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Eight years of forest-floor CO₂ exchange in a boreal black spruce forest: Spatial integration and long-term temporal trends



D. Gaumont-Guay^{a,*}, T.A. Black^b, A.G. Barr^c, T.J. Griffis^d, R.S. Jassal^b, P. Krishnan^e, N. Grant^b, Z. Nesic^b

^a Biometeorology Research Laboratory, Vancouver Island University, BC, Canada

^b Biometeorology and Soil Physics Group, University of British Columbia, BC, Canada

^c Climate Research Branch, Meteorological Service of Canada, SK, Canada

^d Department of Soil, Water and Climate, University of Minnesota, MN, USA

^e National Oceanic and Atmospheric Administration, Atmospheric Turbulence and Diffusion Division, TN, USA

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ABSTRACT

Automated measurements of the net forest-floor CO₂ exchange (NFFE) were made in a mature (130-yearold) boreal black spruce forest over an 8-year period (2002–2009) with the objectives of (1) quantifying the spatial and temporal (seasonal and interannual) patterns in NFFE, soil respiration (SR) and gross forestfloor photosynthesis (GFFP), and (2) better understanding the key climatic controls on each component at both time scales. Scaling-up of the component fluxes to the stand level showed that the feather moss community accounted for more than 85% of NFFE and SR, and more than 70% of GFFP. The remainder was partitioned almost equally between the sphagnum and lichen communities for all components fluxes, while the exposed mineral soil in hollows accounted for less than 1% of NFFE and SR. Soil temperature (T_s) was the dominant climate variable determining seasonal trends in NFFE and SR. The shape of the exponential response was, however, strongly modulated by soil water content (SWC) in the surface organic horizon, with reduced apparent temperature sensitivity at low SWC. A lowering of the water table depth also had an effect on NFFE and SR, although very weak, with increased CO2 loss from the hollows likely due to improved soil aeration. Air temperature (T_a) was the dominant climate variable determining seasonal trends in GFFP, while plant water status seemed to have played a minor role. Although not statistically significant (p = 0.9907), annual totals of scaled-up NFFE varied from 505 ± 121 to 601 ± 144 g C m⁻² y⁻¹ over the 8-year period. The lowest NFFE was observed in 2004, the coldest and wettest year on record, while the highest was observed in 2005, a warmer year with slightly above-average precipitation. SR, by far the dominant component of the forest-floor CO₂ exchange, closely followed the inter-annual trends in NFFE, while GFFP was lowest in 2004 and highest in 2003, also a cold year but with very low precipitation. Over the 8-year period, winter NFFE contributed 7% to annual NFFE while GFFP during the growing season reduced losses due to SR by 18%.

While strong correlations were observed between the component fluxes and temperature (T_s or T_a) and SWC at the seasonal time scale, the mean annual values of these climate variables were poor predictors of the inter-annual trends when considered individually. Combining multiplicatively T_s and SWC for NFFE and SR, and T_a and SWC for GFFP, significantly increased the predictive ability of the models. The difference in predictability of the two time scales poses some interesting challenges for interpreting and modeling the long-term temporal trends in NFEE and its components. The results obtained in this relatively long-term study suggest that the inter-annual variability in the component fluxes was not driven by the mean annual climate conditions, but rather the shorter time scale changes in climate conditions, i.e. changes that occurred within days, weeks and/or seasons. Moreover, it appeared that the timing of the climatic changes within each year was also critical, spring and summer conditions having a far greater impact than fall and winter conditions in this stand.

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* Corresponding author at: Faculty of Science and Technology, Department of Biology, Vancouver Island University, 900 5th street, Nanaimo, BC, Canada V9R5S5. Tel.: +1 250 753 3245x2314; fax: +1 250 740 6482.

E-mail address: david.gaumont-guay@viu.ca (D. Gaumont-Guay).

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1. Introduction

Black spruce forests are an intrinsic part of the Canadian boreal landscape. Because of their extensive coverage (Viereck and Johnston, 1990), they play an important role in the North-American biosphere-atmosphere exchange of carbon dioxide (CO₂). Recent studies of stand-level net ecosystem CO₂ exchange (NEE) made with the eddy covariance technique in mature stands (>100-yearold) have demonstrated that these forests are nearly carbon neutral and that the inter-site and/or inter-annual variability in their sink or source strength depends mainly on their responses to temperature and soil water regimes (Bergeron et al., 2007; Dunn et al., 2006; Krishnan et al., 2008). Since black spruce forests contain more carbon than any other forests in the boreal biome (Gower et al., 1997) and that they are currently undergoing significant changes in terms of these climate drivers (IPCC, 2007), there is a need to better understand the biophysical processes influenced by these changes so a better quantification of the consequences on their sink or source strength can be achieved.

Various studies (Dunn et al., 2006; Krishnan et al., 2008) have clearly demonstrated that ecosystem respiration (ER) is a key driver of the temporal variability in NEE in these forests, and that belowground carbon dynamics play a significant role in determining ER. Automated chamber measurements of the net forest-floor CO₂ exchange (NFFE) have since supported this hypothesis and have indicated that this component represents more than two-thirds of ER in these forests (Bergeron et al., 2009; Davidson et al., 2006c; Gaumont-Guay et al., 2009).

In boreal black spruce forests, NFFE is a balance between the production of CO₂ through various metabolic processes associated with roots, mycorrhizae and decomposers at multiple depths in the soil profile, as well as vegetation at the forest-floor, and the assimilation of CO₂ by forest-floor vegetation photosynthesis. In practical terms, when measured with transparent chambers, NFFE can be partitioned into its two contributing components, i.e. soil respiration (SR, which incorporates plant respiration in this study) and gross forest-floor photosynthesis (GFFP) (Goulden and Crill, 1997; Swanson and Flanagan, 2001; Gaumont-Guay et al., 2009). SR is by far the dominant component of NFFE, while GFFP usually contributes a smaller fraction, i.e. approximately 15% (Bergeron et al., 2009; Gaumont-Guay et al., 2009).

