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Forest Floor Carbon Exchange of a Boreal **Black Spruce Forest in Eastern Canada**

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Abstract

This study reports continuous automated measurements of forest floor carbon (C) exchange over feathermoss, lichen, and sphagnum micro-sites in a black spruce forest in eastern North America during snow-free periods over three years. The response of soil respiration (R_{s-auto}) and forest floor photosynthesis (P_{ff}) to environmental factors was determined. The seasonal contributions of scaled up R_{s-auto} adjusted for spatial representativeness (R_{s-adj}) and P_{ff} (P_{ff-eco}) relative to that of total ecosystem respiration (R_e) and photosynthesis (P_{eco}), respectively, were also quantified.

Shallow soil temperature explained 67–86% of the variation in R_{s-auto} for all ground cover types, while deeper soil temperatures were related to R_{s-auto} only for the feathermoss micro-sites. Base respiration was consistently lower under feathermoss, intermediate under sphagnum, and higher under lichen during all three years. The R_{s-adj}/R_e ratio increased from spring through autumn and ranged from 0.85 to 0.87 annually for the snow-free period. The R_{s-adj}/R_e ratio was negatively correlated with the difference between air and shallow soil temperature and this correlation was more pronounced in autumn than summer and spring.

Maximum photosynthetic capacity of the forest floor ($P_{\rm ffmax}$) saturated at low irradiance levels (~200 μ mol m⁻² s⁻¹) and decreased with increasing air temperature and vapor pressure deficit for all three ground cover types, suggesting that P_{ff} was more

- ²⁰ limited by desiccation than by light availability. $P_{\rm ffmax}$ was lowest for sphagnum, intermediate for feathermoss, and highest for lichen for two of the three years. P_{ff} normalized for light peaked at air temperatures of 5–8°C, suggesting that this is the optimal temperature range for P_{ff} . The $P_{\rm ff-eco}/P_{\rm eco}$ ratio varied seasonally from 13 to 24% and reached a minimum in mid-summer when both air temperature and $P_{\rm eco}$ were at their
- ²⁵ maximum. On an annual basis, $P_{\rm ff-eco}$ accounted for 17–18% of $P_{\rm eco}$ depending on the year and the snow-free season totals of $P_{\rm ff-adj}$ were 23–24% that of $R_{\rm s-adj}$.

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1 Introduction

Total ecosystem respiration (R_{e}) is a major determinant of the carbon (C) balance of northern forests (Valentini et al., 2000). R_{e} includes respiration by above-ground plant parts (boles, branches, twigs, and leaves) and soil. Soil respiration (R_{s}) is a dominant component of C exchange in boreal ecosystems, accounting for at least half of R_{e} (Black et al., 2005). The temporal variability of respiratory metabolism is influenced mostly by temperature and humidity conditions (Davidson et al., 1998; Gaumont-Guay et al., 2006a). Above- and below-ground processes contributing to R_{e} can respond in different ways to the seasonal variation of air and soil temperature, to the availability of water and to substrate type (Davidson et al., 2006; Jassal et al., 2007).

Coniferous boreal forests typically have relatively open canopies that allow a significant portion of incoming radiation to reach the ground vegetation (Baldocchi et al., 2000). Forest floor photosynthesis is thus a potentially important process that can represent up to 50% of C assimilation in such ecosystems (Goulden and Crill, 1997). The

productivity of the forest floor depends on favourable light, temperature and moisture conditions (Swanson and Flanagan, 2001; Kolari et al., 2006) and also on the composition and relative presence of different forest floor communities in the ecosystem (O'Connell et al., 2003; Heijmans et al., 2004).

The boreal forest in eastern Canada is subjected to climatic conditions that differ significantly from those of other boreal regions in North America and Eurasia. For example, precipitation is generally more abundant in this region than in central Canada, while air temperatures are much cooler than in boreal Scandinavia. Also, the markedly different latitudes of boreal forests in Scandinavia and Canada lead to different light regimes in regards to both photoperiod and intensity. Such differences in climatic condi-

tions can influence the C exchange of boreal forest ecosystems (Bergeron et al., 2007). Furthermore, climate change is expected to have different regional consequences in northern forests (Flannigan et al., 2001). Thus, it is important to characterize the response of C exchange to environmental conditions in the eastern Canadian region of

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the circumpolar boreal forest.

Information on the seasonal contribution of soil respiration to ecosystem respiration is still very limited (e.g., Davidson et al., 2006) since values have been primarily reported on an annual or growing season basis (e.g., Lavigne et al., 1997; Law et al.,

- ⁵ 1999; Janssens et al., 2001; Gaumont-Guay et al., 2006b). Furthermore, there is apparently little information available for the vast area of cool humid boreal forest that is characteristic of eastern North America. On the other hand, photosynthesis of the moss stratum has been studied in different ecosystems (e.g., Swanson and Flanagan, 2001; Heijmans et al., 2004; Botting and Fredeen, 2006; Kolari et al., 2006). However,
- the extent to which it might contribute to the interannual variability in gross ecosystem productivity has apparently not been studied for boreal forests of eastern North America. Moreover, the relative contribution of different boreal micro-sites (sphagnum, feathermoss, lichen) has not been well explored. Such information is important for partitioning the different C sinks within an ecosystem and characterizing their specific response to environmental conditions.

Numerous automated chamber systems have been developed to produce continuous measurements that help gain insight into the seasonal variability of soil respiration and forest floor photosynthesis (e.g., Goulden and Crill, 1997; Pumpanen et al., 2001; Gaumont-Guay et al., 2008). Coupling automated chamber measurements with eddy

- ²⁰ covariance (EC) measurements can provide valuable information on the concomitant response of respiratory and photosynthetic processes of different ecosystem components to environmental variables at fine time scales. However, due to logistical and equipment constraints, automated chamber systems are typically confined to a small portion of the footprint measured by an EC tower. This can lead to a mismatch in
- the source area, resulting in an apparent discrepancy between measurement methods (Drewitt et al., 2002). This source of error can be controlled by assessing the spatial representativeness of soil respiration using a portable manual chamber system (Savage and Davidson, 2003) and by limiting ecosystem C exchange estimates to specific sectors of the tower footprint (e.g., Yuste et al., 2005).

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This study presents continuous automated measurements of ecosystem and forest floor CO₂ exchange for the snow-free period over three years in a boreal black spruce forest ecosystem in eastern North America. The objectives of this study were to (1) quantify the relationship of soil respiration and photosynthesis of different forest floor micro-sites (sphagnum, feathermoss and lichen) to environmental factors and (2) contrast the seasonal contribution of soil respiration and forest floor photosynthesis to that of the entire ecosystem. The spatial representativeness of automated soil respiration measurements in the tower footprint area was also assessed.

2 Methods

10 2.1 Site description

Our study site (Eastern Old Black Spruce, EOBS; 49.692°N, 74.342°W) lies in the commercial boreal forest of Canada and is located about 30 km south of Chibougamau, QC. The study site corresponds to a 500 m radius centered on the tower where at least 90% of the flux footprint originates (Bergeron et al., 2007). Black spruce (Picea mariana) dominates the site and there are sparse jack pine (*Pinus banksiana*) and tamarack 15 (Larix laricinia). The shrub stratum is comprised of sheep laurel (Kalmia angustifolia) and Labrador tea (Rhododendron groenlandicum) on dry micro-sites and alder (Alnus rugosa) on wet micro-sites. The forest floor is covered by feathermoss (Hylcomnium splendens, Pleurozium schreberi), sphagnum (Sphagnum spp.), and lichen (Cladina spp.; see Table 1). Most of the study area originates from fire disturbance that occurred 20 between 1885 and 1915. EOBS is dominated by podzol soils with 15-40 cm organic layers lying on silty-sand parent material. Mean tree height is 13.8 m, mean DBH is 12.7 cm, tree density is 4,490 stems ha⁻¹, black spruce basal area is 22.8 m² m⁻², and hemispherical LAI is 3.7 m² m⁻². The 30-year average of mean annual temperature and total annual precipitation measured at the nearest weather station (15 km NW of 25 the site) are 0.0°C and 961.3 mm, respectively. Additional details can be found in Berg6, 5507-5548, 2009

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eron et al. (2007).

