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EXCHANGES OF CO₂ AND H₂O VAPOUR AT THE FOREST FLOOR OF A
MATURE BLACK SPRUCE FOREST

by

Robert V. Swanson

A thesis submitted to
the Faculty of Graduate Studies and Research
in partial fulfillment of the requirements
for the degree of

Master of Science

Department of Biology

Carleton University

Ottawa, Ontario

July 25, 1997

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EXCHANGES OF CO₂ AND H₂O VAPOUR AT THE FOREST FLOOR
OF A MATURE BLACK SPRUCE FOREST

Submitted by Robert V. Swanson, B.Sc.
in partial fulfillment of the requirements for
the degree of Master of Science

Thesis Supervisor

Chair, Department of Biology

Carleton University

August 21, 1997

Abstract

Measurements of the exchange of CO₂ and H₂O vapour between the forest floor and the atmosphere were made in plant communities dominated by feather mosses and *Sphagnum* moss in a 140 year-old *Picea mariana* forest. Maximum rates of moss gross photosynthesis were approximately 4 μmol m⁻² s⁻¹ for feather moss and 9 μmol m⁻² s⁻¹ for *Sphagnum*. At a uniform soil temperature of 10°C the rate of CO₂ efflux from the forest floor was 2.68 ± 1.34 μmol m⁻² s⁻¹ in the feather moss community and 2.55 ± 0.79 μmol m⁻² s⁻¹ in the *Sphagnum* community. At midday, the forest floor was typically a source of CO₂ in the feather moss community, and a sink of CO₂ in the *Sphagnum* community. Spatial variability in CO₂ flux was addressed. Very low moss tissue water contents decreased forest floor conductance to water vapour in the feather moss community.

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CHAPTER 1
INTRODUCTION

In recent years there has been much interest in global change. The concentration of atmospheric CO₂ is increasing as a result of the combustion of fossil fuels, and as a result of land use changes such as the clearing of forests for agriculture (Holmén 1992). However, based on knowledge of fossil fuel emissions, the observed annual increase in atmospheric CO₂ concentration is less than would be expected, indicating the existence of an unidentified, globally important CO₂ sink (Sundquist 1993). Global patterns of the concentration and stable isotopic composition of atmospheric CO₂ have been used to infer a large terrestrial CO₂ sink in the northern hemisphere (Tans *et al.* 1990; Ciais *et al.* 1995). The circumpolar boreal forest has been the object of numerous studies attempting to resolve this uncertainty in the global carbon budget, and to better understand the ecological implications of global change (eg. Bonan and Van Cleve 1992; Price and Apps 1995; Sellers *et al.* 1995).

The boreal forest is a globally important biome, representing approximately 25% of the earth's closed canopy forest (Natural Resources Canada 1996). It significantly affects the seasonal and annual climatology of much of the northern hemisphere, and the global budget of atmospheric CO₂ (Bonan *et al.* 1995). For example, seasonal change in its activity can account for up to 50% of the change in atmospheric CO₂ concentration at Pt Barrow, Alaska (71°N

157°W s.l.), and up to 30% of the change in CO₂ concentration at Mauna Loa (20°N 156°W 3400 m) (D'Arrigo et al. 1987). The boreal forest is also the major global reserve of soil carbon (Gorham 1991), and so any systematic change to its net ecosystem exchange of CO₂ (NEE) could substantially affect the global CO₂ budget. Recent research has underlined the sensitivity of the productivity of boreal systems to changes in temperature and hydrologic status (Taubes 1995). Detailed information on ecosystem-atmosphere exchanges of CO₂ and water vapour in boreal systems is therefore needed to improve our understanding of global climate and to improve the predictive ability of models of global change.

A detailed accounting of atmospheric CO₂ inputs and outputs requires detailed information about the response of NEE to climate variables. Such detailed information can be obtained by studying an ecosystem's component parts. Biochemically based models of photosynthesis and respiration have been developed that successfully describe CO₂ exchange at the leaf and whole plant levels (Farquhar and Caemmerer 1982; Lloyd et al. 1995), and a generally applicable model of soil respiration has recently been introduced (Lloyd and Taylor 1994). Parameterization of these models in different ecosystems facilitates comparison between ecosystems, and allows the prediction of CO₂ exchange from standard climatological data.

Black spruce (*Picea mariana* (Mill.) B.S.P.) is the dominant boreal forest type (Cauboue and Malenfant 1988). It is generally found on poorly drained sites, either in pure stands or mixed with tamarack (*Larix laricina* (Duroi) K. Koch). In mature black spruce stands, a moss layer dominates the forest floor (up to 100% cover) (Oechel and Van Cleve 1986), overlying peat sometimes deeper than 50 cm (Mueller-Dombois and Ellenberg 1974). In relatively dry black spruce stands the feather moss community (dominated by *Pleurozium schreberi* (Brid.) Mitt., with lesser amounts of *Hylocomium splendens* (Hedw.) B.S.G. and *Ptilium crista-castrensis* (Hedw.) DeNot forms a dense, continuous carpet over approximately 80% of the forest floor (Frego and Carleton 1994). In more open, wet stands, *Sphagnum* spp. are common (Van Cleve et al. 1983). A variety of evergreen and deciduous shrubs make up a multi-layered understorey. Typically, the distribution of the vascular understorey is patchy, and is composed of low shrubs and herbs such as *Ledum groenlandicum* Oeder, *Vaccinium* spp. and *Equisetum* spp., with no one species contributing more than 10% coverage (Van Cleve and Dyrness 1983).

Throughout this manuscript the term forest floor is used to designate the combination of soil, moss, and all vascular vegetation not exceeding approximately 40 cm in height.

The objectives of this study were:

- 1) to determine whether the forest floor of a mature boreal black spruce (*Picea mariana*) stand is a net source or a net sink of CO₂;
- 2) to determine the magnitude of the flux of H₂O at the forest floor, and the magnitudes of plant gross photosynthesis and total respiration at the forest floor;
- 3) to identify the major ecological factors controlling spatial variability in the capacity of the forest floor for photosynthesis and respiration.

This study was part of the Boreal Ecosystems-Atmosphere Study (BOREAS), an international and interdisciplinary study focusing on the exchanges of mass and energy between the boreal forest and the lower atmosphere (Sellers et al. 1995).

CHAPTER 2
LITERATURE REVIEW

2.1 Respiration

The term respiration designates the biological production of carbon dioxide (CO_2) through the oxidation of compounds containing carbon. The rate at which carbon dioxide produced below-ground is released to the above-ground atmosphere is commonly referred to as soil respiration (Rochette et. al. 1991). Carbon dioxide is produced below-ground by those portions of plants extending below-ground (especially roots of vascular plants), heterotrophic soil organisms, and to a lesser extent, chemical oxidation of carbon compounds (Waring and Schlesinger 1985; Lloyd and Taylor 1994). Below-ground CO_2 transport (in unsaturated soil) is a complex physical process, involving convective and diffusive transport in liquid and gas phases, as well as the removal of CO_2 dissolved in water by plant root water uptake (Simunek and Suarez 1993). Concentrating strictly on the gas phase, and assuming that the movement of CO_2 molecules from their place of production to the above-ground atmosphere is driven solely by diffusion, the rate of flux of CO_2 from the soil to the atmosphere can be described by the general equation

$$R = P_i k D_i (dC_i/dz) \quad (2.1)$$

where R is the rate of CO_2 flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$), P_i is the proportion of total soil volume occupied by air (typically 0.25, Brady 1990), k is a tortuosity factor which accounts for the fact that the shortest path to the above-ground

atmosphere is usually blocked by soil particles, D_s is the diffusion coefficient of CO_2 in the gas phase ($1.4 \times 10^{-5} \text{ m}^2 \text{ s}^{-1}$ at 10°C), and dC_s/dz ($\mu\text{mol m}^{-4}$) is the effective gradient in CO_2 concentration that exists between the soil and the above-ground atmosphere (modified from Simunek and Suarez 1993). Over the course of a growing season at a given uniform and undisturbed location, P_s will vary (in theory between zero and the porosity of the soil) in proportion to the water content of the soil, k may change slightly as a result of changes in the soil surface cover or below-ground plant growth, D_s will vary as a function of temperature, and dC_s/dz (in relation to a fixed point of reference) will change as a function of biological activity. A similar relationship exists for the transport of CO_2 in the liquid phase. Despite the complexity of the transport processes involved, soil respiration at a given study site has been shown to respond to temperature in a regular manner (Singh and Gupta 1977; Raich and Schlesinger 1992). Simple models have been widely used to describe the relationship between soil respiration rate and soil temperature. For example, a Q_{10} relationship (Figure 2.1) has often been used to describe the relationship between soil temperature and soil respiration, and the parameter Q_{10} is often used as a means of comparison between sites and between studies (Raich and Schlesinger 1992; Meir *et. al.* 1996). A Q_{10} relationship for soil respiration takes the form

$$R = R_{25} Q_{10}^{(T - 25)/10} \quad (2.2)$$

where R is the observed rate of respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$), R_{25} is the respiration rate at 25°C , and T is the measured soil temperature ($^\circ\text{C}$). Some researchers prefer to express the temperature sensitivity of chemical or biochemical processes in terms of activation energy (eg. Lloyd *et. al.* 1995). Activation energy is defined as the minimum amount of energy (per mol of reactant) needed before a reaction can take place (Nobel 1991), and there is a simple relationship between the Q_{10} of a reaction and the energy of activation (E_a) for that reaction, given by

$$\ln Q_{10} = (13.6 \times 10^{-6}) E_a \quad (2.3)$$

(Farquhar *et. al.* 1980). A temperature response expressed in terms of activation energy is given by

$$R = R_{10} e^{\left(\frac{E_a}{283.15K}\right)\left(1 - \frac{283.15}{T_a}\right)} \quad (2.4)$$

where R ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the rate of reaction at temperature T_a (K), R_{10} is the rate of reaction at 283.15 K, and E_a is the energy of activation of the reaction (Lloyd *et. al.* 1995). The temperature responses described by equation 2.2 (Q_{10} response) and equation 2.4 (exponential response expressed in terms of activation energy) are nearly identical (Figure 2.1), deviating most at high and low temperatures. Recently it was shown that when soil respiration rates at different locations are standardized to the same value at a given soil surface temperature, the

relative change in soil respiration rate as a function of soil surface temperature is similar across a wide range of ecosystem types (assuming no soil moisture limitation) (Lloyd and Taylor 1994). This latter study proposed a model of soil respiration that attributed differences in soil respiration between sites solely to differences in the effective mass of carbon available as respiratory substrate. Also, the model effectively produced a decrease in the activation energy of respiration with increasing temperature (Figure 2.1), a pattern that had been observed previously by other researchers (Schleser 1982 cited in Raich and Schlesinger 1992). The formula of Lloyd and Taylor (1994) for soil respiration is given by

$$R = R_{10} e^{308.56 \left(\frac{1}{56.02} - \frac{1}{T_s - 227.13} \right)} \quad (2.5)$$

where R ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is the rate of soil respiration and T_s (K) is the temperature of the soil. It is therefore possible, in many cases, to accurately predict soil respiration using simple models which focus on the biological production of CO_2 and ignore the complexities of below-ground CO_2 transport. For the purposes of characterizing soil respiration with respect to potential rates and spatial variability in a given ecosystem, and in the context of identifying the capacity of different ecosystems to act as net sources or net sinks of CO_2 , simple models that accurately predict the response of observed CO_2

flux to standard meteorological data are desirable. Unless otherwise noted, the term "soil respiration" will designate the efflux of CO_2 from the soil, recognizing that soil respiration and soil CO_2 efflux are conceptually different, but in practice often equal.

Under natural conditions, the majority of soil respiration originates from microbial and plant root metabolism (Flanagan and Van Cleve 1977). In a black spruce forest in Alaska, tree roots were estimated to contribute up to 90% of the observed soil respiration (Flanagan and Van Cleve 1977), while in an ombrotrophic pine bog in Finland, roots were estimated to contribute approximately 20% of observed soil respiration (Silvola et. al. 1992). However, most studies estimate root respiration to contribute between 30 - 70% of total respiration (Schlesinger 1977). Where moss cover is continuous, it can also be expected to contribute significantly to forest floor respiration. The Q_{10} for tissue respiration of three boreal moss species was found to vary widely (between approximately 1 and 6), with no observable pattern of difference through the growing season, or between species (Longton 1988).

Moisture conditions affect forest floor respiration (Waring and Schlesinger 1985). For example, Savage (1995) found decreased CO_2 evolution from very wet and very dry boreal sites, compared to mesic sites. Similar to photosynthesis (see section 2.2), moss respiration (at some

standard temperature) will depend on water content, consistent with a general metabolic down-regulation during desiccation (Dilks and Proctor 1979). A pulse of respiration is often observed upon rewetting following desiccation for both moss (Skre and Oechel 1981; Silvola 1991) and soil (Funke and Harris 1968). Several hypotheses have been proposed to explain the pulse of respiration following rewetting in mosses (Silvola 1991). It has been suggested that the pulse of respiration is caused by the release of adsorbed CO_2 (Farrar and Smith 1976), and that it is perhaps related to the activity of microbes resident on the plants, which take advantage of the cellular damage that occurred as a result of desiccation (Gupta 1977). If metabolic down-regulation takes place during desiccation (eg. Dilks and Proctor 1979), it is also logical that a burst of CO_2 following rewetting may be the result of metabolic up-regulation. The increase in soil respiration following rewetting has been attributed to an increase in the populations and activity of soil microbes following rewetting (Funke and Harris 1968). In general, the soil underlying moss in boreal systems is less prone to desiccation than the moss itself (Van Cleve *et al.* 1983).

In some cases, measured rates of soil respiration will not be well correlated to soil temperature measurements. For example, low porosity of the uppermost soil horizon can impede diffusion of CO_2 produced in layers beneath (Parkin

1987). Precipitation events can also cause short-term increases in CO_2 evolution from the soil as a result of the filling of soil pore space by water (Rochette *et al.* 1991). Finally, since the concentration of CO_2 in the soil is higher than that in the aboveground atmosphere, CO_2 may be drawn out of the soil by turbulence (and/or pressure fluctuations) at the soil surface (Baldocchi and Meyers 1991).

2.2 Photosynthesis

Photosynthesis at the forest floor is the sum of that of the moss layer and the low vegetation of the vascular plant understorey. Where moss cover is continuous, moss photosynthesis can be expected to be a relatively consistent component of forest floor photosynthesis on an area basis. Since the vascular understorey is generally non-uniform (Van Cleve *et al.* 1983), its contribution to forest floor photosynthesis can be expected to vary widely over small spatial scales.

There is evidence that bryophytes possess a C_3 photosynthetic pathway (Green and Lange 1994). For example, the $\delta^{13}\text{C}$ values of selected bryophytes fall within the range expected for C_3 plants (Rundel *et al.* 1979; Teeri 1981). Photosynthesis is also depressed at 21% oxygen compared to 2% oxygen, and the depression increases at higher temperatures (Green and Lange 1994), consistent with an

increase in the affinity of ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco - the major carboxylating enzyme in green plants) for O_2 compared to CO_2 with increasing temperature (Brooks and Farquhar 1985). The majority of boreal vascular plants are C_3 plants, and in what follows, the response of photosynthesis to environmental variables is discussed for C_3 photosynthesis.

Net photosynthesis for a leaf is equal to the difference between gross photosynthesis and respiration in the absence of light, as

$$P_n = P_g - R_d \quad (2.6)$$

where P_n is net photosynthesis, P_g is gross photosynthesis, and R_d is respiration in the dark (all in units $\mu\text{mol m}^{-2} \text{s}^{-1}$) (Salisbury and Ross 1992). The assumption that dark respiration is occurring at the same rate in the light as in the dark has been used in a detailed biochemical model of moss photosynthesis (Williams and Flanagan 1997), though it has been demonstrated for a higher, vascular C_3 plant (*Eucalyptus pauciflora* Sieb. ex Spreng.) that non-photorespiratory respiration in the light may typically proceed at a rate closer to 0.6 times the measured rate in the dark (Kirschbaum and Farquhar 1984).

Photosynthesis is dependent on the concentration of CO_2 in the chloroplast, which is influenced by the concentration of atmospheric CO_2 (Salisbury and Ross 1992). The rate of net photosynthesis, when plotted against the concentration

of CO_2 in the chloroplast (C_p), is seen to follow a pattern typical of competitive inhibition for an enzyme catalyzed reaction (Figure 2.2) (Stryer 1988). In this case the enzyme in question is Rubisco, and the principal reaction is the combination of ribulose-1,5-bisphosphate (a 5-carbon compound, commonly abbreviated RuBP) and CO_2 , to form two molecules of phosphoglyceric acid (a 3-carbon compound, commonly abbreviated PGA) (Farquhar *et. al.* 1980). This reaction is subject to competitive inhibition from O_2 , since the enzyme Rubisco also catalyzes the reaction of RuBP and O_2 , to form one 3-carbon compound, and one 2-carbon compound. This oxygenation reaction is energetically wasteful, since it ultimately results in the release of CO_2 (photorespiration), following further metabolism of the 2-carbon compound (Lorimer *et. al.* 1978). The maximum velocity of an enzyme catalyzed reaction (as measured by the rate of disappearance of a substrate, for example CO_2), is referred to as V_{max} (Stryer 1988). In ecological studies, evaluation of the maximum carboxylation velocity ($V_{\text{c,max}}$) of the enzyme Rubisco is useful as an indication of maximum photosynthetic potential, or photosynthetic capacity.

In the northern hemisphere, the concentration of atmospheric CO_2 changes seasonally, with the lowest concentration occurring in midsummer (when photosynthetic rates are greatest), and the highest in midwinter (when photosynthetic rates are least) (D'Arrigo *et. al.* 1987).

The amplitude of the annual change in concentration has been estimated at approximately 20 parts per million at 71°N (D'Arrigo et. al. 1987). In a forest, the largest source of CO₂ is the soil, and in periods when atmospheric turbulence is least (during the night), the vertical profile of CO₂ concentration in the forest often becomes stratified, with highest concentrations near the soil, and lowest concentrations at the top of the canopy (eg. Brooks et. al. 1997). Thus the ambient CO₂ concentration to which the forest floor vegetation is exposed will vary seasonally, and diurnally, and in general the local CO₂ concentration around the forest floor vegetation, and particularly around the moss, may be considerably greater than the concentration in the well mixed atmosphere above the forest (Green and Lange 1994).

Photosynthesis of forest floor vegetation will also depend on the flux of photosynthetically active radiation (PFD, or photosynthetic photon flux density - corresponding to the density of quanta ($\mu\text{mol m}^{-2} \text{s}^{-1}$) of electromagnetic radiation between wavelengths of approximately 400 and 700 nm). A generalized response of net photosynthesis to absorbed PFD is shown in Figure 2.3. At low light levels, net photosynthesis increases rapidly as light is increased. The initial slope of a plot of net photosynthesis vs. absorbed PFD is defined as the quantum yield (mol CO₂ fixed/mol PFD absorbed) (Ehleringer and Björkman 1977). In

this region of the curve, photosynthesis is limited by the rate of electron transport (Farquhar et. al. 1980). Net photosynthesis equals zero at the light compensation point, which is approximately equal to the value of PFD at which gross photosynthesis equals dark respiration (Laisk 1977, cited in Woodrow and Berry 1988). In general the light compensation point in bryophytes is lower than that of vascular sun plants (Green and Lange 1994), which suggests that mosses may be physiologically acclimated to conditions of low PFD (Björkman 1981). For a typical C_3 species, the slope of a plot of net photosynthesis vs. PAR decreases with increasing light, until a maximum rate, called the light saturated rate of net photosynthesis, is approached, where the slope is near zero (Proctor 1982). In this region of the curve, photosynthesis is limited by the maximum carboxylation velocity of Rubisco (Farquhar et. al. 1980). The value of PFD beyond which net photosynthesis no longer increases is called the light saturation point. The light saturation point for bryophytes is in general low compared to vascular sun plants (Green and Lange 1994). Therefore it is seen that the process limiting the observed rate of photosynthesis of a leaf changes beyond a certain value of PFD. Below this value of PFD the rate of net photosynthesis is limited by the rate of electron transport, while above this value of PFD, the rate of net photosynthesis is limited by the maximum carboxylation velocity ($V_{c, \max}$) of the enzyme

Rubisco.

In general, a particular location in a forest understorey is subjected to long periods of diffuse sunlight (shade), interrupted by short periods of direct sunlight (sunflecks) (Skre *et al.* 1983; Pearcy and Pfitsch 1994). Though present for typically less than 10% of the time, sunflecks can constitute up to 80% of total PFD available in understorey environments (Chazdon 1988). Since the light compensation and light saturation points of bryophytes are in general low compared to vascular sun plants (Green and Lange 1994), moss photosynthesis can be expected to approach light saturated rates, even when PFD is low. Where the canopy is relatively open, such as in wet areas of a black spruce stand, the forest floor will receive more direct sunlight. In *Sphagnum* spp., very high light intensity has been shown to limit photosynthesis through photoinhibition (Murray *et al.* 1993). High light intensity will also influence moss photosynthesis by increasing leaf temperature, and by increasing transpiration (which will affect moss moisture content - see below).