Although chamber-based measurements of NFFE have been carried out for many decades, there is still an on-going debate regarding the controls on CO₂ production and/or transport in the soil profile. On one side, the vast majority of studies aimed at improving the quantification of NFFE have focused on the dependence of this process and its components on the physical climate system, mainly soil temperature (T_s) and soil water content (SWC). However, new partitioning methods (see Subke et al., 2006 and references therein) and sophisticated analytical techniques (Vargas et al., 2010, 2011) emphasize the point that biological processes themselves directly control NFFE mostly through organic inputs into the soil environment (Kuzyakov and Gavrichkova, 2010). The difficulty in interpreting these new findings is that the direct action of the biological processes is masked by the indirect and simultaneous action of the physical variables. A similar type of phenomenon was highlighted recently when trying to disentangle the confounding effects of T_s and SWC on NFFE (Davidson et al., 1998). One of the most important biological controls suggested to date is the direct link between carbon assimilation by photosynthesis in the aboveground portion of forests and its transport down the phloem to the sites of respiration in the rhizosphere (Ekblad and Högberg, 2001; Kuzyakov and Gavrichkova, 2010).

A few studies have reported and discussed the interannual variability in NFFE and its components in various forest ecosystems (Epron et al., 2004; Fenn et al., 2010; Phillips et al., 2010; Savage and Davidson, 2001; Wang et al., 2011). As observed at shorter time scales, climate variables such as T_s and SWC have been shown to be key drivers of the inter-annual variability of these components. In particular, Phillips et al. (2010) reported that a reduction in spring T_s was mainly responsible for a 5-year decrease in SR in a temperate mixed forest. Wang et al. (2011) reported, however, that SWC through an indirect effect of precipitation frequency rather than amount, was responsible for the inter-annual variability in SR in a subtropical forest. The study of Epron et al. (2004) also hinted at other biological controls, such as photosynthesis-driven belowground carbon dynamics, that could have helped explain the inter-annual variability in SR in a Beech forest.

Given the occurrence of climate change (IPCC, 2007), the potential positive feedback between climate change and NFFE and/or SR (Davidson and Janssens, 2006a), and the realization that process-based models of global carbon dynamics require a better parameterization of soil CO₂ production processes (Bahn et al., 2010) there is need for the investigation of the long-term effects of climate variability and biological factors on these processes in order to improve our predictive capabilities. In an attempt to achieve this in one of the most dominant forest ecosystems of the boreal landscape, the black spruce forest, we report the results of an analysis of 8 years of automated, continuous and high-frequency measurements of NFFE and concomitant climate variables made in a mature (130-year-old) boreal black spruce stand from 2002 to 2009. The specific objectives of this study were to (1) quantify the spatial and temporal (seasonal and interannual) patterns in NFFE, SR and GFFP, and (2) better understanding the key climatic and biological controls on each component.

2. Methods

2.1. Study site

This study was performed in a 130-year-old (age in 2009) black spruce forest located at the southern edge of the boreal forest in Saskatchewan (Fluxnet ID: CA-Obs). The research site was established as part of BOREAS in 1993 and has been operated by the Boreal Ecosystem Research and Monitoring Sites (BERMS) program since 1997. The dominant tree species in this stand were black spruce (*Picea mariana* (Mill.) B.S.P., up to 11 m high), tamarack (*Larix laricina* (Du Roi) K. Kock, 10–16 m high (10% of ground cover)) and occasional jack pine (*Pinus banksiana* Lamb., 13 m high). Tree density was 4330 trees ha⁻¹ with a mean height and diameter at breast height of 7.2 m and 7.1 cm, respectively. LAI was $3.8 \text{ m}^2 \text{ m}^{-2}$ in Chen et al. (2006). The understory vegetation consisted mainly of wild rose (*Rosa woodsii*) and Labrador tea (*Ledum groenlandieum*).

The forest-floor vegetation consisted mainly of mixed feather mosses (*Hylocomium splendens*, *Pleurozium schreberi* and *Ptilium crista-castrensis*) overlaying an organic layer (~70% of total forest-floor coverage, Bisbee et al., 2001), peat moss (*Sphagnum* spp.) in wetter areas (10%), lichens (*Cladina* spp.) in drier areas (10%), standing water in open hollows (10%) and human trails. The soil was classified as a peaty phase gleyed eluviated eutric brunisol (Agriculture and Agri-Food Canada, 1998; Kalyn and Van Rees, 2006) and consisted of an approximately 20–30-cm-deep organic layer overlying a waterlogged sandy clay. This stand had an elevated water table most of the year. Most of the root system was found above the water table, i.e. within 20–30 cm of the soil surface.

2.2. Automated measurements of NFFE and climate variables

The non-steady-state automated chamber system used in this study and the calculations of NFFE have been described in detail elsewhere and only a brief description will be given here (see Drewitt et al., 2002; Gaumont-Guay et al., 2008, 2009). Two identical systems were used during the course of the measurement period (original system in 2002 and 2003 and new system from 2004 to 2009). Each chamber was connected to temperature-controlled housings (TCHs) enclosing data logging, pumping and gas analyzer equipment. All chambers, which were approximately 60 L in volume $(50 \text{ cm i.d.} (\text{internal diameter}) \times 30 \text{ cm high})$, were located within a 25-m radius centered on the TCHs and the locations were chosen to represent the diversity of the forest-floor composition. During the 2002-2003 measurement period, two chamber locations were selected to represent the feather moss community, one to represent a mix of feather moss and herbaceous plants, one to represent the sphagnum community and one to represent the hollows with exposed mineral soil at the surface. During the 2004-2006 measurement period, chamber locations were determined as follows: 4 chambers for feather moss, 2 for sphagnum and 1 for lichen. One less chamber was used for the feather moss community during the 2007-2009 period. One chamber was added in one exposed hollow (mineral soil) during the growing season of 2007 only, temporarily bringing the number of chambers to 8 for that year.

