Global Change Biology (2000) **6** (Suppl. 1), 69–83

Climate and vegetation controls on boreal zone energy exchange

DENNIS BALDOCCHI,* FRANCIS M. KELLIHER,† T. A. BLACK,‡ and PAUL JARVIS§

**Department of Environmental Science, Policy and Management, 151, Hilgard Hall, University of California, Berkeley, CA 94720, USA, †Manaaki Whenua-Landcare Research, PO Box 69, Lincoln, New Zealand, ‡Faculty of Agricultural Sciences, University of British Columbia, 139–2357 Main Mall, Vancouver, BC, Canada V6T 1Z4 , §Institute of Ecology and Resource Management, Schools of Forestry and Ecological Science, University of Edinburgh, Darwin Building, King's Buildings, Mayfield Rd, Edinburgh EH9 3JU, UK*

Abstract

The boreal forest, one of the world's larger biomes, is distinct from other biomes because it experiences a short growing season and extremely cold winter temperatures. Despite its size and impact on the earth's climate system, measurements of mass and energy exchange have been rare until the past five years. This paper overviews results of recent and comprehensive field studies conducted in Canada, Siberia and Scandinavia on energy exchanges between boreal forests and the atmosphere.

How the boreal biosphere and atmosphere interact to affect the interception of solar energy and how solar energy is used to evaporate water and heat the air and soil is examined in detail. Specifically, we analyse the magnitudes, temporal and spatial patterns and controls of solar energy, moisture and sensible heat fluxes across the land–atmosphere interface. We interpret and synthesize field data with the aid of a soil–vegetation–atmosphere transfer model, which considers the coupling of the energy and carbon fluxes and nutrient status.

Low precipitation and low temperatures limit growth of many boreal forests. These factors restrict photosynthetic capacity and lower root hydraulic conductivity and stomatal conductance of the inhabitant forests. In such circumstances, these factors interact to form a canopy that has a low leaf area index and exerts a significant resistance to evaporation. Conifer forests, growing on upland soils, for example, evaporate at rates between 25 and 75% of equilibrium evaporation and lose less than 2.5 mm day^{-1} of water. The open nature of many boreal conifer forest stands causes a disproportionate amount of energy exchange to occur at the soil surface. The climatic and physiological factors that yield relatively low rates of evaporation over conifer stands also cause high rates of sensible heat exchange and the diurnal development of deep planetary boundary layers. In contrast, evaporation from broad-leaved aspen stands and fen/wetlands approach equilibrium evaporation rates and lose up to 6 mm day^{-1}.

Keywords: aspen, biosphere–atmosphere interactions, boreal forest, energy balance, evaporation, hydrology, jack pine, larch, micrometeorology, spruce

Introduction

The biosphere and atmosphere are a coupled system. Temperature, insolation and precipitation affect plant architecture and the physiological functioning of the vegetation (Woodward 1987; Waring & Running 1998). In return, the presence or type of vegetation affects the climate system through its influence on albedo and surface roughness, soil moisture and plant resistance to evaporation (Dickinson 1992; Thomas & Roundtree 1992; Betts *et al.* 1996). Together, the biosphere and atmosphere interact to determine the height of the planetary boundary layer and the entrainment of dry air from the

Correspondence: Dennis Baldocchi, e-mail: baldocchi@nature.berkeley.edu

troposphere (McNaughton & Spriggs 1989; Barr & Betts 1997). This interaction re-enforces both positive and negative feedback loops on evaporation (Raupach 1998). The entrainment of dry air promotes evaporation by increasing the vapour pressure deficit, but it can inhibit transpiration by forcing stomata to close.

The boreal forest is of particular interest and importance to climate and global change scientists due to its great size (12.0–14.7 million km^2) and distinct climate. The boreal forest is the biome occupying the circumpolar region between 50 and 70 degrees north, a land area dominated by the Canadian and Siberian landmasses. It is the world's second largest forested biome, surpassed only by the tropical evergreen forest (Landsberg & Gower 1997).

The boreal region experiences extremely cold winters, warm summers and a short growing season (Table 1). Air temperature can range between –70 and 30 °C (a span of up to 100 °C) over the course of a year, and the growing season is less than 120 days in many locales. Additionally, precipitation input to many of the regions of the boreal zone is low; annual precipitation in Central Canada and Siberia, for example, ranges between 200 and 600 mm per year (Table 1).

Low winter temperatures and low amounts of precipitation limit the northern extreme of this biome. Climatically, the northern extent of the boreal forest correlates with the position of the summer-time arctic front or the 10–13 °C July isotherm (Oechel & Lawrence 1985; Bonan & Shugart 1989; Pielke & Vidale 1995). In central Canada, fire and negative water balance delineate the southern demarcation between the boreal forest and the temperate grassland.

The species diversity of the boreal zone is low due to the relatively recent presence of glaciers and the slow rate at which species can migrate and evolve (McClone 1996). The boreal landscape consists of deciduous broad-leaved forests, deciduous and evergreen conifer forests, fens and lakes. The dominant genera include poplar (*Populus*), birch (*Betula*), willow (*Salix*), alder (*Alnus*), spruce (*Picea*), larch *(Larix)*, pine *(Pinus)*, fir *(Abies) and* hemlock *(Tsuga)* (Oechel & Lawrence 1985; Bonan & Shugart 1989; Landsberg & Gower 1997). The general composition of boreal forests includes pure stands of deciduous broad-leaved and conifer forests, mixed conifer/deciduous forests, pine/lichen and spruce/moss stands. Many forest stands in the boreal zone contain distinct over- and understories. The aspen/hazel stands in Canada (Black *et al.* 1996) is one example. Using a broader categorizing scheme, four major vegetation zones exist in the boreal zone. These are the forest–tundra ecotone, the open boreal woodland, the main boreal forest and the boreal–mixed forest ecotone (Oechel & Lawrence 1985).

With regard to edaphic factors, poorly drained sites are organic (Histosols) while upland sites tend to be coarse-grained and sandy (Entisols) (Landsberg & Gower 1997). Also found in the boreal zone are spodosol soils, which have a thick acidic and organic surface horizon and a nutrient poor mineral horizon.

The biosphere–atmosphere energy exchanges of boreal forests in Siberia (east of the Ural Mountains), Canada and Scandinavia differ from one another for various reasons, despite their similar latitudes and forest functional types. The climate of the eastern Siberian boreal forest, for example, is colder and drier than the climate of the Canadian and Scandinavian boreal forests (Table 1). Furthermore, the Siberian boreal forest grows over a much larger area of continuous and discontinuous permafrost than its Canadian and Scandinavian counterparts (Bonan & Shugart 1989; Shivedenko & Nillson 1994). The presence or absence of permafrost, as well as differences in precipitation and soil texture and water holding capacity affects the availability of soil moisture.

Winter temperatures in Canadian boreal forest are tempered, in comparison to Siberia. Moderating factors include Canada's closer proximity to the Pacific Ocean (on the west), the protrusion of Hudson Bay into the central portion of that landmass and the heat transferred by the Gulf Stream on the eastern side. Maritime factors also temper the boreal climate of Scandinavia.

Table 1 Climate data for representative cities in the boreal zone (Muller 1982)

Site	Lat. (deg)	Long. (deg)	Precipitation (mm y^{-1})	Ave. temp. (°C)	Sunshine (h)
Siberia					
Tunguska	61.6 N	92.2 E	527	−3.8	1646
Yakutsk	62.1 N	129.8 E	213	−10.2	2294
Canada					
Saskatoon	52.1N	106.7 W	352	2.0	2381
Goose Bay	53.3N	60.4 W	610	2.7	n/a
Scandinavia					
Stockholm	59.3 N	18.1 E	555	6.6	1973

A difference in species composition and age structure of the Canadian and Siberian forests is another potential source of variation on mass and energy exchange rates. The majority of the Siberian taiga (54%) is dominated by *Larix*, a deciduous conifer (Shvidenko & Nilsson 1994; Schulze *et al*. 1995). Evergreen conifers (*Picea mariana, P. glauca and Pinus banksiana*) dominate the Canadian boreal landscape (Sellers *et al*. 1995). With regard to age, approximately one half of Canadian forests are between 40- and 100-y-old, according to a 1970 age distribution survey (Kurz & Apps 1993) because disturbance was abated at the beginning of the 20th century. The Siberian forest, by contrast, experienced heavy logging after World War 2 until the 1960s (Shvidenko & Nilsson 1994). One analysis estimates that half of the 654 Mha of forested land in Siberia is considered young and maturing (Kolchugina & Vinson 1995).

Needle-leaf conifer forests have a greater ability to exchange mass and energy with the atmosphere than other vegetation types, e.g. grasslands, crops, shrubs and broad-leaved trees. Conifer forests, for example, are optically darker than broad-leaved forests and short vegetation (Jarvis *et al*. 1976; Sellers *et al*. 1995; Betts & Ball 1997; Kaminsky & Dubayah. 1997). 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 broad-leaved forests, shrubs and herbaceous vegetation. This characteristic enhances their ability to transfer mass and energy with the atmosphere by generating turbulence and increasing the aerodynamic conductance (Jarvis *et al*. 1976; Jarvis & McNaughton 1986). The conical architecture of conifers allows them to shed snow and intercept sunlight quite efficiently (Stenberg *et al*. 1995). The evergreen habit of conifers allows them to photosynthesize and transpire on fine spring days when co-occurring deciduous plants are still dormant (Black *et al*. 1996; Jarvis *et al*. 1997).

