared absorption gas analyzer, developed at NOAA/ATDD (Auble and Meyers 1992). The sensor responded to frequencies up to 15 Hz, had low noise and high sensitivity (30 mg m^{-3} V^{-1}). The water vapor/CO_2 sensor experienced little calibration drift.

Micrometeorological data were digitized, processed and stored using a microcomputer-controlled system and in-house software. Digitization of analog sensor signals was performed at 10 Hz with hardware on the sonic anemometer. Mass and energy flux covariances were computed at 30-min intervals. Previous computations of power spectra and co-spectra indicated that these sampling rates and durations were adequate for measuring fluxes above and below the deciduous and boreal forest canopies (Anderson et al. 1986, Amiro 1990, Baldocchi and Meyers 1991).

Soil heat flux density was measured by averaging the output of three soil heat flux plates (REBS Model HFT-3, Seattle, WA) buried 0.01 m below the surface and randomly placed within a few meters of the flux system. Soil temperatures were measured with two multilevel thermocouple probes. Sensors were spaced at 0.02, 0.04, 0.08, 0.16 and 0.32 m below the surface.

Photosynthetic photon flux density and the net radiation balance were measured above the forest with a quantum sensor (LI-190S, Li-Cor, Inc., Lincoln, NE) and a net radiometer (REBS Model 6), respectively. A more detailed experimental design was implemented at the forest floor because the solar radiation field below a forest canopy is highly variable (Baldocchi and Collineau 1994). To account for this variability, measurements of solar radiation components were made with an instrument package that traversed slowly across a prescribed domain; the measurement domains were 14.5 and 30 m long under the boreal pine and temperate deciduous forests, respectively.

Air temperature and relative humidity were measured with appropriate sensors (Model 207, Campbell Scientific, Logan, UT and Model HMP-35A, Vaisala, Helsinki, Finland). Wind speed and direction were measured with a propeller wind speed/direction monitor (RM Young Model 05701, Traverse City, MI). The temperature, humidity and wind speed sensors were placed alongside the flux instrumentation. Canopy heat storage was calculated by measuring the rate of change in bole temperature at several depths in several tree trunks. Ancillary data were acquired and logged on Campbell CR-21X data loggers. Thirty-minute averages were stored on a computer, to coincide with the flux measurements.

Computations

Vertical flux densities of CO_2 (F_c), latent heat (LE) 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 (see Baldocchi et al. 1988). Positive flux densities represent transfer away from the surface (a gain by the atmosphere) 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 with a digital recursive filter, using a 400 s time constant. Empirical and theoretical calculations suggest that this choice of a filter time constant is adequate for flux density calculations.

It is prudent to employ three-dimensional sonic anemometers when measuring turbulent fluxes over and within forest canopies. Over a forest it is nearly impossible to align a vertical velocity sensor normal to the mean wind streamlines; sensor orientation problems typically arise because of sloping terrain and the practice of extending a long boom upwind from a tower. We circumvented this problem by making numerical coordinate rotations of the three orthogonal wind axes to align the vertical velocity measurement normal to the mean wind streamlines (see Baldocchi et al. 1988). We also applied numerical coordinate rotations to the wind velocities measured near the forest floor. Carbon dioxide flux densities were corrected for the impact of water and humidity fluctuations on the measurement of CO_2 density fluctuations.

Closure of the surface energy balance—the partitioning of net radiation into H, LE and soil heat transfer (S), and canopy heat storage (G)—is one measure of data quality. Past studies at the temperate forest site (Verma et al. 1986, Baldocchi and Harley 1995) verify that the local terrain does not compromise the quality of measurements, as energy balance closure is typically attained. Table 1 documents that we were able to close the local one-dimensional energy balance satisfactorily (within the 95% confidence level) above and below the temperate deciduous forest and above the boreal forest. There was a significant bias between the energy balance components at

Table 1. Statistics on closure of the surface energy balance for a boreal jack pine (JP) forest and a temperate deciduous (TD) forest. The net radiation balance (x) is regressed on the sum of its energy components (y), LE + H + S + G + P.

Location	Slope	Intercept	r^2	n	Mean ± SE
Above the canopy					
JP	1.00	−9.8	0.92	354	R_n: 73.5 ± 6.1 Sum: 63.9 ± 6.44
TD	1.00	3.5	0.92	638	R_n: 160 ± 8.7 Sum: 164 ± 9.11
At the forest floor					
JP	1.12	5.98	0.85	520	R_n: 10.6 ± 1.8 Sum: 17.8 ± 2.2
TD	0.84	1.70	0.63	675	R_n: 11.6 ± 0.67 Sum: 11.5 ± 0.71

the floor of the boreal forest stand, but it was small (only 7 W m^{-2}) and should not prevent use of the data to examine processes.

Results and discussion

Radiation balance

The temperate broad-leaved forest and the boreal jack pine forest differed greatly in canopy architecture in a way that strongly influenced canopy radiation interception. Figure 1 shows that between 20 to 30% of incoming photosynthetic photon flux (Q_P) reached the floor of the jack pine stand at midday, whereas only 5% of incoming Q_P was transmitted to the floor of the temperate forest. Penetration of about one-third of incident solar radiation is common in boreal conifer forests growing on dry sites (Perttu et al. 1980), whereas temperate broad-leaved forests typically intercept between 90 and 95% of incoming solar radiation (Baldocchi and Collineau 1994).

