

Landscape heterogeneity, soil climate, and carbon exchange in a boreal black spruce forest

ALLISON L. DUNN,^{1,2,4} STEVEN C. WOFSY,² AND ALFRAM V. H. BRIGHT³

¹Department of Soil Science, University of Manitoba, 362 Ellis Building, Winnipeg, Manitoba R3T 2N2 Canada

²Department of Earth and Planetary Sciences, Harvard University, 20 Oxford Street, Cambridge, Massachusetts 02138 USA

³School of Engineering, Tufts University, 200 College Avenue, Medford, Massachusetts 02155 USA

Abstract. We measured soil climate and the turbulent fluxes of CO₂, H₂O, heat, and momentum on short towers (2 m) in a 160-yr-old boreal black spruce forest in Manitoba, Canada. Two distinct land cover types were studied: a *Sphagnum*-dominated wetland, and a feathermoss (*Pleurozium* and *Hylocomium*)-dominated upland, both lying within the footprint of a 30-m tower, which has measured whole-forest carbon exchange since 1994. Peak summertime uptake of CO₂ was higher in the wetland than for the forest as a whole due to the influence of deciduous shrubs. Soil respiration rates in the wetland were approximately three times larger than in upland soils, and 30% greater than the mean of the whole forest, reflecting decomposition of soil organic matter. Soil respiration rates in the wetland were regulated by soil temperature, which was in turn influenced by water table depth through effects on soil heat capacity and conductivity. Warmer soil temperatures and deeper water tables favored increased heterotrophic respiration. Wetland drainage was limited by frost during the first half of the growing season, leading to high, perched water tables, cool soil temperatures, and much lower respiration rates than observed later in the growing season. Whole-forest evapotranspiration increased as water tables dropped, suggesting that photosynthesis in this forest was rarely subject to water stress. Our data indicate positive feedback between soil temperature, seasonal thawing, heterotrophic respiration, and evapotranspiration. As a result, climate warming could cause covariant changes in soil temperature and water table depths that may stimulate photosynthesis and strongly promote efflux of CO₂ from peat soils in boreal wetlands.

Key words: black spruce boreal forest; decomposition; evapotranspiration; global change; interannual variability; modified Bowen ratio method; peatland; photosynthesis; *Picea mariana*; soil hydrology and carbon exchange; wetland.

INTRODUCTION

Boreal forests represent 22% of global forest area, covering $\sim 11 \times 10^6$ km² and accounting for more than half of North American forests (Iremonger et al. 1997, Schlesinger 1997). The amount of aboveground biomass in boreal forests is small (13% of global biomass carbon), but the associated peat-rich soils hold nearly half of global soil carbon stores, mostly deposited since the last deglaciation (~ 450 Pg, equivalent to 200 ppm atmospheric CO₂; Gorham 1991, Schlesinger 1997). Climate has warmed in the boreal forest in the past century, and precipitation has increased (Myneni et al. 1997, Keyser et al. 2000, Zhang et al. 2000, Stone et al. 2002). The IPCC Fourth Assessment Report (2007) predicted that the greatest temperature increases over the 21st century will be in the high northern latitudes. The future stability

of boreal forests and peatlands and their large reservoirs of organic carbon under changing hydrological and temperature regimes is unknown. Myneni et al. (1997) suggested that primary production may increase in response to a warmer climate. However, some boreal species are ill-adapted to warmer climates and may be subject to growth declines (Barber et al. 2000, D'Arrigo et al. 2004, Wilmking et al. 2004) and to more insect outbreaks and wildfire (Flannigan et al. 2005), as occurred during the warm 1980s (Stocks et al. 2002).

The boreal landscape is heterogeneous, with varying stand ages and land cover types, complicating attempts to predict the response of the biome to changing climate. Previous studies have shown that these forests can serve as a sink for atmospheric carbon dioxide (Black et al. 2000, Suni et al. 2003) or as a source (Milyukova et al. 2002, Dunn et al. 2007). Fire is an important process in the boreal forest, and generates a mosaic of stand ages and species that alters local carbon trajectories in space and time (Litvak et al. 2003, Goulden et al. 2006). Topography-driven variations in land cover type within a single-aged stand are also common (Harden et al. 1997), but the impact of these variations on ecosystem processes is difficult to resolve with whole-forest carbon

Manuscript received 10 May 2007; revised 15 January 2008; accepted 18 April 2008; final version received 8 July 2008. Corresponding Editor: H. P. Schmid.

⁴Present address: Department of Physical and Earth Sciences, Worcester State College, 486 Chandler Street, Worcester, Massachusetts 01602 USA.
E-mail: adunn@worcester.edu

flux measurements. As a result, it has been difficult to make assessments regarding the strength of the biome as a source or a sink for atmospheric CO₂ due to the high degree of landscape heterogeneity present on a variety of scales (Black et al. 2004).

In this paper, we present the results from a study seeking to quantify the effects of small-scale landscape heterogeneity on ecosystem processes within a single-aged boreal forest stand. This study was conducted at the Northern Old Black Spruce (NOBS) tower flux site, where whole-forest carbon flux data have been collected since 1994 (Dunn et al. 2007). In this study, we installed short flux towers (2 m) within the footprint of the preexisting NOBS tower. These towers were located in two common boreal land cover types that had very different vegetation, drainage, and soil carbon profiles. We conducted intensive, automated monitoring programs of soil climate and CO₂ fluxes in these two land cover types. We developed a modified Bowen ratio technique for measuring fluxes of carbon, water, and heat in areas close to the ground, where traditional flux measurements were impractical. These data provided valuable insight into how two major land cover types of the boreal forest landscape respond to climate and shape the whole-forest pattern of carbon exchange observed at the preexisting NOBS tower.

METHODS

Site selection

The Northern Old Black Spruce (NOBS) tower is located at 55.88° N, 98.48° W, in central Manitoba, Canada, and is situated on the low-relief terrain of the Canadian Shield, near the northern limit of the continuous boreal forest (Trumbore and Harden 1997). The site is 40 km from the nearest town (Thompson), 4 km south of the closest road (Provincial Highway 391), and is accessible only by foot, all-terrain vehicle, or snowmobile. An Environmental Monitoring System (EMS) tower was installed in 1994 as part of NASA's Boreal Ecosystem-Atmosphere Study (BOREAS), an international field experiment examining atmosphere-biosphere interactions in the Canadian boreal forest (Sellers et al. 1995). The EMS tower measures continuous fluxes of carbon dioxide, water vapor, heat, and momentum at a height of 30 m, in addition to a suite of meteorological observations (see Goulden et al. [1997] and Dunn et al. [2007] for more details).

