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The contribution of bryophytes to the carbon exchange for a temperate rainforest

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Abstract

Bryophytes blanket the floor of temperate rainforests in New Zealand and may influence a number of important ecosystem processes, including carbon cycling. Their contribution to forest floor carbon exchange was determined in a mature, undisturbed podocarp-broadleaved forest in New Zealand, dominated by 100–400-year-old rimu (*Dacrydium cupressimum*) trees. Eight species of mosses and 13 species of liverworts contributed to the 62% cover of the diverse forest floor community. The bryophyte community developed a relatively thin (depth <30 mm), but dense, canopy that experienced elevated CO_2 partial pressures (median 46.6 Pa immediately below the bryophyte canopy) relative to the surrounding air (median 37.6 Pa at 100 mm above the canopy). Light-saturated rates of net CO_2 exchange from 14 microcosms collected from the forest floor were highly variable; the maximum rate of net uptake (bryophyte photosynthesis – whole-plant respiration) per unit ground area at saturating irradiance was 1.9 $\mu mol\, m^{-2}\, s^{-1}$ and in one microcosm, the net rate of CO_2 exchange was negative (respiration). CO_2 exchange for all microcosms was strongly dependent on water content. The average water content in the microcosms ranged from 1375% when fully saturated to 250% when air-dried. Reduction in water content across this range resulted in an average decrease of 85% in net CO_2 uptake per unit ground area.

The results from the microcosms were used in a model to estimate annual carbon exchange for the forest floor. This model incorporated hourly variability in average irradiance reaching the forest floor, water content of the bryophyte layer, and air and soil temperature. The annual net carbon uptake by forest floor bryophytes was 103 $g\, m^{-2}$, compared to annual carbon efflux from the forest floor (bryophyte and soil respiration) of $-1010\, g\, m^{-2}$. To put this in perspective of the magnitude of the components of CO_2 exchange for the forest floor, the bryophyte layer reclaimed an amount of CO_2 equivalent to only about 10% of forest floor respiration (bryophyte plus soil) or $\sim$11% of soil respiration. The contribution of forest floor bryophytes to productivity in this temperate rainforest was much smaller than in boreal forests, possibly because of differences in species composition and environmental limitations to photosynthesis. Because of their close dependence on water table depth, the contribution of the bryophyte community to ecosystem CO_2 exchange may be highly responsive to rapid changes in climate.

Keywords: carbon cycle, forest productivity, photosynthesis, podocarp, soil respiration, water deficit, water table

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Introduction

Bryophytes are a prominent feature of many mesic forests, where they can make an important contribution to carbon balance (Goulden *et al*., 1998; Swanson & Flanagan, 2001). On the floor of boreal forests, bryophyte cover is nearly complete and their mass may exceed that of the trees (Goulden *et al*., 1998). *Sphagnum* and feather mosses (*Pleuorizium* and *Hylcomium*) are the dominant taxa in these forests and there is more biomass globally in *Sphagnum* than in any other plant taxa (Clymo & Hayward, 1982). Mature podocarp forests in New Zealand owe their verdant, 'tropical' appearance to the rich bryophyte community living as epiphytes and draping the forest floor, where the most recent checklists list more than 1000 species of mosses and liverworts (Fife, 1995; Glenny, 1998). This bryophyte blanket affects several ecosystem processes through its influence on root-zone water storage, soil temperature and pH, and the retention and cycling of carbon and nutrients (O'Neill, 2000; Brisbee *et al*., 2001).

Respiration from roots and microbial populations in the soil usually represents the largest flux of carbon from forests to the atmosphere (Valentini *et al*., 2000). For example, in pine forests soil respiration originating from microbial decomposition and roots returns 50% to more than 70% of gross primary production to the atmosphere (Hamilton *et al*., 2002). Photosynthesis and subsequent bryophyte productivity captures a portion of this carbon potentially increasing ecosystem productivity. In boreal forests, bryophyte productivity equals or exceeds the productivity of trees (Vasander, 1982; Oechel & Van Cleave, 1986). Because of the strong coupling between bryophyte productivity and water availability (Brisbee *et al*., 2001), the contribution of bryophytes to ecosystem productivity may be highly responsive to changes in the duration and timing of seasonal root-zone water deficits associated with global warming (Weltzin *et al*., 2001).

The extensive mixed conifer broadleaved forests on glacial terraces in southern New Zealand are dominated by large evergreen podocarp species, principally rimu (*Dacryidium cupressinum* Sol. ex Lamb.). Rimu trees can live for 600 years or longer (James & Norton 2002), but survival is often dependent on major disturbance events associated with earthquakes. Low temperatures limit tree growth in the winter (June–August), but frosts are rare, allowing growth to continue throughout the year. Growth rates of rimu are low with annual increments in stem biomass of $\sim 0.8\,\mathrm{Mg\,ha^{-1}}$ (Whitehead *et al*., 2002a). This low productivity is associated with frequent water-logged conditions and low rates of mineralization in the acid, organic soils resulting in very low nutrient availability (Whitehead *et al*., 2002a). Leaf area index of the tree canopy is low, resulting in high transmittance of radiation to the forest floor to support a rich bryophyte community.

The objective of this research was to estimate components of the annual carbon exchange for the floor of an evergreen podocarp forest, emphasizing the role of living bryophytes. The extensive cover of bryophytes on the forest floor, high fraction of radiation transmitted by the forest canopy and moderate air temperatures throughout the year led us to hypothesize that a substantial fraction of CO_2 released by soil respiration would be captured by bryophyte photosynthesis. This suggests that bryophytes could contribute significantly to the net carbon exchange for the ecosystem. Our approach was to measure the response of the bryophyte community to variation in irradiance and water content, and then combine these relationships and a published temperature dependence of photosynthesis with meteorological data to model annual carbon exchanges for the forest floor.

Materials and methods

Site description

Rates of carbon exchange between the forest floor and air below the tree canopy were measured in mixed conifer-broadleaved forest in south Westland, New Zealand (lat. 43.2°S, long. 170.3°E). The site is a on a lowland glacial terrace with soil consisting of >400 mm of decomposed peat over heavily weathered Spodosols and Inceptisols. The annual rainfall of ca. 3400 mm is evenly distributed throughout the year, and poor drainage contributes to a high water table and shallow rooting depth (Jackson, 1984). Frost is rare and the annual average air temperature is 11.3 °C. The tree canopy is dominated by 100–400-year-old rimu trees (*D. cupressinum*; 86% of total basal area; James & Norton, 2002), attaining a canopy height of 25 m and a leaf area index (projected surface area basis) of 2.9 (Whitehead *et al*., 2002a, A. S. Walroft, unpublished data). The forest floor has an extensive cover of bryophytes.

Micrometeorology

Air temperature, relative humidity, incident irradiance (400–700 nm, Q), and rainfall above the forest canopy, air temperature above the forest floor (1 m) and soil temperature (50 mm depth) were measured and recorded at half-hourly intervals using a datalogger for a year from autumn, beginning on 1 April 2001.

To characterize more fully the CO_2 partial pressure in the air near the forest floor, the vertical gradient in partial pressure was measured at 10 random locations in the forest. Measurements were made with an infrared gas analyzer (LiCor 6400, LiCor, Inc., Lincoln, NE) at different heights relative to the leaves of the bryophytes: within the bryophyte mat near the stems (depth of –20 mm), immediately below the leaves (0 mm), immediately above the leaves (+ 10 mm) and at 100 and 2000 mm above the leaves. Measurements were made in mid summer (January) under still conditions between 10:00 and 16:00 h (NZST). Narrow-gauge tubing was supported at each height and the air surrounding the tubes was allowed to equilibrate within the canopy for a minimum of 5 min before a sample was drawn through the gas analyzer.