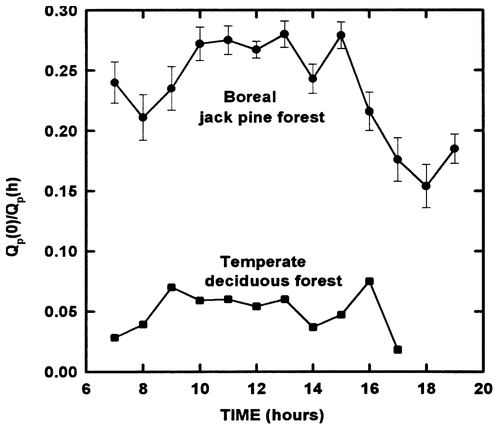

Figure 1. Mean diurnal pattern of intercepted photosynthetically active radiation over a temperate broad-leaved forest and a boreal jack pine stand.

A feature of Figure 1 are the dips in Q_P transmission during the morning and afternoon. When the sun angle is low, photons have a higher probability of striking tree boles, and thus are attenuated more effectively.

Despite the differences in intercepted Q_P, the amount of incident solar radiation converted to net radiation is comparable for the two forest types. Linear regressions of net radiation (R_n) on incoming global radiation (R_g) yield the following results: $R_n = -27.4 + 0.893\,R_g$ and $-23.7 + 0.866\,R_g$ for the jack pine and the broad-leaved forests, respectively.

The regression coefficients fall within the range of values summarized by Jarvis et al. (1976) for various conifer forests and by Shuttleworth et al. (1984) for a tropical forest. The similarity of the data suggests that the efficiency of conversion of solar radiation to net radiation is similar in a wide range of forest types.

Energy balance flux densities

Net radiation is partitioned into various energy streams. Here, we focus on the two most prominent streams, latent and sensible heat transfer. Diurnal variations of net radiation (R_n), latent heat (LE) and sensible heat (H) flux densities are shown in Figure 2 for both the temperate and boreal forest stands. The data represent ideal summertime conditions (the skies were

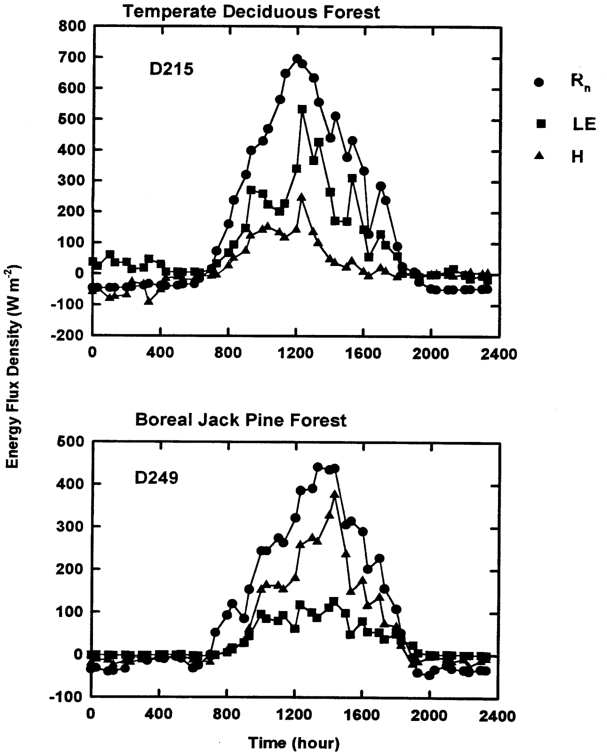

Figure 2. Diurnal variations of net radiation (R_n), and latent (LE) and sensible heat (H) flux densities over a temperate broad-leaved forest and a boreal jack pine stand. The daily sums of net radiation over the temperate broad-leaved forest and boreal jack pine stand were 13.99 and 8.90 MJ m^{-2}, respectively.

relatively clear and peak air temperatures were optimal at about 15 °C in Canada and 25 °C at Oak Ridge, TN). A striking difference occurred in the partitioning of net radiation into LE and *H.* Peak rates of LE over the broad-leaved forest approached and exceeded 400 W m^{-2}, whereas evaporative flux densities over the jack pine stand did not exceed 125 W m^{-2} when the foliage was dry. Over the temperate forest stand, most available solar energy was consumed as LE (Figure 2), whereas over the boreal forest stand most R_n was consumed as *H* (Figure 2). To examine this point further, we plotted LE against available energy ($A = R_n - G - S$) (Figure 3). Regression analysis shows that there was a huge difference between how well LE was coupled to *A* over the two forest stands. Evaporation rates over the temperate forest were closely coupled to *A*, whereas LE over the boreal jack pine forest was weakly coupled to *A.* About 77% of *A* was consumed as LE over the temperate broad-leaved forest, whereas only 36% of *A* drove LE over the boreal jack pine stand. The close relationship between LE and *A*, observed over a dry temperate forest, agrees with our earlier findings (Verma et al. 1986, Baldocchi and Harley 1995). The small magnitude of LE observed over the boreal forest is consistent with measurements by Perttu et al. (1980).

