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Automated measurements of CO₂ exchange at the moss surface of a black spruce forest

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Summary We used an automated, multiplexing gas-exchange system to measure the net exchange of CO₂ at the surfaces of three shady feather moss and three exposed sphagnum moss sites in a black spruce forest during 35 days at the end of the 1995 growing season. Midday gross photosynthesis was 0.5 to 1.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ by feather moss and 0.5 to 2.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ by sphagnum moss. Photosynthesis by sphagnum moss was reduced by approximately 70% at 0 °C, and reached a maximum rate at 8 °C. Nighttime CO₂ efflux, the sum of soil and moss respiration was 1 to 2.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ above feather moss and 0.5 to 1.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ above sphagnum moss at moss temperatures of 0 to 15 °C. The higher rates of respiration at the feather moss sites probably reflected a greater below-ground input of carbon from black spruce, and the lower rates of photosynthesis were probably associated with shading by the black spruce canopy. Photosynthesis by moss accounted for 10 to 50% of whole-forest gross CO₂ uptake measured simultaneously by eddy covariance. Respiration at the moss surface was 50 to 90% of whole-forest respiration, with a decreasing fraction on warm nights apparently because of a disproportionate rise in aboveground respiration.

Keywords: boreal forest, BOREAS, feather moss, gas-exchange methodology, gross production, photosynthesis, soil respiration, sphagnum moss, taiga.

Introduction

Black spruce (*Picea mariana* (Mill.) BSP) forests with a continuous carpet of feather moss (*Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) Schimp. in B.S.G., *Ptilium crista-castrensis* (Hedw.) De Not.) in shaded dry areas and sphagnum moss (*Sphagnum* spp.) in open wet areas dominate much of the North American boreal zone (Larson 1980, Van Cleve et al. 1983). The exchange of CO₂ between these forests and the atmosphere is complex, with important contributions by five physiological processes: black spruce photosynthesis, black spruce respiration, moss photosynthesis, moss respiration and heterotrophic respiration (Oechel and Lawrence 1985, Bonan and Shugart 1989). Information on the rates of and controls on each of these processes are needed to

improve understanding of the current and future carbon balance of boreal forests.

Measurements of photosynthesis and respiration by boreal forest mosses are scarce and are typically based on laboratory studies of excised tissue (e.g., Busby and Whitfield 1978, Skre and Oechel 1981). Similarly, measurements of respiration from boreal forest soils are limited and are often based on less reliable techniques such as soda-lime absorption (e.g., Schlentner and Van Cleve 1985). Net exchange of CO₂ above the moss surface reflects the sum of moss photosynthesis and moss, root and heterotrophic respiration during daylight, and moss, root, and heterotrophic respiration at night. Long-term *in-situ* measurements of CO₂ exchange over diel courses should allow partial separation of these processes and permit an analysis of the associated environmental controls. However, investigations of this type have been limited by the difficulty of obtaining reliable field measurements in remote, inclement regions.

We used an automated, multiplexing gas-exchange system to make continuous, unattended measurements of the net exchange of CO₂ at the moss surface at the Northern Study Area Old Black Spruce site of the Boreal Ecosystem–Atmosphere Study (BOREAS). In this paper, we analyze 35 days of measurements on feather moss and sphagnum moss sites that span the end of the 1995 growing season. Our goals are: (1) to describe the gas-exchange system, (2) to characterize the physical controls on moss-surface photosynthesis and respiration during the late summer to winter transition, and (3) to discuss moss-surface exchange within the context of whole-forest exchange.

Methods

Site

Measurements were made at the Old Black Spruce site in the BOREAS Northern Study Area in central Manitoba (55.879° N, 98.484° W; Goulden et al. 1997). The gas-exchange system was installed 100 m southeast of the eddy-flux tower in September 1995. The system operated continuously

from September 24 to October 26 and was visited every 2 weeks.