Historically, work on boreal forest energy exchange has been done by the Scandinavians (Perttu *et al*. 1980) and Canadians (Amiro & Wuschke 1987). Recent field campaigns, associated with the Northern Wetlands Study (NOWES) (den Hartog *et al*. 1994; Fitzjarrald & Moore 1994), BOREAS (Baldocchi *et al*. 1997; Blanken *et al*. 1997; Jarvis *et al*. 1997; McCaughey *et al*. 1997; Sellers *et al*. 1997), NOPEX (Grelle *et al*. 1997) and Siberian experiments (Kelliher *et al*. 1997, 1998), are extending the available information base and are shedding new light on the interactions between boreal forests and the climate system. In this article, we review energy balance data from recent energy-balance studies across the boreal zone. The overarching question that we address in our analysis is how do the climatic and vegetation attributes of the boreal zone influence air-surface mass and energy exchange rates? We attempt to answer this question with the use of a canopy micrometerological model that is coupled to carbon, water and energy flows.

Measurement and analysis methods

Flux densities of water vapour and sensible heat between the canopy and the atmosphere were measured by most literature citations with the eddy covariance technique (e.g. Black *et al*. 1996; Baldocchi *et al*. 1997; Jarvis *et al*. 1997). This method is a direct measure of mass and energy exchange rates. The eddy covariance measurements, reported in this paper, employed a 3D sonic anemometer, to measure vertical and horizontal wind and temperature fluctuations, and an infrared spectrometer to measure water vapour and carbon dioxide fluctuations.

The canveg model was used to calculate flux densities of energy, water vapour and sensible heat between the canopy and the atmosphere (Baldocchi & Meyers 1998). The model consists of coupled micrometeorological and physiological modules. The micrometeorological model computes leaf and soil energy exchange, turbulent diffusion, scalar concentration profiles and radiative transfer through the canopy. Environmental variables, computed with the micrometeorological module, in turn, drive the physiological models that compute leaf photosynthesis, stomatal conductance, transpiration, leaf, bole and soil/root respiration. The model is driven by a minimal number of external variables that were measured above the forest. Environmental inputs include incident photosynthetic photon flux density (Q_p), air temperature, wind speed, relative humidity and CO_2 concentration. Plant structural variables include leaf area index, leaf angle orientation, a leaf clumping factor and canopy height.

Energy exchange of boreal forest stands

The surface energy budget provides a framework for investigating energy exchange over the boreal landscape. The net radiation (Q^*) absorbed by a forest, fen or lake is equal to the sum of incoming short-wave ($K\downarrow$) and long-wave radiation ($L\downarrow$) minus reflected shortwave, reflected long-wave and emitted long-wave radiation. In turn, this energy is partitioned into latent (Q_E), sensible (Q_H), soil conductive (Q_G) and canopy storage (S) heat flux densities:

$$Q^* = (1-\alpha)K\downarrow + \varepsilon L\downarrow - \varepsilon\sigma T_s^4 = Q_E + Q_H + Q_G + S \qquad (1)$$

The ratio between reflected and incoming solar radiation is called albedo (α). The outgoing longwave radiation is a function of the surface temperature (T_s), its emissivity (ε) and the Stefan–Boltzmann constant (σ).

We used the Penman–Monteith equation to interpret evaporation measurements, as this equation identifies the key abiotic and biotic factors that control canopy evaporation (Jarvis & McNaughton 1986).

$$Q_E = \frac{s(Q^* - Q_G - S) + \rho_a C_p D G_a}{s + \gamma(1 + G_a/G_s)} \tag{2}$$

The most prominent variables are available energy ($Q_a = Q^*\text{-}Q_G\text{-}S$), surface (plant plus soil) (G_s) and aerodynamic (G_a) conductances and the atmosphere's humidity deficit (D). The term s is the slope of the relation between saturation vapour pressure and temperature (is the psychrometric constant, ρ_a is air density, and C_p is the specific heat of air.

Equilibrium evaporation is one limit of Penman–Monteith evaporation theory:

$$Q_{E,eq} = \frac{s}{(s + \gamma)}(Q^* - Q_G - S) \tag{3}$$

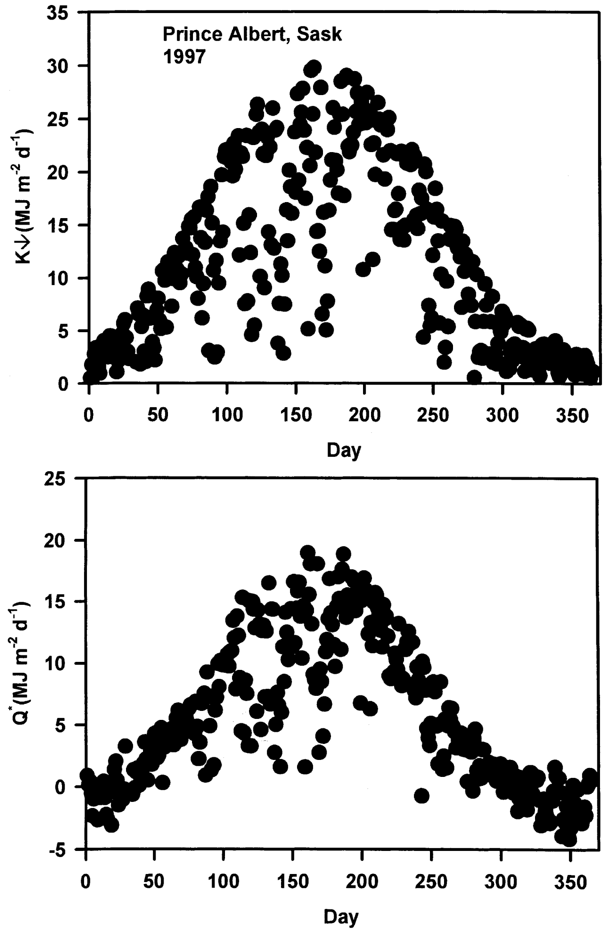

Fig. 1 The yearly course in solar radiation, summed over a day, for Prince Albert, Saskatchewan. The data are for 1997 and are from the BOREAS database.

Equation (3) can be derived via three routes of logic. Mathematically, it describes the case when the aerodynamic conductance goes to zero, as when wind is calm. Physically, the equilibrium evaporation rate is attained by a freely evaporating wet surface (G_s equals infinity) after it saturates the atmosphere with humidity (D equals zero). (Jarvis & McNaughton 1986). Theoretically, one can arrive at the present definition of equilibrium evaporation by examining the time dependence of evaporation into a closed volume and its feedback with the humidity deficit of the volume (McNaughton & Spriggs 1989).

Solar radiation

In northerly latitudes of the boreal zone days are short (less than 8 h) during the winter and long (greater than 18 h) during the summer. Low solar elevation angles, relative to the tropical and temperate zones, cause mid-day values of K↓ to peak below 1000 W m^{-2} during the summer growing season. Much of the boreal zone is south of the Arctic Circle (66°N) so some sunlight is available to most boreal forest stands during the winter. At Prince Albert, Saskatchewan (53°N), for example, the potential magnitude of mid-day solar radiation is on the order of 300 W m^{-2}.

Earth–sun geometry and the absence or presence of clouds modulates the seasonal course of daily summed solar radiation. The upper boundary of data, shown in Fig. 1, represents clear day data, over the course of the year, at Prince Albert, Saskatchewan. Daily sums of K↓ range between 5 and 38 MJ m^{-2} day^{-1}, with lowest and highest values corresponding with the winter and summer solstices, respectively. On an annual basis, incident short-wave radiation in the boreal zone ranges between 3300 and 5025 MJ m^{-2} y^{-1} (Budyko 1974). For comparison, the data in Fig. 1 sum to 5139 MJ m^{-2} y^{-1}, a value which corresponds well with Budyko's data for the southern edge of the boreal zone.

Albedo

The albedo of boreal conifer forests is relatively conservative over the course of a year (Table 2). On average, daily albedo of conifer boreal forests is below 0.083 during the summer. The reported albedo values, for boreal conifers, are similar to values measured over temperate conifer forests (Jarvis *et al.* 1976).

During the winter, albedo is higher than its summertime value, but it is low compared to highly reflective snow-covered surfaces (Betts & Barr 1997); the albedo of snow-covered grass can vary between 0.6 and 0.9 (Sharatt 1998). The low sun angles and the dark evergreen foliage of the trees act to absorb most incoming sunlight. Higher albedos are associated with cloudy conditions (Betts & Ball 1997), as the source of light during cloudy periods comes from all sectors of the sky.

The recent measurements of boreal forest albedo have had a positive impact on weather and climate models. Prior to these recent albedo measurements, meteorological forecasting models assumed that winter albedo over snow-covered forests ranged between 0.6 and 0.8 (Thomas & Roundtree 1992; Betts & Ball 1997). This inaccurate parameterization has resulted in severe underestimation (~15 °C) of forecasted air temperatures (Betts *et al*. 1998).