The area surrounding the NOBS EMS tower is quite heterogeneous (Dunn et al. 2007: Plate 1), comprising a continuum of drainage classes (from moderately well drained to very poorly drained; Harden et al. 1997) and soil carbon profiles. The soils at this site developed atop the relatively impermeable clay/silt sediments of glacial Lake Agassiz in the 8000 years following deglaciation and lake retreat (Trumbore and Harden 1997; H. Veldhuis, R. G. Eilers, and G. F. Mills, *unpublished manuscript*). The area within a 500-m radius of the tower is ~25% well drained, 50% imperfectly to poorly

drained, and 25% very poorly drained (Harden et al. 1997). The well-drained areas are covered by feathermoss with ~160-yr-old, 10-m-tall black spruce trees (*Picea mariana* (Mill.); Gower et al. 1997). The imperfectly to poorly drained areas are covered with feathermoss and *Sphagnum* spp., and have chlorotic, 1–6 m-tall black spruce trees. *Sphagnum* and brown mosses cover the very poorly drained areas.

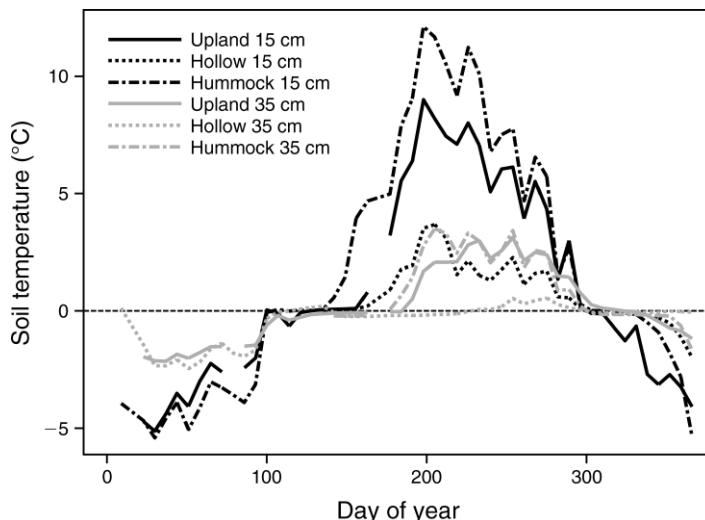
We selected two sites for intensive study of the link between soil hydrology and carbon exchange. The “dry” site was located in a moderately well-drained upland 22 m to the south of the EMS tower (Dunn et al. 2007: Location D; see Plate 1), with a closed canopy of dense, 10-m-tall black spruce trees and a ground cover of feathermosses (*Pleurozium* and *Hylocomium*). Soil carbon stocks at the dry site were modest, 4 kg C/m² (Trumbore and Harden 1997). The “wet” site was located in a poorly drained wetland 130 m to the east-northeast of the EMS tower (Dunn et al. 2007: Location C; see Plate 1), characterized by *Sphagnum* hummocks, chlorotic black spruce, and tamarack (*Larix laricina* (Du Roi) K. Koch). Large amounts of soil organic carbon cover the wet site, ~28 kg C/m² (Trumbore and Harden 1997). The wet site had small-scale microtopography, with *Sphagnum* hummocks and hollows comprised of a mix of *Sphagnum* and feathermosses. Soil organic layers were up to 100 cm thick in the tallest hummocks.

Instrumentation and analysis

Site installation commenced in September 2001 with a suite of instrumentation to measure soil climate. Thermistors for soil temperature were emplaced at multiple depths at two locations at each site. Time domain reflectometry probes for soil moisture were installed at the same locations, at four different depths. Soil heat flux plates were installed at 12 cm in depth at two locations in each site. In the dry site, these measurements were made at two similar locations ~2 m apart. At the wet site, one set of measurements was made in a *Sphagnum* hummock and the other set in an adjacent hollow, with a height difference of 21 cm between the two. An ultrasonic distance detector mounted above a well 10 cm in diameter was installed near the soil climate profiles to measure the height of the water table. Automated measurements began on 21 September 2001, and have continued to the present.

Two 2-m-tall towers were installed during early 2003, one at the wet site and one at the dry site. A sonic anemometer was mounted at 2 m on the tower to measure the three-dimensional components of wind velocity and sonic temperature (derived from the speed of sound and very close to virtual temperature). Air temperature, CO₂ concentration, and H₂O concentration were measured at heights of 0.5 and 2 m. The turbulent transfer coefficient *k* was determined based on the measured sensible heat flux at 2 m and the temperature gradient between 0.5 and 2 m. The turbulent fluxes of CO₂ and H₂O were then calculated

FIG. 1. Soil temperature during 2004 in three boreal land cover types: upland (well-drained soils, dense closed-canopy forest), hollow (microtopographic low point in a poorly drained wetland), and hummock (microtopographic high point in a poorly drained wetland).



using k and the gradient of CO_2 and H_2O between 0.5 and 2 m, following the modified Bowen ratio method (Meyers et al. 1996, Liu and Foken 2001). The flux and associated measurements on the towers began on 17 April 2003, and continued through fall 2006. A detailed description of instrumentation and analysis, as well as the names and addresses of the sources for the equipment, can be found in the Appendix.

RESULTS

Heterogeneity in soil temperatures, interannual variability, and heat fluxes

The seasonal pattern of soil temperature was driven by air temperature. Deeper depths exhibited lagged responses to the seasonal forcing as soil thaw propagated downward from the surface. The seasonal cycle of soil temperature differed between the hummock and hollow at the wet site and the dry site (Fig. 1), although notably all were fixed at $\sim 0^\circ\text{C}$ for long periods in spring

and early summer. Soil temperatures at a given depth were warmest in the hummock and coolest in the hollow, with the upland soil temperatures falling in between the two. It is not surprising that temperatures in the hollow lagged other locales, as these microtopographic lows are close to the water table and high soil moisture levels lead to increased soil heat capacity, as well as high conductance to colder layers below. Wintertime soil temperatures were -3°C to -5°C , much warmer than air temperature, which averaged -18.4°C from January through March. There was pronounced interannual variability in soil temperature at the wet site (Fig. 2). While 2002 and 2003 had mean annual air temperatures of -1.3°C and -1.8°C , respectively, 2004 was cooler with a mean temperature of -2.4°C . These small shifts in air temperature impacted the soils, with summer 2004 soil temperatures being cooler than 2002 and 2003 by more than 2.5°C . There was much less interannual variability in soil temperatures at the dry site, where deep soil temperatures varied by a degree or less.