2.2 Automated measurements of forest floor CO₂ exchange

Soil CO₂ efflux, including daytime forest floor photosynthesis, was measured continuously during the 2004-2006 snow-free periods by a non-steady state, automated chamber system manufactured by the Biometeorology and Soil Physics Group (University of British Columbia, Vancouver, BC, Canada; see Gaumont-Guay et al. (2008) for a complete description). The system is comprised of three temperature-controlled housings enclosing data logging, pumping and gas measurement equipment, as well as 6 to 9 chambers. The chambers are made of a clear acrylic dome fixed with a hinge to a 13-cm high PVC collar inserted 8-12 cm in the forest floor. The chambers 10 are about 50 L in volume and cover an area of 0.216 m². A 50-cm long venting tube is inserted into the top of each chamber to allow pressure equalisation. A pneumatic system controls the opening and closing of the chambers. All chambers are deployed in a 15 m radius around the main equipment stand which is located about 80 m south of the flux tower. In June 2004, a total of six chambers were installed on feathermoss 15 (3 chambers), lichen (2), and sphagnum (1). In June 2005, three more chambers were

set up on feathermoss (2) and sphagnum (1). Shrubs were excluded from the collars. At the time of measurement, chambers were closed for 2.5 min or 3 min (when 6 or 9

chambers were in use, respectively), otherwise the chamber stayed in the open position (83 or 92% of the time based on a 15 or 30 min cycle, respectively). Air was sequentially

(83 or 92% of the time based on a 15 or 30 min cycle, respectively). Air was sequentially circulated at 9 L min¹ through ~35 m of tubing (Synflex 1300, 4.0 mm Internal Diameter, Saint-Gobain Performance Plastics, Wayne, NJ, USA) between the chambers and an infrared gas analyser (IRGA) (model LI-6262, LI-COR Inc., Lincoln, NE, USA). The IRGA was calibrated daily using the same procedure as the EC system (see below).
 Data were sampled at 1 Hz and averaged every 5 s.

Soil CO₂ efflux (F_{cs}) was calculated on a half-hour basis using the equation

$$F_{cs} = \rho_a \frac{V_e}{A} \frac{ds_c}{dt},$$

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(1)

where ρ_a is the density of dry air in the chamber headspace (mol m⁻³), V_e the effective volume of the chamber (m³), *A* the area of ground covered by the chamber (m²) and ds_c/dt the time rate of change of the CO₂ mixing ratio in the chamber head space over a 60-sec interval beginning 5–7 s following lid closure (mol CO₂ mol⁻¹ dry air s⁻¹). V_e was estimated daily using the dilution technique described in detail in Drewitt et al. (2002) and Gaumont-Guay et al. (2006a). A 5-day running mean with a one-day increment

and Gaumont-Guay et al. (2006a). A 5-day running mean with a one-day increment was computed for V_e to minimize day-to-day variation. Multiple F_{cs} measurements performed in the same half-hour were averaged.

2.3 Manual soil respiration measurements

- In June 2004 and May 2005, 45 white PVC collars (height=10 cm; diameter=9.6 cm) were installed in a 80 m by 80 m systematic grid, covering about half of the study area (roughly 400 m×800 m) and corresponding to the portion of the footprint most often upwind from the flux tower. Collars were inserted about 8 cm deep in the forest floor and shrubs were excluded from the collars. Manual soil respiration (R_{s-man}) was measured on a monthly basis during the 2005 area free access using a L 6400 particular.
- ¹⁵ sured on a monthly basis during the 2005 snow-free season using a LI-6400 portable system (LI-COR Inc.) coupled to a LI-6400-09 soil chamber (volume=991 cm³; diameter=9.55 cm; ground area exposed=71.6 cm²). R_{s-man} measurements were made according to the soil chamber manual. More specifically, ambient CO₂ concentration was first measured by laying the chamber on its side on the ground and the LI-6400
- ²⁰ was set to measure CO₂ concentrations 2 to 10 ppm (or higher for greater fluxes on rare occasions) around the ambient concentration. The chamber was then placed on the collar and allowed 10–20 s to equilibrate. Then, three measurement cycles were performed and only the last two measurements were averaged for further analysis. The distance between the forest floor and the top of the collar was measured to cal-
- ²⁵ culate the actual chamber volume during post-processing. The whole measurement sequence was completed within 10 min at each location. Measurements were made between 09:00 and 20:00 (LT) during one single day and measurements began at a

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different location for each measurement date in a latin square fashion as suggested by Davidson et al. (2002).

2.4 Ecosystem CO₂ flux measurements

CO₂ flux at the ecosystem level was measured half-hourly following the EC technique
as described in detail in Bergeron et al. (2007). A closed-path IRGA (model LI-7000, LI-COR Inc.) enclosed in a thermostatic box (37.5±0.5°C) was coupled to a 3-D sonic anemometer-thermometer (model CSAT3, Campbell Scientific Canada corp. (CSC), Edmonton, AB, Canada) to make 10 Hz measurements of CO₂ concentration and vertical wind velocity at a height of 24 m. The IRGA was calibrated daily by injecting dry, CO₂ free nitrogen and an air/CO₂ gas mixture with a CO₂ concentration of approximately 370 ppm (0.001 ppm precision, traceable to NOAA/CMDL standards). Net ecosystem exchange was computed as the sum of CO₂ flux at the ecosystem level and CO₂ storage in the air column below the EC sensors measured with a 5-height profile system.

15 2.5 Ancillary climate measurements

Air temperature (*T_a*) and vapour pressure deficit (VPD) were measured at a height of 24 m with a shielded thermistor and humidity sensor (model HMP45C, CSC). Soil temperature at 5 (*T_{s5cm}*), 50 (*T_{s50cm}*) and 100 cm (*T_{s100cm}*) and soil water content at 5 cm (SWC) below the active moss layer were measured in two soil pits using thermistors
²⁰ (model 107, CSC) and reflectometers (model CS616, CSC), respectively. The two soil pits were located on different micro-sites, the first one under a relatively closed canopy with feathermoss covering the ground surface, the second one under a relatively open canopy with lichens on the ground surface. Photosynthetically active radiation was measured with quantum sensors (model LI-190SB, LI-COR Inc.) at a 24-m height (*PAR*_{24 m}) on the tower and ~30 cm above the forest floor (*PAR*_{30 cm}) beside (<50 cm away) seven of the nine chambers. Three chambers were located within a 2-m radius

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and shared the same quantum sensor. Wind direction was monitored at a 24 m height with a wind monitor (Model 05103-10, RM Young, Traverse City, MI, USA).

2.6 Data analysis

For each chamber of the automated system, soil respiration (R_{s-auto}) and photosynthesis of the forest floor (P_{ff}) were calculated for the snow-free season using a modified version of the Fluxnet-Canada Research Network (FCRN) standard partitioning and gap-filling algorithm described in detail in Barr et al. (2004). In our study, soil respiration refers to CO₂ efflux from autotrophic and heterotrophic respiration originating from below-ground as well as autotrophic respiration from ground cover plants.

¹⁰ First, an exponential temperature function (Eq. 2) was fit to nighttime (mean chamber $PAR_{30 \text{ cm}} < 5 \,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1})F_{cs}$ data to estimate daytime and missing half-hourly R_{s-auto} as follows:

$$R_{\rm s-auto} = R_{10} Q_{10}^{(T_{\rm s5cm} - 10)/10}$$
(2)

$$In(R_{s-auto}) = A + BT_{s5cm}$$

¹⁵ where Q_{10} (= exp(10*B*)) is a temperature sensitivity coefficient and R_{10} (= Q_{10} exp(*A*)) is base soil respiration at 10°C (μ mol m⁻² s⁻¹). A time varying factor was calculated as the regression slope between measured and predicted values using a moving window (100 good measurement points, increment of 20) to adjust for any seasonal variability of the temperature response of R_{s-auto} . T_{s5cm} measured in the soil pit under feathermoss ²⁰ served to estimate daytime R_{s-auto} of chambers installed on feathermoss or sphagnum, while T_{s5cm} measured in the lichen soil pit was used for automated chambers over lichens. The response of R_{s-auto} to T_{s5cm} as presented in Table 3 was characterized using a log transformed Q_{10} function (Eq. 3) as presented by Morgenstern et al. (2004). The transformation provides homoscedasticity to perform linear least squares regres-²⁵ sion. Equation (3) was also used to characterize the response of R_{s-auto} to T_{s5cm} , to

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(3)



calculate R_{s-auto} normalized for soil temperature (R_{s-auto}/R_{s-auto} (T_{s5cm})) and to assess the influence of T_a , T_{s-50cm} and SWC on R_{s-auto} . In all cases, only nighttime non gap-filled measurements were used.