Neither forest stand evaporated at rates predicted by the Priestley-Taylor equation, defined as 1.26 × equilibrium evaporation (LE_{eq}) (see Jarvis and McNaughton 1986). The latent heat flux density of the temperate forest stand was about $0.95 \times LE_{eq}$, whereas LE of the jack pine stand was about $0.60 \times LE_{eq}$. This deviation from rates predicted by the Priestley-Taylor equation is consistent with results reported by Shuttleworth and Calder (1979) for spruce and Scots pine.

The low rates of LE of jack pine relative to *A* reflect, in part, the limited water holding capacity of the sandy soil and its impact on stomatal conductance, even when the soil is wet. A survey of the literature by Kelliher et al. (1993) indicates that LE/*A* is severely limited when volumetric soil water content drops below a threshold value. For the case of *Pinus sylvestris,* LE/*A* decreased from 0.4 to 0.2 as volumetric soil water content decreased from 0.15 to 0.1 m^3 m^{-3}. At our jack pine stand the volumetric water content of the soil never exceeded 18% (Baldocchi et al., unpublished observations), even after a 100 mm rain event. Drawing on the survey of Kelliher et al. (1993), we conclude that pervasively low soil water contents severely limit evaporation rates of the conifer stand.

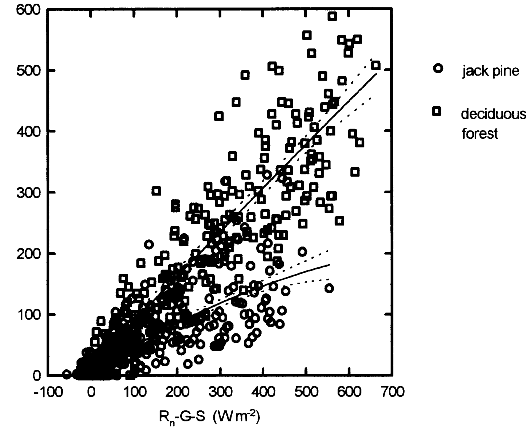

Figure 3. The relation between latent heat flux density (LE) and available energy for a temperate broad-leaved forest and a boreal jack pine stand. A second-order regression was fitted through the data. The dashed lines denote the standard error of the regression estimates.

There were periods when LE over the jack pine stand followed the regression for the broad-leaved forest stand (Figure 3). These data are associated with periods when the foliage and soil were wet. Enhanced rates of evaporation over a wet forest is consistent with earlier measurements over *P. sylvestris* (Shuttleworth and Calder 1979, Lindroth 1985*a*) and *Picea sitchensis* (Bong.) Carr. (Jarvis et al. 1976, Shuttleworth and Calder 1979).

Over the relatively dry jack pine site we consistently observed Bowen ratios ($\beta = H/LE$) approaching and exceeding 3. These results are at variance with the assumption of the climate modeling community that Bowen ratios over the boreal forest stands are low (e.g., Dickinson 1990). The original justification for assuming a low Bowen ratio stems from the proliferation of bogs, fens, lakes and swamps about the boreal landscape. Examination of the literature, however, shows that our high Bowen ratios over a conifer stand are not unique (Lindroth 1985*a*, Amiro and Wuschke 1987, Lafleur 1992, Fitzjarrald and Moore 1994, Fan et al. 1995).

Controls on the partitioning of available energy into sensible and latent heat exchange are explained by climate and by the differential exertion of various resistors as water vapor molecules travel from the canopy to the atmosphere (Jarvis et al. 1976, Lindroth 1985*b*, Jarvis and McNaughton 1986, Kelliher et al. 1993). Theoretically, the Bowen ratio can be defined as:

$$\beta = \frac{1 + R_s/R_{av} - R_i/R_{av}}{s/\gamma + R_i/R_{av}}, \tag{1}$$

where *s* is the derivative of the saturation vapor pressure curve, with respect to temperature, γ is the psychrometric constant, R_s and R_{av} are the surface and aerodynamic resistances for water vapor transfer, respectively, and R_i is a climatological resistance; it is defined as: $\rho C_p VPD/(\gamma A)$ (ρ is air density and C_p is the specific heat of dry air).

The aerodynamic roughness of the jack pine stand exceeds that of the broad-leaved forest. The canopy drag coefficient, which is defined as the ratio between friction velocity and wind speed (u_*/u), equals about 0.2 and 0.13 for the conifer and broad-leaved forest, respectively. On the days under examination, aerodynamic resistances were of the order of 20 and 5 s m^{-1} for the temperate (Day 215, 1992) and boreal (Day 249, 1993) forests, respectively. The relative humidity of the air at the boreal site was less than at the temperate site. However, when air temperature differences are considered, greater VPDs occurred over the temperate stand; VPDs were about 2000 and 600 Pa for the temperate forest and the boreal stand, respectively.

Evaluating the canopy surface resistance is a more complex task, because this variable is a function of both leaf area and the resistances exerted by stomata, the soil surface and the interstitial canopy air layers (Lindroth 1985*b*, Kelliher et al. 1994). Differences in nutrient availability affect canopy surface resistance not only through effects on leaf area index, but also through effects on photosynthetic capacity and, hence, maximum stomatal conductance (Kelliher et al. 1992, 1994, Schulze et al. 1994). A typical value for R_s of the broad-leaved forest is about 100 s m^{-1} (Verma et al. 1986). By taking account of these factors, it can be expected that the R_s of a jack pine forest will be about twice that of a broad-leaved forest, which is consistent with an analysis by Lindroth (1985*b*) for a similar *P. sylvestris* stand and with published leaf conductance data for *P. banksiana* (Admundson et al. 1986). Taking the numerical values in Table 2 to be representative of the broad-leaved and jack pine stands, Bowen ratios were calculated by Equation 1.