The net photosynthesis of a leaf increases with increasing temperature until it reaches a maximum at some optimum temperature (Figure 2.4) (Berry and Raison 1982). The relationship shown is typical of enzyme catalyzed reactions, whereby above the optimum temperature, the enzyme is no longer stable, and further increases in temperature

result in a precipitous drop in enzyme activity (Stryer 1988). The response of net CO_2 uptake to temperature is the summation of multiple effects of temperature on individual steps of the photosynthetic process (Berry and Raison 1982). The maximum velocities of photosynthetic electron transport (J_{max}), carboxylation of RuBP by Rubisco ($V_{\text{c,max}}$), and oxygenation of RuBP by Rubisco ($V_{\text{o,max}}$) increase with temperature, though they do not necessarily have the same temperature sensitivities, or the same temperature optima (Björkman *et. al.* 1980; Farquhar and von Caemmerer 1982). The affinity of Rubisco for O_2 relative to CO_2 also increases with temperature, which favours a decrease in net CO_2 uptake with increases in temperature (Brooks and Farquhar 1985). Dark respiration also increases as temperature increases, however the temperature sensitivity of dark respiration is greater than that of gross photosynthesis, and the optimum temperature for dark respiration is always much higher than that of the major photosynthetic enzymes (Berry and Raison 1982). Thus above the temperature optimum for net photosynthesis, the net photosynthesis of a leaf decreases as a result of an increase in the relative importance of both photorespiration and dark respiration. The optimal temperature for photosynthesis in mosses is typically near 20°C (Proctor 1982; Harley *et. al.* 1989).

Moss photosynthesis is heavily dependent on the

moisture content of its photosynthetic tissue (moss water content) (eg. Skre and Oechel 1981; Titus and Wagner 1984; Murray *et al.* 1989; Silvola 1990; Silvola 1991; Williams and Flanagan 1996). Below an optimum water content, mosses experience a general metabolic slowdown (Figure 2.5), and at very low water content, mosses can become metabolically inactive (Titus and Wagner 1984). Above the point where water is no longer metabolically limiting, further increases in water content cause a decrease in photosynthesis by acting as a barrier to the diffusion of atmospheric CO₂ to the chloroplasts (Williams and Flanagan 1996). Most mosses lack root systems and stomata, so a majority do not exert direct physiological control over their water balance (Proctor 1980; Skre and Oechel 1981). However, moss morphology can affect water balance. For example in *Sphagnum* spp., some branches lie parallel to the stem (pendant branches), and draw water up along the stem by capillarity (Clymo and Hayward 1982). The common boreal forest feather mosses *Pleurozium schreberi* and *Hylocomium splendens* lack any means by which to translocate water from the soil, though the imbricate pattern and concavity of their leaves enable the storage of absorbed water between the leaf and the stem or branch along which it lies (Proctor 1984). Titus and Wagner (1984) suggested that morphology-related differences in water balance can result in species specific levels of desiccation tolerance, and this notion is

supported by the experiments of Silvola (1991). For these reasons the duration, intensity and frequency of rainfall, and other factors affecting wetting and drying (including throughfall, moss morphology, vapour pressure deficit and boundary layer conditions), will all affect moss photosynthesis, however it can be expected that periods of drought will affect the photosynthetic capacity of the major moss types (ie. feather moss and *Sphagnum* spp.) differently. Since very high PFD will increase both moss temperature and transpiration, mosses experiencing intermediate light intensities may fix more carbon over the growing season, than those experiencing very high or very low light intensities.

The photosynthetic capacity of the forest floor vascular vegetation can be expected to vary primarily with leaf habit (eg. deciduous vs. evergreen), but also between species (Small 1972; Chapin and Tryon 1983). Species tending to grow in gaps in the canopy, or in relatively wet areas, could be acclimated to higher light intensities, and therefore have greater rates of light saturated photosynthesis (Björkman 1981). The photosynthesis of both bryophytic and vascular vegetation per unit ground area will depend directly on the ratio of leaf area/ground area. This ratio (for one-sided (ie. projected onto the ground) leaf area) is defined as the leaf area index.

Finally, the capacity of plants for photosynthesis will

change seasonally in response to changes in leaf area, and the concentration of photosynthetic enzymes. For example, over one growing season, Skre and Oechel (1981) attributed a gradual increase in the rates of net photosynthesis in the moss *Pleurozium schreberi* and two species of *Sphagnum* to increasing amounts of young, photosynthetically active tissue. Photosynthesis in deciduous vascular plants in the spring and fall will be heavily dependent on leaf area, and in the fall will decrease as a result of the retranslocation of nutrients from senescing leaves (Salisbury and Ross 1992).

2.3 Evapotranspiration

At equilibrium, water vapour will move from an area where its concentration is high to an area where its concentration is low, at a rate proportional to the gradient in its concentration between the two areas, and a conductance term, as

$$E = g_{t,w} \left[\frac{e_i - e_a}{P} \right] \quad (2.7)$$

where E ($\text{mmol m}^{-2} \text{s}^{-1}$) is evapotranspiration, $g_{t,w}$ ($\text{mmol m}^{-2} \text{s}^{-1}$) is the total conductance to water vapour, e_i (kPa) is the equilibrium vapour pressure of air in the area of high water vapour concentration (for example, at the moss surface in the understorey of a black spruce forest), e_a (kPa) is the vapour pressure of air in the area of low water vapour

concentration (for example outside of the forest floor boundary layer in the black spruce forest understorey), and P (kPa) is the total atmospheric pressure (eg. Meinzer 1993; Meinzer *et. al.* 1993). For the forest floor, the total conductance to water vapour can be further broken down into component parts, as

$$1/g_{t,w} = 1/g_{bl} + 1/g_{ff} \quad (2.8)$$

where the total resistance to water vapour flux ($1/g_{t,w}$) is equal to the sum of boundary layer resistance at the forest floor ($1/g_{bl}$) and a forest floor resistance term ($1/g_{ff}$).

As previously described, feather mosses cannot translocate water from the soil, so their potential for transpiration will depend on moisture input from snowmelt, precipitation and condensation. Although also lacking internal water transport systems, *Sphagnum* spp. can translocate water vertically and laterally, as a result of the capillarity of pendant branches (previously mentioned) and mutually appressed growth habit (Clymo and Hayward 1982). The forest floor conductance will therefore depend on the water content of the moss. For example, Williams and Flanagan (1996) found the maximum moss conductance to water vapour to occur at a water content of approximately 9 (fresh weight/dry weight) in *Pleurozium schreberi* and *Sphagnum* (sect. *acutifolia*). In the same study, total conductance, and average field water content were greater in *Sphagnum* than in *Pleurozium schreberi*. Nichols and Brown (1980)

demonstrated that the presence of an overstorey of grasses and sedges protected *Sphagnum* from desiccation when the water table was low, but did not change total evapotranspiration at any water level.

Transpiration from the vascular understorey will be a function of leaf area index, stomatal conductance, vapour pressure deficit, available energy, and the boundary layer conductance at the forest floor (Roberts *et al.* 1980; Black and Kelliher 1989). Since the distribution of the vascular understorey is patchy (Van Cleve *et al.* 1983), its contribution to forest floor transpiration is likely to be highly variable over small spatial scales. In a Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) stand, Tan *et al.* (1977) found the stomatal conductance of the understorey species salal (*Gaultheria shallon* Pursh.) to be most dependent on soil water potential, vapour pressure deficit, and PFD. Vapour pressure deficit and irradiance have dual effects on transpiration, by affecting stomatal conductance on the one hand, but also acting as the driving forces for water vapour flux (Black and Kelliher 1989). Stomata will tend to open in response to high humidity (low vapour pressure deficit) in the understorey (Pearcy and Pfitsch 1994). Solar irradiance is of course lower in the understorey than above the forest canopy, however it can approach that above the canopy in gaps and sunflecks (Skre *et al.* 1983). High irradiance can cause stomatal opening,

however the increased net radiation and leaf temperature, and subsequent increase in transpiration, can cause loss of turgor and subsequent stomatal closure (Pearcy and Pfitsch 1994).

If sufficient turbulence exists at the forest floor, evapotranspiration from the forest floor will proceed at the equilibrium rate described by equation 2.7 (Baldocchi and Meyers 1991). However, if a sufficiently great boundary layer develops within the forest understorey, the rate of evapotranspiration from the forest floor will become decoupled from the influence of the ambient air vapour pressure, and will proceed at a rate determined primarily by the available energy (McNaughton and Jarvis 1983). Conifer forests are in general aerodynamically rough (Jarvis and McNaughton 1986), and in some situations, periodic large-scale turbulent events that penetrate deep into the canopy are known to prevent the establishment of a thick boundary layer in the understorey (Denmead and Bradley 1985; Crowther and Hutchings 1985). It can therefore be expected that under natural conditions, transpiration from the understorey will be subject to the relationship described by equation 2.7.

CHAPTER 2 FIGURES

Figure 2.1. Theoretical responses of soil respiration to soil temperature. Lines represent equations 2.2 (solid line), 2.4 (dotted line) and 2.5 (dashed line) in the text. The solid and dotted lines represent a Q_{10} for respiration of approximately 2. See section 2.1 in the text for an explanation of the differences between the equations.

Figure 2.2. Generalized response of net photosynthesis of a leaf to the concentration of CO_2 in the chloroplast.

Figure 2.3. Generalized response of net photosynthesis of a leaf to absorbed photon flux of photosynthetically active radiation (PFD).

Figure 2.4. Generalized temperature response of net photosynthesis of a leaf.

Figure 2.5. Generalized response of moss net photosynthesis (percent of maximum rate) to tissue water content.

CHAPTER 3
MATERIALS AND METHODS

3.1 Study Site

The study was conducted at the mature black spruce site in the southern study area (SSA) of the BOREAS project (53.99°N 105.12°W, elevation 617 m). The study site was located in central Saskatchewan, and represented the approximate southern limit of the western Canadian boreal forest. The site occurred on poorly drained clay-sand soil. The forest was approximately 140 years old (S.T. Gower, unpublished data), and was dominated by two distinct community types. The first community type (feather moss community) had an overstorey of black spruce (4150 live stems/ha), with scattered individuals of jack pine (*Pinus banksiana* Lamb.) and tamarack (*Larix laricina* (Du Roi) K. Koch). The black spruce ranged in height up to 12 m, and the understorey was dominated by feather mosses and the vascular evergreen shrub *Ledum groenlandicum* Oeder. In the second community type (*Sphagnum* community) the black spruce overstorey was shorter (up to 6 m) and less dense (3700 live stems/ha), and the understorey contained a greater proportion of *Sphagnum* moss (E.H. Hogg, unpublished data). Vascular species common in the understorey were *L. groenlandicum*, *Vaccinium vitis-idaea* L. and *Equisetum* spp. Field measurements were made during the spring (Julian days 118 to 140), summer (Julian days 193 to 213) and fall (Julian days 273 to 283) of 1996.

3.2 Field Measurements

3.2.1 Gas Flux Measurements

3.2.1.1 Gas Flux System

Fluxes of carbon dioxide and H₂O vapour at the forest floor were measured using a Li-Cor 6200 portable photosynthesis system (Li-Cor Inc., Lincoln, Nebraska), and a dynamic, closed chamber technique, similar to that described by Vourlitis *et. al.* (1993). The concentration of CO₂ inside the chamber was monitored by circulating air from inside the chamber through an infrared gas analyzer (IRGA) (Li-6250, Li-Cor Inc.), and then returning the same air to the chamber. The relative humidity inside the chamber was monitored by a relative humidity sensor located inside the chamber (Vaisala, Li-Cor Inc.). The CO₂ concentration and the humidity of the air returning to the chamber from the IRGA could be controlled by passing all or some of the flow through a column of soda lime and/or a column of desiccant (Mg(ClO₄)₂), however large chamber volumes in this study (see below) prevented the returning air from influencing the composition of the air inside the chamber. The chamber was made of acrylic, and consisted of a portable top (the chamber head) (60 cm x 60 cm x 15 cm), and a permanent base (60 cm x 60 cm x 30 cm) which were sealed together using clamps and a closed cell foam gasket, during each measurement of gas exchange. During gas exchange measurements, air in the chamber was circulated by 1 small

fan (Li-Cor 6200-17, Li-Cor Inc.) operated at 3V (Rochette et. al. 1997). A valve with an adjustable aperture (Nupro, SS-4P4T, Ottawa Valve and Fitting, Ottawa, Ontario) was attached to a length of tubing (60 cm long, 3 mm i.d., volume 4.2 cm³ : Bev-a-line, Warehoused Plastic Sales, Toronto, Ontario) inside the chamber, maintaining equilibrium between the total pressure inside and outside of the chamber during gas flux measurements (Livingston and Hutchinson 1995).

3.2.1.2 Collars

Sixteen different bases (collars) were installed at a variety of sites in both the feather moss community and the *Sphagnum* community in November of 1995. In the feather moss community, collars were installed in feather moss, and in the *Sphagnum* community, collars were installed in *Sphagnum* moss. It should be emphasized however that in the feather moss community the cover of feather moss was not 100%, and in the *Sphagnum* community the cover of *Sphagnum* was not 100% (cf. sections 3.2.6, 4.4.2). Two collars were added in the *Sphagnum* community at the beginning of the summer measurement period. It was necessary to install most of the collars in the fall, as gas flux measurements were to begin early in the spring of 1996, when the ground was expected to be frozen. Collar locations were chosen in order to minimize the cover of vascular shrubs, while at the

same time capture the range of exposure of the forest floor to the sky. Despite the attempt to avoid vascular vegetation, at least a small amount of vascular vegetation was present in most collars in all measurement periods (cf. sections 4.3.1.1, 4.3.2.1). Collar locations were necessarily restricted to where the ground was relatively flat. Collars were installed to depths of between 7 and 20 cm. Care was taken not to sever roots of trees and shrubs, however the minimum depth required for a good seal with the ground and collar stability, resulted in the severance of roots where these were present in the upper soil profile. The sides of the collars protruded between approximately 10 and 23 cm above the surface of the moss, depending on the depth of the soil at each microsite, and the limitations imposed by obstacles such as roots and stones. In a small number of cases a gap existed between the exterior sides of a collar and the surface peat. Where this occurred, long intact sections of peat from nearby areas were cut and pushed gently into the gap, creating a natural appearing moss surface. Short, portable raised platforms were stood upon while working at a collar, in order to avoid trampling of the area around the collar. Table 3.1 summarizes the number of separate visits made to each collar in each season.

3.2.1.3 Gas Flux Measurement Protocol

Gas flux measurements were made with the chamber illuminated and with the chamber darkened. After the chamber head was clamped onto a collar, at least 10 s were allowed to elapse before recording the gas flux data, in order to allow the establishment of steady state conditions. Two or three observations were logged during the minute that the chamber head was clamped onto the collar, corresponding to observational periods of 30 s or 20 s, respectively. When the minute had expired, the chamber head was removed from the collar, allowing the re-establishment of ambient conditions inside the chamber. Each visit to a collar, this process was repeated three times with the chamber illuminated, and two times with the chamber darkened. Thus during each visit to a collar (which lasted a total of approximately 30 minutes), the chamber head was clamped onto the collar, and removed, a total of five times. During the second and third measurements made in the light, transparent plastic sheets were placed over the chamber in order to reduce the natural light intensity incrementally. A specially constructed vinyl cover was used to darken the chamber for measurements of dark respiration.

Air temperature inside the chamber was measured by a chromel-constantan thermocouple (Li-6000-09RJ, Li-Cor Inc.) which was shielded from the sun. Photosynthetic photon flux density inside the chamber was monitored by a PFD sensor

(Li-190SA Quantum Sensor, Li-Cor Inc.). Soil temperature at 15 cm depth (ie. 15 cm below the moss surface) was measured beside the chamber by a soil temperature probe (Li-6000-09TC, Li-Cor Inc.). Moss temperature was measured inside the chamber at approximately 1 cm depth using a copper-constantan thermocouple connected to a digital thermocouple thermometer (Digi-Sense, Omega Inc., Stamford, Connecticut).

3.2.1.4 System Volume and Data Quality

Chamber volume was evaluated at each collar in each measurement period in order to account for any shifting in collar position, and for the growth of moss. Chamber volume was evaluated by measuring the depth from the top of the collar to the moss surface at 36 points in the collar interior, using a specially constructed grid frame. The average depth to the moss surface in the chamber was calculated as the average of the measured depths. The total volume of the chamber varied at each collar location, ranging from 70 to 125 litres. Since the chamber volume was so great relative to the flow rate through the IRGA (approximately $1200 \mu\text{mol s}^{-1}$), it was not possible to scrub the CO_2 concentration to below ambient levels before measuring dark respiration. Neither was it possible to control the relative humidity inside the chamber. Results of tests indicated that the rate of increase in CO_2 concentration in the dark remained approximately linear with

the chamber closed and the fan operating, for as long as 40 minutes (data not shown). Since moss constituted the majority of the vegetation in all chambers, typical problems associated with the response of stomata to changes in relative humidity were not encountered. The chamber head was tested for leaks at the beginning of each measurement period by blowing into it, immediately sealing it to a plexiglas base, and monitoring the decline in CO_2 concentration over time. The results of the tests indicated that the chamber head provided an excellent seal (Li-Cor Inc. 1989).

Since the slope of the change in CO_2 concentration with time (dC/dt) in the dark varied widely as a function of chamber volume and the rate of respiration, data were not rejected on the basis of an *a priori* value of slope or slope coefficient of variability, as this was likely to introduce bias against collars with large volumes and/or low respiration rates, as well as against measurements made in the spring and fall. Data quality was evaluated on the basis of dark runs only, as dC/dt in the light could be expected to be near zero. Table 3.2 summarizes the data quality, as measured by the variability in dC/dt , for each measurement period.

Some measurements were made with snow partially or fully covering the ground inside the chamber, however these were excluded from further analysis. For photosynthesis,

measurements during which light conditions were uneven were excluded from further analysis.

3.2.2 Experimental addition of water

For approximately two weeks in the summer measurement period, the equivalent of 5 mm of water (taken from nearby Candle Lake) was added daily to several collars in both community types. This was done in order to remove moss water stress, and compare the photosynthetic capacity of continually well hydrated moss to that of moss subject to wetting/drying cycles. This was done in the summer measurement period because it was the time period during which moss were most likely to be limited by low tissue water contents.

3.2.3 Moss Water Content

Since the activity of moss is highly dependent on its tissue water content, it was important to record moss water content at the time of each gas exchange measurement. Moss water content was determined gravimetrically from samples collected at the time of each gas exchange measurement. Samples were taken from a quadrat adjacent to each collar. At the end of each visit to a collar, a substantial number of shoots were excised at the approximate base of the photosynthetically active tissue, and sealed in a small plastic bag. Fresh weight was measured within 10 minutes of

excision, and dry weight was measured following drying overnight at 60°C in a food dehydrator.

3.2.4 Meteorological Data

Meteorological data in the understory of the feather moss community were recorded by a solid state datalogger (CR10, Campbell Scientific Inc., Logan Utah), during the majority of the 1996 growing season. Precipitation was measured at ground level, in a canopy gap using a tipping bucket rain gauge, and the total precipitation recorded was output for 15 minute intervals. PFD was measured at one location in the understory, using a PFD sensor (Li-190SA Quantum Sensor, Li-Cor Inc.). Air temperature and relative humidity were measured using two temperature and relative humidity probes (207, Campbell Scientific Inc.). The probes were placed approximately 1.5 m above the forest floor, and were protected by gill radiation shields (41004-5, Campbell Scientific Inc.). Moss temperature (at approximately 2.5 cm depth) and soil temperature (at depths of 15 cm and 27 cm) were each measured by two copper constantan thermocouples installed in May 1996. The PFD and temperature and relative humidity sensors were scanned every 15 s and readings averaged every 15 minutes.

In order to compare the light regimes of the collar locations, PFD was monitored close to each collar in each of the community types for six days in July (days 202 to 207 in

the feather moss community; days 208 to 213 in the *Sphagnum* community). PFD sensors (Li-190SA Quantum Sensor, Li-Cor Inc.) were scanned every 10 s by a datalogger (CR10, Campbell Scientific Inc.) and the readings averaged every 5 minutes. Where two collars were near to each other, a single PAR sensor was used to represent the light environment of both collars. Daily averages were calculated from all five-minute averages in a 24 hour period. In some cases a constant relationship was found to exist between the light environments of two adjacent collars, and the daily average of one of the collars was recalculated based on a constant of proportionality relating PAR readings made during gas flux measurements, and those measured by the nearest PAR sensor.

3.2.5 Spatial variability

In order to help explain spatial variability in measured respiration, a number of measurements were taken at each collar location. The diameter at breast height (dbh) of all trees (dbh > 1.5 cm) within 1 m of any collar edge was measured. In the *Sphagnum* community at the beginning of the summer measurement period, 1.2 m lengths of PVC pipe (3.8 cm i.d.) were drilled with holes and hammered into the peat near each collar. During the summer and fall measurement periods, depth from the moss surface to the water table was measured at each pipe once daily. Vascular

vegetation representative of that inside each collar was collected at the end of the spring and summer measurement periods for later determination of leaf area index (LAI). At the end of the fall measurement period, five 18.1 cm^2 samples of the moss layer were taken from within each feather moss collar for later determination of LAI. At the end of the fall measurement period a soil pit was dug within each collar and the thicknesses of the organic horizons were measured. In the *Sphagnum* community, actual depth to the water table was measured once in the soil pit.