 P_{ff} was then calculated as daytime $F_{cs} - R_{s-auto}$ for each chamber. The P_{ff} record s was gap filled using a rectangular hyperbola function

$$P_{ff} = \frac{\alpha P_{\rm ff\,max} P A R_{\rm 30cm}}{\alpha P A R_{\rm 30cm} + P_{\rm ff\,max}} \tag{4}$$

where α is the apparent quantum yield and $P_{\rm ffmax}$ is the horizontal asymptotic value of P_{ff} . As for $R_{\rm s-auto}$, a time varying adjustment factor (moving window) was included. $R_{\rm s-auto}$ and P_{ff} were then averaged by cover type. Equation (4) was also used with non gap-filled data to characterize the response of P_{ff} to $PAR_{30\,\rm cm}$ and calculate P_{ff} normalized for light (P_{ff}/P_{ff} ($PAR_{30\,\rm cm}$)) to assess the influence of T_a , VPD and SWC on P_{ff} .

10

For three 2-to-6-day periods in 2005 (see Fig. 1 caption), all automated chambers were darkened using Lumite shade fabrics (Synthetic Industries, Gainesville, GA, USA) ¹⁵ to measure daytime R_{s-auto} . Figure 1 presents the relationship of measured to estimated daytime R_{s-auto} using the modified partitioning algorithm described above. Since both variables contain errors due to the measurement techniques, we used geometric mean regression as presented in Jassal et al. (2007). Daytime estimates agreed well with measurements and allowed us to calculate reliable estimates of daytime R_{s-auto} and P_{ff} .

Estimates of soil respiration and forest floor photosynthesis scaled-up to the ecosystem level (R_{s-eco} and P_{ff-eco} , respectively), were computed as a weighted average of R_{s-auto} and P_{ff} , respectively, based on the surface area of each ground cover for the three main cover types in the study area (Table 1). In 2006, one chamber on feathermoss showed spurious results and its measurements were thus discarded for that year. Also, the IRGA yielded unstable measurements in September and October 2006, which led to the exclusion of automated chamber data for this period.

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 $R_{\rm s-man}$ was aggregated by sector and for the whole study area. Sectors were delimited by azimuth angles from the flux tower to include approximately the same number of measurement points per sector (Table 1). Each sector included collars located 120 to 450 m from the tower.

The EC record was quality controlled as described in Bergeron et al. (2007). Night-5 time data under calm conditions ($u_{\star} < 0.25 \,\mathrm{m \, s^{-1}}$) were discarded. Net ecosystem exchange was partitioned into total ecosystem respiration (R_e) and photosynthesis (P_{eco}) using the FCRN standard partitioning and gap-filling algorithm (see Bergeron et al., 2007 for details). EC data were corrected for the lack of closure in the energy budget (82% closure), as suggested by Barr et al. (2006). 10

Monthly totals of R_{s-eco} , P_{ff-eco} , R_e , and P_{eco} were obtained by summing gap-filled values. Regressions were performed using SAS (version 9.1; SAS Institute Inc., Cary, NC, USA), SigmaPlot (version 8.02; SPSS Inc. Chicago, IL, USA) and/or MatLab (version 7.3.0; The MathWorks Inc., Natick, MA, USE) and its curve fitting toolbox (version 1.1.6).

15

2.7 Adjustment of R_{s-eco} for spatial representativeness

Manual soil respiration measurements made within three sectors of the tower footprint showed the same general seasonal patterns as automated measurements made in the immediate vicinity of the flux tower (Fig. 2). Nonetheless, total gap-filled R_{s-eco} was compared to total R_{s-man} for the entire snow-free season in 2005 (16 June to 4 20 October) to assess the spatial representativeness of scaled-up automated soil respiration measurements. $R_{s=eco}$ totals were calculated using daily averages from (1) only nighttime measurements and (2) only daytime measurements, multiplied by 48, and (3) from the sum of both nighttime and daytime measurements to test for the effect of time of measurement. We did this since R_{s-man} was measured during the daytime while 25 daytime R_{s-auto} (thus R_{s-eco}) was estimated using the partitioning algorithm described

above. Total R_{s-man} was estimated using two common techniques, i.e. linear interpolation between sampling dates (e.g., Davidson et al. 2006) and derivation from an 6, 5507-5548, 2009

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exponential temperature function (e.g., Law et al., 1999). R_{s-eco} systematically overestimated soil respiration by 2 to 28% as compared to R_{s-man} regardless of the period of the day used for the calculation (Table 2). As well, total soil respiration estimated from R_{s-man} diverged between summation techniques by less than 10 g C m⁻² for the 80-day period, corresponding to an uncertainty of less than 3% (Table 2). Hence, the method chosen to estimate snow-free season totals of soil respiration from manual measurements did not account for the higher total respiration derived from the automated measurements.

Therefore, the average of all the ratios of automated to manual measurements for ¹⁰ each sector presented in Table 2 (S: 1.24; SW: 1.04; NW: 1.20; All sectors: 1.16) was used as a correction factor to empirically adjust the spatial representativeness of our time series of automated soil respiration measurements. R_{s-eco} adjusted for spatial representativeness (R_{s-adj}) was computed by decreasing each half-hour measurement of R_{s-eco} by the correction factor corresponding to the appropriate sector. Half-hours ¹⁵ when wind direction was from outside the three sectors or when the footprint length did not match the source area defined above were corrected using a correction factor averaged for all three sectors. The footprint length was calculated using an inverse Lagrangian model (Kljun et al., 2004).

3 Results and discussion

20 3.1 Response of soil respiration to environmental factors

3.1.1 Q_{10} and base respiration

 Q_{10} values derived from Eq. (3) ranged from 3.22–4.36 for feathermoss, 3.54–4.42 for lichen, and 3.33–4.04 for sphagnum micro-sites (Table 3) for soil temperatures varying between 0 and 16°C (data not shown). These estimates are within the range of reported values for other boreal forest soils (e.g. Davidson et al., 1998; Rayment and

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Jarvis, 2000; Gaumont-Guay et al., 2006a, 2008). Q_{10} values of sphagnum micro-sites were lowest overall in 2005 and 2006 and were consistently lower than lichen microsites during all three years. Q_{10} values estimated on a growing season basis represent the temperature sensitivity of enzymatic activity and other temperature-dependant pro-

- ⁵ cesses (Davidson et al., 2006) but also include phenological effects (e.g. root growth stage) and microbial population shifts (Janssens and Pilegaard, 2003; Yuste et al., 2004). Hence, our results suggest that the dynamics of the processes influencing the temperature sensitivity of soil CO₂ efflux are to some degree affected by forest floor vegetation type, which is, to some extent, a reflection of underlying soil properties.
- ¹⁰ Base respiration (R_{10}) was consistently lowest under feathermoss, intermediate under sphagnum, and highest under lichen (Table 3). Accordingly, R_{s-auto} was highest under lichen, intermediate under sphagnum, and lowest under feathermoss at any given soil temperature (Fig. 3a–c). The spatial variability of soil respiration has been related to the physical (micro-topography, porosity, organic horizon depth, temperature, humid-
- ity), chemical (nutrient status of mineral and organic horizons, organic matter quantity and quality) and biological (microbial and fine root biomass, microbial community composition) properties of the soil which can influence either the production of CO₂, its transport to the surface or both (Fang et al., 1998; Longdoz et al., 2000; Rayment and Jarvis, 2000; Xu and Qi, 2001; Heijmans et al., 2004; Khomik et al., 2006; Saiz et al.,
- 20 2006). These properties are linked to micro-site structural characteristics that are in turn related to the distribution and composition of mosses and lichens (Bisbee et al., 2001; Sulyma and Coxson ,2001). Our results provide evidence that the heterogeneity of the ground cover vegetation, which can represent the spatial variability of soil properties, should be taken into account when characterizing or simulating the response of soil CO₂ efflux to environmental factors.