Net radiation, latent, sensible and soil heat flux densities

We expect fluxes of energy and water vapour over boreal forest stands to vary spatially and temporally due to variations in solar energy, soil and air temperature, soil moisture, soil texture, photosynthetic capacity and leaf area. The ways by which these factors affect latent, sensible and soil heat flux densities are examined below.

The ratio between incoming solar radiation and net radiation (The $Q^*/K\downarrow$) ranges between 0.70 and 0.80 during the growing season and when the forest is snow-less (Table 3). Values of $Q^*/K\downarrow$ for boreal forest stands resemble data reported for many temperate conifer stands (Jarvis *et al*. 1976). On an annual basis, a different scaling relationship between Q^* and $K\downarrow$ emerges. Budyko (1974) reports that the net radiation balance over land in the boreal latitude band ranges between 800 and 1700 MJ m^{-2} y^{-1}. This value is about 24–33% of annual sum of incident short-wave radiation. A smaller fraction of net radiation is available on an annual basis, than on an hourly basis, because the annual sum of Q^* incorporates losses of long-wave radiation during night. In contrast to the data from forests, about 55% of incoming solar radiation converts to net radiation over a wetland (Lafleur *et al*. 1997). A higher albedo and a colder and wetter surface contribute to this lower efficiency over wetlands.

Table 2 Albedo over the boreal landscape. Sources include: Betts & Ball (1997); Sharatt (1998); Harding & Pomeroy (1996); Perttu *et al*. (1980); McCaughey *et al*. (1997); Lafleur *et al*. (1997)

Daily Ave.	Summer	Snow-covered
Grass	0.2	0.75
Aspen	0.15	–
Conifer sites	0.083	0.13
Aspen-leafless	0.11	0.21
Jackpine	0.09–0.136	0.12–0.15
Spruce	0.076–0.088	0.11
Wetland	0.155–0.18	0.70
Lake	–	0.20–0.88

Diurnal patterns. Mean diurnal variations in Q^*, Q_E, and Q_H are shown in Fig. 2 for three contrasting forests, a broad-leaved aspen stand, a black spruce stand growing on poorly drained peat and a jack pine stand growing on well-drained sand. The data were acquired between days 201 and 220 of 1994 during the second intensive field campaign of the BOREAS experiment in Canada. These mean diurnal patterns of energy flux densities were constructed by binning data hour by hour, then averaging them for the duration of the period. Over the aspen stand, the diurnal trends of Q_E and Q_H follow a parabolic rise and fall of Q^*. Mid-day values of Q_E approach 220 W m^{-2}, on average, and exceed sensible heat flux density by a factor of two. The diurnal patterns of latent and sensible heat fluxes, measured over the black spruce and jack pine stands, contrast with the behaviour observed over the aspen stand. Over both conifer stands the temporal changes in Q_E and Q_H are less sensitive to changes in Q^*. For instance, Q_E remains relatively constant between 10 and 18 h. Of greater note is the observation that mid-day values of Q_H exceed those for Q_E. This behaviour is contrary to typical measurements over broad-leaf forests and crops, where Q_E tends to be larger (Baldocchi & Vogel 1996).

The lowest rates of mid-day evaporation were observed over the jack pine stand throughout the summer. Mid-day Q_E values for jack pine stand during the July August period were 130 W m^{-2}, as compared with 200 W m^{-2} over the black spruce stand. These observations are a common feature of evaporation associated with conifers growing on dry sites in the boreal region. For example, low hourly rates of evaporation (below 150 W m^{-2}) were also observed over Siberian larch (Kelliher *et al*. 1997) and Scots pine stands (Grelle 1997; Kelliher *et al*. 1998), too. The evaporation rates of boreal forests growing on sandy upland sites (such as jack pine, Scots pine and larch) tend to be limited by humidity and soil moisture deficits (Kimball *et al*. 1997; Kelliher *et al*. 1998). In contrast, black spruce, which grow on wet organic soils, have ample soil moisture for transpiration (Kimball *et al*. 1997). Instead, their transpiration rates are inhibited in the spring by cold and water-logged soils and during the summer by elevated atmospheric humidity deficits (Jarvis *et al*. 1997).

Spatial variations. A survey of field measurements reveals a ranking of summertime evaporation rates across the classes of forest stands in the boreal zone (Table 4). The

Table 3 Ratios between net radiation and incoming solar radiation

Surface	$Q^*/K\downarrow$	Intercept	Source
Boreal forest	0.842	-29 (W m^{-2})	Kaminsky & Dubayah (1997)
Wetland	0.55	–	Lafleur *et al.* (1997)
Boreal forest	0.73	-1.96 (MJ m^{-2} d^{-1})	Sharratt (1998)

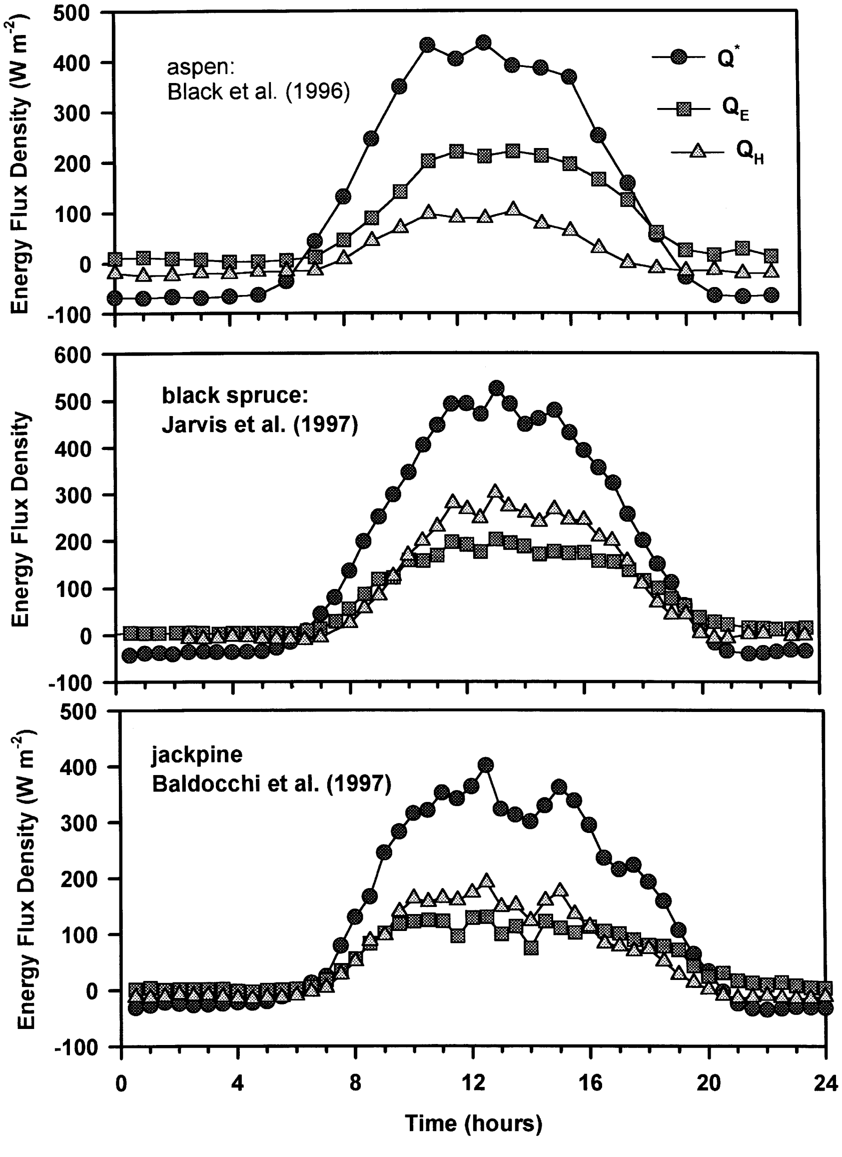

Fig. 2 Diurnal patterns of net radiation and latent and sensible heat flux densities for three contrasting forest stands growing in the Canadian boreal forest. The stands are aspen (Black *et al.* 1996; Blanken *et al.* 1997), black spruce (Jarvis *et al.* 1997) and jack pine (Baldocchi *et al.* 1997).

evaporation fraction, as computed over the course of days and normalized by net radiation (Q_E/Q^*) or available energy [$Q_E/Q_a = Q_E/(Q^*-Q_G)$], is largest over boreal wetland (Lafleur *et al.* 1997). On a daily basis, wetlands evaporate at rates ranging between two-thirds and three-quarters of available radiation. An aspen stand attains summertime evaporation rates near 60% of net radiation (Blanken *et al.* 1997). Evaporation from conifer stands, by contrast, is most conservative. Conifer stands evaporate at rates ranging between one-third and one-half of net radiation (Baldocchi *et al.* 1997; Grelle 1997; Jarvis *et al.* 1997; Kelliher *et al.* 1997, 1998; McCaughey *et al.* 1997).