3.2.6 Vegetation Transects

In order to permit spatial scaling of gas fluxes, it was necessary to obtain an estimate of the percent cover of the major moss types (feather moss and *Sphagnum* spp.) at the study site. The boundaries of feather moss and *Sphagnum* communities in the area comprising the study site had previously been drawn onto an aerial photograph of the study site (J. Niederleitner, unpublished data). Using a colour laser copy of the same aerial photograph, the percent cover of feather moss and *Sphagnum* communities was determined for a circular area of radius 400 m, centred at a meteorological tower, which was within 200 m of all soil collars.

A wedge with an angle of 63° , extending east from the meteorological tower, was excluded from this analysis. This area was excluded in order to facilitate comparison between

the results of this study and the results of gas flux measurements made by an eddy covariance system at the top of the meteorological tower. Since the prevailing winds came from the west side of the meteorological tower, gas fluxes measured by the eddy covariance system would rarely be affected by the ground cover east of the tower. By excluding this wedge-shaped area, the area considered in the determination of cover of moss types corresponded to the approximate wind area boundary (WAB) of the eddy covariance system.

Within the feather moss community the cover of feather moss was not 100%, and within the *Sphagnum* community, the cover of *Sphagnum* was not 100%. It was therefore necessary to quantify the abundance of feather moss and *Sphagnum* in both communities. Vegetation transects were set up in both feather moss and *Sphagnum* community types. A point frame method was used to determine the % cover of the major moss types (feather moss and *Sphagnum* spp.) in both community types. A single pin was lowered perpendicular to the moss surface from a frame (approximately 80 cm high x 40 cm wide), at 5 m intervals along the transects, and the species it touched were recorded. Percent cover of a species was calculated by dividing the number of points at which that species was touched by the total number of points. A total of 167 points were visited in the feather moss community type, and a total of 130 points were visited in the *Sphagnum*

community type.

3.3 Laboratory Measurements

3.3.1 Leaf and Shoot Area Index

For each collar, the one-sided LAI of vascular plants was determined from representative samples of each species present, using a leaf area meter (Li-3100, Li-Cor Inc.). Since it was not practical to remove the leaves from feather moss shoots, a one-sided shoot area index (SAI) was determined for each feather moss collar by passing the green portions of intact shoots from five samples through the leaf area meter. The moss SAI for each feather moss collar was calculated as the total shoot area of the five samples divided by the total ground area of the five samples.

3.3.2 Carbon Isotope Analysis

For each collar, in each measurement period, moss ^{13}C content was determined from the samples used to determine moss water content during gas exchange measurements. Equal amounts of photosynthetically active tissue from all the dried samples for a given collar in a given season were combined, frozen in liquid nitrogen, and ground using a mortar and pestle. Samples were then prepared for measurement of carbon isotopic composition by combustion. A 1-2 mg subsample of ground tissue was sealed in a tin capsule and loaded into an elemental analyzer for combustion

(Carla Erba). The carbon dioxide generated from the combustion was purified cryogenically and passed directly to the inlet of a gas isotope ratio mass spectrometer (Delta S, Finnigan Mat, San Jose, California) at the University of Utah.

Carbon isotope ratios are expressed in delta notation,

$$\delta = \left[\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right] \quad (3.1)$$

where R is the molar ratio of heavy to light isotope ($^{13}\text{C}/^{12}\text{C}$), and the standard used is CO_2 from Pee Dee Belemnite limestone (Ehleringer and Osmond 1989). The δ values are presented as parts per thousand (‰).

3.4 Data Analysis

3.4.1 Respiration

From the two measurements of forest floor dark respiration made per visit to a collar, an average value was calculated for each of dark respiration, soil temperature and moss temperature. These average values (for all measurement periods combined) were used to parameterize three models of soil respiration. For feather moss collars, only visits where moss water content was ≥ 4 (fw/dw) were considered, in order to eliminate variability in the moss respiration rate associated with changes in moss water content. The goodness of fit of each model was evaluated on

the basis of an adjusted R^2 , and the distribution of the residuals (observed values - predicted values).

The adjusted R^2 was calculated as

$$R^2_{adj} = 1 - \frac{MSE}{MST} \quad (3.2)$$

where MSE is the residual mean square (SSE/df where SSE is the residual sum of squares and df is residual degrees of freedom) and MST is the total mean square (SST/df where SST is the total sum of squares and df is the total degrees of freedom). No measure of significance was included in the assessment of goodness of fit of the models of respiration, as strictly speaking, repeated measurements of respiration at the same locations represented time series, rather than independent observations. The approach taken in this study for the measurement of soil respiration, and the presentation of goodness of fit of the models, is not uncommon in the literature (eg. Lloyd and Taylor 1994; Meir *et. al.* 1996). An exception is made in section 3.4.1.4, where for illustrative purposes it was useful to include a measure of significance for the effect of feather moss water content on forest floor respiration.

3.4.1.1 Exponential Regression

In some cases, the response of respiration to soil temperature was clearly exponential (cf. section 4.2), however the apparent Q_{10} (or activation energy) differed between collars. A Q_{10} type response to temperature was

compared to observed values of respiration, allowing both the respiration rate at a standard temperature (interpreted as the amount of available respiratory substrate), and the Q_{10} (or activation energy) to change between collars. The Q_{10} form of the equation was chosen in order to emphasize the empirical nature of the assumption of a different activation energy between collars. The form of the Q_{10} response was

$$R = a e^{bT} \quad (3.3)$$

where R was the measured respiration rate ($\mu\text{mol m}^{-2} \text{s}^{-1}$), T was the soil temperature at a depth of 15 cm, e was the base of the natural logarithm, and a and b were constants predicted by the regression. Q_{10} and R_{10} were evaluated from this regression. For the same Q_{10} and R_{10} , the curve given by equation 3.3 is identical to that given by equation 2.2.

3.4.1.2 Model A

The second model to which total forest floor respiration was compared (Model A) took the form

$$R = R_{10} e^{308.56 \left(\frac{1}{56.02} - \frac{1}{T_s - 227.13} \right)} \quad (3.4)$$

where R ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was the measured respiration rate, and T_s (K) was the soil temperature (at 15 cm depth). In this case, R_{10} represented a collar specific value of respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at 10°C , which could be interpreted as the effective mass of carbon available as respiratory substrate

(Lloyd and Taylor 1994). The best-fit for the parameter R_{10} was calculated for each collar using nonlinear regression and an iterative least squares procedure (SAS Institute Inc. 1989).

Model A was developed by Lloyd and Taylor (equation 11 in Lloyd and Taylor 1994), and effectively produces a decrease in the activation energy of respiration with increasing soil temperature.

3.4.1.3 Model B

The third model to which total forest floor respiration was compared (Model B) took the form

$$R_{tot} = R_{10,deep} e^{308.56 \left(\frac{1}{56.02} - \frac{1}{T_s - 227.13} \right)} + R_{10,shallow} e^{\left(\frac{E_r}{283.15R} \right) \left(1 - \frac{283.15}{T_s} \right)} \quad (3.5)$$

where R_{tot} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) was the measured rate of respiration, T_s (K) was the soil temperature (at 15 cm depth), T_1 (K) was the moss temperature (at 1 cm depth), E_r (set at 53000 J mol^{-1}) was the activation energy of respiration for a shallow stratum (see below), and R was the universal gas constant. $R_{10,deep}$ and $R_{10,shallow}$ represented collar specific values of respiration ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at 10°C for a deep stratum (bulk soil and most roots), and for a shallow stratum (the moss layer, aboveground vascular vegetation, and shallow roots), respectively. The best-fit for the parameters $R_{10,deep}$ and $R_{10,shallow}$ was calculated for each collar

using nonlinear regression and an iterative least squares procedure (SAS Institute Inc. 1989). For feather moss collars, it was necessary to limit the possible values of $R_{0, \text{shallow}}$ to ≥ 0 .

Since the first term of Model B produces a decrease in the activation energy of respiration with increasing soil temperature, and the second term assumes a constant activation energy of respiration (over the temperature range of interest), Model B seems theoretically contradictory. The second term of Model B was expected to be largely influenced by moss respiration. Carefully controlled measurements of moss respiration at the same study site during the same measurement periods as this study indicated that moss respiration was well described by a model of the form given by the second term of Model B, assuming an activation energy for respiration of 53 kJ mol^{-1} (Williams and Flanagan 1997). The first term of Model B was applied based on the evidence of Lloyd and Taylor (1994) for the decrease in activation energy of soil respiration with increasing temperature. An activation energy of 53 kJ mol^{-1} for moss falls between the activation energies at 0°C (37 kJ mol^{-1}) and 40°C (78 kJ mol^{-1}) calculated for soil respiration by Lloyd and Taylor (1994).

3.4.1.4 Effects of Moss Water Content on Total Respiration in the Feather Moss Community

Linear multiple regression was used to illustrate the effects of limiting moss water content on total forest floor respiration in the feather moss community in the summer measurement period. Since the range of soil temperatures encountered in the summer measurement period was relatively narrow (from approximately 8°C to 16°C), it was felt that the relationship between total respiration and soil temperature would be adequately described by a straight line for the purposes of this analysis, bearing in mind that departures from linearity would decrease the probability of finding a significant relationship. All values of total respiration where the feather moss water content was below 5 (fresh weight/dry weight), for the summer measurement period, were included in the analysis. Additionally, one or two points from each collar were included where moss water content was in the range 5 to 6.5, again only from the summer measurement period. Points above 6.5 were not included in the analysis as linear regression was being used, and the relationship between moss water content and moss respiration (and therefore total respiration) was expected to be relatively linear only up to a water content of approximately 5 or 6, beyond which the relationship was expected to be zero order.

Values of total forest floor respiration were

standardized to the modelled respiration rate (from the exponential regression model) at a 15 cm soil temperature of 10°C (R_{10}) by dividing by each value of total respiration at a particular collar by the R_{10} for that collar. Linear multiple regression was carried out with the standardized respiration rates as the response variable, and 15 cm soil temperature and moss water content as the predictor variables.

3.4.2 Photosynthesis

3.4.2.1 Light Saturated Rate of Gross Photosynthesis

Gross forest floor photosynthesis (P_g) was calculated as

$$P_g = NEE - R_d \quad (3.6)$$

where NEE is net ecosystem exchange of CO_2 and R_d is dark respiration. Since there was some uncertainty in the measurement of incident PFD, light saturated rates of gross photosynthesis (as evidenced on a plot of P_g vs. incident PFD) were considered to be the best measure of comparison between collars, between moss types, and between measurement periods. In order to remove bias resulting from differences in the temperature at which light saturated rates of photosynthesis were measured, it was useful to evaluate the maximum carboxylation velocity of Rubisco ($V_{c,max}$) for each collar in each measurement period, as a measure of the maximum capacity for photosynthesis. For the purposes of

calculation of $V_{c,max}$, it was necessary to attribute all photosynthesis to moss, thereby ignoring the complexities introduced by the presence of vascular vegetation. This assumption was not unrealistic, particularly in spring and fall measurement periods, and particularly for collars in the feather moss community, as the leaf area index of vascular vegetation was only very high at two collars in the *Sphagnum* community in the summer measurement period. Because of this assumption, measured and modelled photosynthesis will be referred to as moss photosynthesis, bearing in mind that this is a simplification, as a portion of the observed photosynthesis would have been contributed by vascular vegetation where it was present. For each collar, a light saturated rate of gross photosynthesis, and the moss temperature associated with that rate, were used to calculate $V_{c,max}$ in each measurement period. For collars in the feather moss community, $V_{c,max}$ was evaluated from several different light saturated rates of gross photosynthesis, at a range of moss water contents, in order to evaluate the effect of moss water content on photosynthetic capacity. $V_{c,max}$ was calculated from the equation developed by Farquhar *et. al.* (1980):

$$A_v = V_{c,max} \frac{C_c - \Gamma^*}{C_c + K_c(1 + [O_2]/K_o)} - R_d \quad (3.7)$$

where A_v is the Rubisco-limited rate of net CO_2 assimilation, C_c is the concentration of CO_2 in the

chloroplast, $[O_2]$ is the ambient partial pressure of oxygen, K_c and K_o are the Michaelis-Menten constants for carboxylation and oxygenation of Rubisco, respectively, Γ^* is the CO_2 compensation partial pressure in the absence of dark respiration, and R_d is the measured rate of dark respiration. Since R_d had already been subtracted from the measured values of NEE in order to obtain values of gross photosynthesis, the equation from which $V_{c,max}$ was calculated simplified to

$$P_{g,v} = LAI_{tot} V_{c,max} \frac{C_c - \Gamma^*}{C_c + K_c(1 + [O_2]/K_o)} \quad (3.8)$$

where $P_{g,v}$ was the measured light saturated (Rubisco limited) gross photosynthetic rate, and LAI_{tot} was the sum of vascular plant LAI and moss SAI. The temperature sensitivities of Rubisco specificity (used in the calculation of Γ^*), Γ^* , $V_{c,max}$, K_c and K_o were all described by Q_{10} functions of temperature. See Appendix I for a list of the symbols and values used in the model.

It was necessary to determine a value of C_c in order to evaluate $V_{c,max}$. C_c was calculated from the $\delta^{13}C$ value of the moss in each season by rearranging the equation (Farquhar *et. al.* 1982, 1989)

$$\delta^{13}C_{plant} = \delta^{13}C_{source} - a - (b - a)(C_c/C_a) \quad (3.9)$$

where $\delta^{13}C_{plant}$ and $\delta^{13}C_{source}$ are the carbon isotope ratios of leaf tissue and source CO_2 , respectively, a is the fractionation associated with the slower diffusion of $^{13}CO_2$

compared to $^{12}\text{CO}_2$ (4.4‰, Craig 1953), b is the net fractionation associated with carboxylation (27.5‰, Lloyd and Farquhar 1994) and C_c and C_a are the chloroplastic and ambient concentrations of CO_2 , respectively. The carbon isotope ratio of the source CO_2 was set at $\delta^{13}\text{C}_{\text{source}} = -8.0\text{‰}$, however because soil respired CO_2 is depleted in $^{13}\text{CO}_2$, and because the moss are at located at ground level, this value may be higher than the actual $\delta^{13}\text{C}$ of the source CO_2 for moss photosynthesis (Farquhar *et. al.* 1989).

3.4.2.2 Effects of moss water content on moss photosynthetic capacity

In order to determine the effects of moss water content on moss photosynthetic capacity, the maximum carboxylation velocity of Rubisco ($V_{c,\text{max}}$) was evaluated at each collar on more than one date in each measurement period. For each collar, the maximum value of $V_{c,\text{max}}$ obtained in each measurement period represented the potential physiological capacity for photosynthesis in that measurement period. Each value of $V_{c,\text{max}}$ calculated for a given collar was compared to the maximum $V_{c,\text{max}}$ obtained for the same collar in the same measurement period, in order to evaluate the effect of moss water content on moss photosynthetic capacity.

3.4.2.3 Light Limited Rate of Gross Photosynthesis

For the purposes of scaling of gas fluxes (section 4.5.1), it was necessary to obtain some estimate of the response of photosynthesis to incident PFD. The initial slope of the response of gross photosynthesis to incident PFD was therefore calculated for two feather moss collars, and for all *Sphagnum* collars, in the summer measurement period. The response of gross photosynthesis to incident PFD was assumed to be linear in the range 0 - 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Since there was uncertainty in the measured PFD, geometric mean regression (Sokal and Rohlf 1981) was used to estimate the initial slope of gross photosynthesis vs. incident PFD. The average initial slope of the light response of gross photosynthesis for feather moss collars was calculated as the average of the initial slopes at collars 6 and 7 in the summer measurement period. For *Sphagnum* collars, the average initial slope of the response of gross photosynthesis to incident PFD was calculated as the average of the initial slopes at all *Sphagnum* collars in the summer measurement period. For both communities, the slope of the light response of gross photosynthesis was assumed constant in all seasons, bearing in mind that this is an oversimplification, as the slope would be affected by temperature and CO_2 concentration (Ehleringer and Björkman 1977).

3.4.2.4 Modelled Rate of NEE

For both communities, the rate of respiration was calculated from Model B. Average values from all independent microsites (some collars represented the same micro-environment) were used for $R_{10, \text{deep}}$ and $R_{10, \text{shallow}}$. $R_{10, \text{shallow}}$ was expressed on a ground area basis.

The modelled rate of gross photosynthesis for feather moss was described by the minimum of the straight line describing the initial slope of gross photosynthesis vs. PFD, and the maximum rate of photosynthesis defined by $V_{c, \text{max}}$. Thus the light limited rate of gross photosynthesis varied only as a function of the calculated slope (the intercept was set to zero) and the incident PFD, whereas the light saturated rate varied as a function of temperature. This led to variation in the light saturation point with temperature, with light saturation occurring typically near a PFD of $150 \mu\text{mol m}^{-2} \text{s}^{-1}$. For the *Sphagnum* community, the rate of gross photosynthesis was described by the minimum of three lines, rather than the minimum of two lines as in feather moss. From a PFD of 0 to $150 \mu\text{mol m}^{-2} \text{s}^{-1}$, the rate of gross photosynthesis followed the calculated initial slope (again the intercept was set to zero). Above a PFD of $500 \mu\text{mol m}^{-2} \text{s}^{-1}$, the rate of gross photosynthesis was set by $V_{c, \text{max}}$. Between PFDs of $150 - 500 \mu\text{mol m}^{-2} \text{s}^{-1}$, gross photosynthesis followed the straight line joining the predicted light limited rate at $150 \mu\text{mol m}^{-2} \text{s}^{-1}$, and the

predicted light saturated rate at the maximum daily temperature, and $500 \mu\text{mol m}^{-2} \text{s}^{-1}$. In the spring and fall measurement periods, it was necessary to constrain the slope of this line to ≥ 0 . The use of this third line improved prediction of light limited rates of gross photosynthesis in *Sphagnum* in the summer measurement period because curvature in the response of gross photosynthesis to incident PFD was strong in the range of PFD from 150 - $500 \mu\text{mol m}^{-2} \text{s}^{-1}$.

3.4.2.5 Meteorological Data Used to Model NEE

Models of respiration and gross photosynthesis were referenced to meteorological conditions representative of snow free and relatively cloud-free (on the basis of the strength of sunflecking observed in incident PFD in the feather moss understory) days in each measurement period; day 134 in the spring measurement period, day 206 in the summer measurement period, and day 278 in the fall measurement period.

For both communities, respiration rates were referenced to temperatures recorded at the meteorological station in the feather moss community understory. For both communities, $R_{10,\text{deep}}$ was referenced to soil temperature at 15 cm. For the feather moss community, $R_{10,\text{shallow}}$ was referenced to moss temperature. For the *Sphagnum* community, $R_{10,\text{shallow}}$ was referenced to air temperature.

For both communities, maximum photosynthetic rates were

referenced to temperatures recorded at the meteorological station in the feather moss community understorey. For the feather moss community, gross photosynthesis was referenced to moss temperature, whereas for the *Sphagnum* community, gross photosynthesis was referenced to air temperature.

Incident PFD recorded near each collar on one day in the summer measurement period was used as a basis for the PFD to which light limited gross photosynthesis was referenced. For the feather moss community, predicted light limited photosynthetic rates for day 206 were referenced to averages of incident PFD recorded near each feather moss collar on day 206. For the *Sphagnum* community, predicted light limited photosynthetic rates for day 206 were referenced to averages of incident PFD recorded near each *Sphagnum* collar on day 209. For the spring and fall measurement periods, the PFD to which light limited photosynthetic rates were referenced was the same as for the summer measurement period, multiplied by a constant of proportionality relating incident PAR at the earth's surface (calculated from standard equations, see Jones 1992) for the appropriate two days.

3.4.3 Correlation Analysis

In order to help explain the observed spatial variability in the capacity of the forest floor for respiration and photosynthesis, a correlation analysis was

carried out on a series of variables measured at each collar. Some of the variables were constant across all measurement periods, and some varied between measurement periods. One analysis was made for each of the forest floor communities in each measurement period, for a total of six analyses. For the feather moss community, the variables included in each analysis were $V_{c,max}$, moss SAI, total vascular plant LAI, average daily PAR intensity, $R_{10,tot}$, $R_{10,deep}$, $R_{10,shallow}$, total tree basal area within 1 m of any collar edge, depth of live (green and brown) moss, depth to the organic/mineral soil interface, and average moss water content. For the *Sphagnum* community, the variables included in each analysis were the same as for the feather moss community with the following exceptions: moss SAI could not be evaluated, and so was excluded; the depth of live moss was difficult to evaluate, and so was excluded; depth to the organic/mineral soil interface was replaced by the average depth to the water table, since the depth of the aerated organic layer is more important than the total depth of organic matter to soil respiration in peatlands (Moore and Knowles 1989; Luken and Billings 1985). In the spring, average depth to the water table was not measured, and so could not be included. Average daily PFD for the summer was calculated from the PFD sensors set out near each collar (cf. section 3.2.4). Standard equations for solar radiation at the earth's surface were used to calculate above-canopy

PFD during the summer period, and the proportion of above-canopy PFD reaching the understorey was calculated for each collar. A constant relationship between above-canopy and understorey PFD was assumed, and used to calculate an approximate average incident PFD for each collar in the spring and fall measurement periods.