Shallow soil temperature explained 67–86% of the temporal variation of R_{s-auto} under all ground cover types (Table 3, Fig. 3a–c). R_{s-auto} normalized for soil temperature $(R_{s-auto}/R_{s-auto}(T_{s5cm}))$ showed a significant (p<0.0001) positive linear correlation with air temperature for all three ground cover types (r^2 =0.01–0.07 for feathermoss, 0.02–

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0.13 for lichen, and 0.18–0.28 for sphagnum, Fig. 3d–f). Furthermore, normalized R_{s-auto} of feathermoss micro-sites exhibited a significant (p<0.05), but very weak, positive correlation with deep soil temperature (T_{s50cm}) in 2004 and 2005 (r^2 =0.04 for both years, Fig. 3g–i). Temperature has been demonstrated to exert a major influence on soil respiration (Singh and Gupta, 1977; Raich and Schlesinger, 1992; Lloyd and Taylor, 1994). Studies have also shown that most soil respiration occurs in the upper soil layers in northern forest ecosystems (Drewitt et al., 2005; Jassal et al., 2005). These results again emphasize the need to account for different ground cover vegetation types in soil and ecosystem C exchange studies as they may reflect the spatial variability of soil properties and the distribution of respiratory processes along the soil profile.

3.1.2 Response to substrate moisture

Substrate moisture limitation on R_{s-auto} was apparent only under sphagnum when soil water content near the surface reached values below 0.10 m³ m⁻³ in 2005 (Fig. 3j–l). Soil moisture has been reported to affect the soil respiration of temperate and boreal forest ecosystems (Davidson et al., 1998; Subke et al., 2003; Gaumont-Guay et al., 2006a). However, Gaumont-Guay et al. (2008) also reported no effect of soil moisture on soil respiration for a boreal black spruce site in Saskatchewan. This Saskatchewan site is located in a topographic depression where the water table and soil water content are generally high. Our site is less hydric than the site in Saskatchewan but the wetter climate prevailing in eastern Canada can induce more frequent rainfall throughout the growing season, in addition to larger amounts of water released by snowmelt, compared to ecosystems located in the drier regions of central Canada (Bergeron et al., 2007). As a result, our soils stayed relatively moist, at least in deeper soil horizons (data not shown), thereby partly explaining the lack of a relationship between soil respiration

and soil humidity under feathermoss and lichen. Also, root respiration is potentially less sensitive to the drying of superficial soil layers than soil organic matter decomposition (Gaumont-Guay et al., 2008) likely because tree root systems can access deep

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water that is not available to decomposers in the upper soil layer. In addition, microhabitats dominated by sphagnum in boreal black spruce forests are less favourable for tree root growth as they are associated with wetter and colder conditions (Bisbee et al., 2001), hence microbial decomposition presumably contributes more to soil respiration

⁵ under sphagnum micro-sites. As a result, it is possible that the microbial populations on sphagnum microsites were more sensitive to soil moisture than those on feathermoss or lichen microsites The differences we observed in the response of R_{s-auto} to SWC between ground cover types may therefore reflect different contribution levels of autotrophic (root) and heterotrophic (microbial) respiration between micro-sites.

10 3.2 Contribution of soil respiration to ecosystem respiration

During the study period, monthly values of ratios of R_{s-eco} , not adjusted for spatial representativeness, to R_e ranged from 82–120%, with values exceeding 100% on several occasions (Table 4), suggesting our scaling method overestimated soil respiration at the ecosystem level. On the other hand, adjusted R_{s-eco} (R_{s-adj}) to R_e ratios ranged from 72% to 103% during the snow-free season on a monthly basis and exceeded 100% on only one occasion. These results emphasize the importance of assessing the spatial representativeness of automated soil respiration measurements when scaled up to the ecosystem level to help resolve the mismatch in source area between chamber

- and EC measurements and thus produce comparable estimates. The ratios of R_{s-adj} to R_e on a snow-free season basis ranged from 85–87% (Table 4) over the study period and are within the range, but near the upper end, of other published values for Canadian boreal forest sites. Soil respiration accounted for 48– 71% of total ecosystem respiration for six coniferous boreal sites (Lavigne et al., 1997), 70% in a boreal aspen forest (Gaumont-Guay et al., 2006b), and 80, 67, and 83% for
- ²⁵ boreal aspen, black spruce, and jack pine sites, respectively (Black et al., 2005). In other ecosystems, the soil to ecosystem respiration ratio was found to be 67% in a temperate mixed forest (Yuste et al., 2005), 62% in a costal Douglas-fir stand (Jassal et al., 2007), 76% in a ponderosa pine forest (Law et al., 1999), and 69% in European

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forests (Janssens et al., 2001).

The somewhat higher R_{s-adi} to R_e ratio reported in our study, as compared to sites in the western Canadian boreal forest, could be a result of regional differences within the boreal forest in terms of the various component contributions to total ecosystem ⁵ respiration. Bergeron et al. (2007) showed that total ecosystem C exchange differs between our eastern Canadian site and two other black spruce sites located in central Canada. This difference was partly attributed to higher soil temperatures at 5 and 50 cm. The higher winter temperatures were attributable to a thicker snowpack, at the eastern Canadian black spruce site and led to higher winter soil respiration, which may explain the proportionately higher contribution of soil respiration to total ecosystem 10 respiration at this site. The eastern site also has a greater below-ground biomass (Bergeron et al., 2007) compared to the western coniferous sites which may have led to proportionately higher soil respiration as compared to ecosystem respiration at this site. Furthermore, Bergeron et al. (2007) also observed a lower water table at the eastern site during the second half of the growing season, which may have led to higher 15 soil respiration rates due to the absence of anaerobic conditions. They also noted that soil moisture helped explain anomalies in the response of ecosystem respiration to temperature between sites at the monthly time scale, with our eastern site at the low

end of soil water content. Thus, it is possible that the contribution of soil respiration to
 ecosystem respiration was greater at the eastern site. This finding, and the fact that
 little to no soil respiration restriction due to low soil moisture was found in our study,
 suggests that regional differences may exist in tree root phenology and physiology
 and/or in microbial community composition and dynamics and help explain the high
 soil to ecosystem respiration ratios reported here. However, further study is needed to
 shed light on these regional differences. It is also possible that the lower above-ground

biomass at the eastern site or its associated respiration could help explain the regional differences in the soil to ecosystem respiration ratio.

The R_{s-adj}/R_e ratio had a significant negative linearly correlation with the difference between air and soil temperature for the May–June, July–August and September–

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October periods using daily values (Fig. 5). Furthermore, the R_{s-adj}/R_e ratio calculated from 5-day means tended to increase throughout the snow-free season, showing values of approximately 60% in spring and close to 100% in autumn (Fig. 4). On a monthly basis, a similar general increase was also observed (Table 4). Few studies

- ⁵ have described in detail the seasonal variation of the soil to ecosystem respiration ratio. Black et al. (2005) reported that the soil to ecosystem respiration ratio of a boreal black spruce site was greater in mid-summer and in winter and reached a minimum in spring and early summer. Davidson et al. (2006) showed that the soil to ecosystem respiration ratio was minimal in spring and increased to a maximum in autumn and winter
- ¹⁰ for a temperate deciduous forest. Jassal et al. (2007) also showed a spring to autumn increase for a coastal coniferous forest. This seasonal variation was related to the different phenologies of above- and below-ground ecosystem components, to variations in substrate supply, and to lags between changes in air and soil temperature.

It is worth noting that the R_{s-auto}/R_e ratio close to one in autumn reported here returns to a much lower value by the following spring. This reset likely occurs in springtime when warm air stimulates above-ground respiration and the cold soil limits root growth and organic matter decomposition (Davidson et al., 2006), thus limiting soil CO₂ efflux and decreasing the contribution of soil respiration to total ecosystem respiration to a minimum.

20 3.3 Response of forest floor photosynthesis (P) to environmental factors

3.3.1 Response to light

25

Maximum photosynthetic capacity ($P_{\rm ffmax}$) was higher for feathermoss than sphagnum in 2004 and 2005 (Table 5). $P_{\rm ffmax}$ was lowest for lichen in 2005 and 2006 but highest in 2004. Feathermoss consistently showed lower photosynthetic apparent quantum yield (α) values than sphagnum (Table 5). The same was true for lichen except in 2005 when α was not significantly lower than for sphagnum. Feathermoss and lichen showed significantly different α only in 2004.