Conifer stands in the boreal zone possess either low leaf area indices (less than three) or highly clumped shoots on narrow tree crowns (Chen 1996). This low canopy density allows a disproportionate amount of solar radiation to reach the stand floor or its understorey. For instance, up to 25–35% of incoming sunlight reaches the canopy floor of a jack pine (Baldocchi *et al.* 1997) and a Scots pine stand (Perttu *et al.* 1980). This paucity of foliage allows an ample amount of radiation to be available to drive sensible and latent heat exchange at the forest floor. Forest floor evaporation accounts for 10–40% of canopy evaporation in jack pine (Baldocchi *et al.* 1997). In Siberia, between 38 and 50% of moisture flux measured over a larch stand comes from the soil (Kelliher *et al.* 1997). On average, about 54% of evaporation comes from the soil of a Siberian Scots pine stand, with values ranging between 33 and 92% (Kelliher *et al.* 1998). Subarctic woodlands are most open. As much as 70% of evaporated water can come from the understorey of a subarctic woodland (Lafleur 1992). In contrast, the greater (near five-fold) leaf area of an aspen/hazel stand near Prince Albert, Saskatchewan intercepts over 70% of incident radiation (Chen *et al.* 1997). Consequently, only 5% of canopy evaporation comes from the soil (Black *et al.* 1996; Blanken *et al.* 1997).

Seasonal sums of evaporation and its variation. Published values of annual evaporation from boreal forests are exceedingly rare. Grelle *et al.* (1997) reported that 399 mm of water evaporates from a Swedish Scots pine stand between May and October. Of this total, 243 mm was associated with transpiration, 56 mm comes from the forest floor and 74 mm was associated with the re-evaporation of intercepted precipitation. Over the course of a growing season (May to October), Amiro & Wuschke (1987) reported that a jack pine stand evaporated 240 mm of water. Data from a hydrological water balance model suggests that spruce stands at the southern and northern BOREAS sites evaporated 243 and 212 mm of water, respectively, between 21 May and 21 September. A jack pine stand at the southern extent of the boreal forest evaporated 218 mm (Nijssen *et al.* 1997). In the cited study, 43% of canopy evaporation was derived from transpiration, 12% originated from the evaporation of intercepted precipitation and 45% was from soil evaporation.

The magnitude of these recent measurements of evaporation corresponds reasonably well with the climatic analysis of Budyko (1974), for the 50–70°N latitude band, where evaporation is estimated to range between 300 and 400 mm y^{-1}.

The seasonal pattern of evaporation is affected by seasonal changes in air and soil temperature, insolation, atmospheric humidity deficits, soil moisture and leaf area. Evaporation rates over boreal conifer stands are relatively low in the spring, during clear days with high evaporative demand (Halldin *et al.* 1980; Pattey *et al.* 1997; Baldocchi *et al.* 1997; Grelle 1997; Jarvis *et al.* 1997; Saugier *et al.* 1997). Low evaporation rates occur during spring because cold or frozen soils restrict root uptake of soil moisture (Halldin *et al.* 1980; Teskey *et al.* 1984). The low viscosity of cold or frozen water and the low permeability of cold root cells cause the hydraulic conductivity of roots to be low. This effect reduces leaf turgor and forces the closing of stomata (Teskey *et al.* 1984).

Boreal plants also experience chilling and freezing stresses at the beginning and end of the growing season. Chilling is associated with air temperatures near 0 °C and frost and freezing stresses occur when temperature drops below this threshold. The occurrence of spring and autumn chilling and frost events impacts transpiration through its association with photosynthesis and stomatal conductance. Night frosts during the growing season, for instance, cause a reversible reduction in photosynthetic capacity and stomatal conductance (Schulze *et al.* 1977; Beadle *et al.* 1985; Hallgren *et al.* 1990, 1991), which, in turn, limits transpiration. The reduction in stomatal conductance, however, is not the major factor limiting photosynthesis. Internal CO_2 remains constant or increases, suggesting a decrease in mesophyll conductance or photosynthetic capacity (Hallgren *et al.* 1990).

Between May and August, day-to-day variation in evaporation from coniferous forests resulted from the presence or absence of clouds and changes in atmospheric humidity as fronts passed and re-appeared. Prolonged dry periods restricted canopy evaporation as the soil dried, by forcing stomata to partially close. Peak values of daily evaporation are on the order of 2.5–3.0 mm per day and vary little (Baldocchi *et al.* 1997; Grelle *et al.* 1997; Jarvis *et al.* 1997).

By September, evaporation rates decline with the approach of the autumnal equinox. One plausible explanation for the autumnal decline of Q_E is its covariance with available energy and air temperature, both of which decrease after the summer solstice. But, this explanation does not completely account for the diminution of Q_E, because evaporation rates from pine forests are weakly coupled to available energy and equilibrium evaporation (Lindroth 1985; Jarvis & McNaughton 1986; Table 4). The occurrence of autumnal frost events caused stomatal conductance and transpiration to diminish late in the growing season.

Table 4 Relative measures of energy balance over a variety of boreal forest stands

Northern boreal wetland, fen, sphagnum, tamarack (*Larix laricina*), bog birch (*Betula glandulosa*); Thompson, Manitoba, Lat 55.9°N, 98.4°W; height: < 3 m (Lafleur *et al.* 1997)

	Q_H/Q_A	Q_E/Q_A
Pre-leaf	0.41	0.59
Green	0.31	0.69
Sensescent	0.45	0.55
May–June	0.38	0.62
July–August	0.24	0.76
Sept	0.47	0.53

Aspen/hazel stand (*Populus tremuloides*); lat: 53.63°N, long: 106.2°W; leaf area index: 5.6; Prince Albert National Park, Saskatchewan, Canada 1994 growing season (Blanken *et al.* 1997)

	Pre-leaf	Full-leaf
$Q_E/Q_{E,}$		0.91
Q_E/Q^*	0.10	0.61
Q_H/Q^*	0.73	0.25
Q_G/Q^*	0.09	0.03
Q_S/Q^*	0.08	0.11

Black spruce (*Picea mariana*) forest with lichen and peat; Hudson Bay lowland, Kinosheo Lake, Ontario (Lat. 51°N, 81°W); 29 June to 28 July 1990 (den Hartog *et al.* 1994)

Q_E/Q_A	0.49
Q_H/Q_A	0.51

A mature black spruce stand (*Picea mariana*); Lat: 53.98°N; long 105.11°W (near Candle Lake, Saskatchewan, Canada), age: 112-year-old; LAI projected: 4.5; height: 6 m (Pattey *et al.* 1994; Jarvis *et al.* 1997)

	May–June	July–August	September
Q_E/Q_A	0.344	0.384	0.425
Q_E/Q^*	0.377	0.446	0.369
Q_H/Q_A	0.656	0.616	0.574
Q_H/Q^*	0.576	0.527	0.527
Q_G/Q^*		0.08	

Siberian larch (*Larix gmelinii*), Yakutsk, Russia (lat: 61°N 128°E), 130-year-old stand, leaf area index: 1.9; height: 12 m, 14–23 July 1993 (Kelliher *et al.* 1997)

Q_E/Q_A	0.442
Q_H/Q_A	0.557
Q_G/Q^*	0.06

Scots pine (*Pinus sylvestris*), Zotino, Russia (lat: 61°N; Long. 89°E, leaf area index: 1.5, 215-year-old; height: 16 m, 8–25 July 1996 (Kelliher *et al.* 1998)

Q_E/Q_A	0.476
Q_H/Q_A	0.524

Jack pine (*Pinus banksiana*) in 1994, Nipawin, Saskatchewan, Canada, Lat: 53°N; long: 104°W, height 13 m, leaf area: 2.0. (Baldocchi *et al.* 1997)

	days 144–162	days 163–182
Q_E/Q^*	0.335	0.389
Q_H/Q^*	0.507	0.474
Q_G/Q^*	0.07	0.04

A young jack pine (*Pinus banksiana*) stand, Thompson, Manitoba, Canada, summer 1994; Lat: 55.9°N, 98.29°W, LAI: 1.06; height: 3 m; age 30 years Albedo: 0.136; Par albedo: 0.054 (McCaughey *et al.* 1997)

Q_E/Q_A	0.337
Q_H/Q_A	0.663

Picea mariana, *Picea alba*, Schefferville, Quebec, days 189–215, 1990; Lat: 54.86°N; Long: 66.66°W; (Fitzjarrald & Moore 1994)

Q_E/Q_A	0.35
Q_H/Q_A	0.65

Pinus sylvestris, Jadraas, Sweden, Lat 60°N, long 16°E; canopy ht: 16 m; Tree age: 135 years; Stand density: 350 trees ha^{-1}; Understorey: *Calluna vulgaris, Vaccinium vitisidea* and *Cladonia rangifera*; Leaf area: 3.3, one-sided surface area; August–September 1978 (Lindroth 1985)

Q_E/Q^*	0.59
Q_H/Q^*	0.32
Q_G/Q^*	0.05

A mixed forest stand, *Pinus sylvestris*; *Picea abies*; Understorey: *Vaccinium myrtillus L.*; Norunda, Sweden, Lat 60.5°N, long 17.29°E, Canopy ht: 23 m; Tree age: 100 years; Basal area: 29.3 m^2 ha^{-1}; Leaf area: 4.6, projected; Average diurnal course at 35 m June to September 1996 (Grelle 1997)

Q_E/Q_A	0.38
Q_H/Q_A	0.61

Winter data: Boreal forest, Prince Albert National Park, Lat: 53° 52′N; Long: 106° 8′W; Species: jackpine, *Pinus banksiana*; Ht: 16–22 m; Daily average energy balance: 3,4,19 March (Harding & Pomeroy 1996)

	Snow-free trees	Snow-covered trees
Q_E/Q^*	0.57	3.28
Q_H/Q^*	1.19	−0.53

The annual sum of evaporation from aspen at Prince Albert, Canada was about 403 mm, which was 88% of annual precipitation (Black *et al*. 1996). Annual evaporation is relatively large over the aspen stand although the aspen stand experiences a shorter transpiration period than conifers. The daily sums of evaporation depend strongly on the absence or presence of leaves and can reach 6 mm per day at full leaf (Black *et al*. 1996; Hogg *et al*. 1997; Table 4). In general, leaf development is usually complete one to two weeks before the summer solstice. Leaf senesence and leaf fall occurs by the first two weeks of September (Black *et al*. 1996).