The Bowen ratios thus estimated were less than one for a temperate broad-leaved forest and much greater than one for a boreal conifer forest, which is consistent with field observations. Hence, we argue that climate, aerodynamic roughness, canopy physiology and photosynthetic capacity act in concert to cause the Bowen ratios of the two canopies to differ in a prescribed and expected manner. This conclusion is supported by the work of Jarvis et al. (1976), Lindroth (1985*b*), Verma et al. (1986), Kelliher et al. (1992), Lafleur (1992), and others.

Figure 4 shows that fluxes of R_n, LE and H at the forest floor in the temperate broad-leaved forest were about half those observed in the boreal forest, from which it follows, first, that energy fluxes below a boreal conifer forest are large and, second, such fluxes constitute a significant portion of the canopy's energy flux density. For example, mean midday LE flux densities at the floor of the boreal forest were about 50 W m^{-2}. This value is about half the LE measured above the canopy (Figure 5). Relatively large latent heat flux densities at the floor of the boreal forest stemmed from frequent precipitation events; rainfall occurred four times between Days 241 and 249. During the 1994 study, lower rates of LE were observed because of extended periods of dry weather (Baldocchi et al., unpublished observations).

The magnitude of these forest floor evaporation measurements agree with lysimeter measurements taken under a Swedish *P. sylvestris* stand (Perttu et al. 1980), a forest quite similar to the jack pine stand under investigation. Both studies reinforce the concept that fluxes of mass and energy are significant under a boreal conifer forest.

Peak soil evaporation rates were much smaller under the deciduous forest. They approached 20 W m^{-2} and were less than 5% of peak canopy evaporation rates. Rates of LE below the broad-leaved forest are small because the time scale of intermittent turbulent gusts is shorter than the time scale for equilibrium evaporation. Hence, LE at the forest floor is poorly coupled to available energy (Baldocchi and Meyers 1991). Consequently, understory evaporation rates are capped by the potential rate calculated as the product of the soil conductance to vapor transfer and the VPD. A similar conclusion was drawn by Black and Kelliher (1989) and Kelliher et al. (1990, 1992) for the understory evaporation of various pine stands.

Table 2. Values of R_s, R_{av}, and R_i used in the calculation of Bowen ratios (β) by means of Equation 1.

	Broad-leaved forest	Jack pine stand
R_s/R_{av}	5	40
R_i/R_{av}	3.75	5
β	0.47	6

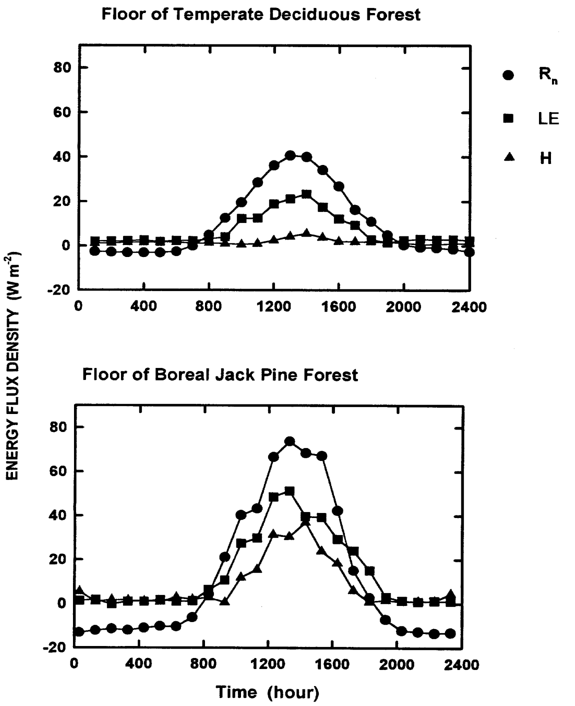

Figure 4. The mean diurnal patterns of net radiation (R_n), latent heat (LE) and sensible heat (H) flux densities measured near the floor of a temperate broad-leaved forest and a boreal jack pine stand. These data were derived from measurements made over the course of the respective experiments.

According to the Omega coupling theory of Jarvis and McNaughton (1986), transpiration from the aerodynamically smoother, broad-leaved forest should be more closely coupled to available energy, whereas transpiration from the jack pine stand should be modulated significantly by VPD. We evaluated transpiration rates (T) of the two forest stands directly, by taking the difference between canopy evaporation and forest floor evaporation rates. Transpiration was more closely coupled to available energy in the broad-leaved forest than in the conifer forest (Figure 6), as indicated by the slopes of the regression lines which were 0.66 and 0.23 for the broad-leaved forest and the jack pine stand, respectively (Table 3). A greater proportion of the variation in broad-leaved forest transpiration was explained by variations in A. The coefficients of determination (r^2) for the relationship between T and A in the broad-leaved forest and the jack pine stand were 0.75 and 0.56,