3.4.4 Evapotranspiration

The forest floor conductance to water vapour was calculated by first determining a total conductance to water vapour from the relationship

$$E = g_{t,w} \left[\frac{e_i - e_a}{P} \right] \quad (3.9)$$

where E ($\text{mmol m}^{-2} \text{s}^{-1}$) was evapotranspiration (measured in the dark), $g_{t,w}$ ($\text{mmol m}^{-2} \text{s}^{-1}$) was the total conductance to water vapour, e_i (kPa) was the equilibrium vapour pressure at the moss surface, e_a (kPa) was the ambient vapour pressure in the understorey, and P (kPa) was the total atmospheric pressure. Evapotranspiration measured in the dark was used instead of in the light as evapotranspiration was found to be positively correlated to incident PFD, which is inconsistent with the equations used to calculate conductance. The effect of PFD on the flux of water vapour was eliminated by using values measured in the dark. Ambient vapour pressure, e_a , was calculated from ambient air temperature and relative humidity. Equilibrium vapour

pressure at the moss surface, e_i , was assumed equal to the saturation vapour pressure at air temperature. Total conductance to water vapour flux is the reciprocal of the total resistance to water vapour flux, $(1/g_{t,w})$, which is equal to the sum of boundary layer resistance at the moss surface $(1/g_{bi})$ and a forest floor resistance term $(1/g_{ff})$:

$$1/g_{t,w} = 1/g_{bi} + 1/g_{ff}. \quad (3.10)$$

The boundary layer conductance inside each chamber depended on the total volume of the chamber, the angle and roughness of the moss surface, the presence or absence of vascular vegetation, the orientation of any vascular vegetation present, and the fan speed. Of these factors, the fan speed alone did not change between collars, however the other factors were in general similar between collars. At any one collar, boundary layer conductance inside the chamber can be assumed to have been constant. Where the total conductance reached a maximum (determined from a plot of $g_{t,w}$ vs. moss water content), g_{ff} was assumed infinite, leaving $g_{t,w} = g_{bi}$. In this way the boundary layer conductance for a collar could be evaluated from the maximum total conductance, and reductions in total conductance attributed to changes in forest floor conductance.

CHAPTER 3 TABLES

Table 3.1. Number of separate visits to each collar in each season. In the summer, collars 5, 6, 9, 10, 11, 12, 15 and 17 were visited four times each in the course in one of two twenty four hour periods. Visits where snow partially or fully covered the ground were not included.

Community	Collar	Measurement period		
		Spring	Summer	Fall
Feather moss	1	4	5	3
Feather moss	2	4	4	3
Feather moss	3	3	5	3
Feather moss	4	3	4	3
Feather moss	5	4	7	3
Feather moss	6	4	7	3
Feather moss	7	3	4	3
Feather moss	8	3	-	-
Feather moss	9	6	7	3
Feather moss	10	7	8	3
<i>Sphagnum</i>	11	5	6	3
<i>Sphagnum</i>	12	6	6	3
<i>Sphagnum</i>	13	6	4	3
<i>Sphagnum</i>	14	7	4	3
<i>Sphagnum</i>	15	2	6	3
<i>Sphagnum</i>	16	1	4	3
<i>Sphagnum</i>	17	-	6	3
<i>Sphagnum</i>	18	-	4	3

Table 3.2. Variability in flux of CO_2 during dark respiration in both feather moss and *Sphagnum* communities in spring, summer and fall measurement periods. Values are averages $\pm$ s.d. The number of comparisons is given in brackets.

	Measurement Period		
	Spring	Summer	Fall
Slope (dCO_2/dt)	0.07 ± 0.04 (162)	0.37 ± 0.2 (342)	0.12 ± 0.06 (306)
C.V. of slope (%)	7.4 ± 5.3 (162)	2.2 ± 2.0 (342)	2.8 ± 0.9 (306)
% difference in slope between 2 consecutive measurements	13.8 ± 12.6 (43)	6.1 ± 5.3 (58)	5.4 ± 3.7 (51)

CHAPTER 4

RESULTS

4.1 Environmental conditions

The main variables affecting respiration and photosynthesis differed substantially between measurement periods. Predictable seasonal changes in temperature and light conditions are reflected in temperature and light conditions recorded during gas flux measurements (Table 4.1). In both feather moss and *Sphagnum* communities, average air and moss temperatures in the summer measurement period were approximately 10 to 15 °C greater than those in the spring and fall measurement periods. Average moss temperature was similar to air temperature. Soil temperature (at 15 cm) showed a lag in seasonal change compared to air temperature, with temperatures near freezing persisting in the spring, and relatively warm temperatures persisting in the fall. PFD was greater, and fluctuated more widely in the *Sphagnum* community than in the feather moss community. In both communities, PFD was greatest in the summer, and least in the fall measurement periods. Average above-canopy PFD between 10:00 and 16:00, for all days in each measurement period (calculated from standard equations, for 53.99°N, 105.12°W, Jones 1992) is given for comparison. The above-canopy PFD is also reduced by a factor of 0.7, in order to simulate the reduction in light intensity caused by the chamber.

4.2 Respiration

In the following discussion, respiration rates are given a positive (+) sign, recognizing that in the context of NEE, respiration acts in the opposite direction to photosynthesis

4.2.1 Feather moss community

4.2.1.1 Models

In the feather moss community, forest floor dark respiration rates showed a strong exponential increase with temperature (Figure 4.1). Three models were tested for goodness of fit to the observed temperature response of dark respiration at each collar in the feather moss community. Each of the models explained a relatively high proportion of the variability in measured dark respiration rate (Table 4.2).

The dark respiration rate was best described best by exponential least squares regressions of measured dark respiration rate against soil temperature at 15 cm (Figure 4.2), despite its having a lower R^2_{adj} , than the other two models. The exponential regressions explained an average of $85 \pm 15\%$ ($R^2_{adj} \pm \text{s.d. at } n = 9 \text{ collars}$) of the variability in dark respiration rate (Table 4.2). The residuals of the model (plotted against soil temperature) indicated a good fit of the model at low soil temperatures, but showed a tendency for the model to underestimate respiration rate at

high temperature (Figure 4.3). There was also a slight increase in the variance with increasing soil temperature. Predicted values corresponded closely to observed values, deviating slightly in the mid-range of values of respiration rate (Figure 4.4). The exponential regression model therefore provided a relatively unbiased estimate of dark respiration as a function of soil temperature at 15 cm, for the range of temperature from approximately 0 to 20°C.

A good fit also existed between measured forest floor dark respiration rate and a model of soil respiration rate that effectively produced a decrease in the energy of activation of respiration with increasing soil temperature (Model A) (Figure 4.5). Model A explained an average of $88 \pm 8\%$ ($R^2_{adj} \pm \text{s.d. at } n = 9 \text{ collars}$) of the variability in dark respiration rate (Table 4.2). While this proportion was greater than that explained by the exponential regressions, the residuals of the model (plotted against soil temperature at 15 cm) showed a tendency for the model to overestimate the respiration rate at low soil temperatures, and underestimate the respiration rate at high soil temperatures (Figure 4.6).

A good fit also existed between measured forest floor dark respiration rate and a two-term model of dark respiration rate, with one term referenced to moss temperature, and one term referenced to soil temperature at 15 cm (Model B) (Figure 4.7). Model B explained an average

of $86 \pm 9\%$ ($R^2_{adj} \pm \text{s.d.}$ at $n = 9$ collars) of the variability in dark respiration rate (Table 4.2). While this proportion was also greater than that explained by the exponential regressions, the residuals of the model (plotted against soil temperature at 15 cm) again showed a tendency for the model to overestimate the respiration rate at low soil temperatures, and underestimate the respiration rate at high soil temperatures (Figure 4.8). This was seen in a plot of predicted vs observed respiration, where despite an overall close fit, the points were slightly above the 1:1 line at low values of forest floor respiration, and slightly below the 1:1 line at high values of respiration (Figure 4.9).

4.2.1.2 Diurnal cycle

Forest floor dark respiration was measured at 6 hour intervals between approximately 14:00 hours on day 211 and 6:00 hours on day 212 in the summer measurement period, at four collars in the feather moss community. At collar 9 (Figure 4.10), the maximum respiration rate occurred in the evening (~19:30), and the minimum respiration rate occurred in the early morning (~5:45). Of the four collars measured over a diurnal cycle in the feather moss community, two showed a peak in respiration in the evening (eg. Figure 4.10), and two showed a peak in respiration at midday (data not shown). At the meteorological station in the feather moss understorey (located within 15 m of all four collars

measured over the diurnal cycle), soil temperature measured at a depth of 15 cm reached a minimum at 9:00, while air temperature reached a minimum at 6:00 (data not shown). Forest floor respiration predicted by the exponential model followed observed respiration closely (Figure 4.10 B), however, the observed points represented a portion of those used to parameterize the model.

4.2.2 *Sphagnum* community

4.2.2.1 Models

In general, collars in the *Sphagnum* community showed more variability in the response of respiration to soil temperature, than collars in the feather moss community (compare Figure 4.11 and Figure 4.1). The same three models parameterized for the feather moss community were tested for goodness of fit to the observed rates of forest floor dark respiration at each collar in the *Sphagnum* community. Each of the models explained a relatively high proportion of the variability in measured dark respiration rate (Table 4.3).

The dark respiration rate was best described by a two-term model, with one term referenced to moss temperature, and one term referenced to soil temperature at 15 cm (Model B) (Figure 4.12). Importantly, Model B accounted for what might otherwise have been construed as noise in a plot of forest floor respiration rate versus soil temperature at 15

cm. Model B explained an average of $91 \pm 7\%$ ($R^2_{adj} \pm \text{s.d.}$ at $n = 8$ collars) of the variability in dark respiration rate (Table 4.3). The residuals of Model B (plotted against soil temperature at 15 cm) showed a tendency for the model to overestimate the respiration rate at low soil temperatures, however this bias was removed at high soil temperatures (Figure 4.13). There was a slight increase in the variance of the residuals as temperature increased. Model B provided a close fit to observed respiration rates, however predicted values were slightly above measured values at low values of respiration (Figure 4.14).

A relatively good fit existed between measured forest floor dark respiration rate and a model of soil respiration rate that effectively produced a decrease in the energy of activation of respiration with increasing soil temperature (Model A) (Figure 4.15). Model A explained an average of $82 \pm 16\%$ ($R^2_{adj} \pm \text{s.d.}$ at $n = 8$ collars) of the variability in dark respiration rate (Table 4.3). The residuals of Model A (plotted against soil temperature at 15 cm) showed a tendency for Model A to overestimate respiration at low soil temperatures, and a marked lack of homogeneity of variance (Figure 4.16).

Exponential least squares regression of measured dark respiration rate against soil temperature at 15 cm provided a reasonable estimate of forest floor respiration (Figure 4.17). The exponential regressions explained an average of

$84 \pm 10\%$ ($R^2_{adj} \pm \text{s.d. at } n = 8 \text{ collars}$) of the variability in dark respiration rate (Table 4.3). The residuals of the model (plotted against soil temperature) were distributed relatively independently, however similar to Model A, there was a marked lack of homogeneity of variance (Figure 4.18). This was very apparent in a plot of predicted versus observed values (Figure 4.19), where it was clear that the ability of the model to accurately predict measured forest floor respiration decreased as the respiration rate increased.

4.2.2.2 Diurnal cycle

Forest floor dark respiration was measured at 6 hour intervals between approximately 12:00 hours on day 202 and 6:00 hours on day 203 in the summer measurement period, at four collars in the *Sphagnum* community. At collar 11, the maximum measured respiration rate occurred at midday (~12:30), and minimum rate occurred in the early morning (~6:00) (Figure 4.20). Of the four collars measured over a diurnal cycle in the *Sphagnum* community, two showed a peak in respiration at midday (eg. Figure 4.20), and two showed a peak in respiration in the evening (data not shown). Forest floor respiration predicted by Model B followed observed respiration closely (Figure 4.20 B), however the observed points represented a portion of those used to parameterize the model.

4.2.3 Average R_{10} and Q_{10} in feather moss and *Sphagnum* communities

There was considerable variation in the absolute rate of dark respiration, and the temperature response of dark respiration, between collars. This was seen in collective plots of dark respiration vs soil temperature for each community (Figure 4.21). In these plots, the scarcity of data points between approximately 6 and 8°C in the feather moss community (Figure 4.21 A), and the absence of data points between 6 and 10°C in the *Sphagnum* community (Figure 4.21 B) emphasized the differences in soil temperature between measurement periods (cf. Table 4.1), since data points above approximately 8°C corresponded to respiration measurements made during the summer measurement period. Average respiration at 10°C (R_{10} , averaged from exponential regressions at each collar) tended to be greater in the feather moss community ($3.0 \pm 1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$) than in the *Sphagnum* community ($2.2 \pm 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$) (Table 4.4). In the feather moss community, a very high Q_{10} (> 5) was calculated for three collars. These three sites corresponded to the sites with the three shallowest organic horizons, such that the measurement of soil respiration at 15 cm was made just below the organic-mineral soil interface. This was undesirable, as the temperature measurement was intended to represent the temperature of the respiratory substrate (ie. organic matter). Since the

calculation of Q_{10} was particularly sensitive to errors in soil temperature, these three collars were not included in the calculation of the average Q_{10} for the feather moss community, reducing the number of independent microsites for this calculation from 6 to 4. Average Q_{10} (averaged from exponential regressions at each collar) was greater in the feather moss community (3.8 ± 0.6) than in the *Sphagnum* community (2.7 ± 0.5) for the range of soil temperatures observed (approximately 0 to 20°C) (Table 4.4).

4.2.4 Contribution of shallow and deep strata to total forest floor respiration

Bearing in mind the limitations of Model B described above, the two parameters estimated by Model B provide an opportunity to partition forest floor dark respiration into components originating from shallow and deep forest floor strata. For all collars in both community types, the rate of respiration at 10°C of the shallow stratum, $R_{10, \text{shallow}}$, was less than that of the deep stratum, $R_{10, \text{deep}}$. The average $R_{10, \text{shallow}}$ in the feather moss community was less than in the *Sphagnum* community, while the average $R_{10, \text{deep}}$ in the feather moss community was greater than in the *Sphagnum* community (Table 4.5). The average proportion of total respiration originating from the shallow stratum (respiration in both strata standardized to 10°C) is greater in the *Sphagnum* community than in the feather moss community (Table 4.5).

The ratio of the temperature of the shallow stratum (represented by moss temperature) to soil temperature at 15 cm changes diurnally (Figure 4.22), and seasonally (cf. Table 4.1). The effect of this ratio on the percent contribution of the shallow stratum to total forest floor respiration will be examined in section 4.5.1.

4.2.5 Effects of Moss Water Content on Total Respiration in the Feather Moss Community

In spite of moss water content limitation, the positive relationship between total forest floor respiration and 15 cm soil temperature was evident for the respiration rates standardized to the R_{10} from exponential regression (Figure 4.23 A). The relationship between respiration rate and moss water content was less evident (Figure 4.23 B), though in both Figure 4.23 A and B there appeared to be a slight downward concavity. The fact that there was a negative correlation (Pearson correlation coefficient $r = -0.27$) between moss water content and 15 cm soil temperature accounts at least in part for this observation, as when soil temperature was high (stimulating respiration), water content would have been low (inhibiting respiration), and vice versa. The linear multiple regression model of total forest floor respiration vs 15 cm soil temperature and moss water content was highly significant ($p < 0.0001$), and the slope of both predictor variables was significantly

different from zero (Table 4.6). Residual plots for soil temperature and moss water content indicate that the linear approximation is relatively unbiased (Figure 4.24). A scarcity of values above approximately 12°C, and one very negative residual (bottom right of Figure 4.24 A) give an appearance of downward concavity to the soil temperature residuals, however downward concavity is unlikely here, as over the full range of temperatures experienced in this study, respiration was shown to respond to soil temperature exponentially (ie. concave upwards). A case could be made for downward concavity of the moss water content residuals, or for an effective decrease in the slope with increasing moss water content (Figure 4.24 B). This would not be unrealistic, as above a water content of approximately 5 or 6 (fw/dw) the relationship between moss water content and moss respiration was expected to be zero order. A curvilinear relationship between feather moss photosynthetic capacity and moss water content will be demonstrated in section 4.3.2, and it is reasonable to expect that the effects of moss water content on moss respiration (for the process of desiccation, Williams and Flanagan 1997) would in fact follow a similar curvilinear relationship.

4.3 Photosynthesis

4.3.1 Seasonal change in vascular plant leaf area index and moss photosynthetic capacity

In both communities, the LAI of vascular plants was greatest in the summer measurement period (Figure 4.25). The LAI of vascular plants increased more dramatically in the *Sphagnum* community in the summer measurement period compared to the feather moss community.

The maximum carboxylation velocity of Rubisco ($V_{c,max}$) for the moss in each collar was determined in each measurement period, from light saturated rates of gross photosynthesis (Figure 4.26 A-B) (cf. Materials and Methods section 3.5.2). In the summer measurement period, the average $V_{c,max}$ was significantly greater (student t-test, $p < 0.05$) for *Sphagnum* than for feather moss (Figure 4.27). The $V_{c,max}$ of *Sphagnum* was also significantly greater (student t-tests, $p < 0.05$) in the summer than in the spring and fall measurement periods. The effect of the seasonal change in moss photosynthetic capacity on potential rates of CO_2 exchange in each measurement period will be examined in section 4.5.1.

4.3.2 Effects of moss water content on moss photosynthetic capacity

The average moss water content for *Sphagnum* was greater than that for feather moss in all measurement

periods (Figure 4.28). *Sphagnum* water content also changed less between measurement periods than feather moss water content (Figure 4.28), and rehydration following rain events was not as apparent for *Sphagnum* as for feather moss (Figure 4.29 A-C).

The optimum water content (fresh weight/dry weight) for photosynthesis in *Sphagnum fuscum* and *Sphagnum sect. acutifolia* has been reported as approximately 7 (Silvola 1990; Williams and Flanagan 1996). Since a moss water content below 7 was only recorded on one occasion for *Sphagnum* (moss water content 6.8), it was reasonable to assume that photosynthetic capacity in *Sphagnum* was unaffected by low water content in any measurement period.

Feather moss water content regularly fell below an average reported optimum of approximately 6 (fresh weight/dry weight) (Skre and Oechel 1981; Williams and Flanagan 1996) in all measurement periods, and rehydration was evident following rain events (Figure 4.29). The CO₂ limited photosynthetic capacity of feather moss increased with increasing moss water content until it reached a maximum at a moss water content of approximately 5 (fresh weight/dry weight) (Figure 4.30). Values of $V_{c,max}$ shown are from all measurement periods, from all collars for which the appropriate data existed.

4.3.3 Light response of photosynthesis

An estimate of the initial slope of the light response of gross photosynthesis was obtained for all *Sphagnum* collars in the summer measurement period, and for two feather moss collars in the summer measurement period. The response of photosynthesis to incident PFD in the range 0 - 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was determined from plots of gross photosynthesis versus incident PFD (Figure 4.31 A-B). In the summer measurement period, the average initial slope of the light response of gross photosynthesis was greater for *Sphagnum* (0.024) than for feather moss (0.018), however there were too few data to make a strict comparison between the moss types.

4.3.4 Carbon isotope ratio of moss photosynthetic tissue

The $\delta^{13}\text{C}$ values for feather moss were lower than those for *Sphagnum* (Figure 4.32). The less negative $\delta^{13}\text{C}$ in *Sphagnum* compared to feather moss indicated that *Sphagnum* had a consistently lower chloroplastic CO_2 concentration (C_c) than feather moss, during the time periods when CO_2 uptake was greatest (Farquhar et. al. 1989). Greater light intensity (Table 4.1), greater photosynthetic capacity (Figure 4.27) and a moss water content consistently favourable for photosynthesis (Figure 4.28) in *Sphagnum* would all contribute to a lower C_c in *Sphagnum*.

The decreased $\delta^{13}\text{C}$ in feather moss in the summer

measurement period indicated that C_i was typically higher during photosynthesis in the summer compared to the spring and fall measurement periods. This was consistent with water content limitation of photosynthesis in the summer, despite an increase in maximum (not limited by moss water content) photosynthetic capacity. For *Sphagnum*, the increase in $\delta^{13}\text{C}$ in the summer measurement period was consistent with an increase in the photosynthetic capacity of the moss, which would have contributed to a reduction in C_i during photosynthesis.

4.4 Spatial Variability in CO_2 flux

4.4.1 Feather moss community

For a given location at the feather moss forest floor, there was a significant negative correlation between total respiration at a uniform soil temperature of 10°C , and the average PFD incident at the forest floor, in all measurement periods (Table 4.7). Since respiration in the dark was independent of incident PFD, the correlation that existed between these two variables was likely the result of an indirect effect of PFD on dark respiration, via another variable or variables that affected the effective mass of carbon available as respiratory substrate. In all measurement periods, PFD was also significantly negatively correlated with the total thickness of organic soil ($\text{depth}_{\text{org}}$) and the total basal area of trees within

approximately 1 m. In the summer measurement period, PFD was significantly negatively correlated to vascular LAI. Average incident PFD thus exerted a large influence on most of the variables that were expected to influence forest floor dark respiration.