Wintertime energy partitioning by conifers depends on whether or not snow is present on the trees (Harding & Pomeroy 1996). When conifer trees are snow free, the net radiation balance is positive and sensible heat is directed towards the atmosphere. When the trees are covered with snow, substantial evaporation occurs at the expense of sensible heat extracted from the atmosphere. This behaviour causes Q_H to be directed downward (Table 3).

Over an aspen stand, Q_H increases with time after the winter solstice until snowmelt and leaf expansion. Peak values of Q_H reach 120 W m^{-2}, on a 24-h basis (Blanken *et al*. 1997).

Energy fluxes over smooth frozen lakes are very small. Q^* and Q_H tend to be directed downward and Q_E remains near zero during the leafless winter period. (Harding & Pomeroy 1996). Sensible heat is directed downward over frozen boreal lakes because the surface is often cooler than the air. The thermal stratification of the air over a frozen lake is very stable and suppresses turbulent mixing.

Constraints on latent heat exchange: the role of environmental and biological factors. From inspection of (3) one can conclude that cooler zones in the northern portion of the boreal climate have a lower potential to evaporate than locales in the southern zone (see Table 1; Nijssen *et al*. 1997). One explanation for this observations stems from the fact that the factor, $s/(s+\gamma)$, is a strong function of temperature. For example, $s/(s+\gamma)$ is 0.32 at –5 °C and 0.47 at 5 °C, a 47% difference for a 5 °C increase in temperature.

Normalizing measured evaporation by estimated rates of equilibrium evaporation helps diagnose how biotic factors control daily forest evaporation relative to the amount of available energy. Figure 3 shows the empirical relation between Q_E/Q_E and surface resistance (R_s), the inverse of surface conductance, for a spectrum of boreal forest canopies. Values of $Q_E/Q_{E\,eq}$ decrease nonlinearly with increasing surface resistance. This relationship is consistent with the theoretical finding of McNaughton & Spriggs (1989). The lowest $Q_E/Q_{E\,eq}$ values (below 0.5) are associated with dry and low productivity boreal forest systems, such as jack pine, Scots pine and larch. Wetter and more productive forests (e.g. spruce, aspen) achieve $Q_E/Q_{E\,eq}$ values close to one. In general, evaporation rates from all boreal forests are below peak values that are achieved for well-watered, fertilized and closed crops, which are near 1.26 (deBruin 1983; Jarvis & McNaughton 1986; McNaughton & Spriggs 1989; Baldocchi *et al*. 1997).

Surveys of stomatal resistance data (Korner 1994; Dang *et al.* 1997a; Sullivan *et al*. 1997) and the data in Fig. 3 indicate that canopy resistances of boreal conifer stands tend to be inherently large. Elevated canopy resistances for boreal vegetation originate from a variety of sources. Contributing short-term factors include partial stomatal closure due to soil moisture deficits (Kelliher *et al*. 1997) and high vapour pressure deficits (Arneth *et al*. 1996; Kelliher *et al*. 1997; Saugier *et al*. 1997). Long-term factors include low leaf area and low maximal stomatal conductance, which we attribute to biogeochemical constraints. We elaborate on these factors next.

The daily averaged canopy stomatal conductance of boreal forest stands decreases linearly with decreasing soil water content or the days since the last rainfall (Kelliher *et al*. 1997, 1998). Physiologically, low soil water potentials cause abscisic acid (ABA) to be released from the roots. When ABA is sensed by the stomata, stomatal closure occurs (Gollan *et al*. 1986). Dry periods also lead to a reduction in understorey evaporation (Kelliher *et al*. 1998). Because understorey evaporation is a significant fraction of canopy evaporation (Baldocchi *et al*. 1997; Blanken *et al*. 1997), any factor reducing understorey evaporation will also limit evaporation from the total stand.

Several interlinking processes cause long-term biogeochemical factors to impact the canopy's surface conductance and limit the ability of a boreal pine stands to transpire. From a climate perspective, boreal pine forests experience cold and cool temperatures most of the year (annual mean temperatures near and below 0 °C), modest amounts of precipitation (< 500 mm) and a growing season that is short (about 120 days) (e.g. Table 1). Furthermore, many pine stands grow on well-drained, sandy soils. Together, these factors cause low rates of decomposition and limit the cation exchange capacity of the soil, so the availability of nutrients is limited and the potential for growth is low (Chapin 1991, 1993). Consequently, unproductive and dry sites can only sustain canopies with a low leaf area (Woodward 1987; Waring & Running 1998). Because canopy stomatal conductance scales with leaf area and photosynthetic capacity (Kelliher *et al*. 1995; Korner 1994), and photosynthetic capacity scales with leaf nutrition (Field 1991; Dang *et al*. 1997a,b), many boreal canopies have low surface conductances. The chronically low productivity of such forests can also impart a hydraulic impact on

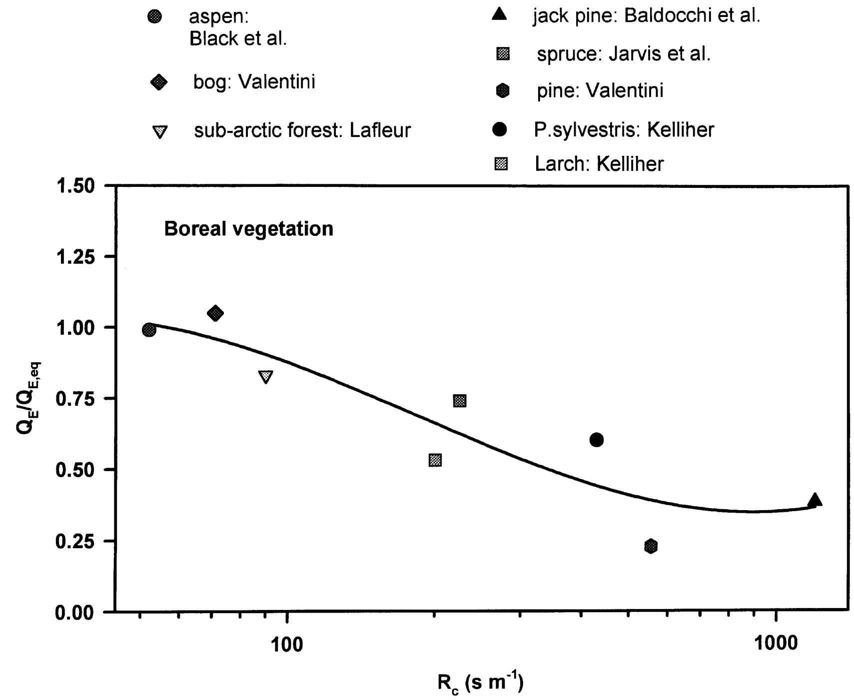

Fig. 3 The relationship between latent heat flux, normalized by the equilibrium rate ($Q_E/Q_{E,}$) vs. canopy surface resistance (R_c).

transpiration. Sapwood cross-sectional area is positively correlated with leaf area index (Waring & Running 1998). Narrow growth rings cause the permeability and the cross-sectional area of the sapwood to be low and restrict the hydraulic conductivity of xylem.

Model calculations, presented in Fig. 4, attempt to distill the coordinated impacts of limited nutrition, leaf area and available soil moisture on $Q_E/Q_{E\,eq}$ for a generic boreal forest. The model used here (CANVEG) considers feedbacks among leaf energy balance, photosynthesis and stomatal conductance (Baldocchi & Meyers 1998). In our calculations we use maximum carboxylation velocity (V_{cmax}) as a measure of leaf nutrition since it is a function of leaf nitrogen (Dang *et al.* 1997a). An additional factor complicating the behaviour of $Q_E/Q_{E\,eq}$, with varying values of the independent variable, V_{cmax} times LAI, is the availability of soil moisture and its impact on stomatal conductance. Field and modelling studies suggest that soil moisture deficit correlates with the value of the Ball–Berry–Collatz (Collatz *et al.* 1991) stomatal conductance factor (k). For instance, k of temperate forest species varies from about 10 to 7 as soil dries from field capacity (Sala & Tenhunen 1996; Baldocchi 1997). Here, we explore the plausible response of $Q_E/Q_{E\,eq}$ to varying levels of soil moisture by changing the Ball–Berry–Collatz stomatal conductance coefficient (k) in such a fashion.