The chamber lids were made of transparent acrylic and were attached to a fixed collar about 10 cm long inserted 3-4 cm into the soil. Snowfall during the winter entirely filled the collar area. Snow removal on the chamber gaskets was done approximately bi-weekly and following significant snowfalls with the help of a contractor to ensure good seals between the lids and the collars. The systems measured the change of CO₂ concentration in the headspace of each chamber over a given time interval (5min and 2.5-min intervals, respectively, for the two systems) sequentially allowing all chambers to be measured once every half-hour. Fluxes were calculated from slopes of the linear regression relationships using 1-s measurements for 1 min starting 20 s after lid closure. The effective volumes of individual chambers, which take into account vegetation growth and snow accumulation in the chambers, as well as adsorption of CO₂ on the chamber walls and litter, was measured daily using a gas injection technique described in Drewitt et al. (2002). The infrared gas analyzer (Model LI-6262, LI-COR, Inc., Lincoln, NB) used to measure CO₂ concentrations was calibrated daily by sequentially using CO₂-free nitrogen (N) gas (offset calibration) and a gas of known CO₂ concentration (\sim 360 μ mol mol⁻¹, balance dry air) (gain calibration) from gas cylinders calibrated against a standard from the Meteorological Service of Canada (MSC), Downsview, ON, Canada.

Soil temperature (T_s) was measured half-hourly at a depth of 2 cm inside each chamber using copper-constantan thermocouples. Volumetric soil water content at the 7.5-cm depth (SWC) was measured every 4 h at 2 locations in the feather moss community using soil water reflectometers (Model CS-615, Campbell Scientific, Inc., Logan, UT). The probes were tested regularly in situ with a onepoint calibration check by removing a known volume of organic material and calculating the bulk density and gravimetric water content. Checking for accuracy of measurements was also done by calibrating the reflectometry probe with similar-type probes in the laboratory. Water table depth (WTD) was measured at one location using a vibrating-wire pressure transducer (Druck PTX depth pressure transmitter, Geokon model 4580-2, Lebanon, NH) in a piezometer tube. Photosynthetically active radiation (PAR) was measured at four different locations at 1 m above the forest-floor using quantum sensors (Model LI-190-SB, LI-COR, Inc., Lincoln, NE).

Air temperature (T_a) was measured at 1 m above the forest-floor with copper-constantan thermocouples.

2.3. Data analysis and statistical analyses

Data quality was evaluated monthly over the course of the 8year measurement period using in-house quality/control software (Jassal et al., 2012) using Matlab (Version 6.5.1, The Mathworks, Inc.). Partitioning of NFFE between SR and GFFP and gap-filling of missing data for each component (40.1% of the dataset, on average over the 8-year period, especially during winter due to snow conditions) was performed at the half-hourly time scale for each chamber independently using the following procedure. First, daytime SR and missing nighttime SR were estimated with a Q₁₀ model (SR = SR₁₀Q₁₀^{$(T_s-10)/10$} where SR₁₀ is SR at 10 °C) using the relationship between measured nighttime NFFE (taken as SR) and $T_{\rm s}$ at the 2-cm depth (see Gaumont-Guay et al., 2006). Second, measured daytime NFFE was subtracted from estimated daytime SR to obtain GFFP. Third, missing daytime GFFP was estimated with a Michaelis-Menten type function (see Griffis et al., 2003) using the relationship between GFFP and PAR. All calculations were performed using a 15-day moving window at 1-day intervals for the growing season (T_s at the 2-cm depth > 0 °C) to account for the potential changes in the short-term temperature sensitivity parameters with other forcing climatic or biological variables (Gaumont-Guay et al., 2006; Davidson et al., 2006b). During winter (T_s at the 2-cm depth ≤ 0 °C), only the effect of T_s on NFFE was considered because of the presence of a frozen soil surface, a snow pack and potentially no photosynthesis. Two separate relationships were developed from the entire dataset for the winter and for all chambers combined: one during the winter-spring transition, i.e. from early January to snow melt (SR₁₀ = 328.9 g C m⁻² d⁻¹ and Q_{10} = 671.9), and one during the fall-winter transition, i.e. from the beginning of soil freezing to late December (SR₁₀ = $2.7 \text{ gCm}^{-2} \text{ d}^{-1}$ and Q_{10} = 8.6). These large values of R_{10} and Q_{10} were the results of fitting the Q_{10} model to low wintertime fluxes over a narrow temperature range $(-10 < T_s < 0 \circ C)$ and the relationships were only used for gap-filling the winter flux data. Half-hourly data were averaged over 24-h periods to obtain daily values. Un-scaled annual totals of NFFE, SR and GFFP were obtained by calculating the sum of the gap-filled daily component fluxes for each forest-floor community separately. The sum was then weighted according to the percent coverage of each forest-floor community as described by Bisbee et al. (2001) to obtain the stand level scaled-up values. Since measurements were not made in the lichen community before 2004, 80% and 10% coverage were attributed to the feather moss and sphagnum communities, respectively, while 10% was attributed to hollows. After 2004, 70% of the coverage was attributed to feather moss, 10% to sphagnum, 10% to lichens and 10% to hollows. All gapfilling and model fitting procedures, as well as statistical analyses were performed with Matlab (Version 6.5.1, The Mathworks, Inc.). Single and multivariate regression analyses between the interannual trends in NFFE, SR and GFFP and climate variables were made with linear models. One-way analyses of variance were carried out on the annual totals of the component fluxes using the uncertainty (see below) as the upper and lower limits on the mean annual values.