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These results contrast with other published values of light response curve parameters. Swanson and Flanagan (2001) reported higher maximum photosynthetic capacity and quantum yield for sphagnum compared to feathermoss from measurements made at an old black spruce site in Saskatchewan. Goulden and Crill (1997) also observed ⁵ higher maximum photosynthetic capacity values for sphagnum than feathermoss at the Northern Old Black Spruce flux site in Manitoba. In both studies, ecological differences between sphagnum and feathermoss micro-sites were greater than in the present study. At these central Canadian sites, sphagnum occupied open, wet microsites in lower elevations (hollows) where the water table is near or at the surface, while ¹⁰ feathermoss was found in shady, dry upland areas (hummocks) where the water ta-

- ble depth is greater. Furthermore, black spruce ecosystems in central Canada are associated with wet sites where small topographic variations can have a large influence on vegetation composition (Trumbore and Harden, 1997). In eastern Canada, black spruce ecosystems are commonly found on less hydric sites where micro-habitat
- ¹⁵ conditions do not differ as much with microtopography, as was the case at our site. The micro-site differences in light and water table regimes described for central Canadian sites were much less pronounced at our site, hence the differences among the studies in question could be attributed to different environmental conditions between micro-sites. Therefore, the photosynthetic response of the ecosystem ground cover to environmental conditions appears to depend on the interaction between ground cover
- type (feathermoss, sphagnum and lichen) and microhabitat environmental conditions.

The response of lichen photosynthesis to light is not well documented and specific information about the physiology of *Cladina* spp. is rare. Lichens are considered to have photosynthetic rates similar to bryophytes when hydrated (Green and Lange, 1994).

²⁵ Coxson and Wilson (2004) reported values of maximum photosynthesis per mass unit of *Cladina mitis* similar to those reported for feathermoss and sphagnum. Our results provide evidence that bryophytes and lichens have photosynthetic rates per unit ground area that are similar in range. However, our study shows that lichen has distinct light response curve parameters and provides values for these parameters that can be used

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to simulate the photosynthetic response of lichen to light.

The photosynthesis of feathermoss, sphagnum and lichen saturated at relatively low irradiance values (~200 μ mol m⁻² s⁻¹; Fig. 6a–c) that correspond to the maximum daytime irradiance below the canopy for most days of the snow-free season (data not 5 shown). This was expected, since bryophytes and lichen would likely be well adapted to shade conditions (Green and Lange, 1994). The saturating light levels observed here are consistent with those measured by Whitehead and Gower (2001) and Kolari et al. (2006) for feathermoss and with those reported by Swanson and Flanagan (2001) for sphagnum. For lichen photosynthesis, Coxson and Wilson (2004) reported lower saturating light levels that decreased with temperature. Kolari et al. (2006) observed 10 that light levels at the forest floor of a Scots pine forest in Finland were high enough for photosynthesis to saturate most of the time. On the other hand, Bisbee et al. (2001) suggested that the photosynthetic production of the forest floor is light limited. Given that P_{ff} reached saturation at low light levels that are typical of the understory environment on our site, our results support the idea that factors other than light (i.e., 15 temperature and/or water stress) limit the photosynthesis, and thus the carbon uptake, of forest floors composed of sphagnum, feathermoss or lichen. Furthermore,

canopy dieback) generally increases the abundance of understory vascular plants thus leaving unchanged the light regime at the forest floor (Hart and Chen, 2006).

3.3.2 Response to other environmental variables

The response of P_{ff} normalized for light $(P_{ff}/P_{ff}(PAR_{30 \text{ cm}}))$ to air temperature and vapor pressure deficit was similar for all three ground cover types (Fig. 6d–i). $P_{ff}/P_{ff}(PAR_{30 \text{ cm}})$, peaked at T_a =5–8°C and decreased at temperatures below and above this range, suggesting that forest floor photosynthesis is optimal at temperatures ranging from 5–8°C. These results are consistent with those of Goulden and Crill (1997) for feathermoss and sphagnum. Coxson and Wilson (2004) reported an optimal temperature for *Cladina mitis* photosynthesis of about 15°C, which is somewhat higher

increased light availability due to non-stand replacing disturbances (e.g., windthrow,

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than reported here. Normalized P_{ff} of sphagnum showed a sharper decline at temperatures above 8°C compared to feathermoss and lichen, decreasing from 1.4 to 0.6, while normalized P_{ff} of feathermoss and lichen decreased from 1.2 to 0.8. This indicates that light response curves can overestimate sphagnum photosynthesis by up to

⁵ 40% under high air temperature conditions while this overestimation is limited to 20% for feathermoss and lichen. Sphagnum also showed a stronger decrease of normalized P_{ff} when VPD values were above 1 kPa and P_{ff} was overestimated by as much as 50% for sphagnum (normalized P_{ff} =0.5) compared to about 25% for feathermoss and lichen (normalized P_{ff} =0.75). No restriction of P_{ff} was observed at low SWC for any of the three ground cover types (Fig. 6j–l).

Air temperature and vapor pressure deficit can be viewed as surrogates for desiccation as opposed to SWC that may not reflect the desiccation status of the ground cover vegetation (Fig. 6j–l). Bryophytes and lichen are poikilohydric plants and the reduction of their photosynthetic capacity under desiccating conditions is well doc-¹⁵ umented (Green and Lange, 1994; Williams and Flanagan, 1996; Schipperges and Rydin, 1998). Our results suggest that sphagnum photosynthesis is more sensitive to desiccation than feathermoss and lichen. More direct measurements of the vegetation water status would likely help us better understand and predict bryophyte and lichen photosynthesis.

20 3.4 Contribution of P_{ff} to P_{eco}

The mean *P_{ff}*/*P*_{eco} ratios on a snow-free season basis were consistent between years at 0.17–0.18 (Table 4). These results agree with published values for mature black spruce ecosystems in other regions of Canada. Swanson and Flanagan (2001) reported that moss photosynthesis accounted for 13% of gross ecosystem productivity (GEP) for the growing season. Goulden and Crill (1997) estimated the contribution of moss photosynthesis to GEP ranged between 10 and 50% on a daily basis with a greater contribution observed after rain events. In our study, the forest floor vegetation accounted for as much as 45% of daily ecosystem photosynthesis toward the end of

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the snow-free season (data not shown). Snow-free season totals of P_{ff} were 23–24% that of R_{s-adj} (Table 4). Drewitt et al. (2002) also measured a decrease in daytime soil CO₂ efflux of up to 25% due to moss photosynthesis. Morén and Lindroth (2002) observed an offset of soil respiration of about 20% due to forest floor photosynthesis.

- ⁵ Our results demonstrate that C fixation by forest floor photosynthesis is a significant component of C exchange of boreal ecosystems and that mature black spruce ecosystems in the eastern portion of North America seem to obtain a similar proportion of their assimilated carbon from the forest floor compared to black spruce forests in other regions.
- ¹⁰ The contribution of P_{ff} to P_{eco} was not constant over the course of the snow-free season for any of the three years, varying from 13 to 24% (Fig. 7, Table 4). The seasonal variability of the P_{ff}/P_{eco} ratio was best related to changes in air temperature $(r^2=0.09, \text{ Table 6})$. This relationship, although weak, shows that the contribution of forest floor vegetation decreased as air temperature increased up to 20°C and varied little
- for further increases up to 30°C (data not shown). This observed temperature limitation of the *P_{ff}/P_{eco}* ratio is consistent with the limitation of photosynthesis at temperatures above 8°C mentioned earlier (Fig. 6d, f). On the other hand, boreal forest GEP is dependent on light levels but also on air temperature (van Dijk et al., 2005; Bergeron et al., 2007; Fig. 8g–o) and thus shows a pronounced seasonal variation with maximum values reached during mid-summer when air temperature is high (Black et al., 2005, Fig. 8j–o). These two contrasting responses, along with the fact that the seasonal variability of *P_{eco}* is almost an order of magnitude greater than that of *P_{ff}*, can explain the seasonal pattern of the *P_{ff}/P_{eco}* ratio.

4 Conclusions

This study reports on C exchange of the forest floor within a boreal black spruce forest in eastern Canada and its seasonal contribution to ecosystem C exchange. We have shown that the response of soil respiration to environmental factors differs beBGD



tween micro-sites. Soil respiration was a dominant component of ecosystem respiration during the study period, accounting for 85–87% of total ecosystem respiration on a snow-free season basis. However, the contribution of soil respiration to ecosystem respiration varied seasonally, ranging 72 to 103% from May to October and this variation
 ⁵ was related to the difference between air and soil temperature.