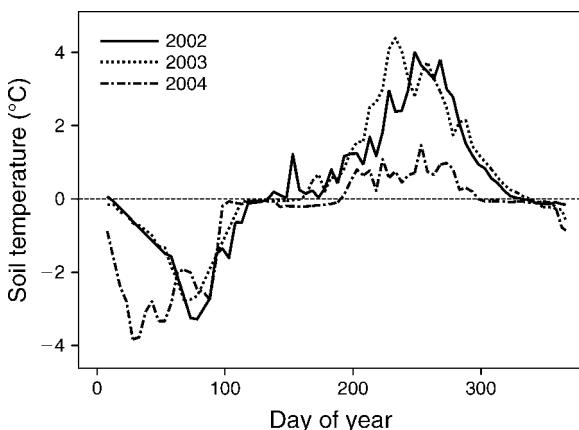


FIG. 2. Interannual variability in soil temperature in a microtopographic hollow at the wet site during the three years of this study.

Soil heat fluxes were an important component of the overall energy balance of the ecosystem, providing long-term sources or sinks for heat (Fig. 3). Both the wet and dry sites absorbed heat through the warm months (mid-May through mid-October), and lost heat through the long boreal winter. The wet site was a larger sink for heat in the summertime, with a peak absorption of 8 W/m^2 , compared to 6 W/m^2 in the dry site. The likely reason for this difference was the higher heat capacity of moist soils in the wet site, which allowed absorption of more energy through the growing season than was observed at the dry site. Wintertime differences in soil heat fluxes between the sites were small.

Water table and soil moisture

The time series of water table depths is shown in Fig. 4. Spring thaw periods were characterized by a slow, fairly steady drawing down of the water table, which remained perched above the frost line as it receded

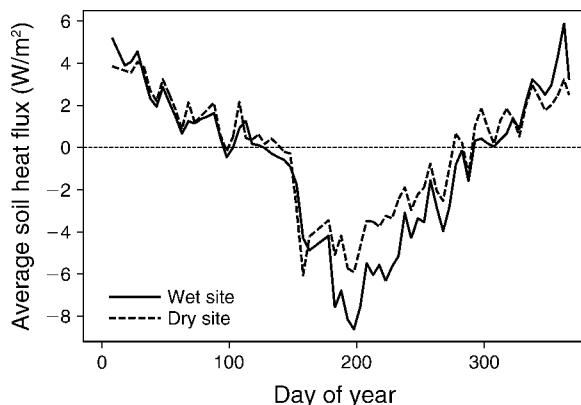


FIG. 3. Soil heat flux at wet and dry sites during 2004.

deeper into the soil. This is the reason why soil temperatures remain fixed at $\sim 0^{\circ}\text{C}$ for long periods in the spring. At the dry site, the water table depth dropped below the depth of the well (30 cm) and into the deeper clay layers by June of each year. At the wet site, however, the water table was always detectable in the 35-cm well, generally fluctuating between 20 cm and 30 cm from the surface. Water tables in the wet site responded strongly to precipitation events, rising as much as 10 cm in response to large rainstorms, most likely reflecting both local rainfall and drainage from upland areas. In the midsummer, the water table slowly dropped following each rainfall, reflecting evapotranspiration demands and slow runoff at this site (H. Veldhuis, *personal communication*). By September and October, the water table began to stabilize, with relatively little drawdown following rainfall events.

The early and midsummer patterns of water table depths in the wetland were coupled to snowmelt and soil thaw, and there was a strong correlation between soil temperature and water table depth. The connection between soil thaw and water table depths is illustrated in Fig. 5, which shows soil temperatures and water table depth in the hollow at the wet site. The vertical lines identify the timing of persistent (as opposed to short-lived) thaw ($T > 0.5^{\circ}\text{C}$) at depths of 5, 10, and 25 cm. The timing of thaw at a given depth and the descent of the water table were coupled, with the water table descending below a given depth only after thaw at that depth was complete. The timing of thaw in the soil column therefore represented an important control on early season water table depth. Until thaw was complete, water table depths did not reflect the free water table, but instead were perched at the depth of the impermeable frost line. This caused the May–June water table depths to exhibit a slow, steady drop (Figs. 4 and 5), tracking the descent of the frost line.

Water table and evapotranspiration

We observed diurnal fluctuations in water table depth on the order of 1–2 cm during the growing season that

were not present during the dormant season at the wet site. The highest water tables were observed just prior to dawn, and the lowest water tables occurred just before sunset. We tested the hypothesis that these fluctuations were driven by evapotranspiration (ET) demands by extracting the amplitude of the diurnal cycle from the half-hourly data. We found that daily rates of whole-forest ET, as measured from the EMS tower, accounted for 30% of the variability in the amplitude of the water table depth ($P < 0.001$). This suggests that the daytime depression of water table depth during the growing season reflected changes in pore pressures due to transpiration demands from the forest and evaporative demands from the atmosphere, wherein the peat acted like a sponge in response to changing internal pressures.

We tested to see if daily ET, as measured by the EMS tower, was affected by water table depths at our site. We saw no evidence of suppression of ET under deep (>30 cm) water table conditions; instead, ET increased with increasing water table depths. As the deepest water tables were found in mid to late summer, when both the conifers and deciduous understory are photosynthesizing, this increase in ET with water table depth was likely due to transpiration rather than evaporation. The absence of ET suppression during times of deep water tables suggests that photosynthesis at the NOBS tower flux site as a whole is not water limited, as ET was largest at times of lowest water availability.