The combination of low leaf area and low maximum carboxylation capacity yields low values of $Q_E/Q_{E\,eq}$ (less than 0.60). In contrast, the combination of high leaf areas and V_{cmax} result in theoretical values of $Q_E/Q_{E\,eq}$ that approach 1.2, a value similar to that of closed and fertilized crops (deBruin 1983; Baldocchi *et al.* 1997). For productive stands, with closed canopies (high V_{cmax} times LAI values), $Q_E/Q_{E\,eq}$ drops by over 20% as k decreases from 10 to 7. Forest stands with low productivity, on the other hand, are less sensitive to water stress, as evidence by a 10–15% drop in $Q_E/Q_{E\,eq}$ with a 30% decrease in k.

Where do various boreal forests fall on the abscissa of Fig. 4? To address this question, we draw on data from Dang *et al.* (1997a,b) and Sullivan *et al.* (1997). Dang *et al.* (1997a,b) observed a ranking of photosynthetic capacity of among boreal trees. The ranking is, progressing from highest to lowest values, aspen, upland black spruce, old black spruce, old jack pine, and young jack pine. At the upper end of the ranking, photosynthetic capacity was 14.5 µmol CO_2 m^{-2} s^{-1}. At the lowest end, it was 3.6 µmol m^{-2} s^{-1} (such low rates of photosynthetic capacity were also reported by Sullivan *et al.* 1997). We also know that leaf area of the conifers ranged between 1 and 3 (Chen 1996) and the leaf area of the aspen/hazel stand was over five (Black *et al.* 1996). If we assume V_{cmax} is about 2.5 times photosynthetic capacity (A_{max}) (Kell Wilson, personal communication), we calculate that values of V_{cmax} times LAI for conifers ranged between 10 and 120. The aspen/hazel stand, on the other hand, would have an index nearer 200. If one compares theoretical values of

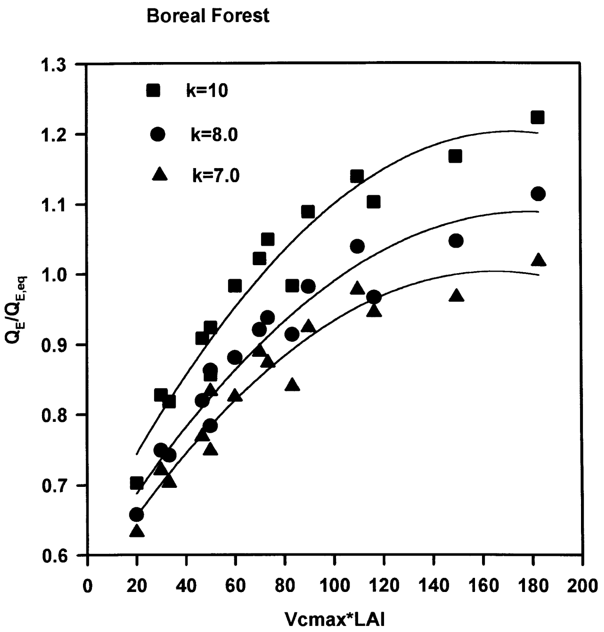

Fig. 4 Model calculations of the relationship between latent heat flux, normalized by the equilibrium rate ($Q_E/Q_{E,}$), and ecological factors pertaining to leaf area index and maximum carboxlyation velocity (V_{cmax}). The later variable is a strong function of leaf nitrogen and is an index of site fertility. The CANVEG model (Baldocchi & Meyers 1998) was used to perform the computations. Meteorological conditions for day 207 of 1994 at Prince Albert, Sask., were used (average air temperature as 19 °C, the daily sum of net radiation was 14.7 MJ m^{-2} and the mean vapour pressure deficit was 0.97 kPa). Sensitivity runs were conducted for cases when leaf area index equalled 2, 3 and 5 and V_{cmax} equalled 15, 25, 35, 45, and 55 µmol m^{-2} s^{-1}. The impact of soil moisture deficits is simulated by varying the value of the Ball–Berry–Collatz stomatal conductance factor, *k*. Well-watered conditions are associated with *k* equal to 10. The data represent averages for conditions when day time periods, when photosynthetically active radiation exceeded 100 µmol m^{-2} s^{-1}.

$Q_E/Q_{E\,eq}$ shown in Fig. 4 with many of the empirical values reported in Fig. 3, one will find reasonable correspondence between theory and observations. In other words, canopies with low leaf areas and low photosythetic capacity have low values of $Q_E/Q_{E\,eq}$ and high canopy resistances.

The results presented above relate only to dry surfaces. Evaporation rates over conifers differ markedly when the surface is wet. In general evaporation rates from wet stands exceed values over dry stands by factors of 50% and greater (Lindroth 1985; Baldocchi *et al.* 1997; Kelliher *et al.* 1997). In extreme conditions, evaporation from wet boreal stands can exceed available energy. Wet evaporation surfaces can become cooler than the air above. When this occurs, sensible heat is extracted from the air mass and promotes evaporation by providing a nonradiative source of energy.

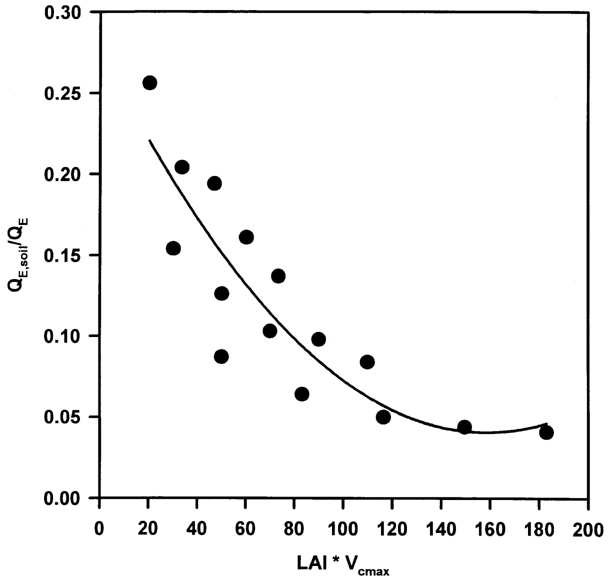

Fig. 5 Model calculations of the ratio between soil and canopy evaporation and ecological factors pertaining to leaf area index and maximum carboxlyation velocity (V_{cmax}).

Returning to soil evaporation, it has been noted already that the open nature of low leaf-area forest stands allows the soil to contribute significantly to canopy evaporation. Model computations were made to examine how the ratio between Q_E over a dry soil surface and the forest stand will vary with changes in leaf area and canopy photosynthetic capacity. As for field data, the theoretical fraction of soil evaporation is very low (about 5%) over forest stands with high leaf areas and high transpiration potential (Fig. 5). By contrast, model calculations indicate that the evaporation contribution from the soil increases nonlinearly with decreasing leaf area and photosynthetic capacity. Theoretical values of $Q_{E\ soil}/Q_E$ approach 25% when the data are averaged over the course of a day, and they reach 40% when these ratios are expressed on an hourly basis.

With regard to factors controlling forest floor evaporation, Kelliher *et al.* (1998), report that evaporation from the forest floor of Scots pine in Siberia is a linear function of available energy. However, the slope of the relationship drops by a factor of three, within three days of after rainfall. Consequently, the daily sum drops, asymptotically, from about 1.6–0.4 mm d^{-1} with increasing number of days after rainfall or with decreasing soil water content. When the soil surface is wet, evaporation rates can exceed available energy (Lindroth 1985; Baldocchi *et al.* 1997).

Ramifications of boreal forest energy balance partitioning. The attainment of relatively large sensible heat flux densities (Q_H), 300 W m^{-2} or greater, is one consequence of the unique albedo and stomatal control of energy partitioning of boreal forests. An outcome of the large values of Q_H is the diurnal growth of a very deep planetary boundary layer (PBL) (McNaughton & Spriggs 1989). Over Canadian boreal forests, the planetary boundary layer grows to a depth of about 1.75 km, on average during the summer (Barr & Betts 1997; Wilzcak *et al*. 1997). On individual days, the depth of the planetary boundary layer can approach 3 km (Wilzcak *et al*. 1997). The planetary boundary layer in Siberia does not grow to the extreme depths observed in Canada (Hollinger *et al*. 1995), despite the occurrence of large rates of sensible heat flux (Kelliher *et al*. 1997). Subsidence due to the existence of the Siberian High Pressure zone seems to limit the daily growth of the planetary boundary layer in that region (Jon Lloyd, pers. comm.).

Deep boundary layers entrain a substantial amount of dry air. And it is the dryness of the air that affects the potential for evaporation and modulates stomata. Over the Canadian boreal forest, near Prince Albert, the bulk entrainment heat flux is about 21% of the surface virtual heat flux (Barr & Betts 1997). A feature of deep planetary boundary layers is their difficulty to humidify. This response can have a negative feedback on stomatal conductance and a positive feedback on sensible heat transfer and PBL growth (McNaughton & Spriggs 1989).