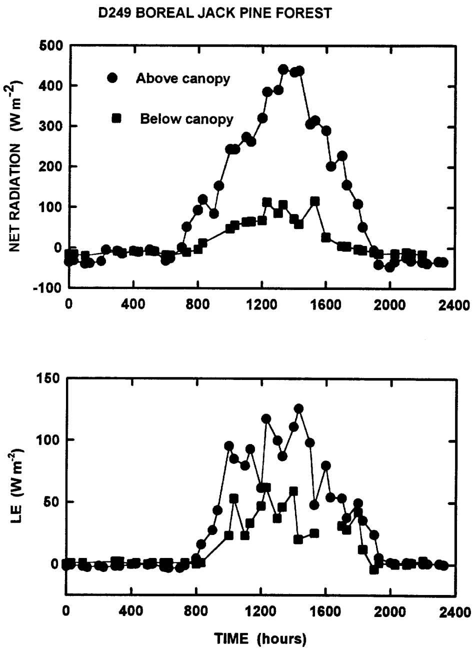

Figure 5. Diurnal trends of net radiation and latent heat (LE) flux densities, measured above and below the boreal jack pine stand on Day 249, 1993.

respectively. The impact of VPD on *T* differed between the forests. Increasing VPD resulted in increased *T* over the temperate forest, but decreased *T* over the boreal pine forest. Statistically, the slope of the *T* versus *A* relationship increased from 0.56 to 0.645, over the temperate forest, when the data were separated for low and high VPD conditions (VPD < 4 g m^{-3} and VPD ≥ 4 g m^{-3}). For the boreal pine forest, the slope of the *T* versus *A* relationship decreased from 0.263 to 0.186 as VPD increased.

The increase in *T* with increasing VPD that occurred in the broad-leaved forest reflects the relative insensitivity of stomata of many broad-leaved species to VPD. Moreover, broad-leaved trees have thicker leaf diffusive boundary layers than conifers, so that VPD values measured over the canopy are much greater than those experienced by the leaves (see Grantz and Meinzer 1990, Meinzer et al. 1993, Kelliher et al. 1993). Over the jack pine stand, increasing VPD exerts a negative feedback on transpiration, presumably because of stomatal closure.

Numerous studies and surveys (e.g., Tan and Black 1976, Lindroth 1985*b,* Sanford and Jarvis 1986, Kelliher et al. 1993, Korner 1994) report stomatal closure in conifers exposed to elevated VPDs. The responses of stomata of broad-leaved trees to water vapor deficit vary. In some cases, stomatal closure occurs as VPD at the leaf surface increases (Meinzer et al. 1993, Harley and Baldocchi 1995), but other data show a weak link between stomatal conductance and VPD in broad-leaved species (e.g., *Q. alba,* Hinckley et al. 1978).

Because *H* fluxes over the two forests differed, their links with the overlying atmosphere will have differed too (see Jacob and deBruin 1992). Growth rates of the convective boundary layer and the development of clouds are directly linked to sensible heat flux density (McNaughton and Spriggs 1986, Culf 1992). To demonstrate this point, we applied our measurements to a formula that predicts the rate of growth of the convective boundary layer:

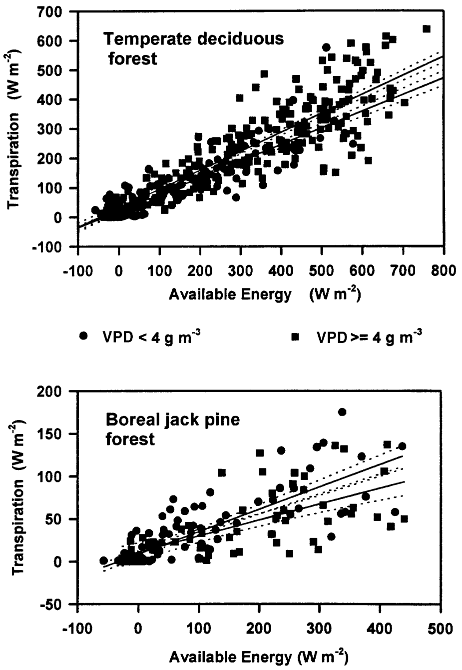

Figure 6. The relationship between canopy transpiration and available energy for two vapor pressure deficit classes. Data are presented for measurements made over the temperate broad-leaved forest and the boreal jack pine stand. A linear regression is fitted through the data. The dash lines denote the standard error of the regression estimates.

$$\frac{dZ_i}{dt} = \frac{H_v}{\rho C_p Z_i \gamma}, \qquad (2)$$

where Z_i is the height of the convective boundary layer, H_v is

Table 3. Regression statistics of transpiration (*T*) versus available energy (*A*). The regression model is: $T = B_0 + B_1A$.

	Broad-leaved forest	Jack pine stand
All Data		
B_0	13.5	10.1
B_1	0.66	0.23
r^2	0.75	0.56
VPD < 4 g m^{-3}		
B_0	20.58	8.78
B_1	0.56	0.263
r^2	0.81	0.69
VPD ≥ 4 g m^{-3}		
B_0	29.9	11.3
B_1	0.645	0.186
r^2	0.82	0.46

the virtual heat flux density, ρ is the density, C_p is the specific heat of air at constant pressure, and γ is the strength of the inversion at the top of the boundary layer. Figure 7 shows how the idealized growth rates of the convective boundary layer differ over boreal and temperate forests. The convective boundary layer approaches 3000 m over the boreal forest and about 1500 m over the temperate forest. These computed values are consistent with observations over these distinct regions (McNaughton and Spriggs 1986, Barr and Betts, unpublished observations, NOAA CD-ROM on radiosonde data of North America).