This study also showed that C assimilation by the moss and lichen stratum can significantly impact ecosystem C exchange in the boreal forest of eastern North America, accounting for 17–18% of the total ecosystem C assimilation. The contribution of forest floor to ecosystem photosynthesis did not vary significantly between years but showed

- a pronounced seasonal variation, ranging 13 to 24% on a monthly basis and even more on a daily basis, indicating that the different vegetation strata do not respond similarly to environmental conditions. The three ground cover types showed some differences in photosynthetic responses to environmental conditions but light did not appear to limit photosynthesis of bryophytes and lichen during the snow-free season.
- ¹⁵ To better understand and predict the consequences of the modification of temperature and precipitation regimes under different climate change scenarios, process models could utilize the parameters and response functions described in this paper to better characterize the physiological processes governing C exchange of the soil and ground cover of boreal ecosystems in eastern North America.
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References

5

- Baldocchi, D., Kelliher, F. M., Black, T. A., and Jarvis, P.: Climate and vegetation controls on boreal zone energy exchange, Glob. Change Biol., 6, 69–83, 2000.
- Barr, A. G., Black, T. A., Hogg, E. H., Kljun, N., Morgenstern, K., and Nesic, Z.: Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem

production, Agr. Forest Meteorol., 126, 237–255, 2004.

- Barr, A. G., Morgenstern, K., Black, T. A., McCaughey, J. H., and Nesic, Z.: Surface energy balance closure by the eddy-covariance method above three boreal forest stands and implications for the measurement of the CO₂ flux, Agr. Forest Meteorol., 140, 322–337, 2006.
- Bergeron, O., Margolis, H. A., Black, T. A., Coursolle, C., Dunn, A. L., Barr, A. G., and Wofsy, S. C.: Comparison of carbon dioxide fluxes over three boreal black spruce forests in Canada, Glob. Change Biol., 13, 89–107, 2007.

Bisbee, K. E., Gower, S. T., Norman, J. M., and Nordheim, E. V.: Environmental controls on ground cover species composition and productivity in a boreal black spruce forest, Oecolo-

¹⁵ gia, 129, 261–270, 2001.

- Black, T. A., Gaumont-Guay, D., Jassal, R. S., Amiro, B. D., Jarvis, P. G., Gower, S. T., Kelliher, F. M., Dunn, A., and Wofsy, S. C.: Measurement of CO₂ exchange between boreal forest and the atmosphere, in: The carbon balance of forest biomes, edited by: Griffiths, H., Jarvis, P.J., Taylor and Francis Group, New York, 151–186, 2005.
- Botting, R. S. and Fredeen, A. L.: Net ecosystem CO₂ exchange for moss and lichen dominated forest floors of old-growth sub-boreal spruce forests in central British Columbia, Canada, Forest Ecol. Manag., 235, 240–251, 2006.

Coxson, D. S. and Wilson, J. A.: Carbon gain in *Cladina mitis* from mixed feather moss mats in a sub-alpine spruce-fir forest: The role of soil respiratory carbon dioxide release, Symbiosis,

²⁵ **37**, **307–321**, **2004**.

Davidson, E. A., Belk, E., and Boone, R. D.: Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest, Glob. Change Biol., 4, 217–227, 1998.

Davidson, E. A., Richardson, A. D., Savage, K. E., and Hollinger, D. Y.: A distinct seasonal

³⁰ pattern of the ratio of soil respiration to total ecosystem respiration in a spruce-dominated forest, Glob. Change Biol., 12, 230–239, 2006.

Davidson, E. A., Savage, K., Verchot, L. V., and Navarro, R.: Minimizing artifacts and biases in

BGD

6, 5507–5548, 2009

Forest Floor Carbon Exchange of a Boreal Black Spruce Forest in Eastern Canada



chamber-based measurements of soil respiration, Agr. Forest Meteorol., 113, 21–37, 2002. Drewitt, G. B., Black, T. A., and Jassal, R. S.: Using measurements of soil CO₂ efflux and concentrations to infer the depth distribution of CO₂ production in a forest soil, Can. J. Soil Sci., 85, 213–221, 2005.

⁵ Drewitt, G. B., Black, T. A., Nesic, Z., Humphreys, E. R., Jork, E. M., Swanson, R., Ethier, G. J., Griffis, T., and Morgenstern, K.: Measuring forest floor CO₂ fluxes in a Douglas-fir forest, Agr. Forest Meteorol., 110, 299–317, 2002.

Fang, C., Moncrieff, J. B., Gholz, H. L., and Clark, K. L.: Soil CO₂ efflux and its spatial variation in a Florida slash pine plantation, Plant Soil, 205, 135–146, 1998.

- Flannigan, M., Campbell, I., Wotton, M., Carcaillet, C., Richard, P., and Bergeron, Y.: Future fire in Canada's boreal forest: paleoecology results and general circulation model – regional climate model simulations, Can. J. Forest Res., 31, 854–864, 2001.
 - Gaumont-Guay, D., Black, T. A., Griffis, T. J., Barr, A. G., Jassal, R. S., and Nesic, Z.: Interpreting the dependence of soil respiration on soil temperature and water content in a boreal aspen stand, Agr. Forest Meteorol., 140, 220–235, 2006a.
- Gaumont-Guay, D., Black, T. A., Griffis, T. J., Barr, A. G., Morgenstern, K., Jassal, R. S., and Nesic, Z.: Influence of temperature and drought on seasonal and interannual variations of soil, bole and ecosystem respiration in a boreal aspen stand, Agr. Forest Meteorol., 140, 203–219, 2006b.

15

Gaumont-Guay, D., Black, T. A., Barr, A. G., Jassal, R. S., and Nesic, Z.: Biophysical controls on rhizospheric and heterotrophic components of soil respiration in a boreal black spruce stand, Tree Physiol., 28, 161–171, 2008.

Goulden, M. L. and Crill, P. M.: Automated measurements of CO₂ exchange at the moss surface of a black spruce forest, Tree Physiol., 17, 537–542, 1997.

- Green, T. G. A. and Lange, O. L.: Photosynthesis in poikilohydric plants: a comparison of lichens and bryophytes, in: Ecophysiology of photosynthesis, edited by: Schulze, E. D., Caldwell, M. M., Springer-Verlag, New York, 319–341, 1994.
 - Hart, S. A. and Chen, H. Y. H.: Understory vegetation dynamics of North American boreal forests, Crit. Rev. Plant. Sci., 25, 381–397, 2006.
- Heijmans, M. M. P. D., Arp, W. T., and Chapin, F. S.: Carbon dioxide and water vapour exchange from understory species in boreal forest, Agr. Forest Meteorol., 123, 135–147, 2004.
 - Janssens, I. A., Lankreijer, H., Matteucci, G., Kowalski, A. S., Buchmann, N., Epron, D., Pilegaard, K., Kutsch, W., Longdoz, B., Grunwald, T., Montagnani, L., Dore, S., Rebmann, C.,

6, 5507-5548, 2009

Forest Floor Carbon Exchange of a Boreal Black Spruce Forest in Eastern Canada





Moors, E. J., Grelle, A., Rannik, U., Morgenstern, K., Oltchev, S., Clement, R., Gudmundsson, J., Minerbi, S., Berbigier, P., Ibrom, A., Moncrieff, J., Aubinet, M., Bernhofer, C., Jensen, N. O., Vesala, T., Granier, A., Schulze, E. D., Lindroth, A., Dolman, A. J., Jarvis, P. G., Ceulemans, R., and Valentini, R.: Productivity overshadows temperature in determining soil and ecosystem respiration across European forests, Glob. Change Biol., 7, 269–278, 2001.

- Janssens, I. A. and Pilegaard, K.: Large seasonal changes in Q(10) of soil respiration in a beech forest, Glob. Change Biol., 9, 911–918, 2003.
- Jassal, R., Black, A., Novak, M., Morgenstern, K., Nesic, Z., and Gaumont-Guay, D.: Relationship between soil CO₂ concentrations and forest-floor CO₂ effluxes, Agr. Forest Meteorol., 130, 176-192, 2005.