2.4. Errors associated with measurements and calculations

The systematic error associated with the infrared gas analyzer (IRGA) was negligible at <0.1% (LI-COR, Inc.). The random error associated with the IRGA calibrations, calculations of daily effective volumes and non-linearity of the CO₂ signal in the chamber headspace following lid closure were estimated at $\pm 4\%$ (Jassal et al., 2012). No error was attributed to the use of the two chamber



Fig. 1. Scaling-up of the component fluxes to the ecosystem level. (a) NFFE: net forest-floor CO_2 exchange, (b) SR: soil respiration and (c) GFFP: gross forest-floor photosynthesis. F_m : feather moss, S_m : sphagnum moss, L_i : lichens, H_0 : hollows, S_u : stand level un-scaled, S_s : stand level scaled. The analysis is presented for 3 June to 14 October 2007, when flux data for hollows were available. The line inside the box, the edges of the box and the whiskers represent the median, the 25th and 75th percentiles and the most extreme data points, respectively.

systems during the 8-year measurement period as the measurement methods were identical. A comparative analysis of NFFE measured in the feather moss community from August to October 2003 confirmed the excellent agreement between the two systems $(y=0.993x+0.003, r^2=0.85, P<0.001)$. The random error associated with the gap-filling procedure, especially during winter when data availability was low, was estimated at $\pm 10\%$ after the application of a Monte Carlo gap-filling simulation (Gaumont-Guay et al., 2009). Gaumont-Guay et al. (2009) have demonstrated previously that annual relationships between nighttime NFFE and T_s are not representative of winter NFFE in this boreal black spruce forest. The use of separate winter relationships derived from measurements over the 8-year record significantly reduced this error. It is well known also that annual relationships tend to overestimate the temperature sensitivity of NFFE or SR at shorter time scales (Gaumont-Guay et al., 2006, 2009) and probably affects the diurnal amplitude of the component fluxes. This problem was alleviated by using the 15-day moving window gap filling procedure. The random error associated with the spatial variability between chamber locations for each forest-floor community, when more than one chamber was available per community, was estimated at $\pm 10\%$ by using an estimate of the standard deviation within the communities. A total error of $\pm 24\%$ was added to the scaled-up annual totals of the component fluxes.

3. Results and discussion

3.1. Spatial variability and scaling

An analysis of the spatial variability of the component fluxes is presented for 2007 when data for hollows were available (Fig. 1). The positive NFFE for all forest-floor communities and hollows indicated a general efflux of CO₂ to the atmosphere in the stand at the daily time scale (Fig. 1a). The feather moss community showed the greatest NFFE (median of 4.25 g C m⁻² d⁻¹), followed by the lichen and sphagnum communities (2.41 and 1.37 g C m⁻² d⁻¹, respectively). NFFE from the hollows was considerably smaller $(0.18 \text{ gCm}^{-2} \text{ d}^{-1})$ which reflected the limited potential for CO₂ efflux from the exposed mineral soil with standing water. SR had a spatial distribution similar to that of NFFE across the communities (Fig. 1b). In contrast, the sphagnum community showed the greatest GFFP (median of $1.11 \text{ g C m}^{-2} \text{ d}^{-1}$) followed by the lichen and feather moss communities (0.72 and $0.70 \text{ g C m}^{-2} \text{ d}^{-1}$, respectively) (Fig. 1c). A small but not negligible photosynthetic uptake was detected in the hollows during extreme drying events.

The observation of higher NFFE and SR in the feather moss community was consistent with the results obtained by Swanson and Flanagan (2001) in the same stand and by Goulden and Crill (1997) in a similar mature northern black spruce stand in Manitoba. Bergeron et al. (2009) found, however, that SR was consistently lower in the feather moss community as compared to the sphagnum community in a mature eastern black spruce forest. In their study SR for the lichen community was the highest. The observation of higher GFFP in the sphagnum community was also in agreement with the results of Swanson and Flanagan (2001) and Goulden and Crill (1997) but again contrasted with those of Bergeron et al. (2009) who observed lower GFFP for the sphagnum community in their eastern black spruce forest. Although we did not attempt to physically characterize each chamber location in this study, Rayment and Jarvis (2000) have shown that the most important factor explaining the spatial variability of NFFE in the same stand was the thickness of the dead brown moss mat, which could be as much as 50 mm at some locations. A general observation of the moss mat thickness and rooting patterns in the stand suggested that the greater CO₂ efflux in the feather moss community could be attributed to the greater depth of the organic horizon beneath the moss and its potential for greater microbial decomposition, but also to live roots which could have increased the contribution of rhizosphere-derived respiration to SR. Many other factors could have influenced the spatial variability in NFFE and SR in this stand, including the quantity and quality of organic material throughout the soil profile, the amount, composition and activity of the respiring biomass (including roots and decomposers), the type of vegetation present at the forest-floor, various chemical and physical characteristics (e.g., C:N ratio, N content, porosity, etc.) as well as the spatial variability of T_s and SWC (see the following references for a discussion of the effects of various factors on different forest ecosystems, Fang et al., 1998; Khomik et al., 2006; Scott-Denton et al., 2006; Singh et al., 2007; Xu and Qi, 2001), but they were not quantified in this study.

