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Carbon, energy and water fluxes at mature and disturbed forest sites, Saskatchewan, Canada

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Abstract

Fire and harvesting are important disturbances in the boreal forest, driving net biome production. Measurements of net ecosystem production (NEP) over mature forest stands have been made from flux towers for about a decade at the Boreal Ecosystem Research and Monitoring Sites (BERMS) in central Saskatchewan, Canada. Over the last few years, the network of towers has been expanded to include stands that were recently disturbed by fire or harvesting. These new towers are part of Fluxnet-Canada, a national network that ties into the international Fluxnet network. Data from 2001 and 2002 show that forests burned in 1998 (F98) or harvested in 1994 (HJP94) were net carbon sources to the atmosphere with annual NEP values in the range of -50 to -130 g C m^{-2} y^{-1}. A site burned in 1989 (F89) was a carbon sink of about 68 g C m^{-2} y^{-1} in 2002. NEP at a mature jack pine site (SOJP) ranged from 41 to -23 g C m^{-2} y^{-1} in this period, whereas, an old black spruce site (SOBS) ranged from 68 to 21 g C m^{-2} y^{-1}. A mature aspen site (SOA) had the greatest NEP with 361 g C m^{-2} y^{-1} in 2001 and 139 g C m^{-2} y^{-1} in 2002, the contrast between years attributed to differences in spring temperature and leaf emergence, as well as a long-term drought at the site. Evapotranspiration (ET) followed similar patterns although the F89 site had the highest ET. The deciduous tree components of SOA and F89 are likely responsible for lower summer Bowen ratios with greater energy going into ET, compared to coniferous sites. These data indicate that there is still a broad gap in our knowledge of carbon fluxes to forest stands between about 10 and 50 years of age. This is especially true in understanding the dynamics of the growth of successional vegetation along with heterotrophic respiration, highlighted by predictions of more boreal fire disturbance in the future.

Keywords: Carbon exchange rate; Fire; Boreal forest; Energy balance; Evapotranspiration; Eddy covariance; Harvesting

1. Introduction

The international network of flux towers measures the exchange of carbon dioxide, water vapour and energy between the biosphere and atmosphere (Aubinet et al., 2000; Law et al., 2002; Wilson et al., 2003). In Canada, the network of flux towers in forested areas

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began during the BOREAS experiment where fluxes along a north–south climatic gradient of the boreal forest were measured (Sellers et al., 1997). After the termination of BOREAS in the mid-1990s, some of the flux towers continued operation at both the northern (Goulden et al., 1998) and southern study areas. The group of three main flux towers at the southern study area formed the basis of the Boreal Ecosystem Research and Monitoring Sites (BERMS). The southern old aspen (SOA) flux tower has run since BOREAS times, and the southern old black spruce (SOBS) and southern old jack pine (SOJP) flux towers were started again in 1999, providing valuable data on inter-annual variability of fluxes and the processes that drive surface-atmosphere exchange (Black et al., 2000; Griffis et al., 2003).

Despite the important information gained to date on mature forest functioning, especially related to carbon exchange, we have less knowledge of the boreal forest biome as a whole. This is because of the mosaic of boreal stand ages and types that are continuously being renewed through natural and human disturbances. Indeed, the carbon balance of the Canadian boreal forest is driven by these disturbances (Kurz and Apps, 1999), and it is possible that water and energy balances that govern climate are also dictated by disturbance-generated surface conditions. Over the past few years, the BERMS program has begun to investigate spatial and temporal variability, characterized by forest disturbances. The main disturbances in the Canadian boreal forest are fire, insects, disease, windthrow and harvesting. Of these, fire is often regarded as the main stand-renewing agent, averaging more than 2 million ha burned annually over the past few decades, mostly as crown fires (Stocks et al., 2003). In addition, about 1 million ha are harvested annually in Canada, and this is a major stand-replacing mechanism in the managed part of the forest, mostly in the south. Although we recognize that the other disturbances are important for forest ecosystem function, we are presently concentrating on the effects of fire and harvesting. Hence, over the past few years, the BERMS program has added flux towers at sites burned in 1998, 1989 and 1977, and sites harvested in 1995 and 2001. An additional site harvested in 1975 was re-established in 2004 (this is the southern young jack pine site monitored during BOREAS). This strategy provides data on various age classes reflecting the present landscape to help with scaling the boreal forest biome as a whole. It also provides temporal information as a chronosequence of events. In parallel, a fire chronosequence has also been established at the BOREAS northern study area (Litvak et al., 2003). The combination of these studies provides a significant improvement in our knowledge of boreal forest functioning, compared to the previous focus on mature stands alone. In 2002, the Fluxnet-Canada network was formed, establishing sites that incorporate forest harvesting in British Columbia, Ontario, Quebec and New Brunswick and components of the BERMS program were incorporated into the network. This will allow the carbon and water dynamics to be compared in different climates and forest types. This network contributes to the international Fluxnet network data sets (e.g., Falge et al., 2002; Gu and Baldocchi, 2002; Law et al., 2002) by providing additional data for both mature and young northern forests.