The site was heterogeneous, with large changes in vegetation over small gradients in elevation. Upland areas were dominated by dense, 10-m-tall, 120-year-old black spruce, with a minor shrub layer and continuous feather moss. Lower areas were dominated by sparse, 1- to 6-m-tall spruce and continuous sphagnum moss. Chambers 1 to 3 were placed in an upland area of well-developed feather moss (mainly *Pleurozium schreberi* with some *Ptilium crista-castrensis* and *Hylocomium splendens*). Chambers 8 to 10 were placed in a lower area dominated by sphagnum moss (*Sphagnum fuscum* (Schimp.) Klinggr. and *S. warnstorffii* Russ.). The other chambers were placed at intermediate (4 to 6) or lichen-covered (7) locations. The current analysis focused on the chambers above pure feather moss and sphagnum moss because these are the most common types of ground cover at the site and because they represent the end members of the ecological gradient. The observations at Chambers 1 and 8 were consistent with those at Chambers 2, 3, 9 and 10, but less reliable because of atmosphere leaks (Chamber 1) or unstable temperature measurements (Chamber 8). We therefore confined our analysis to Chambers 2, 3, 9, and 10.

An automated system for measuring CO₂ exchange at the moss surface

Measurements of CO₂ exchange above moss surfaces are sensitive to errors that are not usually encountered when working above bare soil. Moss is extremely porous, creating uncertainty in chamber volume and also increasing the risk of mass flow. Transient changes in moss physiology and in the direction of CO₂ movement may confound dark respiration measurements made by shading during daytime. Because the physiological activity of moss is sensitive to water content, chambers that remain in place for extended periods must not alter evaporation or precipitation. Finally, the CO₂ exchange above moss is complex, and therefore many measurements may be required to separate the environmental controls on photosynthesis and respiration. As a result of these and other uncertainties, discrepancies among methods used to measure moss-surface exchange in BOREAS have been large (Norman et al. 1996), and it is unclear which, if any, chamber design provides accurate results.

We designed an automated gas-exchange system to circumvent most of these problems. The system sequentially sampled 10 clear, closed-type chambers, completing a circuit every 3 h. Power consumption was less than 300 W at 115 VAC. The system was shipped and operated in three weather-tight boxes that sat on the forest floor within 15 m of the chambers (Figure 1). Box 1 contained equipment used to select a chamber. Box 2 contained instruments and data acquisition equipment. Box 3 contained devices using alternating current.

The tubing and mixing volume were flushed and allowed to equilibrate during the first 8 min of each run (Figure 1). The selected chamber was then closed slowly and the change in CO₂ monitored for the next 10 min. Chamber closure had no

discernible effect on the temperature within a chamber during fall 1995. Subsequent measurements in midsummer 1996 revealed some warming (1 to 2 °C), which occasionally resulted in condensation on the walls of chambers exposed to direct sun.

Air was drawn from the chamber throughout the run and passed through a CO₂ and H₂O infrared gas analyzer operated in absolute mode (IRGA, Model 6262, Li-Cor, Inc., Lincoln, NE). The flow through the IRGA was controlled at 80 cm³ s⁻¹ (MKS Instruments, Andover, MA). The pressure of the sample flow was measured with a pressure transducer (MKS Instruments) immediately after it had exited the IRGA and was assumed equal to the pressure in the sample cell. All tubing and connectors were selected to minimize water vapor and CO₂ absorption and permeability.

The chambers were 38 × 38.5 × 25 cm boxes built of clear lexan and aluminum angle (Figure 1). The lid was pneumatically actuated and held vertical when the chamber was not in use (94% of the time). The chambers were sunk 10 to 15 cm into the moss, resulting in an enclosed height of 10 to 15 cm. This depth was well above the zone of maximum root density. Air entered a chamber through 100 holes in a manifold around the wall. The manifold was made of square brass tube, and the size of the outlets (0.040 cm diameter) and the brass thickness (0.071 cm) were selected to insure nearly equal flow throughout the chamber. Air exited the chamber through a single outlet in the middle. The flow pattern was intended to minimize dead volume without risking a leak or forcing advective exchange with the soil.

Soil temperature at 5 cm beneath the moss surface and air temperature were measured in each chamber with type-T thermocouples (Omega Engineering, Stamford, CT). Horizontal, photosynthetically-active photon flux density (PPFD) was measured at each chamber with a gallium arsenide phosphide photodiode (Hamamatsu, Bridgewater, NJ).