Scaling-up of the component fluxes to the stand level according to the percent coverage of the forest-floor communities (as determined with the 2007 data) showed that compared to not scaling, the median for NFFE was increased by 61% ($2.06 \text{ gCm}^{-2} \text{ d}^{-1}$ for stand-level un-scaled to $3.33 \text{ gCm}^{-2} \text{ d}^{-1}$ for stand-level scaled in Fig. 1a) and by 53% for SR ($2.66 \text{ gCm}^{-2} \text{ d}^{-1}$ for stand-level un-scaled to $4.07 \text{ gCm}^{-2} \text{ d}^{-1}$ for stand level scaled, respectively in Fig. 1b). This was because of the higher values of these component fluxes for the feather moss community and also because of the dominance of this community in the stand. Even though GFFP for the sphagnum and lichen communities was greater than for the feather moss community, scaling had no effect on stand-level GFFP (median of $0.67 \text{ gCm}^{-2} \text{ d}^{-1}$ for both stand-level un-scaled and stand-level scaled in Fig. 1c), because of the smaller areas of the former communities in the stand.

Overall, the feather moss community accounted for more than 85% of stand-level NFFE and SR, the remainder being partitioned almost equally between the sphagnum and lichen communities (\sim 7%). The contribution of hollows was negligible, at less than 1%. The feather moss community accounted for approximately 70% of scaled-up GFFP, leaving the contribution of the sphagnum and lichen communities at \sim 15% for this component. Again, the



Fig. 2. Seasonal trends in daily climate variables and un-scaled component fluxes for the feather moss community in 2008, an average year in terms of temperature, precipitation and soil water content conditions. (a) PAR: photosynthetically active radiation at 1 m above forest-floor, (b) T_s 2 cm: soil temperature at the 2-cm depth and T_a 1 m: air temperature at 1 m above forest-floor, (c) SWC 7.5 cm: volumetric soil water content at the 7.5 cm depth and P: precipitation, (d) NFFE: net forest-floor CO₂ exchange, (e) SR: soil respiration and (f) GFFP: gross forest-floor photosynthesis.

contribution of hollows to GFFP was negligible at less than 1%. For the sake of simplicity, the remainder of the analysis of the seasonal trends is presented for the dominant feather moss community with un-scaled values, except for a discussion of the effects of changing water table depth on NFEE from the exposed mineral soil in the hollows. The inter-annual analysis of the component fluxes is presented, however, with gap-filled scaled-up fluxes, accounting for the spatial distribution of the forest-floor communities reported by Bisbee et al. (2001). In this inter-annual analysis, we also assumed a constant mean daily flux in the hollows of 0.18, 0.26 and 0.07 g Cm⁻² d⁻¹ for NFFE, SR and GFFP, respectively, when data were unavailable for this component (based on the scaling analysis in Fig. 1).

3.2. Seasonal trends

An example of the seasonal trends in the component fluxes is presented for 2008, an average year in terms of temperature, precipitation, soil moisture and light conditions in the stand (Fig. 2). The minimum and maximum un-scaled daily NFFE for the feather moss community were slightly greater than 0 and 5.6 g C m⁻² d⁻¹, respectively. NFFE normally peaked in mid-summer (July) and reached its lowest value in winter (January–February). During the snow period, the chambers showed that NFFE was sustained and positive during the winter months even when the forest-floor was covered by snow and soil surface temperature was near 0 °C. SR normally peaked at the same time as T_s in mid-summer. GFFP peaked at the same time as T_a , but about a month later than PAR.

An increase in T_s was always associated with an exponential increase in NFFE at the seasonal time scale (Fig. 3). The relationship usually showed two phases, with a step change near 0 °C, which reflected a rise in microbial decomposition during snow melt (Gaumont-Guay et al., 2008). The shape of the seasonal temperature response was affected by SWC. In the example presented in Fig. 3, an intense drought in 2003 reduced the apparent temperature sensitivity significantly (Q_{10} = 2.5) as compared to 2004 (Q_{10} = 4.1), when calculated using the Q_{10} model presented in Section 2.3.

A reduction in SWC was usually associated with a small decrease in NFFE during the growing season as shown by the temporal trends in temperature-normalized NFFE for 2004 in Fig. 4 (residuals were calculated as the ratio of measured to modeled NFFE, which is the seasonal NFFE vs T_s relationship in Fig. 3). NFFE responded positively, however, to large and/or sustained rain events even at high SWC (Fig. 4a and b). NFFE pulses have been observed in other forest ecosystems (Borken et al., 2002; Orchard and Cook, 1983; Xu et al., 2004) and have been attributed, at least partly, to microbial access to available carbon substrate and to the population health of microorganisms, a phenomenon referred to as the "Birch effect" (Birch, 1958a,b; Jarvis et al., 2007; Wu and Lee, 2011). New evidence suggests that the increase in NFFE observed at SWC > 0.4 m³ m⁻³ (Fig. 4b) could be associated with priming effects of the rhizosphere in response to increased photosynthesis (Gaumont-Guay et al., submitted).

In normal conditions, the mineral soil was usually saturated with water in this stand with standing water showing in the hollows. However, in 2007, extended drying events led to a lowering



Fig. 3. Relationship between un-scaled daily nighttime net forest-floor CO_2 exchange (night NFFE) and nighttime soil temperature at the 2-cm depth (night $T_s 2 \text{ cm}$) for the feather moss community in 2003 and 2004, two contrasting years in terms of soil water content conditions. Lines represent the best fits of a Q_{10} model (NFFE = NFFE₁₀ $Q_{10}^{T_s-10/10}$) for each dataset separately (NFFE₁₀ 3.1 g C m⁻² d⁻¹ and Q_{10} 2.5 for 2003, NFFE₁₀ 4.7 g C m⁻² d⁻¹ and Q_{10} 4.2 for 2004, significant at the 99% probability level).