In the summer and fall measurement periods, there was a significant negative correlation between moss shoot area index and moss $V_{c,33x}$. In the summer measurement period, moss $V_{c,33x}$ was significantly positively correlated to average incident PFD. Vascular LAI was significantly positively correlated to the total thickness of organic soil in all measurement periods, and to the total tree basal area within 1 m in the summer measurement period. In the summer measurement period, vascular LAI was significantly negatively correlated to average incident PFD. A significant positive correlation existed between the $\delta^{13}C$ value of the moss, and the total thickness of organic soil, in the spring and fall measurement periods.

4.4.2 *Sphagnum* community

For a given location at the *Sphagnum* forest floor, there was a significant positive correlation between total respiration at a uniform soil temperature of 10°C ($R_{10,tot}$), and the total basal area of trees within 1 m, in all measurement periods (Table 4.8). In the fall measurement period, there was a significant positive correlation between

$R_{g,tot}$ and vascular LAI. Tree basal area was also significantly positively correlated to vascular LAI in all measurement periods.

In the spring measurement period, there was a significant negative correlation between $V_{c,max}$ and vascular LAI, and in the summer measurement period, there was a significant positive correlation between $V_{c,max}$ and the $\delta^{13}C$ value of the moss. In the summer and fall measurement periods, tree basal area was significantly negatively correlated to the $\delta^{13}C$ value of the moss.

4.5 Modelling Diurnal variation in CO₂ flux

The environmental variables that control net CO₂ exchange at the forest floor change substantially over 24 hours, and over the growing season. The amount of photosynthetically competent plant material (eg. Figure 4.25), and the physiological capacity of this vegetation for photosynthesis (eg. Figure 4.27) also change over the growing season. In order to present the effects of these many changes on the net flux of CO₂ at the forest floor over time, it was instructive to reference a model of gross photosynthesis, and a model of forest floor respiration (Model B was used for both feather moss and *Sphagnum* collars) to meteorological data recorded in the feather moss community understorey in each measurement period. In what follows, all CO₂ flux (photosynthesis and respiration)

reported for the feather moss community assumes that the feather moss is well hydrated. Other assumptions of the photosynthesis model are described in Materials and Methods section 3.4.2. One day in each measurement period was chosen as an example of a typical day in that measurement period. Air, moss and soil temperatures in the feather moss understorey are shown for days 134 (spring), 206 (summer) and 278 (fall), in Figure 4.33 A - C. PFD in the understorey of each community, on the same days, is shown in Figure 4.34 - 4.35.

4.5.1 Feather moss community

On day 134 in the spring measurement period, the maximum modelled value of gross photosynthesis for feather moss was approximately $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 4.36 A). PFD was saturating (ie. $> 150 \mu\text{mol m}^{-2} \text{s}^{-1}$) for most of the period between 11:00 and 16:00 (Figure 4.34 A). There was a relatively small change in the magnitude of total forest floor respiration over the 24 hour period, and total respiration was approximately equal to the maximum rate of gross photosynthesis. Maximum CO_2 uptake occurred between approximately 13:00 and 17:00 hours. Between 10 and 20 % of total respiration originated in the shallow stratum (Figure 4.36 B). There was a sharp increase in the contribution of the shallow stratum to total respiration between approximately 10:00 and 12:00.

On day 206 in the summer measurement period, maximum gross photosynthesis was higher than in the spring measurement period (Figure 4.37 A). Understorey PFD was nearly identical to that on day 134 (Figure 4.34 B). Maximum total respiration, and the amplitude of the diurnal change in total respiration rate were greater than in the spring measurement period. Because of the increase in both photosynthesis and respiration, maximum net CO_2 flux remained at approximately zero. The proportion of total respiration originating in the shallow stratum was slightly reduced compared to the spring measurement period. Again there was a sharp increase in the proportion of total respiration contributed by the shallow stratum early in the day, however the increase occurred earlier in the day than in the spring (Figure 4.35 B). For approximately 30 minutes near midday, the respiration rate of the shallow stratum rose to over 20% of the total respiration rate, in response to a brief spike in moss temperature.

On day 278 in the fall measurement period, gross photosynthesis reached approximately the same maximum as for day 134 in the spring (Figure 4.38). The relatively high photosynthetic capacity of feather moss in the fall (Figure 4.27) permitted the maintenance of maximum gross photosynthetic rates above $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ in spite of lower moss temperature than in the summer (Figure 4.33), and lower light intensities and a shorter photoperiod than in the

spring and summer measurement periods (Figure 4.34). PFD was saturating for a slightly shorter period of time compared to the spring and summer measurement periods. Total respiration rate was intermediate between the spring and summer measurement periods, and the contribution of the shallow forest floor stratum to total forest floor respiration was lowest in the fall measurement period (Figure 4.38 B).

The maximum calculated rate of photosynthesis in each measurement period is shown as function of temperature for a range of moss temperatures likely to have occurred in each measurement period (Figure 4.39). The rate of gross photosynthesis of feather moss is not likely to have exceeded $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the spring and fall periods, while in the summer measurement period, it is conceivable that gross photosynthesis might have exceeded $4 \mu\text{mol m}^{-2} \text{s}^{-1}$. However, the rates shown assume adequate moss hydration, and the moss were less likely to be adequately hydrated in the summer than in the spring and fall. Since the rates shown are for conditions of light saturation, they are most likely to have occurred at midday.

4.5.2 *Sphagnum* community

On day 134 in the spring measurement period, the maximum gross photosynthesis of *Sphagnum* reached approximately $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 4.40 A), which was

nearly twice the value for feather moss on the same day. PFD was saturating (ie. greater than $500 \mu\text{mol m}^{-2} \text{s}^{-1}$) for almost the entire period from 10:00 to 17:00 (Figure 4.35 A), and the *Sphagnum* forest floor was a net sink of CO_2 for most of the day. The amplitude of diurnal change in total respiration was greater in *Sphagnum* than in feather moss. The greater sensitivity of total respiration to diurnal temperature change was a result of a greater proportion of total respiration originating in the shallow forest floor stratum (Figure 4.40 B). Also, respiration of the shallow stratum in *Sphagnum* was referenced to air temperature (cf. section 3.4.2.5), which may have a greater amplitude of diurnal change than the temperature of the moss in the spring and fall measurement periods (eg. Figure 4.33 A, C). During the night the shallow stratum contributed approximately 20 % of total forest floor respiration, however during most of the light period (10:00 to 17:00), its contribution stayed constant at between 55 and 60 % of the total. Similar to the feather moss community, there was a sharp increase in the proportion of total respiration originating from the shallow stratum relatively early on in the day.

On day 206 in the summer measurement period, the *Sphagnum* forest floor was a net sink of CO_2 for most of the day, despite an increase in total respiration compared to the spring measurement period. The maximum rate of gross

photosynthesis was greater than $6 \mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 4.41 A), which was much greater than the rate of gross photosynthesis of the feather moss forest floor on the same day. The maximum contribution of the shallow stratum to total forest floor respiration (occurring in midday) was between 40 and 45 %, while the minimum contribution (occurring in early morning) was approximately 15 % (Figure 4.41 B).

On day 278 in the fall measurement period, net CO_2 exchange of the *Sphagnum* forest floor was approximately zero at midday (Figure 4.42 A). This was slightly greater than the net CO_2 exchange of the feather moss forest floor on the same day. PFD was saturating for most of the period between 10:00 and 15:00, though on average it was much reduced compared to the spring and summer measurement periods (Figure 4.35 C). The maximum and minimum contributions of the shallow stratum to total forest floor respiration were similar to the values for day 206, though total respiration was considerably less than in the summer measurement period.

The maximum calculated rate of photosynthesis in each measurement period is shown as function of temperature for a range of moss temperatures likely to have occurred in each measurement period (Figure 4.43 A-C). The rate of gross photosynthesis for *Sphagnum* would typically have reached $2 \mu\text{mol m}^{-2} \text{s}^{-1}$ on warm days in the spring and fall measurement periods, while in the summer, gross photosynthesis can be

expected to have regularly exceeded $7 \mu\text{mol m}^{-2} \text{s}^{-1}$.

4.5.3 Comparison of modelled values to averages of discrete measurements

Averages of CO_2 flux measurements made in each measurement period are shown in Figure 4.44 A-C, and the environmental conditions associated with those measurements were given in Table 4.1. The values shown in Figure 4.44 represent daytime (between approximately 10:00 and 17:00) conditions during each measurement period. Comparing the averages of measured values to modelled values between the hours of approximately 10:00 - 17:00 can help locate any systematic errors in modelled values, and identify limitations imposed by the assumptions of the model.

It can be expected that the model will predict a higher rate of gross photosynthesis than the measured values, for two reasons. First, light conditions inside the chamber were always reduced compared to natural light conditions, because light had to pass through the acrylic chamber top before reaching the PFD sensor, and the moss. PFD inside the chamber was typically approximately 70% of that outside the chamber. Therefore fluxes that were measured under conditions of light limitation should be multiplied by a factor of between 1 and 1.4 in order to be comparable to modelled fluxes. Second, and important only in the feather moss community, modelled values of gross photosynthesis

assume no moisture limitation, whereas measured averages include measurements made when moss water content was limiting. This is important to modelled rates of gross photosynthesis in the summer measurement period. Since the average feather moss water content in the summer measurement period was approximately 3.5, modelled values should be multiplied by a factor of approximately 0.7 (cf. Figure 4.28) in order to account for the effects of moss water content on photosynthetic capacity.

With this in mind, for the feather moss community, there was relatively good agreement between modelled gross photosynthesis and the average measured gross photosynthesis, in all measurement periods. Modelled values were above average measured values in all measurement periods, as expected. The difference between the average measured value and the average modelled value between 10:00 and 17:00 was greatest in the summer measurement period, where the average measured value of gross photosynthesis was approximately one half of the maximum modelled daytime value. Modelled values dropped to as low as approximately $0.25 \mu\text{mol m}^{-2} \text{s}^{-1}$ in mid-afternoon, and the average modelled gross photosynthetic rate between 10:00 and 17:00 was clearly below $2 \mu\text{mol m}^{-2} \text{s}^{-1}$. A further correction for the average feather moss water content in the summer measurement period would bring the average modelled gross photosynthetic rate to below $1.4 \mu\text{mol m}^{-2} \text{s}^{-1}$, which compares well to the

average measured rate of approximately $1 \mu\text{mol m}^{-2} \text{s}^{-1}$.

For days 134 and 278, the modelled values of respiration were close to the average for their respective measurement periods, however modelled respiration was lower than measured respiration in the summer measurement period. The average measured temperature of the soil at 15 cm was up to several degrees higher than the corresponding temperature measured at the meteorological station (compare midday soil temperature in Figure 4.33 B with average soil temperature in Table 4.1). A systematic 2°C increase in the soil temperature to which the model is referenced would increase maximum respiration to $3.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is slightly above the average measured value of dark respiration. It might also be expected that the model would underestimate respiration at high soil temperatures, since it has been shown that Model B has a tendency to underestimate respiration at high soil temperatures, in the feather moss community (cf. section 4.2.1).

In the *Sphagnum* community, modelled gross photosynthesis between 10:00 and 17:00 was greater than the average measured gross photosynthesis in all measurement periods. Again this was to be expected, as the PFD to which the model was referenced was considerably above the average measured light (compare Figure 4.35 B and Table 4.1 B).

Modelled respiration for day 134 was approximately $1.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ during the day, while the average measured

spring value of approximately $0.85 \mu\text{mol m}^{-2} \text{s}^{-1}$. Since the soil temperature to which the model was referenced (Figure 4.33 A) was similar to the average measured soil temperature (Table 4.1 B), the discrepancy between modelled and measured respiration was likely a result of the tendency for Model B to overestimate dark respiration at low soil temperatures. Modelled respiration on day 206 was less than the average measured respiration for the summer measurement period, and modelled respiration on day 278 was greater than the average measured respiration for the fall measurement period. The discrepancies in the summer and fall measurement periods can be explained by the difference between the average measured soil temperature and the maximum soil temperature used in the simulation. For example, the average measured soil temperature for the summer measurement period (Table 4.1 B) was approximately 3.5°C greater than the maximum temperature used for the simulation on day 206 (Figure 4.33 B). If 3.5°C were added to the soil temperature used in the simulation, the maximum total respiration would increase to $3.4 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is close to the measured average of $3.85 \mu\text{mol m}^{-2} \text{s}^{-1}$. Modelled respiration on day 278 could be similarly corrected.

4.5.4 Spatial scaling of CO_2 flux

At the study site, 55% of the forest corresponded to a feather moss community type forest floor, and 45%

corresponded to a *Sphagnum* community type forest floor (determined from aerial photos). However, within the feather moss community the cover of feather moss was not 100%, and within the *Sphagnum* community, the cover of *Sphagnum* was not 100%. It was therefore necessary to quantify the abundance of feather moss and *Sphagnum* in both communities, and then multiply the abundance values by the scaling factors 0.55 (for the feather moss community) and 0.45 (for the *Sphagnum* community), in order to obtain a value for the cover of feather moss and *Sphagnum* at the ecosystem level. Applying this technique, an estimate of the percent forest floor cover of the major moss types at the study site was obtained (Table 4.9). The majority of the forest floor at this study site had a cover of feather moss (includes *Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis*). *Sphagnum* spp. made up a small, but not insignificant proportion of the forest floor cover at the study site.

From these results, gas flux measurements from collars containing feather moss, expressed on a ground area basis, had to be multiplied by a factor of 0.63 in order to represent an estimate for the entire ecosystem. Similarly, gas flux measurements from collars containing *Sphagnum*, expressed on a ground area basis, had to be multiplied by a factor of 0.16 in order to represent an estimate for the entire ecosystem. A significant proportion of the forest

floor cover at the study site consisted of elements for which no estimate of gas flux is provided here.

Using the appropriate scaling factors, combined estimates of CO_2 flux were obtained for the three days examined in section 4.5.1. It should be emphasized again that the CO_2 fluxes for feather moss (gross photosynthesis and respiration) assume that the moss was well hydrated.

On day 134 in the spring measurement period, the combined net CO_2 flux of feather moss and *Sphagnum* forest floors was slightly above zero at midday (Figure 4.45 A). For most of the day, it was clear that gross photosynthesis of both feather moss (Figure 4.45 B) and *Sphagnum* (Figure 4.45 C) was limited by temperature. Light limitation was evident at the beginning and end of the light period, and in the feather moss community, during periods of fluctuating light at midday. At the ecosystem level, *Sphagnum* gross photosynthesis was less than one half that of feather moss, while *Sphagnum* respiration was approximately one third that of feather moss. Both the feather moss and *Sphagnum* community forest floors contributed approximately $0.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ to the total forest floor NEE of approximately $0.2 \mu\text{mol m}^{-2} \text{s}^{-1}$. *Sphagnum* photosynthesis was less affected by changing light conditions at the forest floor compared to feather moss photosynthesis.

On day 206 in the summer measurement period, ecosystem net CO_2 flux was again close to zero at midday (Figure 4.46

A). Changing light conditions in the feather moss understory resulted in total (feather moss + *Sphagnum*) forest floor NEE dropping to as low as $-1 \mu\text{mol m}^{-2} \text{s}^{-1}$ in mid-afternoon. At the ecosystem level, gross photosynthesis was greater for feather moss (Figure 4.46 B) than for *Sphagnum* (Figure 4.46 C), however the *Sphagnum* community forest floor was a stronger sink for CO_2 than the feather moss community forest floor (the feather moss community forest floor was a source of CO_2 , even at midday).

On day 278 in the fall measurement period, the forest floor was a net source of CO_2 for the entire day (Figure 4.47 A). The *Sphagnum* community forest floor was a sink for CO_2 between approximately 12:00 and 17:00 (Figure 4.47 C), while the feather moss community forest floor was a source of CO_2 for the entire day (Figure 4.47 B). Gross photosynthesis for both feather moss and *Sphagnum* was limited by temperature for most of the day. Light limitation was evident at the beginning and end of the light period for both communities, and in the feather moss community, during periods of fluctuating light at midday. Additionally, the photoperiod was shorter in this measurement period than in the spring and summer.

4.6 Evapotranspiration

In both forest floor communities, the average measured transpiration was below $1 \text{ mmol m}^{-2} \text{ s}^{-1}$ in all measurement periods (Figure 4.48). In spring and summer measurement periods, average transpiration was greater for *Sphagnum* than for feather moss, however the difference was only significant (student t-test, $p < 0.01$) in the spring, as the variability was high in *Sphagnum* in the summer. In both communities, average transpiration was greatest in the summer, and least in the fall measurement period.

Presentation of conductances is restricted to those calculated in the summer measurement period, as the temperature of the air (which was used as a measure of the moss leaf temperature in the calculation of the leaf - air vapour pressure deficit) was felt to be a more reliable estimate of moss leaf temperature in the summer than in the spring and fall measurement periods.

The total resistance to water vapour flux in the chamber can be expressed as

$$1/g_{\text{tot}} = 1/g_{\text{bl}} + 1/g_{\text{ff}}$$

where g_{tot} is the total conductance to water vapour flux, g_{bl} is the boundary layer conductance inside the chamber, and g_{ff} is the conductance of the forest floor to water vapour flux. It was expected that the conductance of the forest floor to water vapour flux would change with the water content of the moss.

In the *Sphagnum* community, no relationship was found between moss water content and total conductance to water vapour (Figure 4.49). This was partly a result of the maintenance of a relatively high water content in *Sphagnum*.

In the feather moss community, the total conductance to water vapour increased as the moss water content increased from 1 to approximately 5, but total conductance decreased again above a moss water content of 5 (Figure 4.50). The boundary layer conductance inside each chamber depended on the total volume of the chamber, the angle and roughness of the moss surface, the presence or absence of vascular vegetation, the orientation of any vascular vegetation present, and the fan speed. Of these factors, the fan speed alone did not change between collars, however the other factors were in general similar between collars. The maximum measured total conductance at a collar was assumed to represent the boundary layer conductance of that collar, and it was expected that the maximum conductance to water vapour would occur at high moss water content. The average maximum total conductance in the feather moss community (calculated as the average $\pm$ s.d. of the maximum measured total conductance at each collar) was $105 \pm 80 \text{ mmol m}^{-2} \text{ s}^{-1}$ (data not shown), so it was assumed that the average collar boundary layer conductance was also close to this value. Assuming a maximum total conductance of $105 \text{ mmol m}^{-2} \text{ s}^{-1}$, and a boundary layer conductance of $120 \text{ mmol m}^{-2} \text{ s}^{-1}$ (ie. close

but not equal to the maximum total conductance), the resulting maximum forest floor conductance is approximately $840 \text{ mmol m}^{-2} \text{ s}^{-1}$ (Table 4.10).

Despite being similar to the maximum moss conductance measured in laboratory studies of *Pleurozium schreberi* (approximately $1000 \text{ mmol m}^{-2} \text{ s}^{-1}$, Williams and Flanagan 1996), there was clearly a very large potential for error in the calculation of forest floor conductance with such a low boundary layer conductance. For example, it could be assumed that the range of values of total conductance (% of maximum) above a moss water content of 5 in Figure 4.47 was a result of experimental variability. The standard deviation of these points is 13%. If this amount of variation is assumed to exist around a total conductance of $105 \text{ mmol m}^{-2} \text{ s}^{-1}$, and a boundary layer conductance of $120 \text{ mmol m}^{-2} \text{ s}^{-1}$ is once again assumed, the relative error in the resulting value of forest floor conductance is approximately 60% (Table 4.10). In absolute terms the average maximum total conductance of $105 \text{ mmol m}^{-2} \text{ s}^{-1}$ had a standard deviation of $80 \text{ mmol m}^{-2} \text{ s}^{-1}$ (mentioned above), which translates into a coefficient of variability of 76% (ie. six times greater than the % error assumed in the above calculation of relative error in forest floor conductance). Estimation of absolute forest floor conductance from the data collected in this study is therefore subject to an unreasonably high degree of error.

CHAPTER 4 TABLES

Table 4.1. Environmental conditions in feather moss and *Sphagnum* communities in spring, summer and fall measurement periods. Values are averages $\pm$ s.d. of discrete measurements made during gas flux measurements.

		Measurement Period		
Feather moss		Spring	Summer	Fall
Temperature (°C)	Air	10.2 ± 1.4	22.6 ± 2.2	9.1 ± 4.0
	Moss	10.7 ± 1.3	21.4 ± 2.0	8.6 ± 4.0
	Soil (15 cm depth)	0.34 ± 0.19	11.8 ± 2.1	4.4 ± 0.67
PFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Below canopy ^a	104 ± 33	115 ± 67	56 ± 20
	Above canopy ^b	1224	1261	704
<i>Sphagnum</i>		Spring	Summer	Fall
Temperature °C	Air	14.5 ± 1.5	24.9 ± 4.5	8.7 ± 1.1
	Moss	13.8 ± 1.4	23.2 ± 2.1	7.2 ± 0.7
	Soil (15 cm depth)	0.4 ± 0.2	13.4 ± 1.2	2.7 ± 0.7
PFD ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Below canopy ^a	289 $\pm$ 87	333 $\pm$ 238	124 $\pm$ 43
	Above canopy ^b	1224	1261	704

a - measured

b - calculated from standard equations for incident PFD at the earth's surface (Jones 1992), adjusted to represent PFD inside an acrylic collar on a flat surface

Table 4.2. Proportion of the variability in measured forest floor respiration rate explained by three models of forest floor respiration, for $n = 9$ soil collars in the feather moss community. R^2 values are averages $\pm$ s.d. See text section 3.5 for a description of the models. The number of points used to parameterize the models at each soil collar ranged from 6 to 10.