Data were recorded and the system managed with a datalogger (Campbell Scientific, Logan, UT). The raw CO₂ and H₂O signals were sampled every 2 s and averaged every minute. The other signals were sampled every 2 s and averaged every 9 min. The solenoids used for chamber selection, chamber closure, and calibration were controlled with a pair of 16-channel control modules. The set points for the mass flow controllers were provided by a 4-channel analog output module. The signals from the thermocouples and light sensors were multiplexed with a thermally insulated 32-channel multiplexer. The data were transferred to a storage module every 3 h and subsequently transferred to a computer every two weeks.

Each chamber was calibrated at least once a day by standard addition. Every 21 h, the system added 0.08 cm³ s⁻¹ of 10% CO₂ to the return flow throughout a 3-h circuit (Figure 1). The calibration accounted for the IRGA response, the chamber volume and, to a lesser extent, leaks with the atmosphere. The calibration multiplier for each chamber was calculated as the ratio of the rate of addition to the increase in the rate of CO₂ rise. The increase in rise was calculated as the difference between the background rise determined by linear interpolation of the previous and subsequent measurements for the

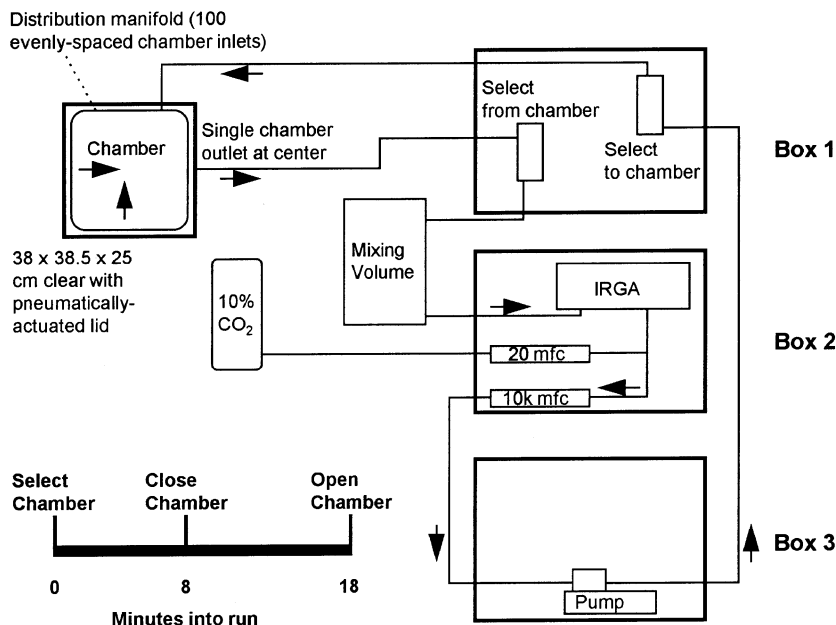


Figure 1. Flow through the multiplexing gas-exchange system. The system sequentially measured the CO₂ exchange in 10 closed-type chambers, completing a circuit every 3 h. Air was circulated between the selected chamber and the CO₂ gas analyzer (IRGA) and mass flow controller (mfc) at 80 cm³ s⁻¹ following the arrows. The system was shipped and operated in three weather-tight boxes that sat on the forest floor within 15 m of the chambers. The system was calibrated every 21 h by standard addition of 10% CO₂. A 25-l polyethylene container with two fans inside may be placed in line during periods with high flux to increase the overall volume of the system and reduce the rate of CO₂ increase.

chamber and the rise during the calibration. Calibrations with a substantial difference in the background rise between the previous and subsequent measurements (greater than 40%) were not used because of uncertainty about the background flux.

The calibration multiplier differed from chamber to chamber by up to 30%, and varied with time for an individual chamber by 10%. The multiplier for Chamber 1 increased by about 30% on Day 280, probably because of a leak. The multipliers for Chambers 3, 8, 9, and 10 decreased by 10 to 20% on Day 290 because of a decrease in volume following snow. We are unaware of previous uses of standard addition for routine calibration of soil- or moss-surface, trace gas exchange, and suspect that the approach can be used for other gases or chamber designs.