Fig. 4. (a) Seasonal trends in un-scaled daily nighttime temperature normalized net forest-floor CO₂ exchange (nighttime NFFE residuals, left axis, open circles), precipitation (*P*, right axis, bars) and volumetric soil water content at the 7.5-cm depth (SWC 7.5 cm expressed in %, right axis, line) for the feather moss community during the growing season of 2004, an extremely wet year. (b) Relationship between nighttime NFFE residuals and SWC 7.5 cm during the same period.

of the WTD (Fig. 5a), which was associated with a small, but significant, increase in NFFE (Fig. 5b). The increase in NFFE was concomitant with an increase in the temperature response (Q_{10} values of 2.3 vs 5.7, for high and low WTD, respectively) (Fig. 5c), which indicated that the temperature control on decomposition was regained during lowering of the water table and improved aeration. These results suggest competing effects of SWC on NFFE and, most importantly, decomposition in waterlogged ecosystems. As discussed above, drying of the organic horizon (as seen with a reduction of NFFE in the feather moss community between rain events) had the potential to reduce microbial decomposition (or root respiration) processes in this horizon. In contrast, drying of the mineral horizon had the potential to increase microbial decomposition processes in this horizon. The higher NFFE following drying in the latter horizon could also have been due to an increase in soil aeration and CO₂ transport (diffusivity). Similar observations of the effect of WTD were made with EC in a northern black spruce stand in Manitoba (Dunn et al., 2009). These authors reported that warmer temperatures and a lowering of WTD increased microbial decomposition in that stand. However, contrasting responses to changes in WTD on respiration processes have been reported for water-dominated ecosystems in North America. Sulman et al. (2010) showed that ER increased and decreased with a lowering of WTD for various fens and bogs in this region, respectively, and attributed the complexity of this response to the impacts of oxygen availability on decomposition processes. Interestingly, the difference between the maximum daily value of 5.6 g C m⁻² d⁻¹ for NFFE in the feather moss community (where the thickest organic horizons were located) (Fig. 2d) and 1.3 g C m⁻² d⁻¹ in the hollows (where mineral soil was exposed) (Fig. 5c) in this study suggest that most (\sim 75%) of the CO₂ production occurred in the organic horizon, i.e. in the first 20-30 cm soil layer. Therefore, SWC in the surface organic horizon had likely the dominant impact on NFFE compared to the mineral soil, given the fact that the hollows contributed little (<1%) to scaled-up NFFE.



Fig. 5. Seasonal trends in daily (a) water table depth (WTD) and (b) un-scaled nighttime net forest-floor CO₂ exchange (night NFFE) in the hollows (exposed mineral soil) from June to October 2007. (c) Relationship between nighttime NFFE and soil temperature at the 2-cm depth (T_s 2 cm) during periods of low (<-20 cm) and high (>-20 cm) WTD. Lines represent the best fits of a Q₁₀ model (NFFE = NFFE₁₀Q₁₀^{(T_s -10)/10}) for each dataset separately (NFFE₁₀ 0.1 g Cm⁻² d⁻¹ Q₁₀ 2.3 for WTD <-20 cm and NFFE₁₀ 0.5 g Cm⁻² d⁻¹ and Q₁₀ 5.7 for WTD > -20 cm, significant at the 99% probability level).

As shown in Fig. 6, T_a was a significant climate variable associated with variations of GFFP at the seasonal time scale for the feather moss community. Overall, GFFP increased exponentially with T_a (corresponding to GFFP₁₀ and Q_{10} values of 0.8 g C m⁻² d⁻¹ and 3.1, respectively, when calculated using the Q_{10} model). These results contrast with those of Bergeron et al. (2009) who observed a bell-shaped response of GFFP to T_a . In their study, GFFP peaked between 5 and 8 °C for the same community with a range of T_a of ~0-25 °C. Past studies have shown that PAR-saturated photosynthesis for these plant communities occurs at relatively low PAR values (Bergeron et al., 2009; Kolari et al., 2006; Whitehead and Gower, 2001). This type of vegetation is therefore adapted to low light conditions under the closed forest canopy (Green and Lange, 1994). Other factors, such as plant water status, are likely to have a greater impact at the seasonal time scale. This is supported by findings like those of Cui et al. (2009) who reported that photosynthesis responded positively to an increase in air relative humidity for two forest bryophytes. An analysis of the time series of temperaturenormalized GFFP in this study showed a small positive response to precipitation events (and increased SWC) although, overall, the effect was difficult to quantify (Fig. 6).

3.3. Inter-annual trends

Although annual totals of the component fluxes were not statistically different between years (see below), we provide a short analysis of their inter-annual trends to contrast with

Table 1

Gap-filled and scaled-up annual totals (\pm uncertainty) of the net forest-floor CO₂ exchange (NFFE), soil respiration (SR), gross forest-floor photosynthesis (GFFP), as well as total winter NFFE, ratio of winter NFFE to annual NFFE and ratio of GFFP to SR with associated annual climate variables, i.e. mean soil temperature at the 2-cm depth (T_s 2 cm), mean air temperature at 1 m above the forest-floor (T_a), growing season length (GS length), total precipitation (P) and mean volumetric soil water content at the 7.5-cm depth (SWC 7.5 cm) over the 8-year measurement period.