Carbon fluxes at two meters

The seasonal cycle of carbon exchange near the ground was markedly different at the wet and dry sites, and both differed from the fluxes observed atop the 30-m EMS tower (Fig. 6). The 2-m tower at the wet site was

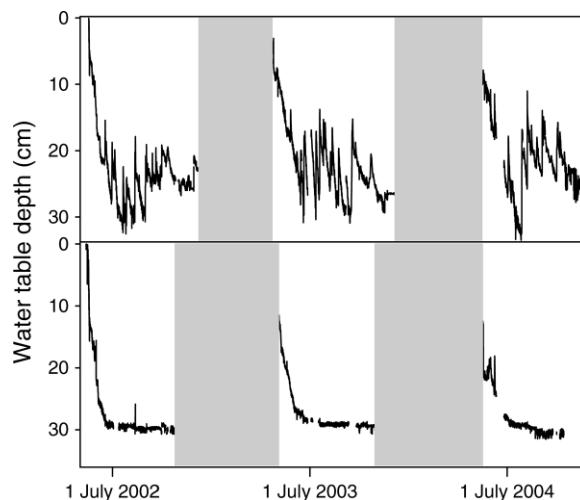
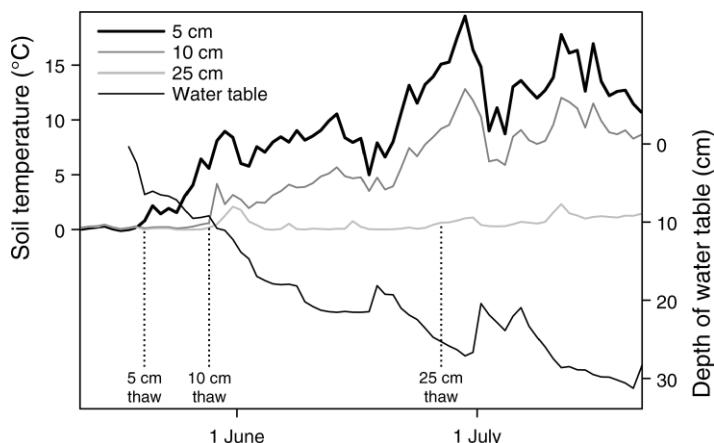


FIG. 4. Water table depth at wet and dry sites. Note the rapid fall of the water table in spring at the dry site contrasted with frequent summer rises and falls at the wet site. Shaded regions represent periods when measurements were absent because ice was present in the well or a sensor failed due to cold temperatures.

FIG. 5. Depth to water table and soil temperature at the wet site in a microtopographic hollow. The water table fell to deeper depths as springtime thaw proceeded. Note the close correspondence of timing of sustained thaw at each depth with descent of water table below that depth.



higher than the canopy of shrubs and mosses, although below the tops of the sparse trees at the site. The tower was situated well above the hummocks and hollows, and measured fluxes therefore represented an integration of the microtopography at the site. All three sites showed the forest to be a source of carbon before the start of the growing season and from October onwards. In 2004, strong negative fluxes (indicating carbon uptake) were first observed at the EMS tower in mid to late May (Fig. 6). This reflected the relatively cool spring experienced in the region, with mean April and May temperatures of -3.7°C and 2.0°C , much cooler than the long-term average of -2.2°C and 6.5°C , respectively. Uptake of CO_2 in the wet site began in June, later than in the forest as a whole (Figs. 6 and 7). Daily maximum uptake was low, the most negative fluxes being $-2 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (the EMS tower, in contrast, showed uptake of over $-5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ at the same time). However, in July and August, peak uptake of CO_2 at the wet site increased markedly to $-10 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, larger than the maximum observed by the EMS tower in any month (Fig. 7). In September, rates of daytime uptake at both the wet site and EMS tower began to decline in advance of the long dormant season. The dry site was a net source of carbon at 2 m (below the thick spruce canopy) all year long, peaking in late July and early August.

Respiration losses at each of the sites and at the EMS tower were estimated using nighttime CO_2 fluxes for well-mixed atmospheric conditions (friction velocity, $u^* > 0.2 \text{ m/s}^2$; representing 62% of valid nighttime measurements). There were significant ($P = 0.05$) differences in respiration rates between the wet and dry sites (Table 1, Fig. 8). During the dormant winter period (November–April), observed respiration at the EMS tower and wet site were similar, whereas the dry site had much smaller respiration losses, likely due to its understory location, which excluded respiration by the forest overstory (Ryan et al. [1997] found that the overstory represented 37% of total autotrophic respiration at this site). Respiration rates increased during spring, peaking at all sites during the month of August.

While EMS and wet site respiration rates were similar during the spring, respiration rates in the wet site exceeded those at the EMS tower from July through October.

Controls on respiration and the role of landscape heterogeneity

Previous studies (Goulden et al. 1998, Wang et al. 2003, Dunn et al. 2007) found that temperature and drainage were important controls on whole-forest respiration at this site. In this study, we observed that soil temperatures in the wetland were significantly and positively correlated with wetland respiration rates, and depth to water table was also a contributor. Soil temperatures at 15 cm in depth in the wetland explained most of the variance in the mean weekly growing season nighttime respiration ($r^2 = 0.33, P < 0.001$), and increased depths to water table slightly stimulated respiration ($r^2 = 0.08, P = 0.06$). Water table depths and soil temperature were positively correlated ($r^2 = 0.32, P < 0.001$), reflecting the effects of moisture on the heat capacity and conductivity of soils. Carbon efflux from the wetland was significantly correlated to whole-forest respiration rates, accounting for 78% of the variance in average monthly effluxes ($P = 0.0001$). Our

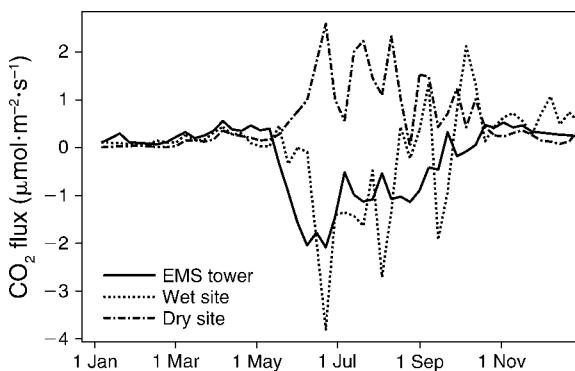


FIG. 6. Weekly average CO_2 flux during 2004 at the 30-m EMS tower and at the 2-m wet and dry sites.