The penetration of photosynthetically active (400–700 nm, Q) and near-infrared (700–1200 nm) radiation through the bryophyte mat was measured with a fiber-optic probe connected to a diode-array spectroradiometer (Unispec, PP Systems, Haverhill, MA). Sections of the bryophyte mat were gently lifted from the forest floor and placed on a steel mesh. The fiber optic was advanced in 10 mm intervals from the lower side of the mat up through the moss canopy toward a diffuse sky; three replicated measurements were made at each interval from 400 to 1200 nm in 3 nm intervals. The spectral distribution was normalized at each height by dividing values by the solar spectrum. To infer the depth profile of chlorophyll concentration, a normalized chlorophyll index [$C = (Q_{750} - Q_{705})/(Q_{750} + Q_{705})$, where Q_{750} and Q_{705} are the irradiance at 750 and 705 nm, respectively] was calculated following Gamon & Surfus (1999) and Stylinski *et al*. (2002).

Carbon dioxide exchange

The response of CO_2 exchange by bryophytes to variation in incident irradiance and water content was measured on microcosms removed from the forest floor. At 19 locations, selected to represent the variation in species composition, the bryophyte layer was gently lifted from the underlying organic soil. A circular sample (91.6 cm^2) was removed at each location and placed in a 50 mm deep pot; the top of the bryophytes extended approximately 30 mm above the top of the pots. A fine mesh on the bottom of the pots permitted drainage. Five microcosms were used to measure the photosynthetic response to incident irradiance and 14 were used to measure the response to water content.

Carbon dioxide exchange was measured by placing the microcosms in a mixed 4 L cuvette connected to a closed infrared gas-analysis system (LiCor 6200, LiCor, Inc., Lincoln, NE). Prior to each measurement the bottom of each microcosm was covered with a plastic film. The gas sample was dried before entering the analyzer to eliminate potential errors in measuring CO_2 associated with water vapor in the gas stream. The change in CO_2 partial pressure in the cuvette was measured over 60 s from an initial partial pressure of $\sim$40 Pa. A halogen lamp projected through an infrared filter provided irradiance, and a fan directed at the cuvette maintained nearly constant air temperature during the measurement (variation $\leq$0.1 °C). The rate of CO_2 exchange for each microcosm was calculated from the rate of change of CO_2 in the cuvette and the volume of the gas exchange system, with appropriate corrections for temperature and pressure (Field *et al*., 1989; Hooper *et al*., 2002). Rates were expressed as flux densities on a unit ground area basis.

Soon after collection, the microcosms for the drying experiment (n = 14) were immersed in water for 30 min to ensure full hydration. The water was in equilibrium with the CO_2 partial pressure of the atmosphere. After draining freely for 60 min, each pot was weighed and gas exchange was measured at an incident irradiance of 533 $\mu mol\, m^{-2}\, s^{-1}$ (400–700 nm) and in darkness. Measurements were repeated as the microcosms dried in conditions of diffuse irradiance for 3 days.

The response of CO_2 exchange to incident irradiance was measured on five additional microcosms. Samples were collected early in the morning following heavy rain and it was assumed that the bryophytes were fully hydrated. Each microcosm was measured initially at an irradiance of 1470 $\mu mol\, m^{-2}\, s^{-1}$, then irradiance was reduced subsequently in eight steps to complete darkness by placing neutral density cloth or black felt over the cuvette. The samples were exposed to each level of irradiance for 2–3 min and the cuvette atmosphere was refreshed prior to each measurement.

The species composition of each microcosm was determined from visual estimates of the frequency and percentage cover of mosses, liverworts and vascular plants. The species names and authorities are from Beever *et al*. (1992) and Glenny (1998).

An *in situ* estimate of CO_2 uptake by the forest floor was made once during the autumn (March 2002) using a large, clear hemispherical 9.7 L cuvette connected to a closed-gas analysis system described above. Irradiance was measured with a quantum sensor (LI 190SA, LiCor, Inc.) mounted in the center of the dome and soil (50 mm depth) and air temperatures were measured with thermistors. At least two days prior to measurements, circular mounting platforms were inserted 50 mm into the bryophyte layer at four locations in the forest understory, providing an airtight seat for the cuvette. The rate of mixing in the cuvette was controlled with fans to provide a stable, linear rate of change in the CO_2

partial pressure during the measurement (Hooper *et al.*, 2002). Each sampling location was measured during a sunfleck and then again with the cuvette darkened; the difference between measurements made with the darkened cuvette (bryophyte and soil respiration) and in the light (bryophyte and soil respiration, plus bryophyte photosynthesis) provided a direct estimate of bryophyte photosynthesis.

In situ measurements of respiration flux density from the forest floor, which included respiration from the soil and bryophyte layer, were made at intervals throughout the year using a darkened 1.1 L chamber and portable infrared CO_2 analyzer (SRC-1 and EGM-1, PP Systems, Hitchin, UK) as described by Blanke (1996). The automated gas-exchange system was configured in 'closed' mode, and each measurement was completed in approximately 120 s. The chamber was placed on plastic rings inserted 25 mm into the surface and circumscribing 0.007 m^2 of ground area. Measurements were made at 28 locations at approximately monthly intervals. Soil temperature at a depth of 50 mm was recorded simultaneously with a thermistor.

Forest floor cover

The percentage of the forest floor covered by bryophytes, angiosperms, ferns, leaf and woody litter, and open space was estimated visually in 0.1 m^2 circular plots. Forest floor vegetation was categorized arbitrarily as all vegetation 100 mm or shorter. A sampling ring was tossed onto the forest floor at 40 random locations and the percentage cover by class was estimated by two observers (repeatability $\pm 5\%$, Anderson, 1986). Because of the small size of the sampling ring, large woody debris was not included in the estimate of cover. The 'open' category included exposed soil and living roots of large trees.

Data analysis

Equations relating physiological variables to environmental variables were fitted using least-squares regression with SYSTAT (ver. 7.0 for Windows, SPSS, Inc., Chicago, IL, USA). The nonquadratic hyperbola describing the relationship between incident irradiance and carbon exchange was fitted using the Nelder-Mead minimization routine in Photosynthesis Assistant (ver. 1.1.2, Dundee Scientific, Dundee, Scotland, UK).

Model of annual forest floor carbon exchange and water balance

A two-compartment model (bryophyte layer and underlying soil) was used to calculate annual values of hourly CO_2 exchange for each component independently for day and night. Night- and daytime respiratory flux densities from the bryophyte layer and soil were designated B_N, B_D, S_N and S_D, respectively; photosynthesis flux density by the bryophyte layer was designated B_P. All values were calculated hourly for the year from May 2001. The convention adopted throughout this paper is to indicate uptake of CO_2 (photosynthesis) with a positive sign and release of CO_2 to the atmosphere (respiration) with a negative sign.

The total night-time respiration flux density from the forest floor ($B_N + S_N$), based on *in situ* measurements described above, was calculated as a function of temperature (50-mm depth) with a modified Arrhenius function (Lloyd & Taylor, 1994; Fang & Moncrieff, 2001). S_N was calculated by subtracting an independent estimate of B_N from the total night-time flux density [$= (B_N + S_N) - B_N$].

B_N was calculated as a function of temperature and tissue water content. The maximum rate of respiration was calculated from a regression of respiration flux density versus water content (Fig. 5) and this value was then modified according to temperature. The temperature dependence of B_N was modeled as the 'Q_{10}' response $R = R_0 e(T_{ln}(Q_{10/10}))$, where R_0 is the respiration rate at 0 °C (0.29 $\mu mol\, m^{-2} s^{-1}$), T is the soil temperature at 50 mm depth and the value for Q_{10} was assumed to be equal to 2 (Drewitt *et al.*, 2002). The slope of the relationship between bryophyte respiration flux density and water content was then used to reduce the temperature-determined respiration rates by the depth of water stored in the bryophyte layer.