Model	R^2	R^2_{adj}
Exponential Regression	0.90 ± 0.10	0.85 ± 0.15
'A'	0.90 ± 0.07	0.88 ± 0.08
'B'	0.90 ± 0.06	0.86 ± 0.09

Table 4.3. Proportion of the variability in measured forest floor respiration rate explained by three models of forest floor respiration, for $n = 8$ soil collars in the *Sphagnum* community. R^2 values are averages $\pm$ s.d. See text section 3.5 for a description of the models. The number of points used to parameterize the models at each soil collar ranged from 7 to 15.

Model	R^2	R^2_{adj}
Exponential Regression	0.87 ± 0.08	0.84 ± 0.10
'A'	0.84 ± 0.14	0.82 ± 0.16
'B'	0.93 ± 0.06	0.91 ± 0.07

Table 4.4. Average respiration rate ($\pm$ s.d.) at 10°C (R_{10}) and Q_{10} for forest floor respiration at n independent microsites in feather moss and *Sphagnum* communities. Respiration rate at 10°C and Q_{10} were calculated from exponential regressions of measured dark respiration rate vs soil temperature at 15 cm depth.

Community	R_{10} ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	n	Q_{10}	n
Feather moss	3.0 ± 1.1	6	3.8 ± 0.6	4
<i>Sphagnum</i>	2.2 ± 0.5	6	2.7 ± 0.5	6

Table 4.5. Average respiration rate ($\pm$ s.d.) at 10°C (R_{10}) of shallow and deep forest floor strata (per ground area), as determined by Model B (see text section 3.5 for a description of Model B), for $n = 6$ independent microsites in feather moss and *Sphagnum* communities. The average percent of total respiration rate attributed to the shallow forest floor stratum, at a uniform soil temperature of 10°C, is also evaluated.

Community	$R_{10, \text{shallow}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	$R_{10, \text{deep}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Contribution of $R_{10, \text{shallow}}$ to $R_{10, \text{total}}$ (%)
Feather moss	0.18 ± 0.14	2.5 ± 1.2	7.0 ± 15
<i>Sphagnum</i>	0.45 ± 0.18	2.1 ± 0.61	21 ± 20

Table 4.6. Regression statistics and ANOVA for multiple regression of feather moss community forest floor respiration (proportion of respiration rate at 15 cm soil temperature of 10°C^a; dependent variable), 15 cm soil temperature (°C; independent variable) and moss water content (fresh weight/dry weight; independent variable). See text section 3.4.1.4 for a description of the dataset used in the regression.

Dependent Variable: Forest Floor Respiration					
Regression Statistics					
Multiple R	0.82				
R ²	0.68				
Adjusted R ²	0.66				
Observations	38				
ANOVA					
	df	SS	MS	F	p
Regression	2	2.99	1.49	37.1	< 0.001
Residual	35	1.41	0.04		
Total	37	4.40			

Table 4.6 (continued)

	Coefficients	Standard Error	Lower		Upper		t	p
			95%	C.I.	95%	C.I.		
Intercept	-0.509	0.196	-0.908		-0.110		-2.59	0.014
Soil Temperature	0.131	0.0152	0.100		0.162		8.60	< 0.001
Moss Water Content	0.039	0.0163	0.006		0.072		2.40	0.022

a: R_{10} taken from results of exponential regression

Table 4.7. Correlation matrix for gas exchange parameters and selected site variables at n = 9 collars in the feather moss community in spring, summer and fall measurement periods. See Appendix II for definitions and units of the variables entered in the analysis.

spring	$V_{C,max}$	LAI_{vasc}	SAI_{moss}	$Moss_{wat}$	PFD	$\delta^{13}C$	$R_{10,tot}$	$Depth_{org}$	$Basal_{tree}$
$V_{C,max}$	1	-0.45	-0.09	0.41	0.52	0.03	-0.22	-0.25	-0.38
LAI_{vasc}		1	0.15	0.09	-0.55	0.59^a	-0.07	0.92^b	0.42
SAI_{moss}			1	-0.04	-0.26	-0.07	-0.02	0.20	0.39
$Moss_{wat}$				1	0.53	0.15	-0.84^b	0.24	-0.45
PFD					1	-0.45	-0.73^b	-0.59^a	-0.64^a
$\delta^{13}C$						1	0.18	0.65^a	0.41
$R_{10,tot}$							1	-0.04	0.46
$Depth_{org}$								1	0.44
$Basal_{tree}$									1

Table 4.7 (continued)

Summer	$V_{c,max}$	LAI_{vasc}	SAI_{moss}	PPD	$\delta^{13}C$	$R_{10,tot}$	$Depth_{org}$	$Basal_{tree}$
$V_{c,max}$	1	0.06	-0.70 ^b	-0.62 ^a	0.13	-0.44	-0.04	-0.28
LAI_{vasc}		1	0.11	-0.57 ^a	0.65 ^a	0.07	0.82 ^b	0.59 ^a
SAI_{moss}			1	-0.26	0.09	-0.02	0.20	0.39
PPD				1	-0.29	-0.73 ^b	-0.59 ^a	-0.64 ^a
$\delta^{13}C$					1	0.08	0.53	0.27
$R_{10,tot}$						1	-0.04	0.46
$Depth_{org}$							1	0.44
$Basal_{tree}$								1

Table 4.7 (continued)

Fall	$V_{c,max}$	LAI_{vasc}	SAI_{moss}	$Moss_{wat}$	PFD	$\delta^{13}C$	$R_{10,tot}$	$Depth_{org}$	$Basal_{tree}$
$V_{c,max}$	1	-0.38	-0.91^b	-0.42	0.36	-0.18	0.09	-0.47	-0.34
LAI_{vasc}		1	0.15	0.46	-0.55	0.81^b	-0.07	0.92^b	0.42
SAI_{moss}			1	0.17	-0.26	-0.06	-0.02	0.20	0.39
$Moss_{wat}$				1	-0.59^a	0.58^a	0.29	0.49	0.08
PFD					1	-0.27	-0.73^b	-0.59^a	-0.64^a
$\delta^{13}C$						1	-0.3	0.74^b	-0.04
$R_{10,tot}$							1	-0.04	0.46
$Depth_{org}$								1	0.44
$Basal_{tree}$									1

a: Significant, $p < 0.1$ b: Significant, $p < 0.05$

Table 4.8. Correlation matrix for gas exchange parameters and selected site variables at collars in the *Sphagnum* community in spring, summer and fall measurement periods. Results for n = 6 collars in the spring, and n = 8 collars in the summer and fall. See Appendix II for definitions and units of the variables entered in the analysis.

spring	$V_{c,max}$	PFD	LAI_{vasc}	$\delta^{13}C$	$R_{10,tot}$	$Basal_{tree}$
$V_{c,max}$	1	0.14	0.79^a	-0.26	0.41	0.70
PFD		1	-0.08	-0.42	-0.66	-0.57
LAI_{vasc}			1	-0.4	0.60	0.75^a
$\delta^{13}C$				1	-0.90^b	-0.49
$R_{10,tot}$					1	0.80^a
$Basal_{tree}$						1

Table 4.8 (continued)

Summer	$V_{c,max}$	PFD	LAI _{vasc}	$\delta^{13}C$	$R_{10,tot}$	Basal _{tree}
$V_{c,max}$	1	-0.23	0.20	0.61^a	0.25	-0.18
PFD		1	-0.54	-0.28	-0.59	-0.61
LAI _{vasc}			1	-0.35	0.55	0.62^a
$\delta^{13}C$				1	-0.54	-0.72^b
$R_{10,tot}$					1	0.70^a
Basal _{tree}						1

Fall	$V_{c,max}$	PFD	LAI _{vasc}	$\delta^{13}C$	$R_{10,tot}$	Basal _{tree}
$V_{c,max}$	1	-0.52	-0.36	0.18	0.38	-0.10
PFD		1	-0.06	-0.28	-0.59	-0.61
LAI _{vasc}			1	-0.83^b	0.66^a	0.63^a
$\delta^{13}C$				1	-0.59	-0.62^a
$R_{10,tot}$					1	0.70^a
Basal _{tree}						1

a: Significant, $p < 0.1$ b: Significant, $p < 0.05$

Table 4.9. Ground cover (% of ground covered) at the mature *Picea mariana* study site. The ecosystem was comprised of 55% feather moss community and 45% *Sphagnum* community (determined from aerial photographs). Based on data collected using a point frame method at a total of 297 points, at 5 m intervals, on 5 separate transects. Total cover is > 100% because of the co-occurrence of lichen and moss. Tree basal area was not considered during data collection, but was insignificant (maximum 30 m²/ha). Stems of vascular shrubs were not considered during data collection.

Percent of ground covered by:		Feather moss							
Community		<i>Pleurozium schreberi</i>	<i>Hylocomium splendens</i>	<i>Ptilium crista-castrensis</i>	<i>Sphagnum</i>	Other moss	Lichen (<i>Cladina</i> spp.)	Bare peat and open water	
Feather moss	58	19		4	2	5	15		4
<i>Sphagnum</i>	32	8		0	33	5	28		5
Ecosystem	47	14		2	16	5	21		4

Table 4.10. Effect of error in total conductance to water vapour (g_{tot}) on relative error in forest floor conductance (g_{ff}), for different boundary layer conductances (g_{bl}). The error estimate for g_{tot} is ± 1 s.d., calculated from the variation in g_{tot} (% of maximum) at feather moss collars, where moss water content was > 5 (see Figure 4.50). Average g_{tot} is the average of maxima from $n = 9$ collars. Note that $1/g_{tot} = 1/g_{bl} + 1/g_{ff}$.

Conductance ($\text{mmol m}^{-2} \text{s}^{-1}$)			
g_{tot}	g_{bl}	g_{ff}	% error in g_{ff}
119	110	-1523	
105	110	2310	77
91	110	542	
119	120	9922	
105	120	840	54
91	120	384	
119	200	291	
105	200	221	24
91	200	168	
119	300	196	
105	300	162	18
91	300	132	
119	1000	135	
105	1000	117	13
91	1000	101	

CHAPTER 4 FIGURES

Figure 4.1. Temperature response of measured respiration for four collars in the feather moss community: A) collar 2, B) collar 4, C) collar 9, D) collar 10. Data points shown span spring, summer and fall measurement periods, and had a moss water content > 4 (fresh weight/dry weight).

Figure 4.2. Comparison of observed respiration (solid circles) and respiration predicted by exponential regression (open circles) for collar 2 in the feather moss community. See text section 3.4.1.1 for a description of how the exponential regression was fit to the observed data points.

Figure 4.3. Residuals of the exponential regression model for soil respiration in the feather moss community, plotted against the predictor variable (soil temperature). See text section 3.4.1.1 for a description of the form of the exponential regression.

Figure 4.4. Observed (measured) respiration vs respiration predicted by exponential regression, for the feather moss community. The line of perfect fit is shown for comparison. See text section 3.4.1.1 for a description of the form of the exponential regression.

Figure 4.5. Comparison of observed respiration (solid circles) and respiration predicted by Model A (open circles) for collar 2 in the feather moss community. See text section 3.4.1.2 for a description of Model A.

Figure 4.6. Residuals of Model A for soil respiration in the feather moss community, plotted against the predictor variable (soil temperature). See text section 3.4.1.2 for a description of Model A.

Figure 4.7. Comparison of observed respiration (solid circles) and respiration predicted by Model B (open circles) for collar 2 in the feather moss community. See text section 3.4.1.3 for a description of Model B.

Figure 4.8. Residuals of Model B for soil respiration in the feather moss community, plotted against one of two predictor variables (soil temperature). The second predictor variable was moss temperature. See text section 3.4.1.3 for a description of Model B.

Figure 4.9. Observed (measured) respiration vs respiration predicted by Model B, for the feather moss community. The line of perfect fit is shown for comparison. See text section 3.4.1.3 for a description of Model B.

Figure 4.10. Diurnal time course of A) air temperature (squares), moss temperature (circles), 15 cm soil temperature (triangles), and B) measured respiration (solid circles) and respiration predicted by exponential regression (open circles) for collar 9 in the feather moss community on days 211-212.

Figure 4.11. Temperature response of measured respiration for four collars in the *Sphagnum* community: A) collar 12, B) collar 13, C) collar 16, D) collar 18. Data points shown span spring, summer and fall measurement periods.

Figure 4.12. Comparison of observed respiration (solid circles) and respiration predicted by Model B (open circles) for collars 11 (A), 12 (B), 16 (C) and 18 (D) in the *Sphagnum* community. See text section 3.4.1.3 for a description of Model B.

Figure 4.13. Residuals of Model B for soil respiration in the *Sphagnum* community, plotted against one of two predictor variables (soil temperature). The second predictor variable was moss temperature. See text section 3.4.1.3 for a description of Model B.

Figure 4.14. Observed (measured) respiration vs respiration predicted by Model B, for the *Sphagnum* community. The line of perfect fit is shown for comparison. See text section 3.4.1.3 for a description of Model B.

Figure 4.15. Comparison of observed respiration (solid circles) and respiration predicted by Model A (open circles) for collar 12 in the *Sphagnum* community. See text section 3.4.1.2 for a description of Model A.

Figure 4.16. Residuals of Model A for soil respiration in the *Sphagnum* community, plotted against the predictor variable (soil temperature). See text section 3.4.1.2 for a description of Model A.

Figure 4.17. Comparison of observed respiration (solid circles) and respiration predicted by exponential regression (open circles) for collar 12 in the *Sphagnum* community. See text section 3.4.1.1 for a description of how the exponential regression was fit to the observed data points.

Figure 4.18. Residuals of exponential regression for soil respiration in the *Sphagnum* community, plotted against the predictor variable (soil temperature). See text section 3.4.1.2 for a description of the exponential regression.

Figure 4.19. Observed (measured) respiration vs respiration predicted by exponential regression, for the *Sphagnum* community. The line of perfect fit is shown for comparison. See text section 3.4.1.1 for a description of the form of the exponential regression.

Figure 4.20. Diurnal time course of A) air temperature (squares), moss temperature (circles), 15 cm soil temperature (triangles), and B) measured respiration (solid circles) and respiration predicted by Model B (open circles) for collar 11 in the *Sphagnum* community on days 202-203.

Figure 21. Measured forest floor respiration at all collars in all measurement periods for A) feather moss and B) Sphagnum communities. For the feather moss community, only data for which moss water content was > 4 (fresh weight/dry weight) are shown.

Figure 4.22. Daily time course of the ratio of moss temperature (at approximately 2 cm depth) to 15 cm soil temperature on day 209 at a meteorological station in the feather moss community.

Figure 4.23. Forest floor respiration in the feather moss community (standardized to the rate at 10°C) where moss water content was < 6.5 , as a function of A) soil temperature and B) moss water content. Data points are for the summer measurement period only.

Figure 24. Residuals plotted against predictor variables for multiple regression of feather moss forest floor respiration with moss water content < 6.5 (response variable), 15 cm soil temperature (predictor variable) and moss tissue water content (predictor variable). Data points are from the summer measurement period only.

Figure 4.25. Seasonal change in the average leaf area index of low understorey vascular vegetation within collars in feather moss (blank columns) and *Sphagnum* (shaded columns) communities. Error bars are one standard deviation. For feather moss, $n = 6$; for *Sphagnum*, $n = 5$ in spring, $n = 6$ in summer and fall.

Figure 4.26. Response of gross photosynthesis to incident PFD at A) collar 7 and B) collar 12 in the feather moss and Sphagnum communities, respectively, in the summer measurement period. The horizontal line passes through the point from which summer $V_{c,\max}$ was calculated.

Figure 4.27. Seasonal change in maximum moss photosynthetic capacity (measured as the maximum carboxylation velocity of Rubisco, $V_{C,max}$) for feather moss (blank columns) and *Sphagnum* (shaded columns). Values are averages and error bars are one standard deviation. For feather moss, $n = 6$; for *Sphagnum*, $n = 5$ in spring, $n = 6$ in summer and fall.

Figure 4.28. Seasonal change in average tissue water content of feather moss (blank columns) and *Sphagnum* (shaded columns). Only moss subject to natural wetting/drying cycles were included in the average. Error bars are one standard deviation. For feather moss, $n = 6$ in spring and fall, $n = 5$ in summer; for *Sphagnum*, $n = 5$ in spring and summer, $n = 6$ in fall.

Figure 4.29. Time series of A) feather moss (circles) and *Sphagnum* (triangles) average tissue water content and B) precipitation, for dates in the spring measurement period.

Figure 4.29 (continued). Time series of C) feather moss (circles) and *Sphagnum* (triangles) average tissue water content and D) precipitation, for dates in the summer measurement period.

Figure 4.29 (continued). Time series of E) feather moss (circles) and *Sphagnum* (triangles) average tissue water content and F) precipitation, for dates in the fall measurement period.

Figure 4.30. Effect of moss tissue water content on photosynthetic capacity (relative to the maximum capacity in a given measurement period) for feather moss. Data points (circles) are from all collars for which moss water contents below 4 (fresh weight/dry weight) occurred, in all measurement periods. The line is a third order polynomial forced through the point (1,0).

Figure 4.31. Response of gross photosynthesis to incident PFD at A) collar 7 and B) collar 12 in the feather moss and *Sphagnum* communities, respectively, in the summer measurement period. The initial slope was calculated as a geometric mean regression (see section 3.4.2.3) through points between 0 and 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PFD.

Figure 4.32. Seasonal change in the average $\delta^{13}\text{C}$ value of moss photosynthetic tissue for feather moss (blank columns) and *Sphagnum* (shaded columns). Only moss subject to natural wetting/drying cycles were included in the average. Error bars are one standard deviation. Note that the units of $\delta^{13}\text{C}$ are negative. For feather moss, $n = 6$ in spring and fall, $n = 5$ in summer; for *Sphagnum*, $n = 5$ in spring and summer, $n = 6$ in fall.

Figure 4.33. Air (solid line), moss (dashed line) and 15 cm soil (dotted line) temperatures recorded at a meteorological station in the feather moss community on days A) 134, B) 206 and C) 278. The lines join 15 min. averages; sensors were scanned every 30s.

Figure 4.34. Photon flux density of photosynthetically active radiation in the feather moss community understory on days A) 134, B) 206 and C) 278. See text section 3.2.4 and 3.4.2.5 for details of understory light measurements in the summer, and the calculation of understory PFD for the spring and fall, respectively.

Figure 4.35. Photon flux density of photosynthetically active radiation in the *Sphagnum* community understorey on days A) 134, B) 206 and C) 278. See text section 3.2.4 and 3.4.2.5 for details of understorey light measurements in the summer, and the calculation of understorey PFD for the spring and fall, respectively.

Figure 4.36. A) Modelled moss gross photosynthesis (circles), forest floor respiration (squares) and forest floor net ecosystem exchange (triangles) for the feather moss community on day 134. Negative fluxes represent efflux to the atmosphere. B) Proportion of modelled forest floor respiration attributed to the upper (shallow) forest floor stratum. See text section 3.4.2.4 for a description of the model.

Figure 4.37. A) Modelled moss gross photosynthesis (circles), forest floor respiration (squares) and forest floor net ecosystem exchange (triangles) for the feather moss community on day 206. Negative fluxes represent efflux to the atmosphere. B) Proportion of modelled forest floor respiration attributed to the upper (shallow) forest floor stratum. See text section 3.4.2.4 for a description of the model.

Figure 4.38. A) Modelled moss gross photosynthesis (circles), forest floor respiration (squares) and forest floor net ecosystem exchange (triangles) for the feather moss community on day 278. Negative fluxes represent efflux to the atmosphere. B) Proportion of modelled forest floor respiration attributed to the upper (shallow) forest floor stratum. See text section 3.4.2.4 for a description of the model.

Figure 4.39. Temperature response of light saturated gross photosynthesis for feather moss in A) spring, B) summer and C) fall measurement periods. See text section 3.4.2.1 for the formula for gross photosynthesis.

Figure 4.40. A) Modelled moss gross photosynthesis (circles), forest floor respiration (squares) and forest floor net ecosystem exchange (triangles) for the *Sphagnum* community on day 134. Negative fluxes represent efflux to the atmosphere. B) Proportion of modelled forest floor respiration attributed to the upper (shallow) forest floor stratum. See text section 3.4.2.4 for a description of the model.

Figure 4.41. A) Modelled moss gross photosynthesis (circles), forest floor respiration (squares) and forest floor net ecosystem exchange (triangles) for the *Sphagnum* community on day 206. Negative fluxes represent efflux to the atmosphere. B) Proportion of modelled forest floor respiration attributed to the upper (shallow) forest floor stratum. See text section 3.4.2.4 for a description of the model.

Figure 4.42. A) Modelled moss gross photosynthesis (circles), forest floor respiration (squares) and forest floor net ecosystem exchange (triangles) for the *Sphagnum* community on day 278. Negative fluxes represent efflux to the atmosphere. B) Proportion of modelled forest floor respiration attributed to the upper (shallow) forest floor stratum. See text section 3.4.2.4 for a description of the model.

Figure 4.43. Temperature response of light saturated gross photosynthesis for *Sphagnum* in A) spring, B) summer and C) fall measurement periods. See text section 3.4.2.1 for the formula for gross photosynthesis.