5

15

Jassal, R. S., Black, T. A., Cai, T. B., Morgenstern, K., Li, Z., Gaumont-Guay, D., and Nesic, Z.: Components of ecosystem respiration and an estimate of net primary productivity of an intermediate-aged Douglas-fir stand, Agr. Forest Meteorol., 144, 44-57, 2007.

Khomik, M., Arain, M. A., and McCaughey, J. H.: Temporal and spatial variability of soil respiration in a boreal mixedwood forest, Agr. Forest Meteorol., 140, 244–256, 2006.

- Kljun, N., Calanca, P., Rotach, M. W., and Schmid, H. P.: A simple parameterisation for flux footprint predictions, Bound.-Lay. Meteorol., 112, 503-523, 2004.
 - Kolari, P., Pumpanen, J., Kulmala, L., Ilvesniemi, H., Nikinmaa, E., Gronholm, T., and Hari, P.: Forest floor vegetation plays an important role in photosynthetic production of boreal forests,

Forest Ecol. Manag., 221, 241-248, 2006. 20

- Lavigne, M. B., Ryan, M. G., Anderson, D. E., Baldocchi, D. D., Crill, P. M., Fitzjarrald, D. R., Goulden, M. L., Gower, S. T., Massheder, J. M., McCaughey, J. H., Rayment, M., and Striegl, R. G.: Comparing nocturnal eddy covariance measurements to estimates of ecosystem respiration made by scaling chamber measurements at six coniferous boreal sites, J. Geophys. Res.-Atmos., 102, 28977–28985, 1997. 25
 - Law, B. E., Ryan, M. G., and Anthoni, P. M.: Seasonal and annual respiration of a ponderosa pine ecosystem, Glob. Change Biol., 5, 169-182, 1999.
 - Lloyd, J. and Taylor, J. A.: On the Temperature-Dependence of Soil Respiration, Funct. Ecol., 8, 315-323, 1994.
- ³⁰ Longdoz, B., Yernaux, M., and Aubinet, M.: Soil CO₂ efflux measurements in a mixed forest: impact of chamber disturbances, spatial variability and seasonal evolution, Glob. Change Biol., 6, 907–917, 2000.

Morén, A. S. and Lindroth, A.: CO₂ exchange at the floor of a boreal forest, Agr. Forest Meteo-

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rol., 101, 1–14, 2000.

5

15

- Morgenstern, K., Black, T. A., Humphreys, E. R., Griffis, T. J., Drewitt, G. B., Cai, T. B., Nesic, Z., Spittlehouse, D. L., and Livingstone, N. J.: Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fir forest during an El Nino La Nina cycle, Agr. Forest Meteorol., 123, 201–219, 2004.
- O'Connell, K. E. B., Gower, S. T., and Norman, J. M.: Comparison of net primary production and light-use dynamics of two boreal black spruce forest communities, Ecosystems, 6, 236–247, 2003.

Pumpanen, J., Ilvesniemi, H., Keronen, P., Nissinen, A., Pohja, T., Vesala, T., and Hari, P.:

- ¹⁰ An open chamber system for measuring soil surface CO₂ efflux: Analysis of error sources related to the chamber system, J. Geophys. Res.-Atmos., 106, 7985–7992, 2001.
 - Raich, J. W. and Schlesinger, W. H.: The Global Carbon-Dioxide Flux in Soil Respiration and Its Relationship to Vegetation and Climate, Tellus B, 44, 81–99, 1992.

Rayment, M. B. and Jarvis, P. G.: Temporal and spatial variation of soil CO₂ efflux in a Canadian boreal forest, Soil Biol. Biochem., 32, 35–45, 2000.

Saiz, G., Green, C., Butterbach-Bahl, K., Kiese, R., Avitabile, V., and Farrell, E. P.: Seasonal and spatial variability of soil respiration in four Sitka spruce stands, Plant Soil, 287, 161–176, 2006.

Savage, K. E. and Davidson, E. A.: A comparison of manual and automated systems for soil

- ²⁰ CO₂ flux measurements: trade-offs between spatial and temporal resolution, J. Exp. Bot., 54, 891–899, 2003.
 - Schipperges, B. and Rydin, H.: Response of photosynthesis of Sphagnum species from contrasting microhabitats to tissue water content and repeated desiccation, New Phytol., 140, 677–684, 1998.
- ²⁵ Singh, J. S. and Gupta, S. R.: Plant decomposition and soil respiration in terrestrial ecosystems, Bot. Rev., 43, 499–528, 1977.
 - Subke, J. A., Reichstein, M., and Tenhunen, J. D.: Explaining temporal variation in soil CO₂ efflux in a mature spruce forest in Southern Germany, Soil Biol. Biochem., 35, 1467–1483, 2003.
- ³⁰ Sulyma, R. and Coxson, D. S.: Microsite displacement of terrestrial lichens by feather moss mats in late seral pine-lichen woodlands of north-central British Columbia, Bryologist, 104, 505–516, 2001.

Swanson, R. V. and Flanagan, L. B.: Environmental regulation of carbon dioxide exchange at

6, 5507-5548, 2009

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the forest floor in a boreal black spruce ecosystem, Agr. Forest Meteorol., 108, 165–181, 2001.

Trumbore, S. E. and Harden, J. W.: Accumulation and turnover of carbon in organic and mineral soils of the BOREAS northern study area, J. Geophys. Res.-Atmos., 102, 28817–28830, 1997.

5

- Valentini, R., Matteucci, G., Dolman, A. J., Schulze, E. D., Rebmann, C., Moors, E. J., Granier, A., Gross, P., Jensen, N. O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C., Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A. S., Vesala, T., Rannik, U., Berbigier, P., Loustau, D., Guomundsson, J., Thorgeirsson, H., Ibrom, A., Morgenstern, K., Clement, R., Moncrieff,
- J., Montagnani, L., Minerbi, S., and Jarvis, P. G.: Respiration as the main determinant of carbon balance in European forests, Nature, 404, 861–865, 2000.
 - van Dijk, A. I. J. M., Dolman, A. J., and Schulze, E. D.: Radiation, temperature, and leaf area explain ecosystem carbon fluxes in boreal and temperate European forests, Global Biogeochem. Cy., 19, GB2029, doi:2010.1029/2004GB002417, 2005.
- ¹⁵ Whitehead, D. and Gower, S. T.: Photosynthesis and light-use efficiency by plants in a Canadian boreal forest ecosystem, Tree Physiol., 21, 925–929, 2001.

Williams, T. G. and Flanagan, L. B.: Effect of changes in water content on photosynthesis, transpiration and discrimination against (CO₂)-C-13 and (COO)-O-18-O-16 in Pleurozium and Sphagnum, Oecologia, 108, 38–46, 1996.

- ²⁰ Xu, M. and Qi, Y.: Soil-surface CO₂ efflux and its spatial and temporal variations in a young ponderosa pine plantation in northern California, Glob. Change Biol., 7, 667–677, 2001.
 - Yuste, J. C., Janssens, I. A., Carrara, A., and Ceulemans, R.: Annual Q(10) of soil respiration reflects plant phenological patterns as well as temperature sensitivity, Glob. Change Biol., 10, 161–169, 2004.
- Yuste, J. C., Nagy, M., Janssens, I. A., Carrara, A., and Ceulemans, R.: Soil respiration in a mixed temperate forest and its contribution to total ecosystem respiration, Tree Physiol., 25, 609–619, 2005.

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Table 1. Sector characteristics and number of manual measurement points by sector.

Sector	Azimuth angles		Cover	type						
	from the tower	Feathermoss	Lichen	Sphagnum	Other					
		Proport	Proportion of ground cover (%)							
S	150–205°	73 (81)	8 (9)	8 (9)	11 (0)	15				
SW	205–257°	70 (80)	2 (2)	16 (18)	13 (0)	14				
NW	257–322°	69 (76)	3 (4)	19 (20)	9 (0)	18				
All	150–322°	70 (79)	5 (5)	14 (16)	11 (0)	48				
		Number	of measu	urement points	S	Total				
S	150–205°	8	3	1	3	15				
SW	205–257°	6	4	2	4	16				
NW	257–322°	9	1	2	2	14				
All	150–322°	23	8	5	9	45				

Number in brackets corresponds to the proportion of ground cover excluding the category Other.