Differences in the depth of the convective boundary layer have a distinct role in determining differences between the forest types in the water content and chemistry of the overlying atmosphere. For example, it is much harder to humidify or pollute the convective boundary layer over a boreal forest because it occupies a deeper volume. Links between surface fluxes and the convective boundary layer are important and need to be appreciated by forest physiologists because they reinforce high VPDs, which act to close stomata and reduce transpiration (see Jacob and deBruin 1992).

The peak flux densities of soil heat transfer were of the order of 30 W m^{-2}. Canopy heat storage was nil over the course of a 24-h day, but during 30-min periods, there were canopy heat flux densities up to 100 W m^{-2}.

Transfer of CO_2

Relatively few studies exist on CO_2 exchange of temperate broad-leaved and boreal conifer forests (Verma et al. 1986, Wofsy et al. 1993, Fan et al. 1995). Yet, it is important to examine CO_2 and water vapor exchange in concert because carbon and water exchange processes are linked—stomatal conductance is a slave of photosynthesis (Collatz et al. 1991). Figure 8 compares the diurnal patterns of CO_2 flux density over the temperate deciduous and boreal jack pine stands. During the night, CO_2 was lost from both forest canopies as a result of leaf, bole, root and microbial respiration. Nighttime respiration rates were often erratic over the temperate broad-leaved forest, oscillating in a sinusoidal manner between zero and 15 µmol m^{-2} s^{-1}. Nighttime respiration rates of the jack pine stand, on the other hand, were smaller (of the order of 1 to 2 µmol m^{-2} s^{-1}) and were more consistent.

The stability of the nocturnal boundary and the intermittency of nighttime turbulent transfer explains some variation in CO_2 flux over the temperate broad-leaved and boreal jack pine forests. During quiescent periods, CO_2 builds up in the stagnant layer below the eddy flux sensors (Wofsy et al. 1993). With periodic breakdowns of the nocturnal boundary layer (Nappo 1991), CO_2 is periodically vented past the eddy sensor. Wofsy et al. (1993) advocate measurement of the CO_2 storage term. We did not make detailed measurements of this term during the 1992 and 1993 studies, but we measured it during our 1994 study, and the results suggest that errors associated with CO_2 storage in the air layer under the measurement system were small during daytime periods, as long as turbulent mixing was sufficient. However, the bias error could be significant at night (of the order 1 and 2 µmol m^{-2} s^{-1}). For example, when storage of CO_2 is added to the eddy fluxes measured over the jack pine stand, the typical net ecosystem exchange rate during the night was of the order of 5 µmol m^{-2} s^{-1} (Baldocchi et al., unpublished observations).

Maximum rates of CO_2 uptake occurred near midday over the temperate forest, and during midmorning over the jack pine stand. It is noteworthy that F_c rates over the jack pine stand diminished as the day progressed, even though the amount of solar radiation was adequate to maintain higher rates of carbon uptake (see Figure 2).

Consistent with the findings on LE, greater magnitudes of

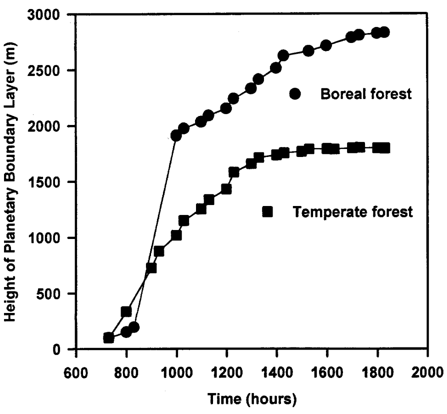

Figure 7. Theoretical growth of the planetary boundary layer over the temperate broad-leaved forest and boreal jack pine stand.

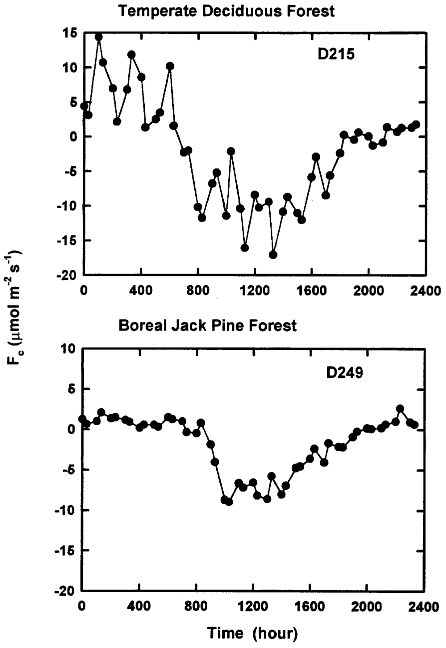

Figure 8. Typical diurnal patterns of CO_2 flux densities measured over a temperate broad-leaved forest and a boreal jack pine stand. The total sums of net carbon exchange were 2.13 and 1.88 g C m^{-2} day^{-1} for the broad-leaved and jack pine forests, respectively.

F_c were observed over the temperate forest stand. This point is reinforced with data presented in Figure 9, a plot between F_c and incident Q_P. At a reference Q_P value of 1500 μmol m^{-2} s^{-1}, the mean value of F_c over the jack pine stand approached –12 μmol m^{-2} s^{-1}, whereas the mean value of F_c over the broad-leaved forest was about –28 μmol m^{-2} s^{-1}.