Figure 4.44. Seasonal change in measured flux of CO_2 in feather moss (blank columns) and *Sphagnum* (shaded columns) communities. Values are averages of fluxes at collars that were subject to natural wetting/drying cycles; error bars are one standard deviation. For feather moss, $n = 6$ in spring and fall, $n = 5$ in summer; for *Sphagnum*, $n = 5$ in spring and summer, $n = 6$ in fall.

Figure 4.45. Moss gross photosynthesis (circles), forest floor respiration (squares) and forest floor net ecosystem exchange (triangles) for the combined feather moss and *Sphagnum* communities (A) and for feather moss (B) and *Sphagnum* (C) communities separately on day 134, spatially scaled to the ecosystem level. Negative fluxes represent efflux to the atmosphere. See text section 3.4.2.4 for a description of the scaling procedure.

Figure 4.46. Moss gross photosynthesis (circles), forest floor respiration (squares) and forest floor net ecosystem exchange (triangles) for the combined feather moss and *Sphagnum* communities (A) and for feather moss (B) and *Sphagnum* (C) communities separately on day 206, spatially scaled to the ecosystem level. Negative fluxes represent efflux to the atmosphere. See text section 3.4.2.4 for a description of the scaling procedure.

Figure 4.47. Moss gross photosynthesis (circles), forest floor respiration (squares) and forest floor net ecosystem exchange (triangles) for the combined feather moss and *Sphagnum* communities (A) and for feather moss (B) and *Sphagnum* (C) communities separately on day 278, spatially scaled to the ecosystem level. Negative fluxes represent efflux to the atmosphere. See text section 3.4.2.4 for a description of the scaling procedure.

Figure 4.48. Seasonal change in evapotranspiration rate in feather moss (blank columns) and *Sphagnum* (shaded columns) communities. Values are averages of discrete measurements made at collars subject to natural wetting/drying cycles; error bars are one standard deviation. For feather moss, $n = 6$ in spring and fall, $n = 5$ in summer; for *Sphagnum*, $n = 5$ in spring and summer, $n = 6$ in fall.

Figure 4.49. Total conductance to water vapour (g_{tot}) as a function of moss water content for collars in the *Sphagnum* community. Data are for the summer measurement period only.

Figure 4.50. Total conductance to water vapour (g_{tot}) as a function of moss water content for collars in the feather moss community (circles). Data are for the summer measurement period only. The line is a third order polynomial forced through the point (1,0).

CHAPTER 5
DISCUSSION

5.1 Respiration

Most models of soil respiration are referenced to a single estimate of soil temperature (eg. Witkamp 1966; Chapman 1979; Howard and Howard 1979; Schlentner and Van Cleve 1985; Raich and Schlesinger 1992; Lloyd and Taylor 1994). However in theory, a soil could be divided into any number of strata, and the respiratory activity of each stratum modelled separately. While exponential regression and Model A as defined in this study were reasonable predictors of forest floor respiration (especially exponential regression in the feather moss community), both showed a marked lack of homogeneity of variance in the *Sphagnum* community, indicating a decrease in predictive ability at high soil temperatures. Including terms referenced to shallow and deep forest floor strata in a model of boreal forest floor respiration clearly gives it more versatility to respond to changes in above-ground temperature that are not immediately transmitted to deeper soil layers. This is particularly useful for modelling short-term (eg. diurnal) changes in forest floor respiration rate, and it can help partition respiration between the moss layer and deeper sources of CO₂, where a relatively deep organic soil is insulated from the atmosphere by a continuous carpet of moss.

The values of dark respiration at 10°C determined for the shallow stratum in each community in this study

corresponded closely to those determined for *Pleurozium schreberi* and *Sphagnum* spp. from on-site laboratory studies made during the same measurement periods in 1996 (Williams and Flanagan 1997). This study reports an average ($\pm$ s.d.) shallow-stratum dark respiration at 10°C (on a ground area basis) of $0.18 \pm 0.14 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the feather moss community, and $0.45 \pm 0.18 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the *Sphagnum* community. Williams and Flanagan (1997) report average dark respiration at 10°C (converted from leaf area to ground area basis using moss shoot area indices from the present study) of $0.28 \pm 0.11 \mu\text{mol m}^{-2} \text{s}^{-1}$ for feather moss, and $0.48 \pm 0.09 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Sphagnum*. While the variability in the respiration of the shallow stratum in the feather moss community is high (C.V. = 78%), the averages for both moss types are very close to those reported by Williams and Flanagan (1997), indicating that respiration of the shallow stratum can reasonably be interpreted as moss respiration. The relatively high variability in the estimate of feather moss respiration reported by this study can be attributed to higher overall rates of respiration and lower rates of moss respiration in the feather moss community, compared to the *Sphagnum* community. These results indicate good agreement between results obtained using a large closed chamber in the field with a partitioning of respiration based on the temperature response of total respiration, and carefully controlled laboratory measurements of gas exchange on

excised moss shoots.

With moss respiration and photosynthesis as known quantities, an estimate of the respiration of heterotrophic soil organisms could be calculated if the amount of vascular litterfall from this ecosystem were known, and a steady state of carbon input and output for the forest floor assumed. This would also result in an estimate for the contribution of roots to the observed soil respiration. Based on the moss respiration rates and total respiration rates determined here, and typical (recorded) diurnal changes in moss and soil temperatures, an upper limit to the contribution of roots to total respiration can be estimated. In the feather moss community (Figures 4.34 - 4.36), this upper limit varies diurnally between approximately 80 and 90% in the spring, between 85 and 95% in the summer, and between 88 and 95% in the fall measurement periods. This compares well with the results of Flanagan and Van Cleve (1977), who estimated that up to 90% of total soil respiration in a black spruce feather moss community was contributed by tree roots. In the *Sphagnum* community (Figures 4.38 - 4.40), the upper limit to the contribution of tree roots to total respiration varies diurnally between approximately 40 and 80% in the spring, and between 55 and 85% in the summer and fall measurement periods.

While Model B of forest floor respiration permits the partitioning of respiration into moss and other components,

it was demonstrated to overestimate respiration at low soil temperatures. The effects of temperature on the diffusion coefficient of CO_2 in air may be partly responsible for this discrepancy (Meir *et. al.* 1996). Since the models of respiration compared in this study assumed that it was only the production of CO_2 that changed with temperature, it would have been appropriate to correct observed respiration for the effects of temperature on the rate of diffusion of CO_2 . Since the diffusion coefficient of CO_2 in air at 0°C (a typical spring soil temperature) and 1 atm is approximately 92% of the value at 12°C (a typical summer soil temperature) and 1 atm (Nobel 1991), it would be appropriate to multiply respiration rates measured in the spring by a factor of 1.1 in order to standardize the rate of diffusion to summer conditions, thereby correcting observed respiration rates for the effect of temperature on the diffusion of CO_2 . Such a correction would have the effect of improving the fit of Model B at low temperatures in both the feather moss and *Sphagnum* communities. Measurements made in the fall could be similarly corrected, though the correction factor would be smaller.

The strength of the correlation between soil respiration and measurements of soil temperature will greatly depend on how closely the measurements of soil temperature approximate the temperature of the material that is being oxidized. Comparison of the temperature responses

of respiration determined in this study with those determined in other studies therefore requires that consideration be made of the depth at which soil temperature was measured. For example, respiration rates at 10°C reported here were in a similar range, but slightly above those reported for the 1995 growing season at similar black spruce feather moss and *Sphagnum* sites in northern Manitoba (R_{10} of approximately $2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for a feather moss community, approximately $1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for a *Sphagnum* community, Goulden and Crill 1997). However, the temperature measurement of Goulden and Crill was taken at 5 cm depth, while for this study it was taken at 15 cm depth. This discrepancy would lead to an overestimation of the respiration rate in this study compared to that of Goulden and Crill, and correction for the methodological difference would create closer agreement between estimates from the two studies. Q_{10} values reported here, for both communities, were also above those reported in the latter study (Goulden and Crill report Q_{10} values of approximately 2 for both feather moss and *Sphagnum* communities), and agreement between Q_{10} from the two studies would again be improved by consideration of the different depths of temperature measurements. For the feather moss community, the average ($\pm$ s.d.) Q_{10} value reported here (3.8 ± 0.6) was above the range (1.3 to 3.3) reported by Raich and Schlesinger (1992), while for *Sphagnum*, the average value reported here ($2.7 \pm$

0.5) fell within the range reported by Raich and Schlesinger. None of the studies for which Q_{10} values are tabulated by Raich and Schlesinger (1992) were conducted in boreal systems (most were temperate forest or grassland). Additionally, since the activation energy of soil respiration is higher at lower temperatures (Lloyd and Taylor 1994), it is reasonable to expect the Q_{10} values calculated over the relatively low temperature range in this study (the majority of points correspond to soil temperatures between 0 and 15°C) to be relatively high. The activation energy of respiration, and the change in activation energy of respiration with temperature, have also been shown to differ between enzymes involved in carbohydrate metabolism, and between species (ap Rees *et. al.* 1988; Hochachka and Somero 1984). Therefore it is not unreasonable to expect spatial variability in the Q_{10} of soil respiration, as it would be affected by the relative proportions of the organisms contributing to total respiration.

The models of respiration compared in this study do not take into account soil moisture changes or differences between sites, and the models were evaluated only for dates on which moss water content was ≥ 4 (fw/dw, for feather moss), in order to avoid variability in respiration associated with moss water content. The importance of confining the modelled fit of total respiration to data

points where moss water content was not limiting was developed in the introduction (cf. section 2.1). The results of the multiple regression demonstrated simply that this was an important consideration in this study, though as discussed, the relationship between moss water content and moss respiration (and therefore total respiration) is expected to be zero order above a moss water content of between 5 and 6. For the organic soil layer, Schlentner and Van Cleve (1985) report an optimum soil water content of 150% (water mass as a percent of dry matter mass in the entire organic layer) for soil respiration in boreal white spruce, birch and aspen stands, however the pattern of change in respiration above and below this level was not consistent at different soil temperatures, and also differed between the models they tested. In a black spruce stand in the same study, soil water contents varied minimally (ranged between 150 to 157%) in two consecutive growing seasons, however an optimum water content for respiration was not determined. Savage (1995) found decreased CO_2 efflux at very dry and very wet black spruce sites in northern Manitoba, and this pattern has been observed in other forest types (eg. Singh and Gupta 1977). The volumetric water content of the upper 15 cm of soil in the feather moss community (manual Time Domain Reflectometry measurements at approximately weekly intervals, at 10 sites in the feather moss community; 2 to 4 measurements at each site were

averaged each date) was $38\% \pm 19\%$ in May, $27\% \pm 16\%$ in July and $38\% \pm 24\%$ in October (S. Kelly, preliminary unpublished data). Thus from maxima in the spring and fall, the volumetric water content of the upper portion of the organic soil decreased by approximately 30% (on average) in July. Calculation of the soil water content as a percent of the dry weight of soil requires values for the bulk density of soil, and the calculation is very sensitive to the values of bulk density used. Additionally, the bulk density depends on profile development, which varied substantially between microsites. In the present study the moss/litter layer (includes live and dead moss) extended to a depth of 13 ± 8 cm, giving way to humus which extended to a depth of 24 ± 12 cm. Using bulk density values ($\text{g dry weight}/\text{cm}^3$ soil) for moss/litter (includes green and brown moss) and humus of 0.02 and 0.344, respectively (S. Trumbore *et. al.*, unpublished data), and assuming a linear change from dead moss at 13 cm to humus at 15 cm, the average water content of the upper organic layer at this site was $149 \pm 88\%$ of dry weight. This exactly brackets the optimum water content (150%) suggested by Schlentner and Van Cleve (1977) for organic soil respiration. However, this calculation is highly sensitive to the value of bulk density used. For example, if the upper 15 cm of the organic layer are assumed to be comprised only of moss and litter, for the same volumetric water content, the water content as a percent of

dry mass rises to $1354 \pm 800\%$, which is unrealistic, given that the maximum water holding capacity of live moss measured in the study was approximately 900% (fresh weight/dry weight - 1 = weight of water as a percent of live moss dry weight). The strong temperature responses demonstrated for data across the three measurement periods are evidence that water content effects on forest floor respiration were minimal during this study. Also, averages of total respiration for feather moss collars that were watered during the summer measurement period were not significantly different ($p > 0.5$) from those that were not watered.

In the *Sphagnum* community, water content limitation to respiration from soil layers beneath the moss surface could not have occurred, as the water content of the surface moss never dropped below approximately 600% of dry weight, and the water content of the peat below the surface would have been equal to (Tenhunen *et. al.* 1994) or greater than (Clymo and Hayward 1982) that of the moss at the surface .

A two-term model of forest floor respiration is well suited to systems with a moss layer, and particularly so for treed *Sphagnum* peatlands where the water table is not at the moss surface. Where the water table is at the moss surface it can be expected that the temperature of the shallow and deep strata will be more similar than was typically the case in this study (since wet moss will conduct heat more readily

than dry moss, Oechel and Van Cleve 1986), and that the relative importance of the flux of carbon in methane compared to the flux of carbon in carbon dioxide will be greater (Moore and Knowles 1989).

The most important variable affecting differences in respiration between collars was the total tree basal area in the immediate surroundings of each collar. In the *Sphagnum* community, this was clearly demonstrated by significant positive correlation between tree basal area and $R_{10,tot}$ ($p < 0.1$). A significant positive correlation between tree basal area and vascular LAI ($p < 0.1$) suggests that part of the increase in total respiration near trees can be attributed to an increase in the respiration associated with vascular understorey plants. In the feather moss community, the most important variable affecting differences in respiration between collars appeared to be the daily average incident PFD. In this community daily average incident PFD was significantly negatively correlated to each of $R_{10,tot}$ ($p < 0.05$), tree basal area ($p < 0.1$), depth to the mineral soil ($p < 0.1$), and vascular LAI ($p < 0.1$, summer measurement period only). A greater daily average incident PFD could decrease total respiration by drying the moss layer, thereby reducing the respiration of this component of total respiration. Indeed in the fall measurement period, there was a significant negative correlation ($p < 0.1$) between PFD and moss water content. However in the spring measurement

period, there was a significant positive correlation between PFD and moss water content. The significant negative correlation between daily average PFD and respiration could alternatively be interpreted in terms of the significant negative correlation between daily average PFD and tree basal area, coupled with the positive correlation between $R_{10, tot}$ and tree basal area. Where tree basal area was greater, less light reached the forest floor, and forest floor respiration was greater. The lack of significance in the positive correlation between tree basal area and $R_{10, tot}$ can be explained by the sampling protocol for tree basal area. In the feather moss community, it is likely that the 1 m distance within which tree basal area was measured around each collar was insufficient to encompass all the trees that may have influenced total respiration at a particular collar. For example, root respiration is likely to have contributed to the effect of trees on total respiration. In a study of root morphology of boreal tree species (Strong and La Roi 1983a), root spread to tree height ratios in three excavated black spruce trees were 0.32, 0.68 and 0.75 for trees 11 m, 3.5 m and 4 m tall, respectively. In the present study, the trees surrounding the collars in the feather moss community ranged upwards in height to approximately 12 m. For a conservative root spread : tree height ratio (eg. 0.32), tall trees up to 3 m from a collar may have had roots extending beneath the

collar, contributing to total respiration. In the *Sphagnum* community, where trees were shorter (typically up to 6 m), and a significant positive correlation existed between total tree basal area and total respiration, a 1 m area surrounding each collar would likely have better reflected the total tree root presence beneath a given collar.

Apportioning of the contribution of live roots to total respiration would require quantification of roots by excavation (eg. Chapman 1979) and an assessment of the extent of damage to roots caused by collar installation. Quantification of roots was not undertaken in this study. Some damage likely occurred to tree roots in both communities in this study, however the majority of tree roots were likely located below the depth of collar installation. The greatest concentration of black spruce roots is found below the live moss layer (Van Cleve and Dyrness 1983), often just above the water table (Strong and La Roi 1983b). The average depth of live moss at collars in the feather moss community was 6 ± 3 cm, while the average depth to the water table in the feather moss community was 29 ± 8 cm ($n = 24$, 2 points from this study, 22 from K. Bisbee, unpublished data). The average depth of collar installation was 12 ± 5 cm, and so on average approximately 25% of the potential tree rooting zone would have been affected by the collar installation. If the roots were located mostly just above the water table, the effect of

collar installation would have been minimal, however if the roots were located mostly just below the live moss, the effect of collar installation would have been substantial. In the *Sphagnum* community, the average depth to the water table for all collars in the summer measurement period was 42 ± 11 cm, and the average depth of collar installation was 15 ± 2 cm. Assuming that roots were excluded from an active moss layer 5 cm deep (a conservative estimate, as live moss may extend up to 10 cm (Clymo and Hayward 1982), the collars would have disturbed on average approximately 27% of the potential tree rooting zone. From these results, it is possible that respiration from live tree roots may have been reduced by approximately 25 - 30% compared to undisturbed ground in both communities, however any roots killed during collar installation would have been subject to microbial degradation, making the net effect of collar installation on total respiration uncertain, but likely less than 25%.

Apart from the direct effects of tree roots on total respiration, greater tree basal area near a collar could also increase respiration indirectly. For example, the significant positive correlation between vascular LAI and total tree basal area in both communities indicates that the respiration of live vascular vegetation was greater where tree basal area was greater. Further, greater total tree basal area immediately surrounding a collar could increase respiration through the input of biomass (litterfall:

needles, branches, bark, cones), and nutrients (leaching in throughfall (Waring and Schlesinger 1985)), to the forest floor.

5.2 Photosynthesis

The photosynthetic capacity of feather moss did not change significantly over the growing season, while that of *Sphagnum* increased in the summer. The realized photosynthetic capacity of feather moss was reduced in the summer as a result of water content limitation. The photosynthetic capacity of *Sphagnum* was greater than that of feather moss in all measurement periods, though it was only significantly greater in the summer measurement period. These conclusions are corroborated by the $\delta^{13}\text{C}$ values of the moss photosynthetic tissue, collected in each season (Figure 4.30), which indicate that the concentration of chloroplastic CO_2 (C_c) was greater in feather moss in summer compared to spring and fall measurement periods, and that C_c was lower in *Sphagnum* in the summer compared to the spring and fall measurement periods. The observed changes in realized photosynthetic capacity for both feather moss and *Sphagnum* would contribute to the observed changes in $\delta^{13}\text{C}$ in the summer measurement period. Additionally, greater photosynthetic capacity in *Sphagnum* compared to feather moss could contribute to the higher $\delta^{13}\text{C}$ values in *Sphagnum*, though increased light intensities in the *Sphagnum* community

understorey, and a moss water content consistently favourable for photosynthesis in *Sphagnum* would also contribute to a lower C_i in *Sphagnum*.

The values of $V_{c, \max}$ reported in this study correspond closely to estimates obtained from measurements made on excised moss at the same study site in the same measurement periods (Williams and Flanagan 1997). This study reports an average ($\pm$ s.d.) Rubisco $V_{c, \max}$ (on a total LAI basis)¹ of 4.0 ± 0.75 , 5.7 ± 0.75 , and $5.0 \pm 0.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ for feather moss in the spring, summer and fall measurement periods, respectively. For *Sphagnum*, the values of $V_{c, \max}$ were 6.0 ± 1 , 14.0 ± 1.5 , and $6.0 \pm 0.8 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the same measurement periods. For the same study site, during the same measurement periods, Williams and Flanagan (1997) report average Rubisco $V_{c, \max}$ (on a moss shoot area basis) of 7 ± 2 , 5 ± 3 and $7 \pm 1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ for feather moss, and 5 ± 1 , 14 ± 4 and $7 \pm 1 \mu\text{mol m}^{-2} \text{s}^{-1}$ for *Sphagnum*. For this study, the average $V_{c, \max}$ for feather moss in the summer measurement period (Figure 4.25) should be adjusted for average moss water content (Figure 4.26) by the third order polynomial given in Figure 4.28. This reduces the realized $V_{c, \max}$ for feather moss in the summer from an average of approximately 5.7 to approximately $4 \mu\text{mol m}^{-2} \text{s}^{-1}$. Values in the spring and fall measurement periods were unaffected by

¹ Equal to the sum of vascular LAI and moss SAI at each collar

moss tissue water content. The averages for the two studies therefore compare well for *Sphagnum* in all measurement periods, and for feather moss they compare well in the summer and fall, while the spring value from this study is slightly below that found by Williams and Flanagan (1997). In the spring measurement period, several of the values of gross photosynthesis from which $V_{L,HI}$ were calculated occurred in what were most likely light limiting conditions, which would have artificially decreased the calculated $V_{L,HI}$. Therefore this study agrees well with the results of Williams and Flanagan (1997), notably finding a significant increase in the photosynthetic capacity of *Sphagnum* during the summer measurement period, and an effective reduction in $V_{L,HI}$ in feather moss in the summer as a result of water content limitation. Precipitation in July 1996 was 86 mm, which was above the 1961 - 1990 average for Prince Albert (55°55'N 106°05'W, 532 m, approximately 50 km southwest of the study site) of 72 mm. It can therefore be expected that feather moss photosynthetic capacity is regularly limited by low tissue water content in mid-summer in an average year.