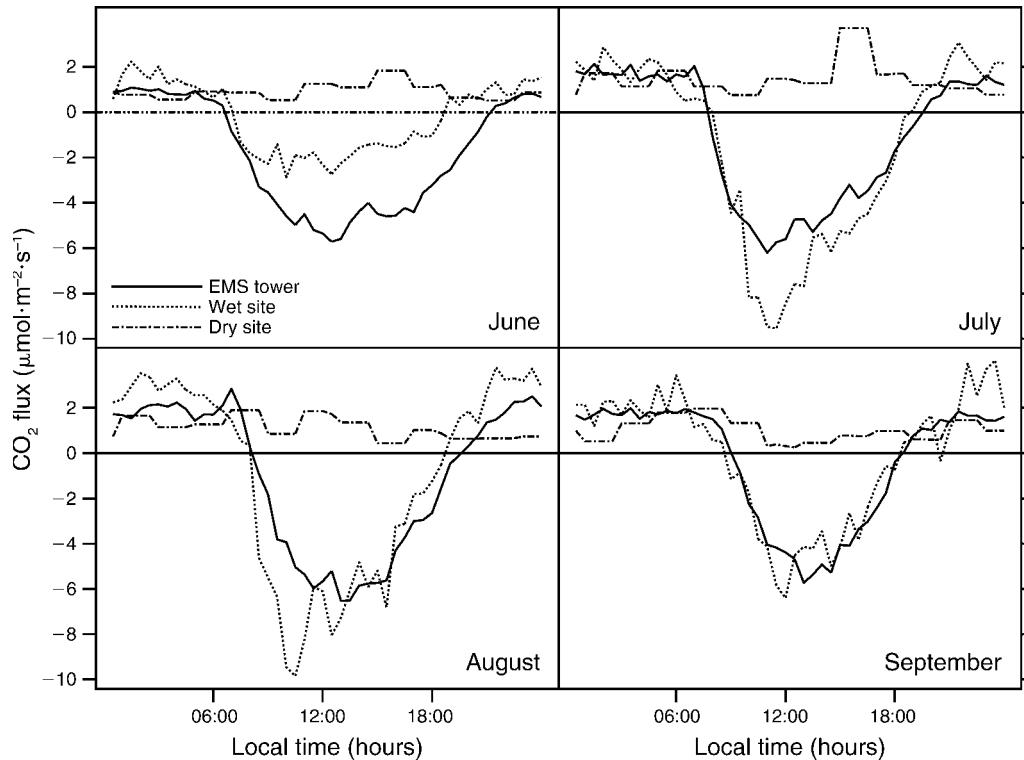


FIG. 7. Diurnal course of CO_2 exchange at wet and dry sites and at the EMS tower during the summer of 2004. Note the delayed onset of photosynthesis and elevated nighttime effluxes at the wet site.

results provide evidence that soil respiration in the wetland is driven by soil temperature and enhanced by lower water tables, exerting a strong control on whole-forest respiration rates.

DISCUSSION

Boreal forests are dynamic landscapes, continually changing in response to post-glacial drainage development, permafrost shifts, forest fire, and climate change. The boreal landscape is very heterogeneous, comprised of a mosaic of wetlands, coniferous forests, and deciduous forests, spanning a wide age structure (Steyaert et al. 1997). The area surrounding the

Northern Old Black Spruce (NOBS) Environmental Monitoring System (EMS) tower is no exception, with differences in drainage class creating a wide spectrum of land cover types in a relatively small area (Trumbore and Harden 1997). Our project sought to study the effects of this landscape heterogeneity on soils and carbon exchange in order to better understand the components of the ecosystem-scale fluxes in this landscape. We found that the site heterogeneity led to marked differences in soil climate and carbon exchange. Below we discuss the observed coupling between soil

TABLE 1. Average monthly nighttime CO_2 effluxes, 2003–2004, from the wet site, the dry site, and the Environmental Monitoring System (EMS) tower.

Time period	Monthly effluxes ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)			Wet site efflux as a portion of whole forest (%)
	Wet site	Dry site	EMS tower	
Winter†	0.34	0.12	0.38	90
May	1.20	0.25	0.96	124
June	1.92	0.68	1.93	99
July	3.82	1.26	3.14	123
August	5.67	1.60	3.60	157
September	3.59	1.15	2.24	160
October	1.60	0.43	1.12	143
Annual	1.65	0.51	1.27	130

† November–April.

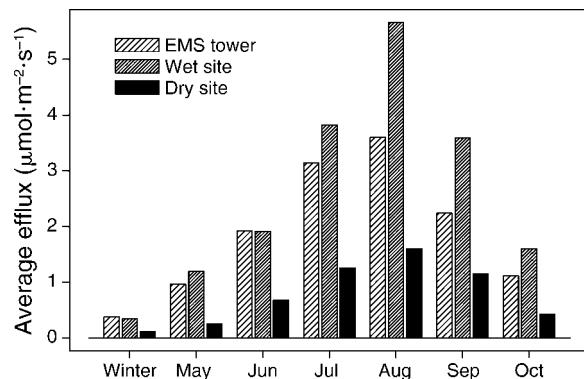


FIG. 8. Average monthly nighttime CO_2 efflux (respiration) at each of three sites. Data presented are averages for the calendar years 2003 and 2004.

thaw, soil drainage, and water table depth, and the implications for carbon exchange. We show how the unique patterns of carbon exchange observed at the 2-m towers help resolve the elements contributing to seasonality in carbon exchange observed at the ecosystem scale by the EMS tower. We then use whole-forest evapotranspiration rates and water table depths to show that photosynthesis in the NOBS area is likely not water limited.

Soil thermal regime, thaw, and drainage

Soil drainage and associated moisture levels had a strong impact on soil thermal characteristics. The high heat capacity of water muted the seasonal cycle of soil temperature at the hollow in the wet site, keeping soils warmer in the winter and cooler in the summer than drier soils (Fig. 1). This higher heat capacity of wet soils also affected the observed soil heat flux (Fig. 3). The wet site was a greater sink for energy during the growing season, absorbing 66 MW/m² of energy during 2004 compared to 44 MW/m² by the dry site. Frost persisted well into the growing season despite the wetland absorbing 50% more heat than the dry site. The interannual variability in soil temperatures (Fig. 2) in the carbon-rich wet site potentially represents an important control on the total heterotrophic respiration of soil organic matter in the wetland portions of this forest.