Bryophyte photosynthesis (B_P) was calculated as a function of irradiance reaching the forest floor, water content and temperature. Irradiance reaching the forest floor (Q_f) was estimated from incident irradiance above the tree canopy (Q) using Beer's law, where $Q_f = (1 - e^{-kL})Q$ and L is the leaf area index for the tree canopy and k is the extinction coefficient (assumed to be equal to 0.5). A nonquadratic hyperbola (Zhang, 1989) was used to describe the response of photosynthesis to incident irradiance. The light-saturated rate of photosynthesis at maximum water content was calculated by regressing photosynthesis against water content. The light-limited rate of photosynthesis for each hour was then 'discounted' with normalized relationships between photosynthesis and water content (derived from Fig. 5) and between photosynthesis and temperature.

A function describing the temperature dependence of photosynthesis was derived from values published by Maseyk *et al.* (1999) for *Sphagnum* species growing near our site. The data were normalized and fit with an equation from Landsberg & Waring (1997), where

$A = A_{max}\,[(T_a - T_{min})/(T_{opt} - T_{min})]*[(T_{max} - T_a)/(T_{max} - T_{opt})]\wedge[(T_{max} - T_{opt})/(T_{opt} - T_{min})]$. The maximum and minimum temperatures supporting photosynthesis were T_{max}: 41.9 °C and T_{min}: −0.7 °C, respectively, and the optimum temperature for photosynthesis was T_{opt}: 20.7 °C. The temperature function was normalized to 1 at 18.3 °C, the average temperature of our measurements. Photosynthesis was reduced by approximately 24% at 10 °C and 53% at 5 °C by this function. It was assumed that irradiance, water content and temperature acted independently on the rate of photosynthesis.

Water balance in the bryophyte layer

For the purposes of estimating annual carbon exchange for the bryophyte layer, a simple water balance model was used to calculate changes in water content in the bryophyte layer at hourly intervals. The maximum water storage in the bryophyte layer (W_{max}) of 4.4 ± 0.6 (SD, $n = 14$) mm was determined from the difference between the mass of samples when they were fully hydrated and at the end of the experimental drying period. The assumption that these limits spanned the range of physiological activity was justified because measured rates of photosynthesis and respiration were negligible at the minimum water content ($\sim 200\%$) attained during the 'dry-down' experiment.

Water content of the bryophyte layer, W_i for the ith hour was estimated as the difference between the gain from net rainfall reaching the forest floor and the loss from evaporation and drainage. Rainfall reaching the forest floor was assumed to be 75% of that measured above the forest canopy (Whitehead *et al*., 2002b). The rate of evaporation from the bryophyte layer was estimated from a relationship between the energy reaching the forest floor and changes in the mass of undisturbed samples from the bryophyte layer placed in plastic-walled lysimeters *in situ* in the forest floor. Six lysimeters (150 mm diameter, 50 mm deep) were prepared and left overnight before measurements began. They were then lifted out of the ground during the subsequent three days and weighed at hourly intervals during the daylight hours. New lysimeters were prepared after 3 days. The measurements were made in mid-summer (January) and repeated in autumn (March).

During the periods when measurements of evaporation were made, the available energy reaching each lysimeter was estimated from measurements of shortwave radiation above the forest canopy and the canopy gap fraction at each site calculated using hemispherical photographs taken with a digital camera (model Coolpix 990, model FC-E8, Nikon). For each hour, the gap fraction was determined from the position of the sun and the solar elevation and zenith for the direct radiation component and an average for the whole canopy for the diffuse component using GLA software (Institute of Ecosystems Studies, Millbrook, NY). In the absence of measurements of net radiation above the forest canopy, it was assumed that available energy was 0.7 times shortwave radiation (Whitehead *et al*., 2002a). These data were used to derive a linear relationship between evaporation rate and available energy.

This relationship was used in the model to estimate hourly rates of evaporation from the bryophyte layer. For each hour during the year, available energy reaching the forest floor was calculated from measurements of incident irradiance above the tree canopy using Beer's law as described earlier. Drainage from the bryophyte layer was assumed to be zero when $W_i \leq W_{max}$ and, if net rainfall resulted in the water storage in the bryophyte layer reaching its maximum (i.e. $W_i > W_{max}$), then it was assumed that the excess rainfall was dispersed either as drainage or surface runoff. The water balance approach provided hourly values of water storage in the bryophyte layer throughout the year. Assuming constant depth of the bryophyte layer, values of water storage were converted into water content and used to estimate rates of photosynthesis and respiration from the experimental relationships described above.

Results

Although not intended to provide a comprehensive description of species composition, the microcosms harvested for gas exchange measurements were representative of the forest floor and contained a diverse community of mosses, liverworts and diminutive vascular plants (Table 1). The species richness and dominance (*dominance = relative cover + relative frequency*; values not shown) of liverworts were greater than for mosses or vascular plants. Two species of mosses, *Dicranoloma billardierei* and *Hypnodendron colenesoi*, and two species of liverworts, *Heteroscyphus billardierei* and *Lepidozia spinosissima* were more dominant than the others. Vascular plants were a minor component of the forest floor community.

Direct sampling of the forest floor indicated that the average bryophyte cover was $62 \pm 20\%$ (SD); angiosperms and ferns contributed $12 \pm 10\%$ and $10 \pm 12\%$, respectively. A small proportion of the forest floor was unoccupied ($4 \pm 12\%$), and cover by leaf and woody litter was 18 ± 20 and $7 \pm 6\%$, respectively. The percentage cover by bryophytes was related inversely to total litter cover (leaf plus woody; $r^2 = 0.36$, $P < 0.01$, $n = 40$), and the samples with the highest proportion of litter

Table 1 Species composition of forest floor microcosms ($n = 19$) harvested from the rainforest site and used for gas exchange measurements; the percentage cover represents the average area occupied by each species, and the percentage frequency is the relative number of microcosms containing a given species. (Trace coverage (<2%) is indicated by 'tr')

Species	Cover (%)	Frequency (%)
Mosses		
Achrophyllum quadrifarium (Sm.) Vitt & Crosby	7	26
Canalohypopterygium tamariscinum (Hedw.) Kruijer	10	5
Dicranoloma billardierei (Brid. ex anon.) Par.	97	11
Hypnodendron comatum (C. Muell.) Mitt. ex Touw	35	53
Hypnodendron colensoi (Hook f. & Wilson) Mitt.	89	21
*Hypnodendron kerrii/menziesii**	19	11
Canalohypopterygium tamariscinum (Hedw.) Kruijer	10	5
Ptycomnion aciculare (Brid.) Mitt.	4	32
Liverworts		
Bazzania novae-zelandiae (Mitt.) Besch. & C. Massal.	10	11
Heteroscyphus billardierei (Schwaegr.) Schiffn.	6	89
Heteroscyphus coalitis (Hook. f.) Schiffn.	tr	5
Leiomitra lanata (Hook.) R.M. Schust.	5	5
Lepidozia spinosissima (Hook. f. & Taylor) Mitt.	42	53
Lepidozia pendulina (Hook.) Lindenb.	32	16
Riccardia colensoi (Steph.) W. Martin	10	5
Riccardia crassa (Schwaegr.) Carrington & Pearson	53	11
Schistochila appendiculata (Hook.) Trevis.	25	26
Schistochila glaucescens (Hook.) A. Evans	4	16
Schistochila nobilis (Hook.) Trevis.	8	26
Tylimanthus saccatus (Hook.) Mitt.	18	26
Trichocolea mollissima (Hook. f. & Taylor) Gottsche	tr	16
Angiosperms and ferns		
Hymenophyllum multifidum (G. Forst.) Sw.	2	16
Luzuriaga parviflora (Hook. f.) Kunth	5	5
Metrosideros diffusa (G. Forst.) Sm.	tr	5
Nertera balfouriana Cockayne	12	26
Nertera dichondrifolia (A. Cunn.) Hook. f.	3	16

*Identification to species is uncertain.

and lowest proportion of bryophyte cover tended to occur in small depressions in the forest floor.