	NFFE $(g C m^{-2} y^{-1})$	$\frac{SR}{(gCm^{-2}y^{-1})}$	GFFP $(g C m^{-2} y^{-1})$	Winter NFFE $(g C m^{-2} y^{-1})$	Winter NFFE/NFFE	GFFP/SR	$T_{\rm s} 2 {\rm cm} (^{\circ} {\rm C})$	<i>T</i> _a (°C)	GS length (days)	<i>P</i> (mm)	SWC 7.5 cm $(m^3 m^{-3})$
2002	556 ± 133	691 ± 166	135 ± 32	34	0.06	0.20	1.9	0.2	157	432	0.29
2003	524 ± 126	669 ± 161	146 ± 35	27	0.05	0.22	2.3	1.0	208	233	0.23
2004	505 ± 121	598 ± 144	93 ± 22	39	0.08	0.16	2.4	-0.3	220	569	0.41
2005	601 ± 144	712 ± 171	110 ± 26	56	0.09	0.15	3.1	1.7	229	500	0.37
2006	522 ± 125	661 ± 159	138 ± 33	31	0.06	0.21	3.6	2.4	218	459	0.33
2007	564 ± 135	673 ± 162	109 ± 26	49	0.09	0.16	3.6	0.8	225	450	0.34
2008	544 ± 131	651 ± 156	107 ± 26	38	0.07	0.16	3.1	0.2	226	371	0.31
2009	541 ± 130	635 ± 152	94 ± 23	34	0.06	0.15	2.8	0.2	222	481	0.37
Avg	545 ± 131	661 ± 159	117 ± 28	39	0.07	0.18	2.9	0.8	213	437	0.33

the patterns observed at the seasonal time scale. Gap-filled and scaled-up annual totals of NFFE varied from 505 ± 121 to $601 \pm 144 \,\mathrm{g}\,\mathrm{C}\,\mathrm{m}^{-2}\,\mathrm{y}^{-1}$ over the 8-year record (Fig. 7 and Table 1, p = 0.9907). The lowest NFFE was observed in 2004, the coldest (mean annual T_a of $-0.2 \circ C$) and wettest (mean annual SWC of 0.41 m³ m⁻³) year on record. The highest NFFE was observed in 2005, one of the two warmest years on record (mean annual T_a of 1.7 °C) with above-average precipitation. Generally, there was an increase in NFFE with increasing warmth and wetness, but also with increasing growing season length, although these relationships were not strong (Table 1). SR followed trends similar to NFFE (inter-annual trends not statistically significantly different, p = 0.9927). GFFP was lowest and highest in 2004 and 2003, respectively (inter-annual trends not statistically significantly different, p = 0.2177). Both years were cold, but 2003 had very limited precipitation. The greatest GFFP in 2003 contradicted with the previous observation that GFFP was stimulated by short-term rain events during the growing season. Overall, winter NFFE accounted for 7% of annual NFFE, over the 8-year period. GFFP offset SR losses by 18%, on average, during the same period (Table 1).

A few studies have reported and discussed the inter-annual variability in NFFE and its components for different forest ecosystems. Similar to the patterns observed in this study, Savage and Davidson (2001) found that prolonged drought decreased SR in an upland forest, but increased SR in a wetland forest. In a beech forest, Epron et al. (2004) argued that the inter-annual variability in NFFE was primarily due to T_s and SWC, but that other factors, such as photosynthesis-driven belowground carbon dynamics, might have accounted for the residuals observed in their data. Similar results were found by Fenn et al. (2010) in a temperate



Fig. 6. (a) Relationship between un-scaled gross forest-floor photosynthesis (GFFP) and daytime air temperature 1 m above the forest-floor (day T_a 1 m) for the feather moss community from July to October 2004. The line represents the best fit of a Q_{10} model (GFFP = GFFP₁₀ $Q_{10}^{(T_a-10)/10}$) (GFFP₁₀ = 0.8 g C m⁻² d⁻¹ and Q_{10} = 3.1, significant at the 99% probability level). (b) Seasonal trends in daily nightime temperature-normalized gross forest-floor photosynthesis (residuals GFFP, left axis, open circles), volumetric soil water content at the 7.5 cm depth (SWC 7.5 cm, right axis, line) and precipitation (*P*, right axis, bars) for the feather moss community.



Fig. 7. Annual totals of gap-filled and scaled-up component fluxes and annual climate conditions from 2002 to 2009. NFFE: net forest-floor CO_2 exchange, SR: soil respiration, GFFP: gross forest-floor photosynthesis, T_s 2 cm: mean soil temperature at the 2-cm depth, T_a 1 m: mean air temperature at 1 m above forest-floor, GS length: growing season length (days), Precipitation: total precipitation, and SWC 7.5 cm: mean soil water content at the 7.5-cm depth. Error bars represent the uncertainty of the annual totals as described in Section 2.



Fig. 8. Relationship between modeled (using single or multivariate linear regression analyses with climate variables presented in each panel) and measured gap-filled and scaled-up annual totals of the components fluxes from 2002 to 2009. NFFE: net forest-floor CO₂ exchange, SR: soil respiration, GFFP: gross forest-floor photosynthesis, *T*_s: mean soil temperature at the 2-cm depth, *T*_a: mean air temperature at 1 m above forest-floor, SWC: mean soil water content at the 7.5-cm depth.

deciduous forest in England. Phillips et al. (2010) reported that a reduction in spring T_s was largely responsible for a 5-year decrease in SR in a temperate mixed forest. Wang et al. (2011) reported for a subtropical forest that SWC, through an indirect effect of precipitation frequency rather than amount, was responsible for the inter-annual variability in SR.

Even though strong correlations were observed between the seasonal trends of the component fluxes and temperature (T_s or T_a) and SWC, as well as some general trends between wet/dry and cold/warm years in this study, overall, the mean annual values of these climate variables, when considered separately, were poor predictors of the inter-annual trends in NFFE, SR and GFFP (Fig. 8).



Fig. 9. Seasonal trends in (row 1) daily soil temperature at the 2-cm depth (T_s 2 cm), (row 2) volumetric soil water content at the 7.5-cm depth (SWC 7.5 cm), gap-filled and scaled-up (row 3) net forest-floor CO₂ exchange (NFFE), (row 4) soil respiration (SR) and (row 5) gross forest-floor photosynthesis (GFFP) for selected pairs of years during the 8-year measurement record. Upper and lower boundaries of the shaded areas represent maximum and minimum daily values of the variables over the 8-year period.

