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



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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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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.

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