Leaves of bryophytes and vascular plants near the forest floor experienced enriched levels of CO_2 partial pressure relative to that in the bulk air below the tree canopy (Fig. 1). The median CO_2 partial pressure at 100 mm above the forest floor was 37.6 Pa (mean 38.2 Pa) and increased to 46.6 Pa (mean 47.3 Pa) immediately below the bryophyte 'canopy' (0 mm). The partial pressure of CO_2 among the bryophyte stems (-20 mm depth) was variable with partial pressures in excess of 100 Pa.

It was assumed that the living bryophyte layer extended to a depth of ca. 80 mm, where it naturally separated from the underlying organic soil. However, the quality of reflected light indicated that only the top 10–20 mm of this layer was photosynthetically active. Irradiance attenuated strongly through the bryophyte canopy (Fig. 2) – the average value decreased to 53% of incident irradiance by 10 mm into the canopy and to less than 5% of incident irradiance at a depth of 40 mm. Attenuation of irradiance through the canopy was accompanied by a strong shift in the spectral distribution (data not shown). The chlorophyll index increased in the first 30 mm, but remained relatively constant thereafter. In so far as this index can be used as a proxy for chlorophyll and the capacity to perform photosynthesis, the rapid increase in the chlorophyll index suggests that the average depth of the photosynthetic layer in the forest floor of this forest was approximately 30 mm (Fig. 2).

There was considerable variation among microcosms in the magnitude of CO_2 exchange measured at full hydration and saturating irradiance (Fig. 3). Two

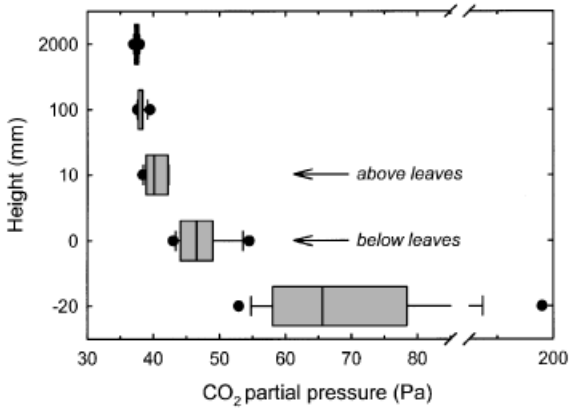

Fig. 1 Vertical gradient of CO_2 partial pressure through the bryophyte layer on the forest floor of a temperate rainforest. Measurements were made in the rhizosphere (designated −20 mm), immediately below (0) and above the photosynthetic tissue (+10 mm), and 100 mm (+100) and 2000 mm (+2000) above the forest floor. The arrows indicate measurements made immediately above and below the bryophyte leaves and indicate the partial pressure of CO_2 available for photosynthesis. The line in the box plot represents the median value ($n = 10$), the ends of the box represent the 25th and 75th percentiles and the whiskers represent the 10th and 90th percentiles. The closed symbols represent statistical outliers.

microcosms (numbers 2 and 3) did not achieve net carbon uptake. Microcosm 2 contained 90% cover of the moss *Hypnodendron colensoi*; microcosm 3 also contained 30% cover of this species with 30% *L. spinosissima* (liverwort) and 30% *Nertora baliforiana* (angiosperm). In sample number 14, with 95% cover of the liverwort *R. crassa*, the light-saturated rates of gross photosynthesis

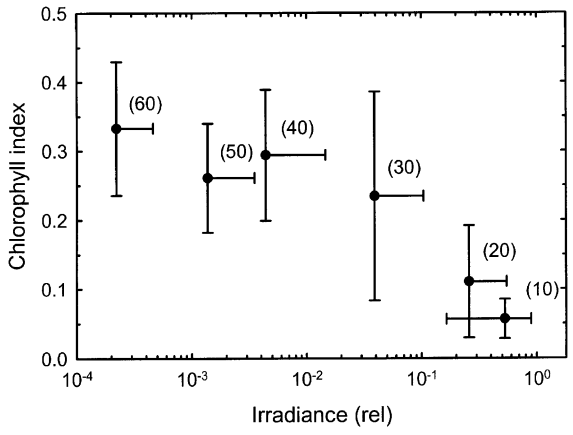

Fig. 2 Profile of the chlorophyll index as a function of relative irradiance (400–700 nm) with depth through the bryophyte layer. Each point is an average of nine independent measurements (±1 SD) and the value in parentheses represents the corresponding depth from the top of the bryophyte canopy.

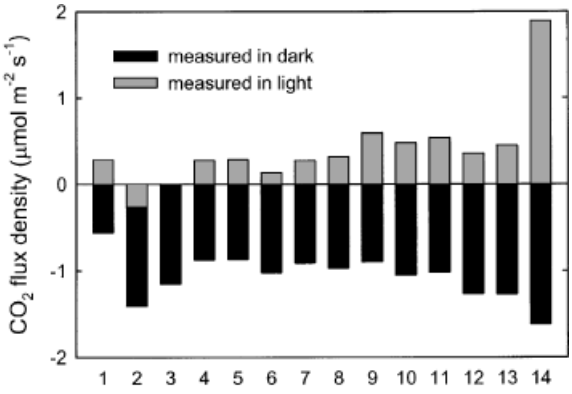

Fig. 3 Rates of net CO_2 exchange measured for bryophyte microcosms removed from the floor. The numbers on the abscissa designate different microcosms. Rates were measured in the dark (closed bars) or in the light (shaded bars). The total height of the bars indicates the sum of the absolute values of net exchange measured in the dark and in the light. Each bar represents the fully hydrated rate of CO_2 flux density for a different microcosm at the beginning of the experimental drying period. The average air temperature during the measurements was 18.3 °C.

(sum of rates measured in the light and in the dark) was approximately 3.5 μmol $m^{-2} s^{-1}$.

These rates represent whole-plant rates of CO_2 exchange per unit ground area, as the microcosms contained intact plants with leaves and stems. Because measuring leaves alone was impractical, the net rate of CO_2 uptake by an intact microcosm in the light plus the rate of CO_2 loss in the dark was taken to represent the photosynthetic capacity of leaves. Because dark respiration by leaves is included, this calculation represents a small overestimate of photosynthesis.

There also was considerable variation among the microcosms used to measure the light-dependence of carbon exchange. Based on the statistical fit of a nonquadratic hyperbola to the data, photosynthesis became light saturated at an irradiance (400–700 nm) of ~160 μmol $m^{-2} s^{-1}$ (Fig. 4), similar to the average annual irradiance reaching the forest understory of 153 μmol $m^{-2} s^{-1}$. The data in Fig. 4 represent gross rates (e.g. the sum of the absolute value of the rate of CO_2 exchange measured in the dark and in the light). As with the microcosms illustrated in Fig. 3, one sample containing 90% of the moss *H. colensoi* did not achieve positive net photosynthesis at saturating irradiance (Fig. 4, diamonds). The highest rates of carbon uptake were from a microcosm containing 70% cover of the liverwort, *L. spinosissima*.