For example, no significant relationships were observed between NFFE and individual climate variables such as T_s and SWC, and there was limited value in using SWC to predict SR ($r^2 = 0.18$). However, the interaction of the two variables, using the multiplication of T_s by SWC, increased the predictive ability significantly to 60% for NFFE and 69% for SR. The inter-annual trends in GFFP were somewhat explained by T_a ($r^2 = 0.27$), but a much higher proportion of the variance in GFFP was explained by SWC ($r^2 = 0.70$). Using the multiplication of the T_a by SWC increased the predictive ability of the model to 85% for GFFP.

A few studies have shown the importance of timing of climate events in determining the inter-annual variability of respiration and photosynthesis in forest ecosystems (McMillan et al., 2008; Phillips et al., 2010; Savage and Davidson, 2001). For example, Black et al. (2000) clearly demonstrated that warm spring conditions had the potential to increase significantly the carbon sequestration potential of a boreal aspen forest, while Piao et al. (2008) and Wu et al. (2013) showed that extended warmer fall conditions were critical in increasing respiration losses from various forest ecosystems. In this study, when contrasting data between years, important trends emerged in response to the intra-annual variability in temperature (T_s or T_a) and SWC conditions, i.e. the timing of climate events within a year and how they influenced NFEE, SR and GFFP (Fig. 9). For example, 2006 and 2009 were contrasting years in terms of T_s (early vs late spring), but were similar years in terms of SWC (except in early spring when it increased slightly earlier in 2009 than 2006 and for July-August when SWC was higher in 2009). The earlier and faster increase in spring T_s led to higher NFFE, SR and GFFP in 2006. The early melt also potentially facilitated water availability in the spring and affected the component fluxes, especially GFFP. The earlier cooling during fall had an opposite effect on all component fluxes (i.e., 2006 values were lower) although the effect was smaller. Overall, annual NFFE in 2009 was slightly greater than in 2006, mainly because GFFP was significantly lower in 2009. When comparing 2003 and 2004, very similar years in terms of $T_{\rm s}$ (both late springs), but very contrasting years in terms of SWC, a strong drying of the organic horizon during the growing season of 2003 had no effect on NFFE and SR, although GFFP appeared to be stimulated. The response of GFFP in 2003 was unexpected as small increases in GFFP were observed during the growing season following rain events, as discussed previously. Annual NFFE for these two years was similar event though the climate conditions, especially SWC were quite different. Finally, a comparison between 2005 and 2007, very similar years both in terms of T_s and SWC, showed that these climate conditions were optimal to provide the maximum NFFE observed over the 8-year record. These two years were characterized by high spring T_s and snowmelt and average fall conditions in terms of T_s. Strong rewetting events in 2005 had a positive influence on NFFE and SR during the late summer.

4. Conclusions

This relatively long-term study, which included 8 years of automated chamber measurements of NFFE, has provided new insights regarding the climatic controls on boreal forest-floor carbon dynamics. The major conclusions are:

1. Feather moss was the dominant forest-floor community in a mature boreal black spruce stand. The contribution of scaled-up NFFE, SR and GFFP was far greater for that community (>85% for NFFE and SR, and >70% for GFFP) than for the sphagnum and lichen communities. Hollows with exposed mineral soil contributed less than 1% to all component fluxes. GFFP during the growing season reduced annual losses due to SR by 18%.

- 2. Seasonal trends in NFFE, SR and GFFP were mainly determined by variations in temperature (T_s or T_a). SWC had competing effects on NFFE at that time scale. Reductions of SWC in the organic and mineral horizons decreased and increased NFFE, respectively, likely mediated through decomposer activity. Plant water status seemed to have played a minor role on GFFP at the seasonal scale, with small increases in photosynthetic activity during rewetting periods.
- 3. The mean annual values of the climate variables (T_s , T_a and SWC) were poor predictors of annual totals of NFFE, SR and GFFP when considered individually. However, accounting for the interaction of these variables by using the product of T_s (or T_a) and SWC significantly increased the predictive ability of the models, highlighting the importance of considering interacting effects of driver-variables in models of ecosystem fluxes.
- 4. The inter-annual trends in NFFE, SR and GFFP depended strongly on the timing of climatic events during each year, spring and summer conditions having a more pronounced impact than fall conditions.

The results of this study, most importantly the different levels of correlation between climate variables and NFFE, SR and GFFP at the seasonal and inter-annual time scales, pose some interesting challenges for interpreting, and also modeling, the complexity of the processes related to carbon dynamics in forest ecosystems. It appears that empirical relationships derived at finer temporal scales, i.e. diurnally (as presented in Gaumont-Guay et al., 2009 in the same stand) or seasonally, are not necessarily representative of processes at longer time scales, i.e. inter-annually, and vice versa. Ultimately, the inter-annual variability in carbon dynamics is dictated by the sum of the processes occurring at finer temporal scales, i.e. within days, weeks and seasons, and how they accumulate over time. As discussed above, the discrepancy between the two time scales used could also have originated from the timing of climatic events within each year and its impact on the component fluxes in this study. Finally, it could also have originated from the amount of data available at each time scale to analyze the temporal trends. For example, hundreds of data points were available to analyze the seasonal trends within each year, whereas only eight data points were available to analyze the inter-annual trends. One could argue that, in order to reconcile the different time scales, measurements should be extended for another decade to increase the statistical power of the long-term analysis and explore alternative explanatory and driver variables and/or their interactions to help identify those that are suitable for characterizing variables at these longer time scales.

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