The rate of change of CO₂ in the chamber typically decreased by 15% in the first 4 min after chamber closure and by 30% over the complete 10-min run. The roll off was more rapid during standard addition indicating that it resulted from the buildup of CO₂ in the chamber, and a suppression of CO₂ movement from the surface or an increase in loss to the atmosphere. We therefore determined the rate of CO₂ change for each run, including those with standard addition, by linearly extrapolating the observations at 2 to 4 min after the chamber closed to the time of closure. This approach should also reduce the occasional effects of shading caused by condensation on the chamber walls. The rate of CO₂ exchange was subsequently standardized using the pressure and temperature measured at the IRGA and the temperature measured in a chamber. The flux was then calculated using the multiplier for each chamber determined by standard addition. All fluxes are presented on a ground-area basis. We did not correct the CO₂ signal for water vapor or for the slightly nonlinear response of the IRGA, and expect associated errors of less than 5% (Li-Cor 1991). Although movement of CO₂ into the moss surface was

considered a negative flux, we discuss photosynthesis as a positive process.

Results and discussion

Carbon dioxide exchange in fall 1995

The second half of the summer of 1995 was cool and wet (Goulden et al. 1997, Shewchuk 1996). The first frost was on Day 250 and the first sustained low temperatures (-5 to 5 °C) were from Days 261 to 266. Air temperatures were moderate from Days 266 to 285 (0 to 15 °C), low from Days 286 to 298 (-5 to 5 °C) and extremely low beginning on Day 298 (less than -5 °C). The daytime temperature of moss was 5 to 15 °C

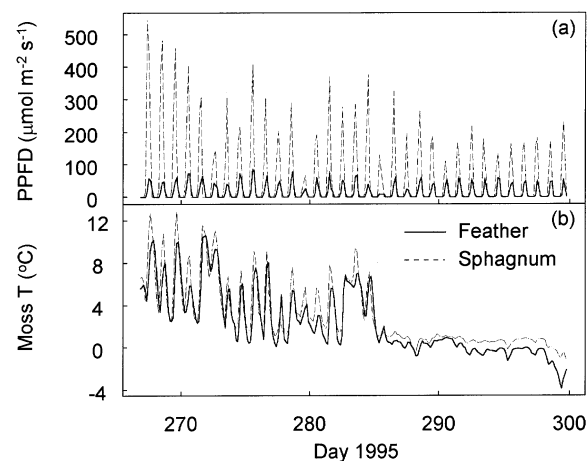


Figure 2. (a) Photosynthetically active photon flux density (PPFD) and (b) temperature at 5-cm depth beneath the moss surface. Lines connect means at 3-h intervals for Chambers 2 and 3 (feather moss = solid line) and Chambers 9 and 10 (sphagnum moss = dashed line).

until Day 285 and near freezing after Day 286 (Figure 2b). The midday PPFD at the sphagnum sites was at least five times greater than at the feather moss sites (Figure 2a). Precipitation occurred every few days except for a dry period from Days 264 to 282 (Shewchuk 1996).

The flux measurements were consistent both for an individual chamber on sequential runs separated by 3 h and also between adjacent chambers on runs separated by 18 min (Figure 3). Nocturnal respiration ranged from 1 to 2.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the feather moss sites and from 0.5 to 1.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the sphagnum moss sites. Respiration at all sites was elevated on warm nights (Figures 2 and 3; Days 272 and 284). The difference between day and night exchange, an approximate measure of midday gross photosynthesis, ranged from 0.5 to 1.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the feather moss sites and from 0.5 to 2.5 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at the sphagnum moss sites. Photosynthesis at all sites continued to the end of the study, including after Day 290 when snow covered part of the surfaces within the sphagnum chambers.

Controls on respiration

Variation in nocturnal respiration was correlated with moss temperature (Figure 4). The Q_{10} at all sites was approximately 2, a pattern consistent with the effects of temperature on moss respiration (Skre and Oechel 1981, Harley et al. 1989) and also on litter decomposition (Schlesinger 1977). The tight relationship between dark respiration and soil temperature at 5-cm depth indicates that much of the respiration has a shallow source. The rates of respiration above feather moss were nearly twice those above sphagnum. The feather moss at the site occurred in association with vigorously growing black spruce, whereas the sphagnum moss was associated with scattered, stunted black spruce. The greater rates of respiration in the