Water table depths in the wet site were strongly affected by soil thaw (Fig. 5) and the overall water balance of the area. We found that drainage of snowmelt and spring rains were impeded by the presence of a soil frost line, leading to a perched water table. This perched water table, in turn, increased the heat capacity of the soils in the wet site relative to the soils in the dry site. The water perched above the frost line was in thermal contact with the frozen layer, and was maintained at a temperature of ~0°C, helping soil frost to persist later in the growing season than it would in drier soils. This close coupling of the soil thermal and hydrological regimes had important implications for the seasonal course of carbon exchange, and for annual respiration totals. The perching of the springtime water tables inhibited heterotrophic respiration of organic matter by inducing anoxia and keeping soil temperatures low. This mechanism explains the seasonal pattern of respiration, which lags photosynthesis at this site (Dunn et al. 2007).

Controls on carbon exchange

The seasonal cycle of carbon exchange at the wet and dry sites was quite different from that observed by the NOBS EMS tower (Figs. 6 and 7). The onset of the growing season (defined as the first day with uptake rates equal to 10% of the seasonal maximum uptake) was earlier at the EMS tower than at the wet site. In 2003, the wet site onset lagged the EMS tower by 30 days, and in 2004 by 38 days. After the initial lag, however, rates of uptake increased rapidly (became

more negative) at the wet site, and were larger than at the EMS during the months of July and August (Fig. 7). Goulet and Crill (1997) measured CO₂ exchange at the moss surface at this location during late summer and found that *Sphagnum* photosynthesis ranged from 0.5 to 2.5 μmol·m⁻²·s⁻¹. This suggests that while bryophytes were an important component of forest-floor photosynthesis at the wet site, they only accounted for a portion of peak summer CO₂ exchange, which reached nearly 10 μmol·m⁻²·s⁻¹. The presence of deciduous shrubs at the wet site and the observed lag in uptake suggests that the intense fluxes in the growing season were dominated by the deciduous components of the footprint of the 2-m tower, whereas the more modest fluxes in early summer, prior to leaf-out, reflected the influence of bryophytes. These observations are in line with those of Kolari et al. (2006), who observed much higher photosynthesis rates by dwarf shrubs than bryophytes in a boreal Scots pine stand. These results therefore suggest that much of the early season EMS flux is derived from the black spruce and mosses in the tower footprint, which begin photosynthesis in early spring (Dunn et al. 2007).

The deciduous “pulse” of uptake in July and August observed at the wet site provides an explanation for the shape of the annual photosynthesis curve at the EMS site (Dunn et al. 2007; Fig. 2). The average seasonal course of photosynthesis began to increase in May, leveled off briefly, and then peaked during the months of July and August. Midsummer peak uptake rates of CO₂ represented an increase of about 25% from the rates in May–June. Our data indicate that this feature was most likely due to contributions from the deciduous understory components of the tower footprint, which have a short but intense growing season that peaks in July and August (Fig. 7). These findings are similar to those of Potter et al. (2001), who estimated that the production of the understory and ground cover accounted for 25% of the total net primary production at this site.

In contrast with the wet site and EMS towers, respiration exceeds photosynthesis at the dry site (below the tree canopy) all season long. Evidently uptake by feathermoss contributes little to the net flux when compared to respiration rates from the upland forest floor, associated with black spruce root respiration. These findings are in line with those of Goulet and Crill (1997), who found the gross photosynthesis of feathermosses at this site to be between 0.5 and 1.0 μmol·m⁻²·s⁻¹, and with those of Wang et al. (2003), who found maximum soil surface effluxes of ~3 μmol·m⁻²·s⁻¹ in the same upland stand.

The lag of respiration relative to photosynthesis at NOBS (Goulet et al. 1998, Dunn et al. 2007; Fig. 2) was directly caused by the slow process of soil thaw and drainage. This effect was seen in the diurnal data at all sites (Fig. 7), which show a steady increase in nighttime flux throughout the course of the summer. By mid to late summer, respiration rates were highest at the wet site and lowest at the dry site (Figs. 7 and 8). It is not



PLATE 1. (Left) Dry site in a moderately well drained upland with 10-m tall black spruce and a feathermoss ground cover, and (right) wet site located in a poorly drained wetland with chlorotic 1–6-m tall black spruce, tamarack, and *Sphagnum* ground cover. Photo credit: A. L. Dunn.

surprising that the wet site showed the largest nighttime effluxes, as the largest stores of soil organic carbon were located in its footprint. In addition, the soils at the wet site remained warm even after photosynthesis had ceased for the year, causing positive fluxes out of the wet soils from October through December (Fig. 6). These findings differ from those of Wang et al. (2003), who found little difference in soil surface CO_2 fluxes between well-drained and poorly drained soils in this area; however, the soil carbon profiles may have been different from those presented in this study.

Respiration rates at the EMS were between those observed at the wet and dry sites, representing an integration of the effluxes across the continuum of land cover types from wet to dry. The footprint of the tower was comprised of 25% well-drained soils and 75% imperfectly to very poorly drained soils (Harden et al. 1997), allowing construction of a simple respiration budget. Total respiration in the upland areas is $\sim 1117 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, based on Ryan et al. (1997), who found $611 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ autotrophic respiration in the well-drained stands of this site ($382 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ from the soils), and Bond-Lamberty et al. (2004), who found that autotrophic respiration accounted for an average of 43% of total soil respiration in boreal forests. In the poorly drained wet site, annual respiration averaged $624 \text{ g C}\cdot\text{m}^{-2}$ during the measurement years of 2003 and 2004. Extrapolating these rates (1117 and $624 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) for the well-drained and poorly drained portions of the EMS tower footprint (25% and 75%, respectively) gives a whole-forest respiration estimate of $747 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$. These data are an independent confirmation of the

average whole-forest respiration reported by Dunn et al. (2007) of $711 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$.

Wet site areas of the tower footprint are clearly a major contributor to whole-forest respiration rates (Table 1, Fig. 8). It appears that these wet site areas have the potential to be an even larger carbon source given favorable environmental conditions. Currently, water tables are high and soil temperatures are low for much of the summer, limiting the window of time when decomposition rates are high. Should climate change cause wet soils to warm more quickly, due to earlier seasonal decline of perched water tables or to decreased moisture availability, effluxes from these areas would be expected to increase, possibly substantially. We note in this context that the peat between 25 and 35 cm in depth appears to contribute most of the increase in CO_2 efflux in July and August, but peat in this area can reach up to 100 cm in depth. In addition, should seasonal thawing occur earlier, the peat would be vulnerable to combustion in forest fires for a longer interval.