Most published values of moss photosynthesis are expressed on a dry weight basis, however this has been done mostly as a matter of convenience (Green and Lange 1994). Values expressed on a ground area basis are less common, but more useful when comparing the field performance of mosses. Net photosynthesis, rather than gross photosynthesis, is

commonly reported. Using the shallow term from Model B of respiration to represent moss respiration, and the temperature functions of maximum gross photosynthesis given in Figure 4.39 and 4.43, maximum (not water or light limited) net photosynthesis can be evaluated for the moss in all measurement periods.

Values of moss net photosynthesis from this study are compared to those determined in other studies in Table 5.1 A-B. For the feather moss community, maximum rates of gross photosynthesis realized by the feather moss are in the same range as those determined by other researchers. At 20°C, feather moss net photosynthesis in this study ranged from 1.46 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the spring measurement period to 1.86 $\mu\text{mol m}^{-2} \text{s}^{-1}$ in the summer measurement period. This is in the range reported for "mosses" by Green and Lange (1994), though it is approximately 50% of the value reported by Silvola (1991) for *Pleurozium schreberi*. Goulden and Crill (1997) report a maximum value of gross photosynthesis of 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$, which is below gross photosynthetic rates measured here. Goulden and Crill subtracted total respiration based on a temperature response of total respiration to soil temperature at a depth of 5 cm from net CO_2 exchange during the day in order to arrive at their values of gross photosynthesis, and from the results of the present study it is clear that this would result in an underestimation of gross photosynthesis, as respiration

would respond strongly to the moss temperature at 1 cm depth. A correction for the protocol of Goulden and Crill would increase their estimates of gross photosynthesis, improving agreement between the two studies. At 25°C, gross moss photosynthesis in the summer measurement period in this study ($2.3 \mu\text{mol m}^{-2} \text{s}^{-1}$) was similar to that measured by Williams and Flanagan (1996) (maximum of $2 \mu\text{mol m}^{-2} \text{s}^{-1}$).

For *Sphagnum*, there was again good agreement between photosynthetic rates reported by this study and published values (Table 5.2), however the range reported by this study, and the range of published values, were greater than for feather moss, owing to the greater seasonal change in photosynthetic capacity. The lowest maximum net photosynthetic rate reported here ($1.3 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the spring measurement period) was above the lowest reported for *Sphagnum* ($0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, Silvola 1991), while the highest value reported here ($5.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the summer measurement period) is lower than that reported for a species in *Sphagnum* sect *acutifolia* by Williams and Flanagan (1996). Thus *Sphagnum* gross photosynthetic rates in the present study are within the range of published values.

In the feather moss community, locations receiving intermediate average daily PFD were associated with the greatest moss growth and vascular understorey plant leaf area. In this community, deep organic soil was positively correlated with the $\delta^{13}\text{C}$ value of the moss photosynthetic

tissue (significant, $p < 0.1$ in the spring, $p < 0.05$ in the fall). This is logical, as an increase in the $\delta^{13}\text{C}$ value of the moss photosynthetic tissue is associated with a decreased C_2 during photosynthesis, indicating a comparatively strong CO_2 drawdown in the chloroplast. A deep organic soil would develop where moss photosynthesis was consistently great. Vascular plant LAI was also significantly positively correlated to the thickness of the organic soil layer ($p < 0.05$), and with the $\delta^{13}\text{C}$ value of the moss photosynthetic tissue ($p < 0.1$ in the spring and summer measurement periods, $p < 0.05$ in the fall measurement period). Thus moss growth, and a strong vascular plant presence (with associated biomass input through root turnover and litter input) were significantly positively correlated with a thick organic soil layer. Average daily PFD was significantly ($p < 0.1$) negatively correlated with the thickness of the organic soil layer. Moss $V_{c,\max}$ was positively correlated to average incident PFD (significant, $p < 0.1$ in the summer measurement period), and negatively correlated to both the moss shoot area index (SAI) ($p < 0.05$ in summer and fall) and the thickness of the organic soil layer. Thus while CO_2 drawdown by the moss was greatest in relatively shaded locations, the maximum photosynthetic capacity of these mosses was low. That the maximum photosynthetic capacity of the moss should be low, and the shoot area high in a relatively shaded environment is

consistent with structural and functional adaptation of the moss to shade, analagous to shade leaves of a tree (Salisbury and Ross 1992). Finally, a thick organic layer tended to be found where tree basal area was greater, however the relationship was not significant in any measurement period. Further, PFD was more strongly negatively correlated with tree basal area than with organic layer depth, and the $\delta^{13}\text{C}$ of the moss photosynthetic tissue was not strongly correlated with tree basal area. It is thus demonstrated that in the feather moss community, while a thick organic layer, consistently high moss photosynthesis, and high vascular plant LAI were found where PFD was low, the light environment that favoured these was intermediate between very bright and very dark. While a high photosynthetic capacity can allow high light saturated rates of photosynthesis, high PFD can cause moss desiccation (eg. significant ($p < 0.1$) negative correlation between moss water content and daily average PFD in the fall measurement period), resulting in failure to achieve high rates of photosynthesis. Since PFD was positively correlated to moss water content in the spring, it is unclear why $V_{c,max}$ was not more strongly positively correlated to the $\delta^{13}\text{C}$ of the moss photosynthetic tissue in the spring.

In the *Sphagnum* community, understorey vascular vegetation was more abundant where tree basal area was greater, and photosynthesis was consistently higher away

from trees and vascular understorey plants, however moss photosynthetic capacity did not show any systematic spatial pattern between sites or across seasons. In this community, vascular vegetation was more abundant where tree basal area was greater (significant ($p < 0.1$) positive correlation), and the $\delta^{13}\text{C}$ value of the moss photosynthetic tissue was higher where tree basal area was lower (significant negative correlation in the summer ($p < 0.05$) and fall ($p < 0.1$)), and where vascular LAI was lower (significant negative correlation ($p < 0.05$) in the fall). High values of both tree basal area and vascular LAI would cause the $\delta^{13}\text{C}$ value of the moss to decrease by shading the moss (tree basal area was negatively correlated with PFD in all measurement periods, and vascular LAI intercepts PFD before it reaches the moss layer). Moss $V_{c,\text{max}}$ did not show a consistent correlation with any spatial features in this community. In the summer measurement period, $V_{c,\text{max}}$ was significantly ($p < 0.1$) positively correlated with the $\delta^{13}\text{C}$ value of the moss, consistent with a decrease in C_c resulting from high moss photosynthetic capacity and high light availability. However in the spring and fall, this relationship was not apparent. In the spring, $V_{c,\text{max}}$ was greatest where tree basal area was greatest, however this too was not apparent in the other measurement periods. Moss $V_{c,\text{max}}$ may have been greater near trees in the spring as snow depth was less near trees (data not shown), and the moss near trees were snow-free

earlier in the season, allowing for an earlier up-regulation of metabolism.

5.3 Net Ecosystem Exchange

The results presented here show that net ecosystem exchange (NEE) was more positive in the *Sphagnum* community than in the feather moss community on all simulation days (compare Figures 4.40 - 4.42 to Figures 4.36 - 4.38), and that despite its comparatively small areal coverage (only 16% of ground area, Table 4.9), the *Sphagnum* community contributed significantly to ecosystem forest floor CO₂ exchange. On simulated days in the summer and fall measurement periods, the contribution of the *Sphagnum* community forest floor to ecosystem CO₂ uptake was greater than that of the feather moss community forest floor (Figure 4.45 - 4.47). Further, the *Sphagnum* community forest floor was a net sink of CO₂ during midday in all measurement periods, while that of the feather moss community was a net sink of CO₂ during midday only in the spring.

These results agree well with those of Goulden and Crill (1997), who showed that NEE at the forest floor was greater (ie. more CO₂ sequestered than lost to the atmosphere) in a black spruce *Sphagnum* community than in a black spruce feather moss community. Goulden and Crill (1997) described their site as a mosaic of patches with high spruce but low moss production (ie. feather moss community)

and low spruce but high moss production (ie. *Sphagnum* community). The results of the present study agree with the results obtained for moss by Goulden and Crill (1997).

Midday forest floor NEE was limited mostly by the temperature of the moss in the *Sphagnum* community, while in the feather moss community, light limitation during the midday period was common. For both communities, the empirical nature of the light response of photosynthesis clearly limited the realism of modelled photosynthesis in the spring and fall measurement periods. For example, the increase in photosynthesis at the beginning of the day for both communities in the summer (the measurement period from which light responses were calculated) showed gradual curvature in the transition from light to CO₂ limitation of photosynthesis before 10:00 and after 15:00 hours. In the spring and fall, the truncation of the increase in photosynthesis at the beginning of the day for both communities was evidence of an abruptness in the change from light limitation to CO₂ limitation that is likely not physiologically realistic.

A further limitation of modelled values of NEE was the use of air and soil temperature recorded in the feather moss community to represent moss and soil temperature, respectively, in the *Sphagnum* community. Temperature averages from gas flux measurements were similar in the two communities, however in the more sheltered environment of

the feather moss community, the amplitude of the seasonal change in air, moss and soil temperature was less than in the *Sphagnum* community (however no consistent significant differences existed between air, moss and soil temperatures in the two communities across all measurement periods). It has been demonstrated that systematic changes in the estimate of soil temperature can lead to notable changes in estimates of CO_2 exchange (cf. section 4.5.1.3), and so a more rigorous evaluation of temperature near the forest floor would increase the predictive ability of the model developed here.

5.4 Evapotranspiration

During gas flux measurements in this study, the speed of the fan circulating the air inside the chamber was kept low in order to avoid problems associated with the degassing of the soil with respect to CO_2 . This resulted in a low chamber boundary layer conductance. Measurements of evapotranspiration inside the chamber were strongly dependent on incident PFD (data not shown), and so it was clear that in the light, the flux of water vapour was driven by the available energy, and not by the gradient in vapour pressure (cf. the reasons for limitation by either of these two sources were explained in section 2.3). Thus although the measured rate of evapotranspiration was greater in the *Sphagnum* community than in the feather moss community in the

spring and summer ($p < 0.01$ in the spring), it is likely that much of the difference can be attributed to higher light intensities in the *Sphagnum* community than in the feather moss community. Measured rates of evapotranspiration in the feather moss community in the summer measurement period compared well to measurements made by a sub-canopy eddy covariance system which made measurements of the flux of H_2O vapour in the feather moss community between days 205 and 213. This study reports an average ($\pm$ s.d.) measured evapotranspiration rate of approximately $0.4 \pm 0.1 \text{ mmol m}^{-2} \text{ s}^{-1}$ for the feather moss community, which compares to an average rate of approximately 0.67 ± 0.17 for 30 minute averages between 10:00 and 17:00, measured by the eddy covariance system in the period mentioned. Thus notwithstanding the difficulties encountered in the calculation of forest floor conductance, the chamber method employed in this study gives results similar to those of a non-invasive gas flux measurement technique (eddy covariance).

By calculating conductances from measured evapotranspiration in the dark, the effect of available energy on water vapour flux was controlled, permitting an examination of the effects of moss water content on conductance. However as was demonstrated (section 4.6), a high boundary layer conductance is necessary for an accurate determination of the conductance of the forest floor.

Therefore although the estimate of maximum forest floor conductance in the feather moss community given here (approximately $840 \text{ mmol m}^{-2} \text{ s}^{-1}$) was close to a previously reported value for feather moss conductance (approximately $1000 \text{ mmol m}^{-2} \text{ s}^{-1}$ for *Pleurozium schreberi*, Williams and Flanagan 1996), there was a large uncertainty in this estimate.

Another factor affecting the estimation of forest floor conductance was the accurate measurement of the temperature of the sites of evaporation (ie. moss leaf temperature). Since the vapour pressure at the moss surface was dependent on the moss temperature, an accurate measurement of moss temperature was essential for the accurate calculation of the vapour pressure deficit between the moss and the air. The dataset from which forest floor conductance was calculated in this study consisted only of measurements made in the summer measurement period, as air temperature was used as an estimate of moss leaf temperature, and it was felt that this assumption was more justified in the summer than in the fall and spring. However, even in carefully controlled laboratory studies of moss, it is difficult to ensure an accurate measurement of moss leaf temperature (Williams and Flanagan 1996). It was therefore clear that the low chamber boundary layer conductances present in this study were an obstacle to reliable estimation of forest floor conductance.

5.5 Conclusion

This study provides measurements of the exchange of CO₂ and H₂O vapour between the forest floor and the atmosphere in plant communities dominated by feather mosses and *Sphagnum* moss in a mature black spruce forest.

The results of this study indicate that the contribution of moss to ecosystem CO₂ uptake is different in feather moss and *Sphagnum* communities for 4 principal reasons: 1) The percent cover of feather moss and *Sphagnum* differs substantially in the two communities, with approximately even cover of feather moss (40%) and *Sphagnum* (33%) in the *Sphagnum* community, and a predominance of feather moss (81%) over *Sphagnum* (2%) in the feather moss community; 2) for well hydrated moss, the photosynthetic capacity of *Sphagnum* is significantly greater than that of feather moss in midsummer; 3) the principal limitations to photosynthesis in the two moss types are different in the field, feather moss being more often limited by tissue water content and light intensity, and *Sphagnum* being more often limited by the activity of Rubisco; 4) larger and more numerous trees in the feather moss community evidently are more productive than those in the *Sphagnum* community. The pattern of high tree productivity and low moss productivity in a black spruce feather moss community, and low tree productivity and high moss productivity in a black spruce *Sphagnum* community, has been demonstrated by Goulden and

Crill (1997). For these reasons it is clear that the moss contribution to whole forest CO₂ uptake requires separate consideration of the two communities in both equilibrium and global change scenarios. For example, since *Sphagnum* photosynthesis in the field is most often limited by the activity of Rubisco, increases in the concentration of atmospheric CO₂ resulting from continued anthropogenic CO₂ production would be expected to result in increased *Sphagnum* photosynthesis, all else remaining equal. An increase in atmospheric CO₂ concentration would increase feather moss photosynthesis at some times (all else remaining equal), however over time the effects would likely be less important than in *Sphagnum*, since feather moss photosynthesis in the field is often limited by tissue water content and light intensity. Similarly, an increase in air temperature due to global warming would affect gross photosynthesis in *Sphagnum* through the temperature response of Rubisco, while in feather mosses, the effect of temperature on photosynthesis would more often be through its effect on electron transport.

This study showed that the photosynthetic capacity of *Sphagnum* increased significantly in midsummer compared to spring and fall, and that it was significantly greater than that of feather moss in midsummer. It also demonstrated that the high productivity of *Sphagnum* was due at least in part to the maintenance of a relatively high moss water

content throughout the growing season. Global change scenarios have been used to predict a drop in the water table in northern fens of up to 22 cm (despite a small increase in daily precipitation, Roulet *et al.* 1992), and it is not unreasonable to expect a similar drop in water table position in poorly drained black spruce systems. It is known that photosynthesis in *Sphagnum* recovers from water stress only very slowly (compared to feather mosses, Silvola 1991). Decreases in *Sphagnum* water content that would accompany plausible global change scenarios could thus have important negative effects on the photosynthetic capacity of *Sphagnum*, with associated effects on the existing CO₂ balance of the black spruce ecosystem.

The balance between moss photosynthesis and total forest floor respiration is also likely to shift with increases in air temperature associated with global change (Shaver *et al.* 1992). Models of the effects of temperature on the CO₂ balance of the forest floor must take into account the thermal stratification of the forest floor. A fruitful and simple approach to the modelling of the effects of temperature on net CO₂ exchange from the forest floor in black spruce forests would be to treat the forest floor as if it were comprised of only two thermally distinct strata: the live moss layer at the surface, and dead and living organic matter beneath the live moss layer.

The spatial distribution of trees was the most

important variable affecting spatial variability in forest floor respiration and moss photosynthetic performance. Increases in the productivity of trees predicted by global change scenarios (eg. through CO₂ fertilization, temperature increases, increased nitrogen deposition and/or increased nitrogen mineralization) can be expected to directly and indirectly affect small scale (< 1 m) to medium scale (stand level) spatial patterns of soil respiration and moss photosynthetic performance.

The precise evaluation of forest floor conductance to water vapour from closed-chamber measurements of evapotranspiration requires that a high boundary layer conductance be maintained inside the chamber. This can be achieved by using a high fan speed. In this study a boundary layer conductance of 1000 mmol m⁻² s⁻¹ would have been sufficient to permit precise measurements of forest floor conductance.

CHAPTER 5 TABLES

Table 5.2. Comparison of maximum photosynthetic rates reported for *Sphagnum* on a ground area basis. Units for photosynthesis are $\mu\text{mol m}^{-2} \text{s}^{-1}$, and have been converted from mass units where necessary. Values are net photosynthesis for 20°C unless otherwise noted.

Study	Photosynthesis	<i>Sphagnum</i> species	Notes
This study	1.3	<i>S. fuscum</i> , <i>S.</i>	Spring
	5.0 (5.5)	<i>warnstorffii</i>	Summer (25°C)
	1.5		Fall
Goulden and Crill 1997	2.5	<i>S. fuscum</i> , <i>S.</i>	gross
		<i>warnstorffii</i>	photosynthesis,
			fall, optimal
Williams and Flanagan 1996	7.0	<i>S. sect acutifolia</i>	temperature (8°C)
Green and Lange 1994	1.9	'Moss'	25°C
			no temperature
Silvola 1991	2.3	<i>S. fuscum</i>	given
Silvola and Heikkinen 1979	1.6	<i>S. fuscum</i>	optimal
			temperature (10 - 15°C)

Table 5.1. Comparison of maximum photosynthetic rates reported for feather moss (groups *Pleurozium schreberi*, *Hylocomium splendens* and *Ptilium crista-castrensis*) on a ground area basis. Units for photosynthesis are $\mu\text{mol m}^{-2} \text{s}^{-1}$, and have been converted from mass units where necessary. Values are net photosynthesis for feather moss at 20°C unless otherwise noted.

Study	Photosynthesis	Species	Notes
This study	1.5	feather moss	spring
	1.9 (2.3)		summer (25°C)
	1.8		fall
Goulden and Crill 1997	1.0	feather moss	gross photosynthesis,
			fall, approx. 12°C
Williams and Flanagan 1996	2.0	<i>P. schreberi</i>	25°C
Green and Lange 1994	< 1.9	'Moss'	no temperature given
Silvola 1991	3.2	<i>P. schreberi</i>	

CHAPTER 6
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APPENDIX I

Table AI.1. List of symbols used in the biochemical model of light saturated photosynthesis, and their units (from Farquhar and Caemmerer 1982).

Parameter	Definition	Units
$P_{g,v}$	measured light saturated rate of moss gross photosynthesis	$\mu\text{mol m}^{-2} \text{ s}^{-1}$
LAI_{tot}	Total leaf area index (equal to the sum of vascular leaf area index and moss shoot area index)	$\text{m}^2 \text{ leaf area/m}^2 \text{ ground area}$
$V_{c,\text{max}}$	maximum velocity of carboxylation of Rubisco	$\mu\text{mol m}^{-2} \text{ s}^{-1}$
C_c	partial pressure of CO_2 in the chloroplast	Pa
Γ^*	CO_2 compensation partial pressure of photosynthesis in the absence of dark respiration	Pa
K_c	Michaelis-Menten constant for Rubisco carboxylation reaction	Pa
K_o	Michaelis-Menten constant for Rubisco oxygenation reaction	kPa
$[\text{O}_2]$	Atmospheric partial pressure of oxygen	kPa
τ	CO_2/O_2 specificity ratio of Rubisco (see note below)	-

Note: $\Gamma^* = [\text{O}_2]/2\tau$

Table AI.2. List of constants and Q_0 for temperature dependence (where applicable) of constants used in the biochemical model of light saturated photosynthesis (from Collatz *et. al.* 1991).

Constant	Value at 25°C (see Table A1 for units)	Q_0
K_c	30	2.1
K_o	30	1.2
$[O_2]$	21	-
τ	2600	0.57
$V_{c,max}$	solved for	2.4

APPENDIX II

Table AII.1. Photosynthetic, respiratory and site variables entered into correlation analysis.

Variable	Definition	Units
$V_{c,max}$	see Table AI.1	see Table AI.1
SAI_{moss}^2	one-sided shoot area index of moss	m^2 shoot area/ m^2 ground area
LAI_{vasc}	one-sided leaf area index of all vascular plants	m^2 leaf area/ m^2 ground area
PFD	average daily photosynthetically active photon flux density	$\mu mol\ m^{-2}\ s^{-1}$
$R_{10,tot}$	total respiration at 10°C (from exponential regression)	$\mu mol\ m^{-2}\ s^{-1}$
$R_{10,shallow}$	respiration of shallow stratum at 10°C (from Model B)	$\mu mol\ m^{-2}\ s^{-1}$
$R_{10,deep}$	respiration of deep stratum at 10°C (from Model B)	$\mu mol\ m^{-2}\ s^{-1}$
$Basal_{tree}$	total tree basal area within 1 m of any collar edge	cm^2
$Depth_{org}$	depth from the moss surface to the organic/mineral soil interface	cm

Table AIII.1 (continued)

Depth _{moSS}	depth of live (green and brown) moss	cm
Moss _{wat}	water content of moss	fresh
	photosynthetic tissue	weight/dry
		weight
Table _{wat} ^b	average depth to the water table	cm

- a *Sphagnum* SAI was assumed to be 1.5 in this study, and was not included in the correlation analysis
- b depth to the water table was only included in the *Sphagnum* community in the summer and fall measurement periods

IMAGE EVALUATION TEST TARGET (QA-3)

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