The CO_2 fluxes observed during the 1993 BOREAS study were higher than those obtained during our 1994 study (Baldocchi et al., unpublished observations). Maximum air temperatures during the 1993 study were 15 to 20 °C, which is the optimum range for photosynthesis of jack pine needles (Manuel Lerdau and Jim Collatz, personal communication). Higher temperatures were observed during the 1994 study and these warmer temperatures seem to have reduced photosynthesis and augmented respiration in jack pine.

Differences between the rates at which CO_2 was evolved from the floor of the two forest stands were small despite substantial differences in soil temperature (Figure 10). Peak CO_2 efflux rates over the temperate and boreal forest soils approached 4 and 3 μmol m^{-2} s^{-1}, respectively. It is noteworthy that forest floor respiration rates constituted a larger proportion of net ecosystem CO_2 exchange of the jack pine stand than the temperate broad-leaved forest, despite the potential for *Cladina* photosynthesis to offset soil respiration. These data indicate that the jack pine forest had, in proportion to aboveground biomass, larger soil respiratory maintenance costs than the broad-leaved forest.

Process studies at the jack pine site indicated that photosynthesis and respiration of the lichen, *Cladina*, over the soil was nil when the lichen was dry (personal communication, Anne Ruimy, University of Paris, Orsay). But lichen photosynthesis was significant when it was wet. Ruimy (personal communication) measured CO_2 uptake rates of 2 μmol m^{-2} s^{-1} after a rain event.

Figure 11 shows that, compared to the conifer stand, the broad-leaved forest absorbed more Q_P, had higher rates of canopy photosynthesis and a higher quantum yield. The slopes of the regression were –0.0148 and –0.0118 mol mol^{-1} for the broad-leaved and conifer stands, respectively, with coefficients of determination (r^2) between 0.5 and 0.6 in both cases. Some scatter in Figure 11 can be attributed to: (1) perennial woody plants having a larger respiratory requirement than annual herbs (Sprugel et al. 1995); (2) respiration rates being highly correlated with temperature (Amthor 1994); and (3) temperature lagging diurnal changes in quantum flux density.

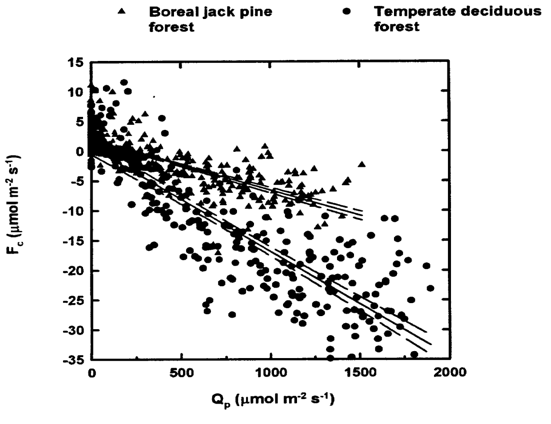

Figure 9. The relationship between canopy CO_2 flux density (F_c) and incident photosynthetic photon flux density (Q_P) of a temperate broad-leaved forest and a boreal conifer stand.

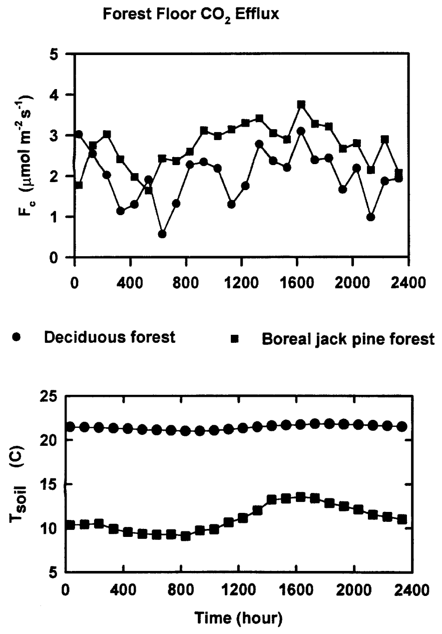

Figure 10. Mean diurnal patterns of CO_2 flux densities and soil temperature measured near the floor of a temperate broad-leaved forest and a boreal jack pine stand.

Canopy CO_2 exchange rates of a temperate broad-leaved forest are insensitive to variations in VPDs (Verma et al. 1986). However, Figure 12 shows that canopy photosynthesis of the jack pine stand diminished with greater VPDs, which accounts, in part, for the gradual diminution of F_c that occurred during the afternoon (Figure 8).

The observed differences between CO_2 uptake rates over the boreal and temperate forest are consistent with noted differences in carbon and nitrogen content and rates of mineralization of the temperate and boreal vegetation (Bonan and Shugart 1989, McGuire et al. 1992). For example, McGuire et al. (1992) demonstrate that the the decrease in soil temperature and soil water availability as one travels north progressively increases the nitrogen limitation of primary productivity. Consequently, McGuire et al. (1992) show that leaves of temperate forest trees contain 45% more nitrogen than leaves of boreal forest species, which enables them, theoretically, to attain a 38% higher photosynthetic capacity (see Field and Mooney 1986). Tight coupling between CO_2 and water vapor fluxes and the role of limited soil water availability on LE (e.g., Kelliher et al. 1993) further constrain the amount of carbon that can be assimilated by the boreal jack pine stand.