The relationships between the CO_2 exchange of microcosms and water content were highly significant, but had uniformly low coefficients of determination

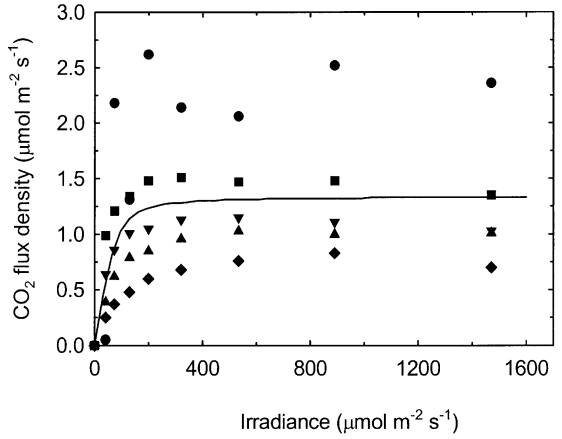

Fig. 4 The rate of CO_2 exchange (sum of the flux densities measured in the light and dark periods) as a function of incident irradiance for five bryophyte microcosms. The solid line represents a nonquadratic hyperbola fit to the data as $A = [\phi Q + A_{max} - (\phi Q + A_{max})^{-1/2} - 4\phi\theta A_{max}))]/2\theta$, where A is the CO_2 flux density at a given irradiance (Q), ϕ is the initial linear rate of A at low Q, θ describes the degree of curvature and A_{max} represents the maximum rate of exchange. The values for ϕ, A_{max}, and θ are 0.0151, 1.34 μmol $m^{-2} s^{-1}$ and 0.88, respectively.

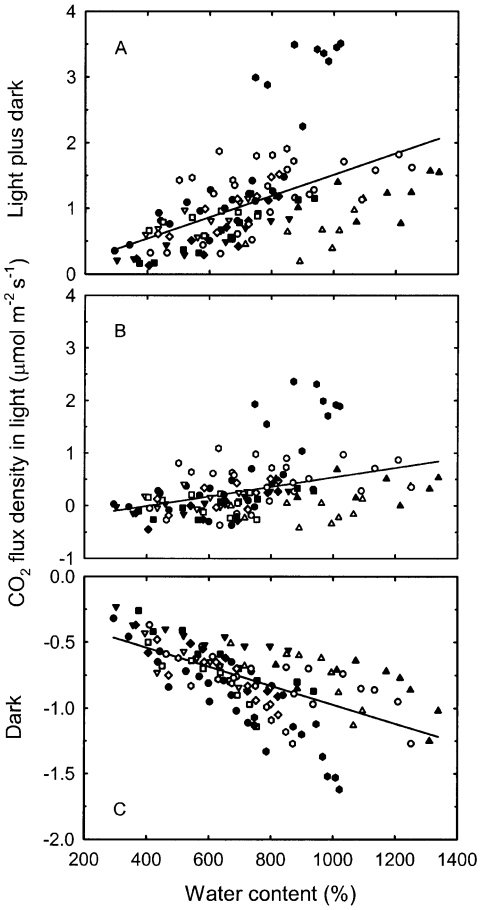

Fig. 5 Sum of the rates of CO_2 flux density measured in the light plus dark (a), measured in the light (b), and measured in the dark (c) for 14 bryophyte microcosms as a function of water content (fresh/dry mass). Each type of symbol represents a different microcosm. The CO_2 exchange in the light was measured under saturating irradiance. The solid lines indicate least-squares regressions (see Results).

(Fig. 5). Rates of CO_2 exchange (μmol $m^{-2} s^{-1}$) in the light ($= 0.002$*water content (%) $- 0.109$, $r^2 = 0.26$, $P < 0.001$, $n = 126$) and the sum of rates in the light and the dark ($= 0.001$*water content $- 0.362$, $r^2 = 0.14$, $P < 0.001$) were positively related to water content in the range from ca. 250% to 1375%. There was a negative relationship between respiration in the dark and water content ($= -0.001$*water content $- 0.254$, $r^2 = 0.40$, $P < 0.001$). When absolute water content was replaced with normalized values, coefficients of determination improved (~ 0.5) and the slopes of these normalized relationships were used as part of the calculation of annual net carbon exchange.

Over the three days of the drying experiment, the absolute decrease in water content for most microcosms was from approximately 300–600%. Microcosm number 14 (Fig. 3) was notable in this regard. Composed of 95% cover of the liverwort *R. crassa*, it had the highest rates of light-saturated photosynthesis at full hydration and had the smallest decrease in water content (274%) over the experimental drying period (filled hexagons; Fig. 5a).

The rate of photosynthesis measured *in situ* on intact bryophyte communities was 1.3 μmol $m^{-2} s^{-1}$; this was calculated as the difference in the rate of CO_2 exchange measured in the dark (-7.3 ± 1.0 μmol $m^{-2} s^{-1}$) and when the forest floor was exposed to a sunfleck (-6.0 ± 0.8 μmol $m^{-2} s^{-1}$; $P = 0.07$, one-tailed t-test, $n = 4$). The average irradiance and CO_2 partial pressure during the sunfleck was 157 ± 206 μmol $m^{-2} s^{-1}$ and 46.5 ± 2.8 Pa, respectively.

There was a significant relationship between evaporation from the bryophyte layer, E (mm h^{-1}) and available energy incident on the forest floor, G (W m^{-2}), where $E = 1.6 \times 10^{-4} G + 0.0118$; $r^2 = 0.69$, $P < 0.01$; Fig. 6). The regression equation was not forced through the origin, recognizing the small enhancement of evaporation due to advection.

Total respiration from the forest floor, including CO_2 efflux from bryophytes and roots and microbial activity in the organic soil, measured with a darkened gas exchange cuvette increased with increasing soil temperature (Fig. 7). The modified Arrhenius function using the common parameter value for activation energy derived from a wide range of soils by Lloyd &

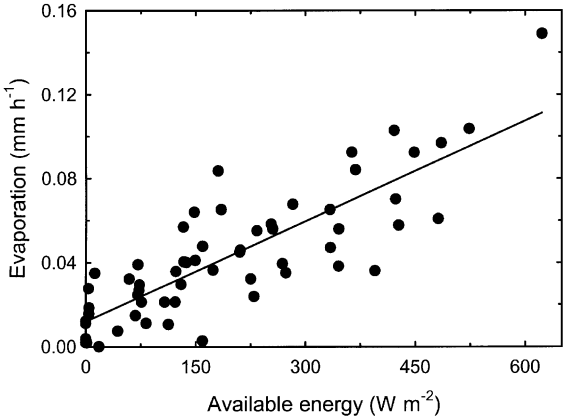

Fig. 6 The relationship between evaporation from the bryophyte layer, E ($mm\,h^{-1}$) and available energy, incident on the forest floor, G (Wm^{-2}). Each point represents an independent measurement and the line is a least-squares linear regression.

Taylor (1994) provided a close fit to measurements at low soil temperatures, but slightly underestimated rates at temperatures above approximately 12 °C.

During the year used for modeling annual net carbon exchange for the forest floor, air temperatures at a height of 1 m were moderate and rarely fell below 0 °C. The average temperature for the year was 10.9 °C (max: 25.8 °C; min: − 1.6 °C), and the average soil temperature (50 mm depth) was 11.7 °C (max: 19.3 °C; min: 2.9 °C). The average daily irradiance above the forest canopy and irradiance reaching the forest floor were 628 and 153 $\mu mol\,m^{-2}\,s^{-1}$, (400–700 nm), respectively. Total rainfall for the year was 3118 mm. Of the rainfall reaching the forest floor (2339 mm), only 122 mm were evaporated. The limited capacity for water storage (maximum 4.4 mm) and poor water retention by the bryophyte layer resulted in frequent periods when the water content fell well below saturation (Fig. 8), even though the rainfall was high and well distributed throughout the year.

Modeled annual net carbon uptake by the bryophyte layer, adjusted for the percentage of forest floor covered by bryophytes, was 103 $g\,m^{-2}$ (Table 2), equivalent to approximately 10% of the total annual CO_2 efflux from the forest floor, including bryophytes and soil ($-1010\,g\,m^{-2}$) and ~11% of soil CO_2 efflux ($-908\,g\,m^{-2}$). The net carbon uptake by bryophytes was small compared to estimates of net primary production (960–1070 $g\,m^{-2}\,yr^{-1}$) or gross primary production (2040 $g\,m^{-2}\,yr^{-1}$) for the trees in the stand (Table 2).