Water table depths and evapotranspiration

The water table depth in the wet site exhibited a pronounced diurnal cycle during the growing season, similar to observations in other *Sphagnum* bogs (Kellner and Halldin 2002). The amplitude of these fluctuations was correlated with rates of whole-forest evapotranspiration observed from the NOBS tower, suggesting that the amplitude reflected daily evapotranspirative demand. Lafleur et al. (2005) found that in a shrub-covered bog in Ontario, evapotranspiration dropped when water tables fell below the rooting depth of the

vascular plants, indicating water stress. We found no evidence of reduced evapotranspiration corresponding to deep water tables at NOBS; instead, whole-forest evapotranspiration increased as water table depths dropped. This finding corroborates that of Ewers et al. (2005), who found that transpiration in mature upland black spruce forests did not saturate with increasing vapor pressure deficits, allowing these forests to continue assimilating carbon in the face of drought. This observation provides strong evidence that the forest as a whole at NOBS is not water limited. Indeed, the increased photosynthesis with water table depth suggests that the soils may be too wet during much of the summer for optimum photosynthesis. This is not surprising, given that the NOBS tower footprint includes wetlands with stunted, 1–6 m-tall spruce that are adversely affected by high water tables. Presumably, deeper water tables would enhance photosynthesis by these trees by making their local soil climate more similar to that of the taller, upland spruce. The lack of observable water stress corroborates the finding of Dunn et al. (2007), who found no enhancement of photosynthesis by precipitation in the 10-yr record of carbon exchange at NOBS. Lack of water limitation for photosynthesis was also observed at six nearby chronosequence sites, which experienced a decrease in photosynthesis associated with increased surface moisture (M. Goulden, *unpublished data*).

Conclusion

Landscape heterogeneity plays a critical role in how boreal forests respond to changes in climate. Our work shows that water, through its abundance and phase changes, has a profound impact on the seasonal cycle of soil thaw and soil drainage in a typical mature boreal forest, with important implications for both ecosystem photosynthesis and respiration. The IPCC Fourth Assessment Report (2007) suggests that high northern latitudes will experience an increase in precipitation in the future, possibly leading to higher water tables. In addition to inundating soils, higher water tables would increase soil heat capacity and mute the seasonal cycle of soil temperature, possibly protecting soil organic carbon against heterotrophic respiration. However, higher water tables may also inhibit photosynthesis by water-logging the soils, keeping evapotranspiration low, and limiting tree growth. If precipitation decreases or remains constant while temperature increases in the future, falling water tables may drain previously saturated portions of the soil column in carbon-rich wetland areas, allowing them to warm more rapidly, stimulating heterotrophic respiration and turning these wetlands into sources of atmospheric carbon. Effects of regionally lower water tables could be compounded by earlier descent of seasonally perched water tables. Drier, more deeply aerobic peat is subject both to increased rates of biological oxidation and to deeper losses due to combustion during fires. The possibility for positive

feedback between water balance, thaw rates, and evapotranspiration rates emerges from the measurements we have presented, and needs to be carefully considered in models of climate change coupled to the carbon and water cycles.

ACKNOWLEDGMENTS

This work was supported by the U.S. National Aeronautics and Space Administration (NAG5-11154, NAG5-7534, and NAG5-2253) and by a NASA Earth System Science Fellowship (R-ESSF/03-0000-0092 to A. Dunn). It was also supported by the Canadian Foundation for Climate and Atmospheric Sciences, NSERC, and BIOCAP Canada Foundation as part of the Fluxnet Canada Research Network, and through a NSERC Discovery Grant to Brian Amiro (University of Manitoba). We especially thank Brian Amiro, John Budney, Carol Barford, Mike Goulden, Lucy Hutyra, Takeshi Ise, Syd Jones, Hugo Veldhuis, and Leo Grenier. We also thank the two anonymous reviewers who provided invaluable assistance in improving this paper.

LITERATURE CITED

- Barber, V. A., G. P. Juday, and B. P. Finney. 2000. Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature* 405:668–673.
- Black, T. A., W. J. Chen, A. G. Barr, M. A. Arain, Z. Chen, Z. Nestic, E. H. Hogg, H. H. Neumann, and P. C. Yang. 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. *Geophysical Research Letters* 27:1271–1274.
- Black, T. A., D. Gaumont-Guay, R. S. Jassal, B. D. Amiro, P. G. Jarvis, A. L. Dunn, S. T. Gower, and F. M. Kelliher. 2004. Measurement of CO₂ exchange between boreal forest and the atmosphere. Carbon balance of forest biomes. Pages 151–186 in H. Griffiths and P. J. Jarvis, editors. *Garland Science/BIOS Scientific Publishers*, Abingdon, UK.
- Bond-Lamberty, B., C. Wang, and S. T. Gower. 2004. A global relationship between the heterotrophic and autotrophic components of soil respiration? *Global Change Biology* 10: 1756–1766.
- D'Arrigo, R. D., R. K. Kaufmann, N. Davi, G. C. Jacoby, C. Laskowski, R. B. Myneni, and P. Cherubini. 2004. Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. *Global Biogeochemical Cycles* 18 [doi: 10.1029/2004GB002249]
- Dunn, A. L., C. C. Barford, S. C. Wofsy, M. L. Goulden, and B. C. Daube. 2007. The long-term carbon balance of a boreal black spruce forest: means, responses to interannual variability, and long-term trends. *Global Change Biology* 13: 577–590.
- Ewers, B. E., S. T. Gower, B. Bond-Lamberty, and C. Wang. 2005. Effects of stand age and tree species composition on transpiration and canopy conductance of boreal forest stands. *Plant, Cell and Environment* 28:660–678.
- Flannigan, M. D., K. A. Logan, B. D. Amiro, W. R. Skinner, and B. J. Stocks. 2005. Future area burned in Canada. *Climatic Change* 72:1–16.
- Gorham, E. 1991. Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications* 1:182–195.
- Goulden, M. L., and P. M. Crill. 1997. Automated measurements of CO₂ exchange at the moss surface of a black spruce forest. *Tree Physiology* 17:537–542.
- Goulden, M. L., B. C. Daube, S.-M. Fan, D. J. Sutton, A. Bazzaz, J. W. Munger, and S. C. Wofsy. 1997. Physiological responses of a black spruce forest to weather. *Journal of Geophysical Research* 102:28987–28996.
- Goulden, M. L., G. C. Winston, A. M. S. McMillan, M. E. Litvak, E. L. Read, A. V. Rocha, and J. R. Elliot. 2006. An