Comparisons of disturbed and mature boreal forest sites during the growing season have shown that very young stands (<20 years) can be strong day-time carbon sinks (Amiro et al., 1999; Amiro et al., 2003) and even modest to strong daily sinks (Amiro, 2001; Litvak et al., 2003). However, longer-term data are not yet available so the annual magnitude of the flux is unknown. We hypothesize that forests remain as an annual carbon source for about 20–30 years after fire, depending on the area. The decomposition of fire-killed vegetation and coarse woody debris likely dominates photosynthetic uptake during this period, but data are needed to understand the magnitude of the net carbon flux. In contrast to fire, harvesting removes much of the coarse material so the respiration dynamics are expected to differ, perhaps causing the forest to become a carbon sink at an earlier age. In the present paper, we report on the comparisons between mature and disturbed sites for 2001 and 2002. For this period, data are available for the three mature sites (SOA, SOBS, SOJP), sites burned in 1998 (F98) and 1989 (F89), and one site harvested in 1994 (HJP94).

2. Site description

The basic attributes of each of the sites are summarized in Table 1 with locations shown in Fig. 1. The normal successional development of forests in the BERMS area can be complicated. Although pure stands of sufficient fetch for tower-based flux measurements exist, they are rare and not typical. Instead, the forest is a mosaic with stand composition often changing on a scale of hundreds of meters. This also affects the successional trajectory following fire, since a mosaic regenerates depending on fire severity, site conditions and establishment method. There is often a competition among trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) BSP), in areas

Table 1
Site characteristics

	SOA	SOBS	SOJP	HJP94	F98	F89
Year of origin	1919	1879	1929	1994	1998	1989
Latitude/Longitude	53.629N, 106.200W	53.987N, 105.117W	53.916N, 104.69W	53.908N, 104.656W	53.917N, 106.078W	54.254N, 105.877W
Canopy height (m)	21	7	13	2	18 (dead) 1 (live)	4
LAI	5.8	4.2	2.5	0.6	1.0	3.0
Tree stem density (>5 cm d.b.h.)	980	5900	1190	8625 Includes young saplings	1100 Dead	4000
Dominant tree d.b.h. (cm)	21	7	13	1	15 Dead	4
Dominant tree species	Aspen	Black spruce	Jack pine	Jack pine	Aspen, jack pine, black spruce	Aspen/poplar, jack pine, black spruce
Leaf-area index	5.2 (2001), 4.0 (2002)	3.9	2.3	0.6–1.0	1.0	3.0
Soil texture	Clay-loam	Organic	Sand	Sand	Loamy sand	Loamy sand
Flux height (m)	33	25	28	5	10, 20	6, 10
Anemometer model	R3	R3	CSAT3	Kaijo SAT-550	CSAT3	CSAT3
IRGA	LI6262	LI6262	LI6262	LI6262	LI6262/LI7500	LI7500
Energy balance closure fraction (r^2 value)	0.87 (0.95)	0.89 (0.97)	0.85 (0.89)	0.81 (0.92)	0.87 (0.73)	0.88 (0.91)
u_* Threshold (m s^{-1})	0.35	0.35	0.3	0.1	0.25	0.25

Canopy characteristics for SOA, SOBS and SOJP are from Gower et al. (1997).

where all three of these were present before fire. Aspen often regenerates through suckering from fire-killed parent trees, grows rapidly but is relatively short-lived. Both jack pine and black spruce regenerate from serotinous seeds, with jack pine growing more quickly, and black spruce eventually catching up and dominating if another fire does not occur. Hence, the mosaic at most fire sites reflects possible trajectories resulting in stands similar to SOA, SOBS or SOJP, but more likely being a combination of species. Hence, we use the data from the three mature stands to characterize the forest mosaic, without any one of these stands being necessarily representative of the landscape as a whole. Harvesting can result in an even-aged monospecific stand, and the HJP94 site represents the condition that would follow harvesting SOJP. Therefore, our comparisons reflect part of the range of conditions experienced on the landscape, and form a basis for decisions regarding research needs.