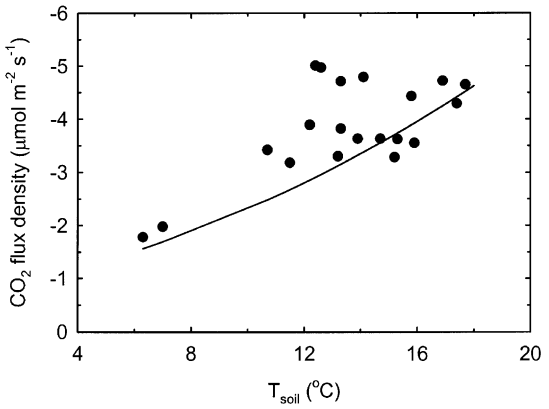

Fig. 7 *In situ* forest floor (bryophyte plus soil) respiration flux density measured in the dark, as a function of temperature (50 mm depth). Each point represents an average of 28 independent measurements made between April 2001 and May 2002. The line represents a least-squared fit of the modified Arrhenius equation (Lloyd & Taylor, 1994) $R = R_{10}\,e_0^{(E/56.02 - 1/(T_s - 227.13))}$; where R is the rate of respiration at soil temperature T_s, E_0 is the activation energy for soils set at 308.56 $J\,mol^{-1}\,K^{-1}$ following Lloyd & Taylor (1994) and R_{10} is the respiration rate at a forest floor temperature of 10 °C (2.35 $\mu mol\,m^{-2}\,s^{-1}$) ($r^2 = 0.40$).

Discussion

The estimate of annual CO_2 exchange from our model suggests that the bryophyte layer contributes to net carbon uptake in this forest, but the contribution is small. We estimated that the annual carbon exchange from the soil of a mature rimu forest was $-908\,g\,m^{-2}\,yr^{-1}$; bryophyte respiration contributed another $-101\,g\,m^{-2}\,yr^{-1}$. Annually, photosynthesis by bryophytes was only 5% of gross primary production by the tree canopy. Assuming that all the CO_2 taken up by photosynthesis was derived from the forest floor and not from the atmosphere, the bryophyte layer captured ~10% of the CO_2 released by soil plus bryophyte respiration, yielding a net carbon release

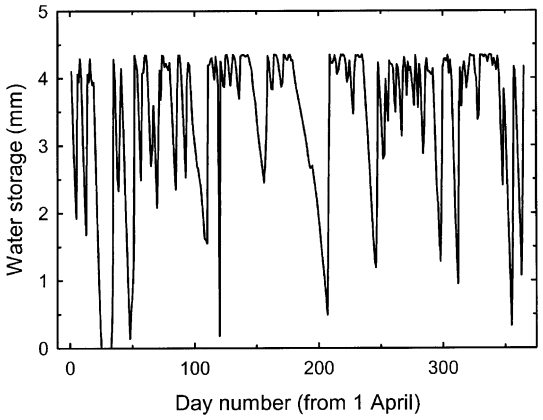

Fig. 8 Daily changes in water storage in the bryophyte layer for one year calculated using the water balance model. The maximum water storage of the bryophyte layer was 4.4 mm.

Table 2 Annual components of carbon exchange ($g\,m^{-2}$) for the bryophyte layer and soil at the rainforest site.

Component	Day flux		Night flux		Total flux
Bryophyte					
Photosynthesis	103	(166)	0	(0)	103
Respiration	−56	(−90)	−45	(−73)	−101
Net	50	(80)	−45	(−73)	2
Forest floor					
Bryophyte & soil respiration	−572	(−606)	−438	(−466)	−1010
Soil respiration	−515	–	−393	–	−908
Net forest floor flux	−469	–	−438	–	−907
Trees					
Net primary production*	–	–	–	–	960–1070
Gross primary production*	–	–	–	–	2040

*Data from Whitehead *et al*. (2002a, b).

Positive values represent net flux densities from the atmosphere to the ground (photosynthesis) and negative values represent net flux densities from the ground to the atmosphere (respiration). The values in parentheses are derived from the model and were not weighted for the amount of bryophyte cover (62%). 'Bryophyte & soil respiration' was calculated as the sum of soil respiration flux density and the area-weighted value for bryophyte respiration flux density. The net exchange for the forest floor is the sum of soil and bryophyte respiration minus bryophyte photosynthesis. 'Day' was defined as the period where irradiances at the forest floor were $\geq 1\,\mu mol\,m^{-2}\,s^{-1}$. The range in values for gross and net primary production for the rimu trees at this site were derived from independent published reports.

by the forest floor of $-907\,g\,m^{-2}\,yr^{-1}$ (Table 2). Comparable data are not currently available for other temperate rainforests in the southern hemisphere. In boreal ecosystems, however, the amount of carbon captured by bryophytes can be substantially higher than at our site.

In a 120-year-old black spruce forest with extensive cover of *Sphagnum* and *Pleurozium*, moss photosynthesis captured 36% of soil respiration between May and October (Swanson & Flanagan, 2001), and on individual days during mid-summer, moss photosynthesis was as high as 50% of whole-forest photosynthesis (Goulden & Crill, 1997). In a mixed boreal forest in Sweden consisting of *Picea abies* and *Pinus sylvestris* trees, photosynthesis by mosses captured ~16% of annual CO_2 efflux from the forest floor (Moren & Lindroth 2000). By comparison, the contribution of bryophytes in this rimu forest to net primary production was small, in part because bryophyte productivity was low and forest productivity was considerably higher than that in a comparable boreal spruce forest (Goulden *et al*., 1998). Our estimate of net CO_2 exchange by the bryophyte layer was not adjusted for the ground area occupied by tree stems, which was less than 1%, and did not include net CO_2 uptake by bryophytes present on stems and branches of the trees. Both these factors would likely have a small effect on our estimates.

The biomass increment of bryophytes was not measured directly in this study, but the net primary production was estimated from the difference between photosynthesis and respiration (Table 2). This estimate of bryophyte net primary productivity of $2\,g\,m^{-2}\,yr^{-1}$ is extremely low relative to that for boreal forests and other peat ecosystems in the Northern Hemisphere, where the long-term average rates of carbon accumulation in peat can exceed $50\,g\,m^{-2}\,yr^{-1}$ (Harden *et al*., 1992). Moss production in forests in Sweden and Canada are from 28 to $>100\,g\,m^{-2}\,yr^{-1}$ and production in temperate and polar bogs can exceed $800\,g\,m^{-2}\,yr^{-1}$ (cited in Rieley *et al*., 1979). High species diversity of mosses and liverworts with low rates of photosynthesis, combined with environmental limitations of carbon assimilation may have contributed to the low bryophyte production in this ecosystem.

Low-energy availability at the forest floor limits photosynthesis and productivity by bryophytes. Even in the fairly bright conditions in the understory of this rimu forest, where approximately 22% of incident irradiance reached the forest floor, annual photosynthesis by bryophytes would increase with higher irradiance. Annual carbon gain in the absence of canopy shade and water limitations, integrated across the response of photosynthesis to irradiance (Fig. 4) using measurements of irradiance alone would be $412\,g\,m^{-2}$. Imposing a light limitation by recalculating irradiance reaching the understory using a tree leaf area index of 2.9 reduced annual carbon gain by ~34%. This is only an approximation, as this estimate does not include possible reductions in photosynthesis caused by persistent photoinhibition (Murray *et al*., 1993; Green &

Lange, 1994). Photosynthetic rates of forest floor microcosms became light saturated at an incident irradiance of $\sim 160\,\mu mol\,m^{-2}\,s^{-1}$ (Fig. 4), similar to the average irradiance at the forest floor. Values of irradiance at light saturation for *Sphagnum* species native to New Zealand are $130–140\,\mu mol\,m^{-2}\,s^{-1}$ (Maseyk *et al*., 1999) and other forest species saturate at $100–300\,\mu mol\,m^{-2}\,s^{-1}$ (Proctor, 2000).