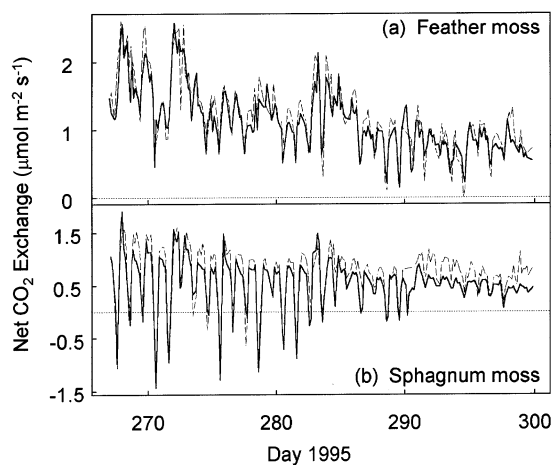


Figure 3. (a) Carbon dioxide exchange at the feather moss surface beneath a thick black spruce canopy (Chamber 2 = solid line, Chamber 3 = dashed line), and (b) CO₂ exchange at the sphagnum moss surface beneath a sparse black spruce canopy (Chamber 9 = solid line, Chamber 10 = dashed line). Lines connect measurements at 3-h intervals from September 24 to October 26, 1995. A positive flux indicates net CO₂ movement out of the moss into the atmosphere.

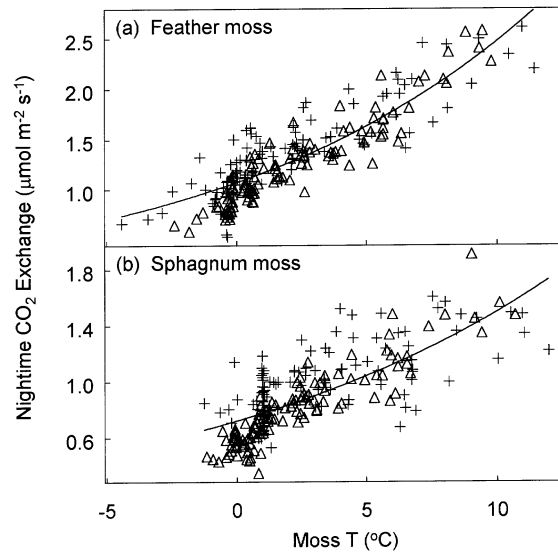


Figure 4. (a) Nighttime CO₂ efflux (moss and soil respiration) as a function of temperature at 5-cm depth for (a) feather moss sites (Chamber 2 = triangles, Chamber 3 = crosses), and (b) sphagnum moss sites (Chamber 9 = triangles, Chamber 10 = crosses). The best fit for feather moss was flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) = $\exp(0.072 + 0.083T_{5\text{cm}})$, $n = 220$. The best fit for sphagnum moss was flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) = $\exp(-0.324 + 0.073T_{5\text{cm}})$, $n = 230$.

feather moss areas probably reflected a greater input of black spruce litter and a higher rate of tree root respiration.

Controls on moss photosynthesis

Measurements of net exchange (Figure 3) were more rigorously separated into respiratory and photosynthetic fluxes by estimating daytime respiration as a function of moss temperature (Figures 2b and 4). The resulting flux, referred to as gross CO₂ exchange or photosynthesis, should equal the combined rate of ribulose-1,5-bisphosphate carboxylase carboxylation and oxygenation. Gross CO₂ exchange does not include the loss of carbon during dark respiration and it is therefore not equivalent to conventional measurements of net assimilation.

Variation in gross exchange was related to light intensity (Figure 5). The gross uptake by sphagnum increased linearly to a PPFD of 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ where it saturated at an uptake rate of 2 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (Figure 5). The response of feather moss to light was less obvious because of the difficulty of separating a small uptake from a large efflux (Figure 3) and probably also because of the patchy light environment on the forest floor. Nonetheless, photosynthesis by feather moss appeared to increase to a PPFD of approximately 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ where it saturated at an uptake rate of 0.5 to 1 $\mu\text{mol m}^{-2} \text{s}^{-1}$. The low rate of photosynthesis by feather moss is consistent with observations on excised tissue (Busby and Whitfield 1978, Busby et al. 1978; approximately 2 $\mu\text{mol m}^{-2} \text{ground s}^{-1}$ if moss to 3 cm depth is light saturated). The light intensity required for saturation is somewhat lower than expected based on investigations of excised tissue (Busby and Whitfield 1978, Skre and Oechel 1981).