2.1. Mature sites (SOA, SOJP, SOBS)

The SOA site is almost pure even-aged trembling aspen with a canopy height of 21 m, generated from a fire in 1919. It has an understory of hazelnut (*Corylus cornuta* Marsh.) to a height of about 2 m. It is located in the southern part of Prince Albert National Park (Fig. 1). The SOJP site is pure jack pine with a canopy height of 13 m, generated from fire in 1929. The subcanopy space has very little vegetation with mostly a lichen ground cover. It is about 110 km east of the SOA site. The SOBS site is dominated by black spruce with a mean canopy height of 7 m, with a few jack pine and tamarack (*Larix laricina* (DuRoi) K. Koch). Some Labrador tea (*Ledum groenlandicum* Oeder) is in the understory with a ground cover of mostly feathermoss (*Pleurozium spp*.). It regenerated from a fire in 1879 and is about 30 km west of SOJP. Further details are given in Table 1 and Appendix A.

2.2. Harvested site (HJP94)

The HJP94 site is about 2 km from SOJP and represents a clearcut of a mature jack pine site. Regeneration of this site since the 1994 harvest was by natural seeding from cones left on the site, but the site had been scarified to aid germination. Regenerated jack pine trees ranged from 1 to 2.6 m tall in 2001. Ground vegetation is sparse with some lichen and moss. Harvested stumps and roots remain along with significant slash remnants on the surface.

2.3. Burned sites (F89, F98)

The 1998 burn site (F98) was in the east part of Prince Albert National Park, Saskatchewan, in the Waskesiu Fire, ignited by lightning that burned about 1700 ha in July 1998. The pre-fire forest consisted of jack pine and black spruce stands, with some intermixed aspen. The fire was severe, consuming much of the top