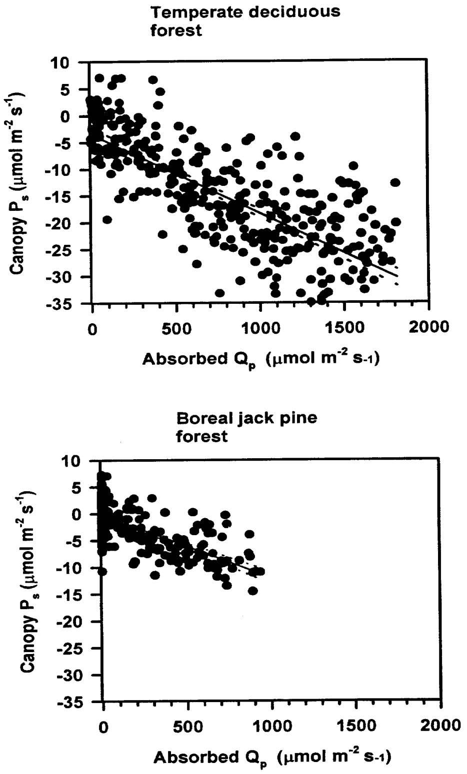

Figure 11. The dependency of canopy photosynthesis (P_S) on the absorbed photosynthetic photon flux density (Q_P) for a temperate broad-leaved forest and a boreal jack pine stand. A linear regression was fitted through the data. The dashed lines denote the standard error of the regression estimates.

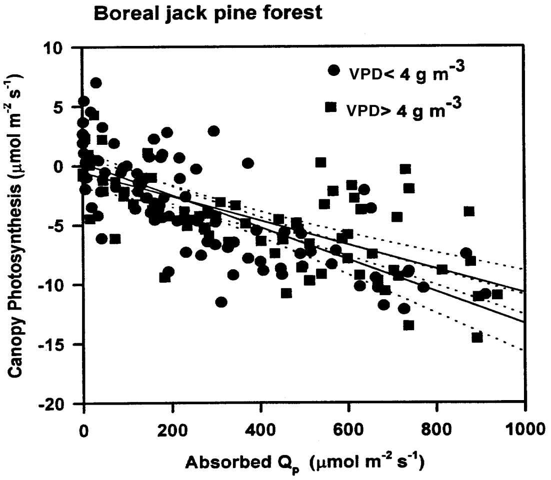

Figure 12. The relationship between canopy photosynthesis and the absorbed photosynthetic photon flux density (Q_P) for two vapor pressure deficit classes.

Conclusions

Carbon and latent heat flux densities of a broad-leaved forest were about three times those observed over a boreal forest. The two forest types also differed in their responses to environmental forcings. Latent heat fluxes over the temperate broad-leaved forest responded mostly to variations in available energy, whereas LE rates of the boreal jack pine forest were sensitive to covariations in available energy and VPDs. Maximum rates of LE by jack pine were limited by the low water holding capacity of the sandy soil.

Carbon dioxide flux densities of both forests were correlated with absorbed quantum flux density. However, variations in photosynthetic photon flux density explained only about 50 to 60% of the variance in CO_2 exchange rates. Because of the openness of the boreal forest stand, water vapor, CO_2 and heat fluxes at the canopy floor were a significant component (20 to 30%) of whole canopy mass and energy exchange rates.

The boreal jack pine forest has about one-third the leaf area of the broad-leaved forest, the difference stemming largely from latitudinal and climate-induced differences in nitrogen availability and productivity (McGuire et al. 1992). The lower leaf area explains in part the lower water vapor and carbon dioxide fluxes associated with the jack pine stand, because both the diffusive source–sink strengths for trace gas exchange and the absorption of solar energy, which drives evaporation and photosynthesis, scale with leaf area index.

Climate-induced nutrient limitation may have a marked feedback on the climate system for three reasons. First, canopy surface conductance is a function of leaf area index and stomatal conductance. Second, stomatal conductance scales with photosynthetic capacity (Collatz et al. 1990). Third, photosynthetic capacity scales with leaf nitrogen content (Field and Mooney 1986). Because the availability of nutrients is reduced in the boreal region, lower rates of carbon uptake cause lower stomatal conductances, lower rates of evaporation, and higher rates of sensible and soil heat exchange (see Schulze et al. 1994, Baldocchi and Harley 1995). Alterations in sensible heat flux impact the climate system because high rates of sensible heat exchange perturb the rate of growth of the planetary boundary layer. Model calculations and preliminary observations from the BOREAS project indicate that the height of the PBL in the boreal region approaches 3000 m, whereas common heights of the PBL in the temperate zone are about 1500 m. Deeper boundary layers in the boreal region are harder to humidify. Consequently, higher VPDs are maintained near the surface, and reinforce a negative feedback on stomatal opening and transpiration and a positive feedback on sensible heat exchange.

From the light and VPD response data, we conclude that it can be misleading to extrapolate surface flux measurements of forest CO_2 exchange to a landscape or regional basis solely in accordance with remotely sensed and radiation-dependent vegetation indices. Effects of temperature, VPD and surface wetness may have to be considered when performing regional gas exchange scaling.

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