Annual precipitation during this study was 3118 mm. Of this total, 2339 mm reached the forest floor, where 122 mm evaporated and the remainder either ran off or percolated to ground water. Water retention and the maximum water storage of the bryophyte layer was low (4.4 mm), so even with this exceptionally high precipitation forest floor bryophytes frequently experienced periods of drying out (Fig. 8). On 188 days in the year, water content of the bryophyte layer was $\leq 90\%$ of its maximum and on 77 days it was $\leq 60\%$ of its maximum. The estimate of net annual carbon uptake by the forest floor if photosynthesis were limited alone by light was $273\,g\,m^{-2}\,yr^{-1}$. Adding a water limitation to the model reduced this value to $199\,g\,m^{-2}\,yr^{-1}$. Thus, water limitations reduced annual carbon uptake by forest floor bryophytes by $\sim 27\%$. The combination of water limitations and suboptimal temperatures reduced photosynthesis from its potential by 39%.

The depth of green tissue and presumably the region of active photosynthesis in the bryophyte community on the forest floor were thin, only 10–30 mm deep, but the canopy effectively harvested 95% of incident irradiance (Fig. 2). Assuming a random distribution of leaf angles, this magnitude of light attenuation would require an equivalent leaf area index of ~ 6 for the forest floor bryophytes. High leaf area index is not unusual for bryophytes. In addition to maximizing light capture for photosynthesis (Whitehead & Gower, 2001), Proctor (2000) suggested that maintaining a high leaf area index might be an adaptation to circumvent diffusion limitations to CO_2 uptake. Because of the absence of stomata, liquid phase conductance between the bulk air and chloroplasts can be quite low for bryophytes (Rice & Giles, 1996; Williams & Flanagan, 1996). In addition to increasing the capacity to absorb incident irradiance, a high leaf area index would also facilitate diffusion by increasing surface area.

As poikilohydric organisms, the metabolism of bryophytes varies directly with external water availability (Proctor, 1982), and even though precipitation in this temperate rainforest is high, the availability of water strongly limited annual photosynthesis by the forest floor community. Rates of photosynthesis and respiration of forest floor microcosms decreased as water content declined (Fig. 5). The linear decline in photosynthesis and respiration with decreasing water content observed in this study was unlike the 'optimal response' to water content widely reported for bryophytes (Maseyk *et al*., 1999; Proctor, 2000). Low diffusive conductance caused by water on leaf surfaces reduces CO_2 exchange at supraoptimal water contents; the microcosms in this experiment were allowed to dry for half an hour prior to the first measurement and by this time no water film was visible on the leaves. There was considerable variation in the relationship between the rates of CO_2 exchange and water content. This was caused in part by differences in the species composition among samples. For example, photosynthesis in the microcosm containing mostly the liverwort *R. crassa* (Fig. 5, closed hexagon symbol) was higher and the rate of water loss was less during the drying experiment than those for most of the other microcosms. This species has very small leaves that are tightly appressed to the substrate, thereby retarding evaporation.

In contrast to the limitations imposed on photosynthesis by water and light, liverworts and mosses on the forest floor experienced elevated levels of CO_2 partial pressure that likely enhanced photosynthesis. The median CO_2 partial pressure during a still day in mid-summer and immediately below the leaves was 48.6 Pa (Fig. 1), and decreased to 38.6 Pa above the level of the photosynthetic tissues. These values are somewhat lower than those reported by Tarnawski *et al*. (1994) for bryophytes on the floor of a broadleaved temperate rainforest, but they sampled the atmosphere at a greater depth, where we observed a median CO_2 partial pressure of >65 Pa. This enrichment in CO_2 partial pressure relative to that in the bulk air suggests that the bryophyte community obtains most of its carbon from CO_2 derived from soil respiration. As with vascular plants, bryophytes may acclimate to prolonged exposure to elevated CO_2 partial pressure (Van Der Heijden *et al*., 2000), but higher rates of photosynthesis and greater nutrient use efficiency than otherwise expected at lower CO_2 partial pressures are likely to occur.

The diversity and species composition of bryophytes may directly influence carbon assimilation and productivity of the forest floor (Brisbee *et al*., 2001). Compared to boreal forests where *Sphagnum* and feather mosses are dominant (Elliott-Fisk, 2000), the species richness of the bryophyte community in the understory of our mature rimu forest was high and the number and frequency of liverworts outnumbered mosses (Table 1). External water conduction is important to all members of the Bryophyta, but where many mosses contain water-conducting parenchyma and other cells that facilitate internal water transfer (Proctor, 1982; Vitt, 2000), most liverworts do not (Hébrant, 1977). In addition to differences among species in their

maximum rates of photosynthesis (Fig. 3), it would be reasonable to expect that liverworts and mosses may respond quite differently to seasonal variation in water availability (Robinson *et al*., 2000). Thus, the balance of these two major taxa may influence the magnitude of carbon cycling by the forest floor.

In addition to their influence on soil thermal and hydrologic regimes and their effect on nutrient retention and mineralization (Rieley *et al*., 1979; Vitt, 2000), bryophytes on the forest floor captured an amount equivalent to approximately 10% of total forest floor CO_2 efflux, therefore contributing directly to ecosystem net primary production. Because bryophytes exist within the boundary layer next to the ground, their function is tightly coupled to variation in CO_2 partial pressure and water content near the forest floor. The depth to ground water, insofar as it affects the rate of soil respiration and the water content of the bryophyte layer will greatly influence their photosynthetic capacity (Johnson *et al*., 1996; Oechel *et al*., 1998). Thus, changes in the activity of forest floor bryophytes may provide an early indicator of the response of mature forests to rapid changes in climate.

Acknowledgements

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References

Anderson EW (1986) A guide for estimating cover. *Rangelands*, **8**, 236–238.

Beever J, Allison KW, Child J (1992) *The Mosses of New Zealand* 2nd edn. University of Otago Press, Dunedin, New Zealand.

Blanke MM (1996) Soil respiration in an apple orchard. *Environmental and Experimental Biology*, **36**, 339–348.

Brisbee KE, Gower ST, Norman JM, Nordheim EV (2001) Environmental control on ground cover species composition and productivity in a boreal black spruce forest. *Oecologia*, **129**, 261–270.

Clymo RS, Hayward PM (1982) The ecology of *Sphagnum*. In: *Bryophyte Ecology* (ed. Smith AJE), pp. 229–289. Chapman & Hall, London.

Drewitt GB, Black TA, Nesic Z (2002) Measuring forest floor CO_2 fluxes in a Douglas-fir forest. *Agricultural and Forest Meteorology*, **110**, 299–317.

Elliot-Fisk DL (2000) The taiga and boreal forest. In: *North American Terrestrial Vegetation* 2nd edn. eds Barbour MG, Billings WD), pp. 21–74. Cambridge University Press, Cambridge.

Fang C, Moncrieff JB (2001) The dependence of soil CO_2 efflux on temperature. *Soil Biology and Biochemistry*, **33**, 155–165.

Field CB, Ball JT, Berry JA (1989) Photosynthesis: principles and field techniques. In: *Plant physiological ecology: field methods and instrumentation* (eds Pearcy RW, Mooney HA, Ehleringer JR, Rundel PW), pp. 209–253. Chapman & Hall, London.

Fife AJ (1995) Checklist of the mosses of New Zealand. *Bryologist*, **98**, 313–337.