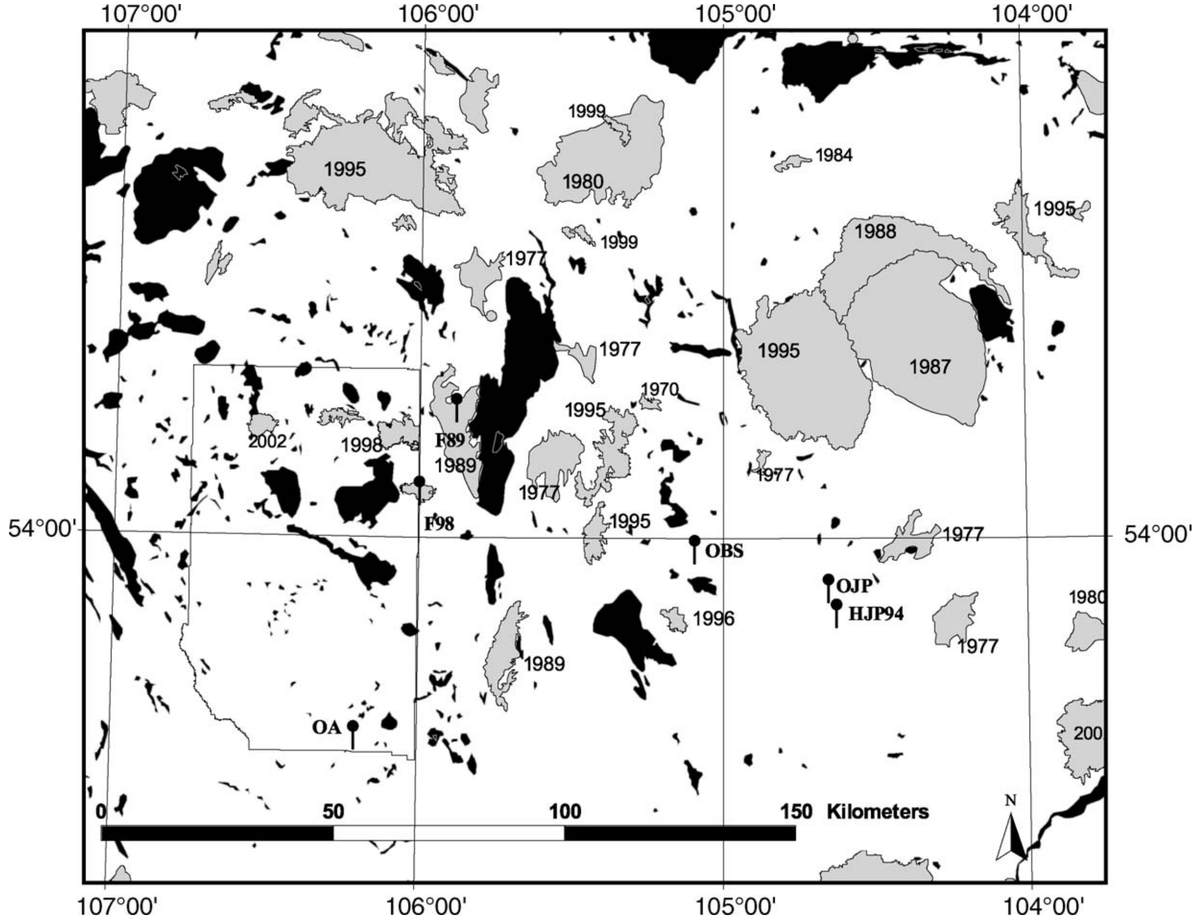

Fig. 1. Map of site locations at BERMS. The six sites described in Table 1 are shown as lollypops. Black areas are lakes. Grey areas are recent fire polygons greater than 1000 ha in size, with the year of the fire indicated (provided by Saskatchewan Environment and Parks, Canada). The rectangular area in the western part of the view is Prince Albert National Park.

layer of organic soil and killing all trees. In 2001, much of the regenerating vegetation consisted of aspen saplings about 1 m tall and shorter jack pine and black spruce seedlings. An overstory of dead, leafless jack pine trees dominated at a height of 18 m. Sparse grass and herbs, such as fireweed (*Epilobium angustifolium* L.) covered the ground. There were a large number of fallen dead trees, mostly perched above the ground and not decomposing quickly.

The 1989 burn site (F89) was northeast of Prince Albert National Park, Saskatchewan, with the human-caused fire covering 13,500 ha. Parts of the area had been logged prior to the fire, and slash residues would have been burned in some locations. Parts of the area were aerially seeded with jack pine seeds in the winter of 1990. The present tree canopy was composed of balsam poplar (*Populus balsamifera* L.), jack pine, trembling aspen, and birch (*Betula papyrifera* Marsh.) and prior to the fire, the stand consisted of these same species as well as black spruce. Dead snags of black spruce and jack pine were still standing, although most had fallen over and formed a leaning mix of dry, dead tree boles. The understory vegetation consisted mostly of black spruce saplings, saplings of the tree overstory species, bearberry, blueberry (*Vaccinium myrtilloides* Michx.), raspberry (*Rubus idaeus* L.), rose (*Rosa acicularis* Lindl.), bunchberry (*Cornus canadensis* L.), and reed grass (*Calamagrostis canadensis* (Michx.) Nutt.).

3. Methods

3.1. Flux measurements

Site-specific instrumentation and methods are given in Appendix A. The basic method for eddy flux measurements used a sonic anemometer coupled with an infra-red gas analyser (IRGA). Both open and closed-path IRGAs were used, depending on the site. The closed-path systems had the IRGA mounted on top of the tower to allow for short (~4 m) lengths of tubing between the intake and the IRGA. Continuous high frequency (20 or 10 Hz) data were archived at most sites and post-processed to calculate the covariance at 30-min intervals. On-line cross-products only were saved at the two burned sites for covariance calculation. Coordinate rotations were done following the method of Tanner and Thurtell (1969), except at HJP94. Energy and mass storage were included in the fluxes, although these terms become very small as daily totals. Net radiation (R_n) was measured using either four instruments (paired Kipp and Zonen CM11, Delft, The Netherlands, and paired Eppley PIR, Newport, USA), or four-component (Kipp and Zonen CNR1), or two-way instruments (e.g., Middleton CN1, Melbourne, Australia or Kipp and Zonen NR-Lite). Down-welling photosynthetically-active radiation (PAR) was measured with quantum sensors (Licor Inc. LI190, Lincoln, NE, USA). Ground heat flux (G) measurements were made at all sites using heat flux plates with storage measured using soil thermocouples. Site-specific details are given in Appendix A.

Soil temperature was measured at a depth of 2 cm using thermocouples at a minimum of three locations at each site. Soil volumetric moisture content was measured using CS616 soil moisture probes (Campbell Scientific Inc., Logan, UT, USA) over a depth of 0–30 cm at a minimum of three locations at each site. Additional temperature and moisture measurements were made at the sites but are not reported in this paper.

3.2. Data analyses and quality control

Quality control included removal of spikes in the high frequency data and periods of clearly bad half-hour data (e.g., caused by precipitation or malfunctions). Data below a specified u_* (friction velocity) threshold were also removed, with this threshold varying slightly among sites (Table 1). The remaining gaps were filled using two simple annual empirical relationships determined from measured data. One used the relationship between ecosystem respiration (R) and soil temperature (T_s) at a shallow depth (usually 5 cm) and the other was between gross ecosystem productivity (GEP) and PAR above the stand. The details of these are given in Appendix B. The 30 min fluxes were then integrated to get daily totals. NEE was calculated as the sum of the CO_2 covariance flux and the CO_2 storage below the flux measurement height. Net ecosystem productivity (NEP) was:

$$\text{NEP} = -\text{NEE} = \text{GEP} - R$$

Our sign convention is that NEE is positive for carbon sources, whereas, NEP is positive for carbon sinks. Note that both GEP and R are given positive signs. Missing data for sensible (H) and latent (LE) heat fluxes were also gap-filled (Appendix B).