- eddy covariance mesonet to measure the effect of forest age on land-atmosphere exchange. *Global Change Biology* 12: 2146–2162.
- Goulden, M. L., S. C. Wofsy, J. W. Harden, S. E. Trumbore, P. M. Crill, S. T. Gower, T. Fries, B. C. Daube, S.-M. Fan, D. J. Sutton, A. Bazzaz, and J. W. Munger. 1998. Sensitivity of boreal forest carbon balance to soil thaw. *Science* 279:214–217.
- Gower, S. T., J. G. Vogel, J. M. Norman, C. J. Kucharik, S. J. Steele, and T. K. Stow. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *Journal of Geophysical Research* 102:29029–29042.
- Harden, J. W., K. P. O'Neill, S. E. Trumbore, H. Veldhuis, and B. J. Stocks. 1997. Moss and soil contributions to the annual net carbon flux of a maturing boreal forest. *Journal of Geophysical Research* 102:28805–28816.
- IPCC. 2007. *Climate Change 2007: the physical science basis. Contribution of Working Group I to the fourth assessment report of the intergovernmental panel on climate change.* Cambridge University Press, New York, New York, USA.
- Iremonger, S., C. Ravilious, and T. Quinton, editors. 1997. *A global overview of forest conservation—including: GIS files of forests and protected areas. Version 2. CD-ROM.* World Conservation Monitoring Centre (WCMC) and Centre for International Forest Research (CIFOR), Cambridge, UK.
- Kellner, E., and S. Halldin. 2002. Water budget and surface-layer water storage in a *Sphagnum* bog in central Sweden. *Hydrological Processes* 16:87–103.
- Keyser, A. R., J. S. Kimball, R. R. Nemani, and S. W. Running. 2000. Simulating the effects of climate change on the carbon balance of North American high-latitude forests. *Global Change Biology* 6(Supplement 1):185–195.
- Kolari, P., J. Pumpanen, L. Kulmala, H. Ilvesniemi, E. Nikinmaa, T. Grönholm, and P. Hari. 2006. Forest floor vegetation plays an important role in photosynthetic production of boreal forests. *Forest Ecology and Management* 221:241–248.
- Lafleur, P. M., R. A. Hember, S. W. Admiral, and N. T. Roulet. 2005. Annual and seasonal variability in evapotranspiration and water table at a shrub-covered bog in southern Ontario, Canada. *Hydrological Processes* 19:3533–3550.
- Litvak, M. E., S. Miller, S. C. Wofsy, and M. L. Goulden. 2003. Effect of stand age on whole ecosystem CO₂ exchange. *Journal of Geophysical Research* 108:8225.
- Liu, H., and T. Foken. 2001. A modified Bowen ratio method to determine sensible and latent heat fluxes. *Meteorologische Zeitschrift* 10:71–80.
- Meyers, T. P., M. E. Hall, S. E. Lindberg, and K. Kim. 1996. Use of the modified Bowen-ratio technique to measure fluxes of trace gases. *Atmospheric Environment* 30:3321–3329.
- Milyukova, I., O. Kolle, A. Varlagin, N. N. Vygodskaya, E.-D. Schulze, and J. Lloyd. 2002. Carbon balance of a southern taiga spruce stand in European Russia. *Tellus* 54B:429–442.
- Myneni, R. B., C. D. Keeling, C. J. Tucker, G. Asrar, and R. R. Nemani. 1997. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386:698–702.
- Potter, C. S., J. L. Bubier, P. M. Crill, and P. M. Lafleur. 2001. Ecosystem modeling of methane and carbon dioxide fluxes for boreal forest sites. *Canadian Journal of Forest Research* 31:208–223.
- Ryan, M. G., M. B. Lavigne, and S. T. Gower. 1997. Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *Journal of Geophysical Research* 102:28871–28883.
- Schlesinger, W. H. 1997. *Biogeochemistry: an analysis of global change.* Second edition. Academic Press, San Diego, California, USA.
- Sellers, P., et al. 1995. The boreal ecosystem-atmosphere study (BOREAS): an overview and early results from the 1994 field year. *Bulletin of the American Meteorological Society* 76: 1549–1577.
- Steyaert, L. T., F. G. Hall, and T. E. Loveland. 1997. Land cover mapping, fire regeneration, and scaling studies in the Canadian boreal forest with 1 km AVHRR and Landsat TM data. *Journal of Geophysical Research* 102:29581–29598.
- Stocks, B. J., J. A. Mason, J. B. Todd, E. M. Bosch, B. M. Wotton, B. D. Amiro, M. D. Flannigan, K. G. Hirsch, K. A. Logan, D. L. Martell, and W. R. Skinner. 2002. Large forest fires in Canada, 1959–1997. *Journal of Geophysical Research* 108. [doi: 10.1029/2001JD000484]
- Stone, R. S., E. G. Dutton, M. Harris, and D. Longnecker. 2002. Earlier spring snowmelt in northern Alaska as an indicator of climate change. *Journal of Geophysical Research* 107. [doi: 10.1029/2000JD000286]
- Suni, T., F. Berninger, T. Markkanen, P. Keronen, Ü. Rannik, and T. Vesala. 2003. Interannual variability and timing of growing-season CO₂ exchange in a boreal forest. *Journal of Geophysical Research* 108:4265. [doi: 10.1029/2002JD002381]
- Trumbore, S. E., and J. W. Harden. 1997. Accumulation and turnover of carbon in organic and mineral soils of the BOREAS northern study area. *Journal of Geophysical Research* 102:28817–28830.
- Wang, C., B. Bond-Lamberty, and S. T. Gower. 2003. Soil surface CO₂ flux in a boreal black spruce fire chronosequence. *Journal of Geophysical Research* 107:8224. [doi: 10.1029/2001JD000861]
- Wilmking, M., G. P. Juday, V. A. Barber, and H. J. Zald. 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology* 10:1724–1736.
- Zhang, X., L. A. Vincent, W. D. Hogg, and A. Niitsoo. 2000. Temperature and precipitation trends in Canada during the 20th century. *Atmosphere and Ocean* 38:395–429.

APPENDIX

Additional description of methods including belowground and aboveground instrumentation, analysis, and post-processing analyses (*Ecological Archives* A019-021-A1).

SUPPLEMENT

Data set containing soil climate and carbon flux data for years 2001–2005 at Northern Old Black Spruce Forest, Manitoba, Canada (*Ecological Archives* A019-021-S1).