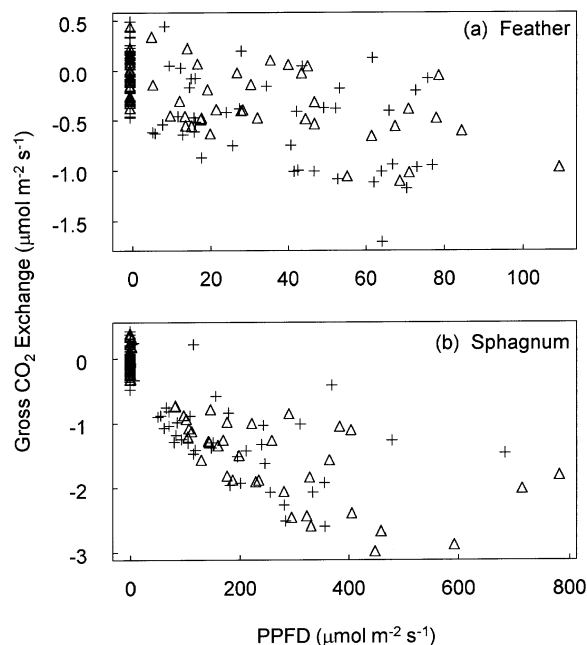


Figure 5. Gross CO₂ exchange during periods with moss temperatures at 5-cm depth greater than 4 °C as a function of local photon flux density (PPFD) for (a) feather moss (Chamber 2 = triangles, Chamber 3 = crosses), and (b) sphagnum moss (Chamber 9 = triangles, Chamber 10 = crosses). Gross exchange was calculated from measured net exchange (Figure 3) by subtracting respiration estimated for each chamber as a function of moss temperature (Figure 4). More negative fluxes indicate increasing moss photosynthesis.

Both the peak rate of photosynthesis and the light required for saturation were higher for sphagnum moss than for feather moss (Figure 5), a pattern consistent with the relative light environment in the two areas. Feather moss dominated beneath a thick canopy of black spruce with a leaf area index (LAI) of 4 to 5 (Gower et al. 1997), whereas sphagnum moss occurred beneath a canopy of stunted chlorotic black spruce with a much lower LAI. The PPFD at the feather moss surface was less than 50 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during 76% of the light periods, and exceeded 100 $\mu\text{mol m}^{-2} \text{s}^{-1}$ only 3% of the time (Figure 2a). The PPFD at the sphagnum moss surface was 50 to 300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 68% of the time.

The uptake of CO₂ by sphagnum under bright light (> 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) was reduced at moss temperatures of less than 8 °C (Figure 6). Appreciable photosynthesis by both feather moss and sphagnum moss was observed at or below 0 °C. The relatively high uptake at low temperatures confirms observations on *S. warnstorffii* by Harley et al. (1989). Moss temperatures above 10 to 15 °C were not observed, and the limitation of photosynthesis by heat or high evaporative demand cannot be assessed. Similarly, the effect of prolonged drought on photosynthesis was not determined.

Moss-surface exchange as a component of whole-ecosystem exchange

Moss photosynthesis was 20 to 30% of whole-forest photosynthesis from Days 267 to 289 and 20 to 50% from Days 290 to

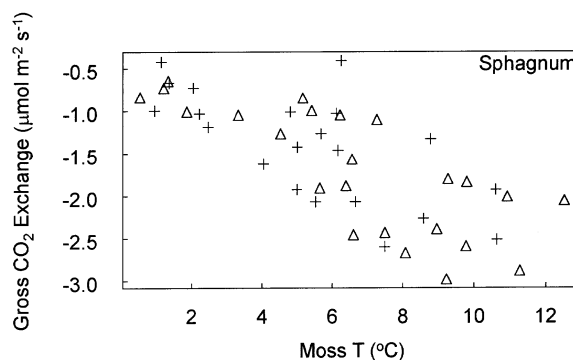


Figure 6. Gross CO₂ exchange before Day 290 as a function of temperature at 5-cm depth during periods with local photon flux densities (PPFD) greater than 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for sphagnum moss (Chamber 9 = triangles, Chamber 10 = crosses).