4. Results

Energy balance closure was calculated based on regression of the gap-filled daily totals of H + LE versus $R_n - G$. Missing periods at the young sites were excluded. Closure ranged from 81 to 89% (Table 1) and gaps ranged from 31 to 47% of the data, mostly at night (Table 2). We believe that our best estimate of NEP needs to include losses due to underestimation of turbulent fluxes indicated by lack of energy balance closure. This is a well-known issue with most studies recognizing the need to include this factor and applying it to underestimations of H, ET and NEE (e.g., Twine et al., 2000; Wilson et al., 2002). Here we report values with closure corrections, but the non-corrected values can be reconstructed using the percentages in Table 1.

4.1. NEP

4.1.1. Daily NEP

Weekly means of daily NEP are shown in Fig. 2 for each of the six sites, with the graphs organized in chronological order from oldest to youngest stand. Data are continuous for the three mature sites but there are data gaps at the younger sites. The HJP94 site began operation on 24 March 2001 and the F89 site began on 6 July 2001. Missing data at the F89 and F98 sites in the winter of 2001/2002 were mostly caused by a power failure during cold temperatures. However, winter data were also excluded at these sites because of lack of confidence in the flux measurements during winter using the open-path gas analysers (see Appendix A for details).

The largest fluxes occurred at SOA. The strong annual cycle is clearly a function of the response of trembling aspen to phenology and weather with strong positive NEP when the leaves are out, particularly in early summer. Net respiration occurred in spring and fall when soil temperatures were warm but there was little photosynthetic activity. Higher fluxes were experienced in 2001 than 2002. The SOBS and SOJP sites showed earlier positive NEP in spring than SOA because of the dominance of evergreen tree species.

Table 2
Flux summaries

Component	SOA	SOBS	SOJP	HJP94	F98	F89
2001 NEP (S.D.) (g C m^{-2} y^{-1})	361 (24)	68 (23)	41 (13)	−55 (16)	−132 (22)	
2002 NEP (S.D.) (g C m^{-2} y^{-1})	139 (23)	21 (21)	−23 (19)	−59 (16)	−87 (41)	68 (44)
%NEP gap-filled	31	37	35		46	47
2001 ET (mm water y^{-1})	441	385	265	267	215	
2002 ET (mm water y^{-1})	323	328	254	252	238	443
2001 Precipitation (mm water y^{-1})	235	408	307			
2002 Precipitation (mm water y^{-1})	286	434	429			
2001 Growing season Bowen ratio	0.4	1.2	2.0	2.0	1.2	
2002 Growing season Bowen ratio	0.9	1.3	2.0	1.7	1.1	0.6

Positive NEP indicates a gain of carbon by the ecosystem. NEP and ET values have been corrected for energy balance closure (see Table 1). The growing season Bowen ratio is calculated as the ratio of the sum of H to the sum of LE from 15 May to 15 September.

Both of these sites had days of negative NEP during summer, which was very rare at SOA. A period in late July 2001 is especially notable when SOBS, SOJP, F89 and F98 all showed negative NEP for several weeks. Winter NEP was less at SOJP than at the other two mature sites.

HJP94 showed a very small flux throughout the year, with more days being negative than positive. Winter respiration tended to be quite similar to that at SOJP.

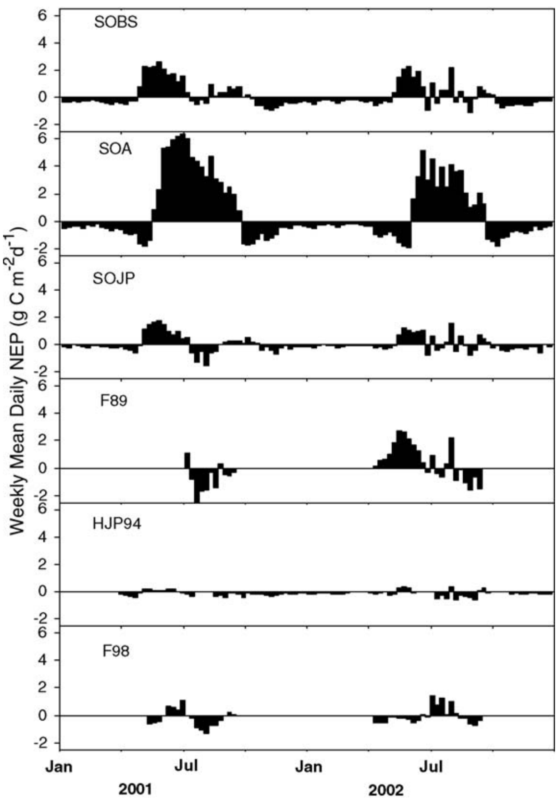

Fig. 2. Daily NEP (g carbon m^{-2} d^{-1}) in 2001 and 2002 as weekly means.