The unique energy partition of boreal forests may have an impact on the position of their northerly extent. Pielke & Vidale (1995) argue that the large rates of Q_H and the deep planetary boundary layers, measured over boreal forests, affect the transport of energy above the PBL, the atmosphere's thickness gradient. It is these factors which determine the positioning of the arctic front. Their finding is contrary to the one drawn by biogeographers, in the past, who concluded that the position of the arctic front set the northern limit of the boreal forest.

New knowledge about the mass and energy exchange of boreal forests has the potential to pay dividends on how we understand the climate and weather of the boreal system by providing information for improving the land surface schemes. For instance, proper partitioning of energy is required to predict the daily cycle of precipitation with accuracy. Current European (ECMWF) and US (NCEP/NCAR) weather forecasting models, however, assume the boreal region is relatively wet and has a low surface resistance to evaporation. A recent analysis shows that these models predict too much evaporation and precipitation for the region since they do not adequately parameterize the stomatal control of evaporation (Betts *et al*. 1998).

Summary

A combination of micrometeorological, biogeochemical and ecological principles have been used to interpret how evaporation from the boreal biome occurs and how it may differ from other functional groups. This approach has the potential to identify a mix of abiotic and biotic mechanisms that control evaporation. It has the potential also to constrain and simplify the parameterization of models that are used to predict evaporation.

The boreal environment is particularly harsh to plant growth and function. Vegetation growing in this region is exposed to very cold winters, a short growing season and a dearth of precipitation. The climate and vegetation of this region interact in such a way to produce short- and long-term forcings on evaporation rates. The short-term forcings are imposed by weather, soil moisture and stomatal physiology which limit the demand and the supply of water vapour to the atmosphere. The long-term forcings are related to the impacts that low precipitation and low temperatures have on growth, photosynthetic capacity and stomatal conductance. These factors interact to form a canopy that has a low leaf area index, and is relatively open. In general, conifer forest stands, growing in upland regions of the boreal zone, evaporate at rates between 25 and 75% of equilibrium evaporation, while evaporation rates from broad-leaved aspen and fen/wetlands approach equilibrium rates. The open nature of many boreal forest stands also causes a disproportionate amount of energy exchange to occur at the soil surface. Two consequences of relatively low rates of evaporation, from upland boreal forests, are high rates of sensible heat exchange and the diurnal development of deep planetary boundary layers.

Acknowledgement

This paper was written in association with a workshop on: Arctic Boreal Processes that Feedback to Climate, conducted at the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #DEB-94–21535), the University of California, Santa Barbara. The senior author acknowledges funding support from the NOAA Office of Global Change, which supported his participation in the BOREAS project, and the NASA, EOS Program, which supported much of the writing under the auspices of his FLUXNET project. Most of this work was conducted while he was employed at the Atmospheric Turbulence and Diffusion Division, NOAA, Oak Ridge, TN. This paper could not have been written without the discussions with and supply of prepublication information from many friends and colleagues. In particular, Drs Peter Lafleur, Achim Grelle, Riccardo Valentini, Werner Eugster and Roger Pielke were especially helpful. We'd also like to thank Dr Eva Falge for providing a thoughtful internal review. Finally, we thank Dr Terry Chapin for his patience and encouragement to write this paper and for spearheading the workshop.

References

Amiro BD, Wuschke EE (1987) Evapotranspiration from a boreal forest drainage basin using an energy balance/eddy covariance technique. *Boundary Layer Meteorology*, **38**, 125–139.

Arneth A, Kelliher FM, Bauer G *et al.* (1996) Environmental regulation of xylem sap flow and total conductance of *Larix gmelinii* trees in eastern Siberia. *Tree Physiology,* **16,** 247–255.

Baldocchi DD (1997) Measuring and modeling carbon dioxide and water vapor exchange over a temperate broad-leaved forest during the 1995 summer drought. *Plant, Cell and Environment,* **20,** 1108–1122.

Baldocchi DD, Vogel CA (1996) A comparative study of water vapor, energy and CO_2 flux densities above and below a temperate broadleaf and a boreal pine forest. *Tree Physiology,* **16,** 5–16.

Baldocchi DD, Meyers TP (1998) On using eco-physiological, micrometeorological and biogeochemical theory to evaluate carbon dioxide, water vapor and gaseous deposition fluxes over vegetation. *Agricultural and Forest Meteorology,* **90,** 1–26.

Baldocchi DD, Vogel CA, Hall B (1997) Seasonal variation of energy and water vapor exchange rates above and below a boreal jack pine forest. *Journal of Geophysical Research*, **102,** 28,939–28,951.

Barr AG, Betts AK (1997) Radiosonde boundary layer budgets above a boreal forest. *Journal of Geophysical Research,* **102,** 29,205–29,213.

Beadle CL, Jarvis PG, Talbot H, Neilson RE (1985) Stomatal conductance and photosynthesis in a mature Scots pine forest. II. dependence on environmental variables of single shoots. *Journal of Applied Ecology*, **22,** 573–586.

Betts AK, Ball JH (1997) Albedo over the boreal forest. *Journal of Geophysical Research,* **102,** 28,901–28,909.

Betts AK, Ball JH, Beljaars CM, Miller MJ, Viterbo PA (1996) The land surface–atmosphere interactions: a review based on observational and global modeling perspectives. *Journal of Geophysical Research,* **101,** 7209–7225.

Betts AK, Viterbo P, Belkaars A, Pan H-L, Goulden M, Wofsy S (1998) Evaluation of land–surface interaction in ECMWF and NCEP/NCAR reanalysis models over grassland (FIFE) and boreal forest (BOREAS). *Journal of Geophysical Research,* **103,** 23,079–23,085.

Black TA, den Hartog G, Neumann H *et al.* (1996) Annual cycles of CO_2 and water vapor fluxes above and within a boreal aspen stand. *Global Change Biology,* **2,** 219–230.

Blanken PD, Black TA, Yang PC *et al.* (1997) Energy balance and canopy conductance of a boreal aspen forest: partitioning overstory and understory components. *Journal of Geophysical Research,* **102,** 28,915–28,928.

Bonan GB, Shugart HH (1989) Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics,* **20,** 1–28.

Budyko MI (1974) *Climate and Life*. Academic Press, New York.

Chapin FS III (1991) Effects of multiple environmental stresses on nutrient availability and use. In: *Response of Plants to Multiple Stresses* (eds Mooney H *et al.*), pp. 67–88. Academic Press, New York.

Chapin FS III (1993) Functional role of growth forms in ecosystems and global processes. In: *Scaling Physiological Processes: Leaf to Globe* (eds Ehleringer J, Field C), pp. 287–312. Academic Press, San Diego, CA.

Chen JM (1996) Optically-based methods for measuring seasonal variation of leaf area index in boreal conifer stands. *Agricultural and Forest Meteorology,* **80,** 135–164.

Chen JM, Blanken PD, Black TA, Guilbeault M, Chen S (1997) Radiation regime and canopy architecture in a boreal aspen forest. *Agricultural and Forest Meteorology,* **86,** 107–126.

Collatz GJ, Ball JT, Grivet C, Berry JA (1991) Regulation of stomatal conductance and transpiration: a physiological model of canopy processes. *Agricultural and Forest Meteorology*, **54,** 107–136.

Dang QLHA, Margolis MSy, Coyea MR, Collatz GJ (1997a) Regulation of branch level gas exchange of boreal trees: roles of shoot potential and vapor pressure differences. *Tree Physiology,* **17,** 521–536.

Dang QLHA, Margolis MSy, Coyea MR, Collatz GJ, Walthall CL (1997b) Profiles of photosynthetically active radiation, nitrogen and photosynthetic capacity in the boreal forest: implications from scaling from leaf to canopy. *Journal of Geophysical Research,* **102,** 28,845–28,860.

deBruin HAR (1983) A model for the Priestley-Taylor parameter. *Journal of Climate and Applied Meteorology,* **22,** 572–578.

den Hartog G, Neumann HH, King KM, Chipanshi AC (1994) Energy budget measurements using eddy correlation and Bowen ratio techniques at the Kinosheo Lake tower site during the Northern Wetlands Study. *Journal of Geophysical Research,* **99,** 1539–1549.

Dickinson RE (1992) Land Surface. In: *Climate System Modeling* (ed. Trenberth KE), pp. 149–172. Cambridge University Press, Cambridge.

Field CB (1991) Ecological scaling of carbon gain to stress and resource availability. In: *Response of Plants to Multiple Stresses* (eds Mooney H *et al.*), pp. 35–65. Academic Press, New York.

Fitzjarrald DR, Moore KE (1994) Growing season boundary layer climate and surface exchanges in a subarctic lichen woodland. *Journal of Geophysical Research, A,* **99,** 1899–1917.

Gollan T, Passioura JB, Munns R (1986) Soil water status affects the stomatal conductance of fully turgid wheat and sunflower leaves. *Australian Journal of Plant Physiology,* **13,** 459–464.

Grelle A (1997) *Long term water and carbon dioxide fluxes from a boreal forest. methods and applications* (PhD Thesis). Acta Universitatis Agriculturae Sueciae,

Grelle A, Lundberg A, Lindroth A, Moren AS, Cienciala E (1997) Evaporation components of a boreal forest: variations during the growing season. *Journal of Hydrology*, **197,** 70–87.