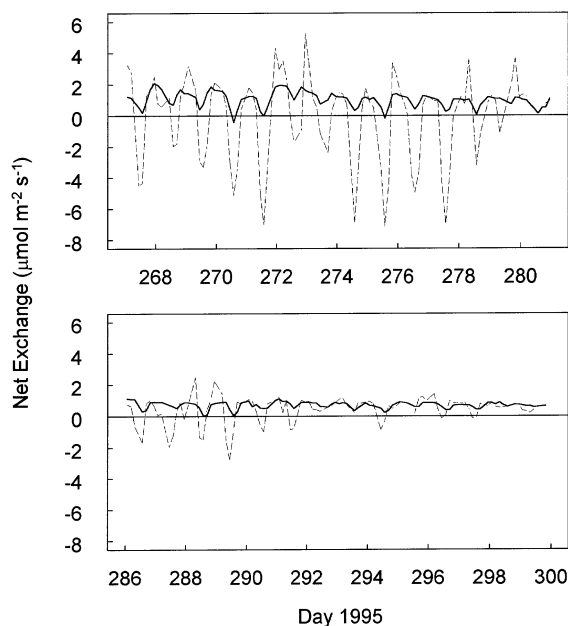


Figure 7. Simultaneous measurements of moss-surface exchange (solid lines connect fluxes at Chambers 2, 3, 9, and 10 averaged at 3-h intervals) and whole-forest net exchange measured by eddy covariance (dashed lines connect observations averaged at 3-h intervals, Goulden et al. 1997). The whole-forest measurements were made 100 m to the northwest of the chambers at an altitude of 30 m, and were calculated as the sum of turbulent flux plus storage change (net ecosystem exchange, NEE). Tower-flux measurements were unavailable from Days 281 to 285.

300 (Figure 7, Goulden et al. 1997), assuming no bias between methods (Goulden et al. 1996, Lavigne et al. 1997). Day-to-day differences in the contribution of moss to whole forest photosynthesis were not associated with cloudiness or the penetration of light to the forest floor (Skre et al. 1983, Goulden et al. 1997).

The nighttime difference between respiration at the moss surface and above the forest increased with increasing air temperature (Figure 7). The difference was consistently large

on Day 272, the warmest night studied (Figure 2). An exponential regression between air temperature at 1 m height and the difference between whole-forest and moss-surface respiration indicated an aboveground respiration of $1.1 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 10°C , a rate that is consistent with direct measurements of stem and foliage respiration near the feather moss sites (Lavigne et al. 1997; $1.7 \mu\text{mol m}^{-2} \text{s}^{-1}$ at 10°C).

The observations allow an estimation of moss gross production. Based on an annual record of feather moss temperature and light (Goulden et al. 1997) and the responses of gross exchange to light (Figure 5) and temperature (Figure 6), we estimate an annual gross production for feather moss of 0.5 Mg C ha^{-1} in 1995. The gross production for sphagnum moss calculated in a similar manner was 1.5 Mg C ha^{-1} in 1995. These values are approximate because they do not incorporate the possibility that photosynthetic response increases in midsummer or that drought decreases production. For comparison, the total gross production at the site was approximately $8 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ (Goulden et al. 1997). The contribution of moss to forest net production is presumably higher than 10% as a result of the relatively low allocation by moss to respiration (Skre and Oechel 1979, Oechel and Van Cleve 1986).

The difference in gross production between moss types, as well as the absolute rates of production, are consistent with the annual moss turnover at the site inferred by ^{14}C analyses (Trumbore and Harden 1997). The higher rate of gross production by sphagnum moss relative to feather moss resulted from greater light availability and a higher maximum rate of photosynthesis. The greater gross production by sphagnum moss compensated partially for the apparent low gross production by the overlying black spruce trees. The site may therefore be viewed as a mosaic of patches with high black spruce production but low moss production and patches with low black spruce production but high moss production. Attempts to model the current and future carbon balance of the site may need to consider separately the physical environments, the physiological responses, and the types of detritus produced in these two types of patches.

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References

Bonan, G.B. and H.H. Shugart. 1989. Environmental factors and ecological processes in boreal forests. *Annu. Rev. Ecol. Syst.* 20:1–28.

Busby, J.R., L.C. Bliss and C.C. Hamilton. 1978. Microclimate controls of growth rates and habitats of the boreal forest mosses, *Tomenthypnum nitens* and *Hylocomium splendens*. *Ecol. Monogr.* 48:95–110.