F89 showed a strong early spring NEP but became negative in late summer in both years. F98 showed a lower flux than F89 and spring NEP was negative. There were a fewer number of summer days when NEP was positive, but NEP was greater than at HJP94.

4.1.2. Annual total NEP

Annual NEP, corrected for energy balance closure, was calculated at the mature sites using the continuous data (Table 2). NEP was greater in 2001 than 2002 at all mature sites by a factor of about three. SOA was the strongest carbon sink with SOJP being close to carbon neutral.

For the younger sites, we filled the missing data periods using a combination of reasonable assumptions and statistical tests. At HJP94, winter NEP values were not significantly different between 2001 and 2002, where winter conditions were defined as the period from day 1 to 90 and day 305 to 365 (paired t-test, SYSTAT, 1997, $P = 0.30$, $n = 57$ days). Hence, we used the 2002 data to fill the missing period in the early winter of 2001 to get annual NEP estimates. Annual NEP was quite similar between years, averaging −57 g C m^{-2} y^{-1}.

We found no significant difference for daily winter NEP between F98 and SOBS (paired t-test, $P = 0.074$, $n = 64$ days) for days when we had data at both sites. We, therefore, filled winter respiration for F98 using SOBS data, although this does not imply that these two sites have similar carbon dynamics. F98 was a stronger source than HJP94 in both years. Although the winter gap filling makes these totals less certain, the site was still clearly a net source of carbon. If winter respiration at F98 was more similar to that at HJP94, then the annual totals would be −102 g C m^{-2} y^{-1} for 2001 and −55 g C m^{-2} y^{-1} for 2002, instead of −132 and −87, respectively. Alternatively, if winter respiration was more like SOA, then the annual NEP would be −144 and −137 g C m^{-2} y^{-1} for the 2 years, respectively.

We could not find an analogue for the F89 site based on statistical tests, largely because we only had about 20 days of F89 winter data that we trusted. F89 has a species mix that is a combination of those found at the three mature sites. Hence, we estimated the missing winter NEP for 2002 at F89 based on four scenarios, three of which use NEP from each of the mature sites, with the fourth being the mean NEP of the three mature sites. This gave total estimates for 2002 ranging from 18 to 106 g C m^{-2} y^{-1} with the mean being 68 g C m^{-2} y^{-1}. This site is clearly a net sink of a stronger magnitude than SOJP but less than SOA. This site started operating too late in 2001 to be able to estimate annual NEP for that year.

4.2. Evapotranspiration and energy

Measured daily ET data are shown in Fig. 3 as weekly means. The younger sites sometimes had strong daily ET, rivalling or even exceeding some of the mature sites. ET started earlier in spring and continued later in the autumn in the coniferous dominated sites compared to SOA. HJP94 had similar daily ET to SOJP (linear regression, $r^2 = 0.58$), and we filled missing HJP94 data using this regression to get annual ET (Table 2). Missing winter data at the F89 and F98 sites were filled using the mean of the three mature sites to get annual total ET. F98 had similar ET to HJP94 in 2002 but F98 was higher in the early part of the 2001 growing season. F89 had high ET throughout the summer and started early in the spring of 2002. For 2002, this site had the greatest annual ET at 443 mm.

Bowen ratios were calculated as the ratio of the weekly sum of H to LE for the 4 June–10 September period, which represents most of the growing season (Fig. 4). SOA and F89 had the lowest values through the summer, although values at SOA in 2002 were greater than those in 2001. The highest ratios were at SOJP, followed by HJP94 and SOBS. SOBS had very similar values for the 2 years. F98 ratios were low in summer, but became quite high in late summer of 2001, as ET became small. Seasonal means of the Bowen ratio show that much more energy went into LE than H at the SOA and F89 sites, both of which have deciduous species (Table 2).