Table 2. Total ecosystem soil respiration as estimated by automated (R_{s-auto}) and manual (R_{s-man}) measurements, and R_{s-auto}/R_{s-man} ratio per sector.

	Totals (g C m ⁻² period ⁻¹)										
Sector	Auto (Night)	Auto (Day)	Auto (All)	Man (Lin)	Man (Exp)						
S	536	515	524	424	420						
SW	523	501	510	492	490						
NW	529	507	517	437	426						
All	531	510	519	452	447						

	Ratios										
Sector	Auto (Night)/ Man (Lin)	Auto (Day)/ Man (Lin)	Auto (All)/ Man (Lin)	Auto (Night)/ Man (Exp)	Auto (Day)/ Man (Exp)	Auto (All)/ Man (Exp)					
S	1.27	1.21	1.23	1.28	1.23	1.25					
SW	1.06	1.02	1.04	1.07	1.02	1.04					
NW	1.21	1.16	1.18	1.24	1.19	1.21					
All	1.18	1.13	1.15	1.19	1.14	1.16					

Data for the period 16 June to 4 October 2005 are included. Totals for automated measurements (Auto) were calculated using nighttime (Night), daytime (Day), or nighttime and daytime data (All). Totals for manual measurements (Man) were calculated using values gap-filled by daily linear interpolation (Lin) and a 5-day exponential soil temperature function (Exp). BGD

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Year	Cover Type	A^1	B^{1} (°C ⁻¹)	Q_{10}^{1}	$R_{10}^1 \ (\mu \text{mol m}^{-2} \text{ s}^{-1})$	r ²	п
2004	Feathermoss	^a 0.057±0.003	^a 0.1170±0.0002	^a 3.22±0.01	^a 3.41±0.01	0.86	2845
	Lichen	^c 0.261±0.007	^c 0.1487±0.0005	^c 4.42±0.02	^c 5.74±0.05	0.71	2845
	Sphagnum	^b 0.196±0.006	^b 0.1397±0.0004	^b 4.04±0.02	^b 4.92±0.03	0.76	2845
2005	Feathermoss	^a -0.299±0.005	^b 0.1472±0.0004	^c 4.36±0.01	^a 3.23±0.02	0.84	3649
	Lichen	^c 0.333±0.007	^a 0.1264±0.0005	^b 3.54±0.02	^c 4.94±0.04	0.74	3649
	Sphagnum	^b 0.067±0.006	^a 0.1228±0.0003	^a 3.41±0.01	^b 3.65±0.03	0.69	3630
2006	Feathermoss	^a -0.364±0.006	^b 0.1456±0.0003	^b 4.29± 0.01	^a 2.98±0.02	0.82	1907
	Lichen	^b 0.026±0.008	^b 0.1447±0.0005	^b 4.25± 0.02	^c 4.36±0.04	0.67	1907
	Sphagnum	^c 0.128±0.005	^a 0.1202± 0.0003	^a 3.33± 0.01	^b 3.78±0.02	0.73	1906

Table 3. Parameter values derived from Eq. (3) relating R_{s-auto} to $T_{s5\,cm}$.

Uncertainty corresponds to 1 SE. Superscripts indicate significant differences (p<0.05) between cover types for each year (beginning with a for lowest values).

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Month		$R_{\rm s-eco}^1$			R_e^1			ŀ	R _{s-eco} /R	e
	2004	2005	2006	2004	2005	2006		2004	2005	2006
May	-	50	55	-	60	61		-	0.83	0.90
Jun	84	119	114	97	145	124		0.88	0.82	0.92
Jul	137	143	169	148	163	161		0.93	0.88	1.05
Aug	149	165	166	153	150	147		0.97	1.10	1.13
Sep	125	128	127	108	121	-		1.16	1.06	-
Oct	78	85	82	68	71	-		1.15	1.20	-
Total	573	690	713	574	710	493	Mean	1.02	0.98	1.00
		$R_{\rm s-adj}^{1}$			R_e^1			I	R _{s-adj} /R _e	9
	2004	2005	2006	2004	2005	2006		2004	2005	2006
May	-	43	47	_	60	61		-	0.72	0.77
Jun	73	104	99	96	145	124		0.76	0.72	0.80

Table 4. Monthly totals of R_{s-eco} , R_{s-adj} , R_{e} , $P_{\rm ff-eco}$ and $P_{\rm eco}$.

		$R_{\rm s-adj}^{1}$			R_e^1			I	R _{s-adj} /R	9
	2004	2005	2006	2004	2005	2006		2004	2005	2006
May	_	43	47	_	60	61		_	0.72	0.77
Jun	73	104	99	96	145	124		0.76	0.72	0.80
Jul	118	123	146	148	163	161		0.80	0.75	0.91
Aug	128	142	142	153	150	147		0.84	0.95	0.97
Sep	107	110	-	108	121	_		0.99	0.91	_
Oct	66	73	-	68	71	_		0.97	1.03	_
Total	492	595	434	573	710	493	Mean	0.87	0.85	0.86

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Table 4. Continued.

		$P_{\rm ff-eco}^1$			$P_{\rm eco}^1$			$P_{\rm f}$	_{f-eco} / P _e	900
	2004	2005	2006	2004	2005	2006		2004	2005	2006
May	_	17	17	-	101	101		-	0.17	0.17
Jun	24	25	25	136	159	162		0.18	0.16	0.15
Jul	24	26	31	165	195	188		0.15	0.13	0.17
Aug	31	31	32	180	177	180		0.17	0.17	0.18
Sep	21	24	_	119	125	-		0.18	0.19	_
Oct	12	14	_	56	58	-		0.21	0.24	_
Total	112	137	105	656	815	631	Mean	0.18	0.18	0.17

¹ Values are in g C m^{-2} month⁻¹. Gap-filled values were used. See Methods for details.

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Year	Cover Type	$\alpha (X \ 10^{-2})^1 (mol \ mol^{-1})$	$P_{\rm ffmax}^1$ (μ mol m ⁻² s ⁻¹)	r ²	n
2004	Feathermoss	^b 4.12±0.11	^b 2.95±0.05	0.62	2907
	Lichen	^a 3.05±0.13	^c 3.44±0.10	0.35	2747
	Sphagnum	^c 5.20±0.30	^a 2.24±0.06	0.26	2677
2005	Feathermoss	^a 5.98±0.25	^c 2.17±0.03	0.32	4204
	Lichen	^{ab} 6.06±0.42	^a 1.68±0.04	0.11	4003
	Sphagnum	^b 7.29±0.39	^b 1.83±0.03	0.20	4074
2006	Feathermoss	^a 3.70±0.14	^b 2.67±0.05	0.48	3048
	Lichen	^a 3.39±0.25	^a 2.03±0.06	0.13	2902
	Sphagnum	^b 4.55±0.18	^b 2.79±0.06	0.41	3000

Table 5. Parameter values derived from Eq. (4) relating P_{ff} to PAR_{30cm}.

¹ Uncertainty corresponds to 1 SE. Superscripts indicate significant differences (p<0.05) between cover types for each year (beginning with a for lowest values).

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Table 6. Relationships of P_{ff}/P_{eco} with air and soil temperatures.

Variables	Parameters	р	r ²
T _a	$y=2.33906 - 0.35617x + 0.01278x^2$	<0.0001	0.09
T _{s5cm}	y=3.13177 - 0.58279x + 0.02737	<0.0001	0.04
T _{s50mm}	$y=3.62913 - 0.79176x + 0.04379x^2$	0.0001	0.04
T _{s100cm}	$y=3.39657 - 0.82296x + 0.05033x^2$	0.0003	0.04

Daily gap-filled values were used. See *Methods* for details.



Fig. 1. Relationship between predicted (with the gap-filling algorithm) and measured daytime soil respiration (R_s) for three periods in 2004 when chambers were darkened (18–19 July , 27 August – 1 September and 22–24 September). A log transformation was used on both x and y to provide homoscedasticity. Given the error associated with x, a geometric mean regression was used.

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Fig. 8. Five-day mean of (**a**–**c**) 5 cm and 50 cm soil temperature (T_s), (**d**–**f**) gap-filled soil and ecosystem respiration (R), (**g**–**i**) total daily photosynthetically active radiation (PAR), (**j**–**I**), air temperature (T_a) and (**m**–**o**) mean gap-filled forest floor and ecosystem photosynthesis (P) for 2004 to 2006.