Busby, J.R. and D.W.A. Whitfield. 1978. Water potential, water content, and net assimilation of some boreal forest mosses. *Can. J. Bot.* 56:1551–1558.

Goulden, M.L., J.W. Munger, S.-M. Fan, B.C. Daube and S.C. Wofsy. 1996. Measurements of carbon sequestration by long-term eddy covariance: Methods and a critical evaluation of accuracy. *Global Change Biol.* 2:169–182.

Goulden, M.L., B.C. Daube, S.-M. Fan, D.J. Sutton, A. Bazzaz, J.W. Munger and S.C. Wofsy. 1997. Gross CO_2 uptake by a black spruce forest. *J. Geophys. Res.* In press.

Gower, S.T., J. Vogel, T.K. Stow, J.M. Norman, S.J. Steele and C.J. Kucharik. 1997. Carbon distribution and above-ground net primary production of aspen, black spruce and jack pine forests in Saskatchewan and Manitoba, Canada. *J. Geophys. Res.* In press.

Harley, P.C., J.D. Tenhunen, K.J. Murray and J. Beyers. 1989. Irradiance and temperature effects on photosynthesis of tussock tundra *Sphagnum* mosses from the foothills of the Philip Smith Mountains, Alaska. *Oecologia* 79:251–259.

Larson, J.A. 1980. The boreal ecosystem. Academic Press, New York, 500 p.

Lavigne, M.B., M.G. Ryan, D.E. Anderson, D.D. Baldocchi, P.M. Crill, D. Fitzjarrald, M.L. Goulden, S.T. Gower, J.M. Massheder, J.H. McCaughey, M. Rayment and R.G. Striegl. 1997. Comparing scaled up chamber estimates of respiration to nocturnal tower flux measurements. *J. Geophys. Res.* In press.

Norman, J.M., C.J. Kucharik and S.T. Gower. 1996. A comparison of five methods for measuring soil surface carbon dioxide fluxes. *Proc. 22nd Conference on Agriculture and Forest Meteorology, American Meteorological Society, Boston*, pp 59–61.

Oechel, W.C. and W.T. Lawrence. 1985. Taiga. *In Physiological Ecology of North American Plant Communities*. Eds. B.F. Chabot and H.A. Mooney. Chapman and Hall, London, U.K., pp 66–94.

Oechel, W.C. and K. Van Cleve. 1986. The role of bryophytes in nutrient cycling in the taiga. *In Forest Ecosystems in the Alaskan Taiga*. Eds. K. Van Cleve, F.S. Chapin III, P.W. Flanagan, L.A. Viereck and C.T. Dyrness. Springer-Verlag, New York, pp 121–137.

Schlesinger, W.H. 1977. Carbon balance in terrestrial detritus. *Annu. Rev. Ecol. Syst.* 8:51–81.

Schlentner, R.E. and K. Van Cleve. 1985. Relationships between CO_2 evolution from soil, substrate temperature, and substrate moisture in four mature forest types in interior Alaska. *Can. J. For. Res.* 15:97–106.

Shewchuk, S.R. 1996. Surface mesoscale meteorological system for BOREAS. *Proc. 22nd Conference on Agriculture and Forest Meteorology, American Meteorological Society, Boston*, pp 42–44.

Skre, O. and W.C. Oechel. 1979. Moss production in a black spruce *Picea mariana* forest with permafrost near Fairbanks, Alaska, as compared with two permafrost-free stands. *Holarct. Ecol.* 2:249–254.

Skre, O. and W.C. Oechel. 1981. Moss functioning in different taiga ecosystems in interior Alaska. I. Seasonal, phenotypic, and drought effects on photosynthesis and response patterns. *Oecologia* 48:50–59.

Skre, O., W.C. Oechel and P.M. Miller. 1983. Moss leaf water content and solar radiation at the moss surface in a mature black spruce forest in central Alaska. *Can. J. For. Res.* 13:860–868.

Trumbore, S.E., and J. Harden. 1997. Accumulation and turnover of carbon in soils of the BOREAS NSA. 1. Methods for determining soil C balance in surface and deep soil. *J. Geophys. Res.* In press.

Van Cleve, K., C.T. Dyrness, L.A. Viereck, J. Fox, F.S. Chapin III and W. Oechel. 1983. Taiga ecosystems in interior Alaska. *Bioscience* 33:39–44.