The three mature sites maintain year-round precipitation gauges. For these 2 years, SOA had less than

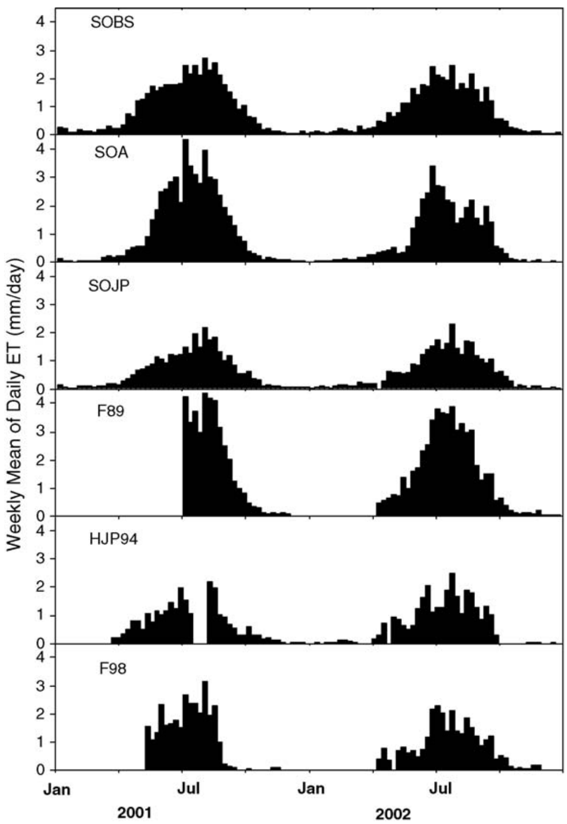

Fig. 3. Daily evapotranspiration (mm water/day) in 2001 and 2002 as weekly means.

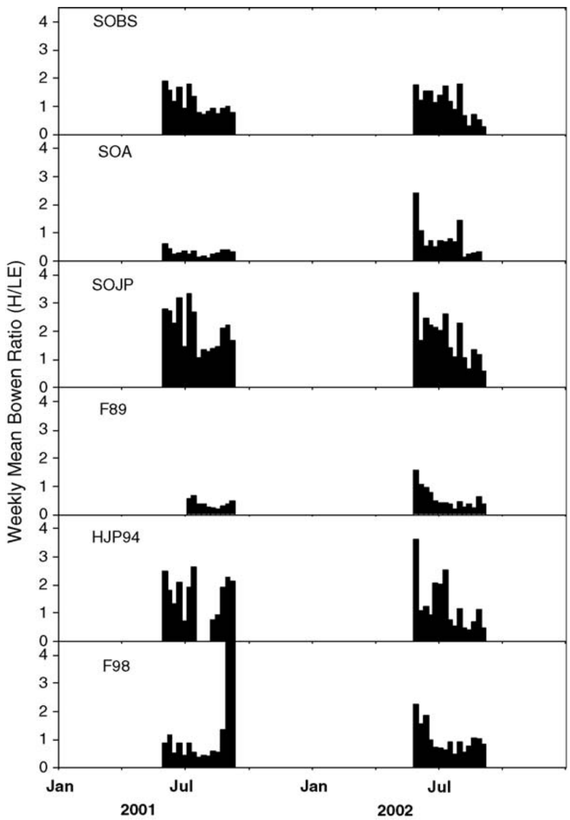

Fig. 4. Weekly mean Bowen ratio (H/LE) for the growing season (4 June–10 September).

300 mm of precipitation, whereas, SOBS had more than 400 mm (Table 2). Although these sites are only 80 km apart, it is clear that there can be large regional variability in precipitation.

5. Discussion

5.1. Disturbance impacts on NEP

It is difficult to construct flux experiments that will allow replications of treatments to compare forests of different ages, especially with similar soil types, drainage and climate. In the BERMS area, the vegetation mosaic dictates that there are few pure stands of sufficient fetch for eddy covariance measurements from towers. The three mature pure stands indicate the range of NEP for mature forests in this area. For these 2 years, we see mature forests ranging from relatively large carbon sinks of about 360 g C m^{-2} y^{-1} at SOA in 2001 to being a small source at SOJP in 2002. The high NEP at SOA in 2001 stands out as one of the highest years for carbon sequestration since annual measurements were made at this site (Black et al., 2000; Griffis et al., 2003). There is clearly a decrease in NEP at SOA, SOBS and SOJP in 2002 compared to 2001 (Table 2). At SOA, this is caused partially by a difference in spring temperature, with an early leaf emergence in 2001 and a late leaf emergence in 2002 (Barr et al., 2004). Data at SOA since 1994 show that warm springs (e.g., 1998) result in greater annual carbon sequestration (Black et al., 2000; Barr et al., 2004). In addition, there were dry conditions in both years with only about half the normal precipitation for this area (the 1971–2000 normal precipitation is 467 mm; Environment Canada, 2004). This also translates to much lower ET at SOA in 2002 compared to 2001. SOBS and SOJP were also drier than normal, but did not experience the extreme drought conditions at SOA. In 2000, SOA, SOBS, and SOJP sequestered 122, 35 and 78 g C m^2 y^{-1} (Griffis et al., 2003). Automated soil and bole respiration chambers are running at these mature sites and root exclusion plots have been established. Autotrophic respiration was estimated to be about 2/3 of total ecosystem respiration in 2001 at SOA (Griffis et al., 2004), but results are not yet available to separate heterotrophic from autotrophic respiration at all sites.