Gamon JA, Surfus JS (1999) Assessing leaf pigment content with a reflectometer. *New Phytologist*, **143**, 105–117.

Glenny D (1998) A revised checklist of New Zealand Liverworts and Hornworts. *Tuhinga*, **10**, 119–149.

Goulden ML, Crill PM (1997) Automated measurements of CO_2 exchange at the moss surface of a black spruce forest. *Tree Physiology*, **17**, 537–542.

Goulden ML, Wofsey SC, Harden JW (1998) Sensitivity of boreal forest carbon balance to soil thaw. *Science*, **279**, 214–216.

Green TGA, Lange OL (1994) Photosynthesis in poikilohydric plants: a comparison of lichens and bryophtes. In: *Ecophysiology of Photosynthesis, Ecological Studies*, **Vol. 100** (eds Schulze E-D, Caldwell MM), pp. 319–342. Springer-Verlag, Berlin.

Hamilton JG, DeLucia EH, George K, Naidu SL, Finzi AC, Schlesinger WH (2002) Forest carbon balance under elevated CO_2. *Oecologia*, **131**, 250–260.

Harden JW, Sundquist ET, Stallard RF, Mark RK (1992) Dynamics of soil carbon during deglaciation of the Laurentitde ice sheet. *Science*, **18**, 1921–1924.

Hébant C (1977) The Conducting Tissues of Bryophytes. J. Cramer, Verlag, FL9490, Vaduz, Germany, 157 pp.

Hooper DU, Cardon ZG, Chapin FS III, Durant M (2002) Corrected calculations for soil and ecosystem measurements of CO_2 flux using the LI-COR 6200 portably photosynthesis system. *Oecologia*, **132**, 1–11.

Jackson RJ (1984) Investigation of the properties and genesis of West Coast wet land soils, South Island, New Zealand. 5. Physical characteristics of soil profiles and soil water regimes. *New Zealand Journal of Science*, **27**, 155–174.

James IL, Norton DA (2002) Helicopter based natural forest management of New Zealand's rimu (*Dacridum cupressinum*, Podocarpaceae) forests. *Forest Ecology and Management*, **155**, 337–346.

Johnson LC, Shaver GR, Giblin AE, Nadelhoffer NJ, Rastetter ER, Laundre JA, Murray GL (1996) Effects of drainage and temperature on carbon balance of tussock tundra microcosms. *Oecologia*, **108**, 737–748.

Landsberg JJ, Waring RH (1997) A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management*, **95**, 209–228.

Lloyd J, Taylor JA (1994) On the temperature dependence of soil respiration. *Functional Ecology*, **8**, 315–323.

Maseyk KS, Green TGA, Klinac D (1999) Photosynthetic responses of New Zealand *Sphagnum* species. *New Zealand Journal of Botany*, **37**, 155–165.

Moren A-S, Lindroth A (2000) CO_2 exchange at the floor of a boreal forest. *Agricultural and Forest Meteorology*, **101**, 1–14.

Murray KJ, Tenjunen JD, Nowak RS (1993) Photoinhibition as a control of photosynthesis and production of *Sphagnum* mosses. *Oecololgia*, **96**, 200–207.

Oechel WC, Van Cleave K (1986) The role of bryophytes in nutrient cycling in the taiga. In: *Forest Ecosystems in the Alaskan Taiga, Ecological Studies*, **Vol. 57** (eds Van Cleave K, Chapin FSIII, Flanagan PW, Viereck LA, Dyrness CT), pp. 121–137. Springer, New York.

Oechel WC, Vourlitis GL, Hatings SJ, Ault RP, Bryant P (1998) The effects of water table manipulation and elevated temperature on the net CO_2 flux of wet sedge tundra ecosystems. *Global Change Biology*, **4**, 77–90.

O'Neill KP (2000) Bryophytes in the global carbon budget. In: *Bryophyte Biology* (eds Shaw AJ, Goffinet B), pp. 344–368. Cambridge University Press, Cambridge.

Proctor MCF (1982) Physiological ecology: water relations, light and temperature responses, and carbon balance. In: *Bryophyte Ecology* (ed. Smith AJE), pp. 333–382. Chapman and Hall, New York.

Proctor MCF (2000) Physiological ecology. In: *Bryophyte Biology* (eds Shaw AJ, Goffinet B), pp. 225–247. Cambridge University Press, Cambridge.

Rice SK, Giles L (1996) The influence of water content and leaf anatomy on carbon isotope discrimination and photosynthesis in *Sphagnum*. *Plant, Cell and Environment*, **19**, 118–124.

Rieley JO, Richards P, Bebbington DL (1979) The ecological role of bryophytes in a North Wales Woodland. *Journal of Ecology*, **67**, 497–522.

Robinson SA, Wasley J, Popp M, Lovelock CE (2000) Desiccation tolerance of three moss species from continental Antarctica. *Australian Journal of Plant Physiology*, **27**, 379–388.

Stylinski CD, Gamon JA, Oechel WC (2002) Seasonal patterns of reflectance indices, carotenoid pigments and photosynthesis of evergreen chaparral species. *Oecologia*, **131**, 366–374.

Swanson RV, Flanagan LB (2001) Environmental regulation of carbon dioxide exchange at the forest floor of a black spruce ecosystem. *Agricultural and Forest Meteorology*, **108**, 165–181.

Tarnawski MG, Green TGA, Buedel B, Meyer A, Zellner H, Lange OL (1994) Diel changes of atmospheric CO_2 concentration within and above cryptogram stands in New Zealand temperate rainforest. *New Zealand Journal of Botany*, **32**, 329–336.

Valentini R, Matteucci G, Dolman AJ (2000) Respiration as the main determinant of carbon balance in European forests. *Nature*, **404**, 861–865.

Van Der Heijden E, Verbeek SK, Kuiper PJC (2000) Elevated atmospheric CO_2 and increased nitrogen deposition: effects on C and N metabolism and growth of peat moss *Sphagnum recurvum* P. Beauv. var *mucranatum*. *Global Change Biology*, **6**, 201–212.

Vasander H (1982) Plant biomass and production in virgin, drained and fertilized sites in a raised bog in southern Finland. *Annals of Botany Fennici*, **33**, 39–44.

Vitt DH (2000) Peatlands: ecosystems dominated by bryophytes. In: *Bryophyte Biology* (eds Shaw AJ, Goffinet B), pp. 312–343. Cambridge University Press, Cambridge.

Weltzin JF, Harth C, Bridgham SD, Pastor J, Vonderharr M (2001) Production and microtopography of boy bryophtes: response to warming and water-table manipulations. *Oecologia*, **128**, 557–565.

Whitehead D, Gower ST (2001) Photosynthesis and light-use efficiency by plants in a Canadian boreal forest ecosystem. *Tree Physiology*, **21**, 925–929.

Whitehead D, Hall GMJ, Walcroft AS (2002a) Analysis of the growth of rimu (*Dacrydium cupressinum*) in South Westland, New Zealand, using process-based simulation models. *International Journal of Biometeorology*, **46**, 66–75.

Whitehead D, Walcroft AS, Griffin KL (2002b) Scaling carbon uptake from leaves to canopies: insights from two forests with contrasting properties. In: Forests at the Land–Atmosphere Interface (eds M. Mencuccini, J. Grace, J. Moncrieff & K. McNaughton). CAB International, Oxford (in press).

Williams TG, Flanagan LB (1996) Effect of changes in water content on photosynthesis, transpiration and discrimination against $^{13}CO_2$ and $C^{18}O^{16}O$ in *Pleuorzium* and *Sphagnum*. *Oecologia*, **108**, 38–46.

Zhang J (1989) Modeling irradiance response of leaf photosynthetic rate in wheat and bamboo. *Photosynthetica*, **22**, 526–534.