Halldin S, Grip H, Jansson PE, Lindgren A (1980) Micrometeorology and hydrology of pine forest ecosystems. II. Theory and models. In: *Structure and Function of Northern Coniferous Forests — an Ecosystem Study* (eds Persson T). *Ecological Bulletin (Stockholm),* **32,** 463–503.

Hallgren JE, Lundmark T, Strand M (1990) Photosynthesis of Scots pine in the field after night frosts during summer. *Plant Physiology and Biochemistry,* **28,** 437–445.

Hallgren JE, Strand M, Lundmark T (1991) Temperature stress. In: *Physiology of Trees* (ed. Raghavendra AS), pp. 301–335. John Wiley, New York.

Harding RJ, Pomeroy JW (1996) The energy balance of the winter boreal landscape. *Journal of Climate,* **9,** 2778–2787.

Hogg EH, Black TA, den Hartog G *et al.* (1997) A comparison of sap flow and eddy fluxes of water vapor from a boreal deciduous forest. *Journal of Geophysical Research,* **102,** 28,929–28,937.

Hollinger DY, Kelliher FM, Schulze ED *et al.* (1995) Initial assessment of multi-scale measures of CO_2 and H_2O flux in the Siberian taiga. *Journal of Biogeography*, **22,** 425–431.

Jarvis PG, McNaughton KG (1986) Stomatal control of transpiration. *Advances in Ecological Research*, **15,** 1–49.

Jarvis PG, James GB, Landsberg JJ (1976) Coniferous forest. In: *Vegetation and the Atmosphere* (ed. Monteith JL), Vol 2, pp. 171–240. Academic Press, London

Jarvis PG, Massheder JM, Hale SE, Moncrieff JB, Rayment M, Scott SL (1997) Seasonal variation of carbon dioxide, water vapor, and energy exchange of a boreal black spruce forest. *Journal of Geophysical Research*, **102,** 28,953–28,966.

Kaminsky KZ, Dubayah R (1997) Estimation of surface net radiation in the boreal forest and northern prairie from shortwave measurements. *Journal of Geophysical Research,* **102,** 29,707–29,716.

Kelliher FM, Lloyd J, Arneth A *et al.* (1998) Evaporation from a central Siberian pine forest. *Journal of Hydrology*, **205,** 279–296.

Kelliher FM, Leuning R, Raupach MR, Schulze ED (1995) Maximum conductances for evaporation from global vegetation types. *Agricultural and Forest Meteorology*, **73,** 1–16.

Kelliher FM, Hollinger DY, Schulze E-D *et al.* (1997) Evaporation from an eastern Siberian larch forest. *Agricultural and Forest Meteorology*, **85,** 135–147.

Kimball JS, White MA, Running SW (1997) BIOME-BGC simulations of stand hydrologic processes for BOREAS. *Journal of Geophysical Research*, **102,** 29,043–29,051.

Kolchugina TP, Vinson TS (1995) Role of Russian forests in the global carbon balance. *Ambio*, **24,** 258–264.

Korner C (1994) Leaf diffusive conductances in the major vegetation types of the globe. In: *Ecophysiology of Photosynthesis* (eds Schulze ED, Caldwell MM), Ecological Studies 100, pp. 463–490. Springer, Berlin.

Kurz WA, Apps MJ (1993) Contribution of northern forests to the global C cycle. Canada as a case study. *Water, Air and Soil Pollution*, **70,** 163–176.

Lafleur PM (1992) Energy balance and evapotranspiration from a subarctic forest. *Agricultural and Forest Meteorology*, **58,** 163–175.

Lafleur PM, McCaughey JH, Joiner DW, Bartlett PA, Jelinski DE (1997) Seasonal trend in energy, water and carbon dioxide fluxes at a northern boreal wetland. *Journal of Geophysical Research*, **102,** 29,009–29,020.

Landsberg JJ, Gower ST (1997) *Application of Physiological Ecology to Forest Management*. Academic Press, San Diego, CA.

Lindroth A (1985) Seasonal and diurnal variation of energy budget components in coniferous forests. *Journal of Hydrology*, **82,** 1–15.

McCaughey JH, Lafleur PM, Joiner DW, Bartlett PA, Costello AM, Jelinski DE, Ryan MG (1997) Magnitudes and seasonal patterns of energy, water, and carbon exchanges at a boreal young jack pine forest in the BOREAS northern study area. *Journal of Geophysical Research*, **102,** 28,997–29,009.

McClone MS (1996) When history matters: scale, time, climate and tree diversity. *Global Ecology and Biogeography Letters*, **5,** 309–314.

McNaughton KG, Spriggs TW (1989) An evaluation of the Priestley-Taylor equation and the complementary relation using results from a mixed layer model of the convective boundary layer. In: *Estimation of Areal Evaporatranspiration* (eds Black TA *et al.*), pp. 89–103. IAHS Publications, Wallingford, UK.

Muller MJ (1982) *Selected Climate Data for a Global Set of Standard Set of Stations for Vegetation Science*. Dr W. Junk, the Hague.

Nijssen B, Haddeland I, Lettenmaier DP (1997) Point evaluation of a surface hydrology model for BOREAS. *Journal of Geophysical Research*, **102,** 29,367–29,378.

Oechel WC, Lawrence WT (1985) Taiga. In: Physiological Ecology of North American Plant Communities (eds Chabot B, Mooney H), pp. 66–94. Chapman & Hall, New York.

Pattey E, Desjardins RL, St. Amour G (1997) Mass and energy exchange over a black spruce forest during key periods of BOREAS 1997. *Journal of Geophysical Research*, **102,** 28967–28975.

Perttu K, Bischof W, Grip H, Jansson PE, Lindgren A, Lindroth A, Noren B (1980) Micrometeorology and hydrology of pine forest ecosystems. I. field studies. In: *Structure and Function of Northern Coniferous Forests-an Ecosystem Study* (eds Persson T). *Ecological Bulletin (Stockholm)*, **32,** 75–121.

Pielke R, PL (1995) Vidale. The boreal forest and the polar front. *Journal of Geophysical Research*, **100,** 25,755–25,758.

Raupach MR (1998) Influence of local feedbacks on land-air exchange of energy and carbon. *Global Change Biology*, **4,** 477–494.

Sala A, J (1996) Tenhunen. Simulations of canopy net photosynthesis and transpiration of *Quercus ilex* L. under the influence of seasonal drought. *Agricultural and Forest Meteorology*, **78,** 203–222.

Saugier B, Granier A, Pontailler J-Y, Baldocchi DD (1997) Transpiration of a boreal pine forest measured by branch bags, sapflow and micrometeorological methods. *Tree Physiology*, **17,** 511–520.

Schulze ED, Fuchs MI, Fuchs M (1977) Spatial distribution of photosynthetic capacity and performance in a mountain spruce forest of northern Germany. *Oecologia*, **29,** 43–61.

Schulze E-D, Schulze W, Kelliher FM *et al.* (1995) Above ground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian Larix stands in eastern Siberia. *Canadian Journal of Forest Research*, **25,** 943–960.

Sellers PJ, Hall FG, Margolis H *et al.* (1995) Boreal Ecosystem-Atmosphere Study (BOREAS): an overview and early results from the 1994 field year. *Bulletin of the American Meteorological Society*, **76,** 1549–1577.

Sellers PJ, Hall FG, Kelly RD (1997) Boreas in 1997: Scientific results, experimental overview and future directions. *Journal of Geophysical Research*, **102,** 28,731–28,770.

Sharratt BS (1998) Radiative exchange, near surface temperature and soil water of forest and cropland in interior Alaska. *Agricultural and Forest Meteorology*, **89,** 269–280.

Shvidenko A, Nilsson S (1994) What do we know about the Siberian Forest? *Ambio*, **23,** 389–404.

Stenberg P, DeLucia EH, Schoettle AW, Smolander H (1995) Photosynthetic light capture and processing from cell to canopy. In: *Resource Physiology of Conifers* (eds Smith W, Hinckley T), pp. 3–38. Academic Press, New York.

Sullivan JH, Bovard BD, Middleton EM (1997) Variability in leaf-level CO_2 and water fluxes in *Pinus banksiana* and *Picea mariana* in Saskatchewan. *Tree Physiology*, **17,** 553–561.

Teskey RO, Hinckley TM, Grier CC (1984) Temperature induced change in the water relations of *Abies amabilis* (Dougl. Forbes). Plant Physiology, **74,** 77–80.

Thomas G, Roundtree PR (1992) The boreal forests and climate. *Quarterly Journal of the Royal Meteorological Society*, **118,** 469–497.

Waring RH, Running SW (1998) Forest Ecosystems. *Concepts and Management*, 2nd edn. Academic Press, London.

Wilzcak JML, Cancillo ML, King CW (1997) A wind profiler climatology of boundary layer structure above the boreal forest. *Journal of Geophysical Research*, **102,** 29,083–29,100.

Woodward FI (1987) *Climate and Plant Distribution.* Cambridge University Press, Cambridge, UK.