Both HJP94 and F98 were annual carbon sources, whereas, F89 was a carbon sink. F98 and F89 are much more dynamic than HJP94, with periods of greater positive and negative flux. This is partly caused by the greater deciduous and herbaceous cover at the post-fire sites, especially suckered aspen trees that have been growing rapidly. Hence, the differences here may mostly be caused by species differences, and not by differences in dynamics of heterotrophic respiration. This is uncertain without measurements of individual ecosystem components. A main difference between burned and harvested stands is that fire removes the fine materials and leaves the coarse woody material, whereas, harvesting typically does the opposite. We would expect greater heterotrophic respiration following harvesting in the early years until the finer material decomposes, whereas, the burned-site heterotrophic respiration would likely not increase until killed trees have reached the ground, becoming moist and decaying. At the F98 site, most of the fire-killed trees are still standing or perched above ground, so very little of this is expected to be decaying and contributing to the respiration flux. Instead, NEP is probably dominated by photosynthesis by suckering aspen (up to 2 m tall), jackpine and black spruce seedlings, and ground vegetation. F89 has far less coarse woody material on the site because of some harvesting before the fire. The smaller values of NEP at HJP94 are a function of the young jackpine ecophysiology since this site is dominated by this one species, with less surface vegetation than at the burned sites. The period of large negative NEP (net respiration) at F89 starting in mid-July 2001 followed a period of rain, where over 80 mm of rain fell within a 4-week period. Although this period of negative NEP is also evident at SOBS, SOJP and F98, it is greatest at F89. Calculations indicate that this was mostly caused by enhanced daytime respiration, i.e., GEP was less affected. Although we do not have independent respiration measurements at this site, we hypothesize that the wetter conditions increased heterotrophic respiration by creating a moister environment for decomposition of coarse woody debris and leaf litter.

Although we believe that differences in the fluxes among sites are largely caused by vegetation differences, there are compounding environmental factors. Figs. 5 and 6 show near-surface soil temperature (2 cm depth) and soil moisture (0–30 cm mean) measurements at the six sites. The soil temperature data show that HJP94 is clearly warmer in summer and colder in winter, largely because of the sparse tree canopy and ground cover. This contrasts with SOBS, which has the least annual variation. There are soil textural differences among the sites (Table 1), but the differences in near-surface soil temperature are mostly driven by differences in radiation penetration to the ground, governed by canopy density. The F98 site shows the next highest summer temperatures because it has more ground

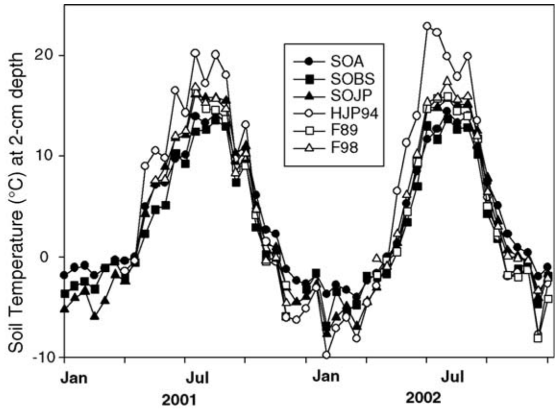

Fig. 5. Mean daily soil temperature at the 2-cm depth. Every 15th day is plotted for clarity.

cover than HJP94. Soil moisture is more interesting, governed by differences in precipitation input, soil conditions, and evapotranspiration rates. It is clear in Fig. 6 that the sandy soils at SOJP and HJP94 are well drained with low volumetric water contents and that these two sites are similar to each other. SOBS is always the wettest and SOA shows very distinct wet springs with summer drying. F89 and F98 have lower soil moisture than SOA. We believe that much of this difference among sites can be attributed to soil drainage conditions, with precipitation and evapotranspiration explaining the annual pattern for a given site. Hence processes, such as heterotrophic respiration, likely differ among sites because of the soil environment. This shows the difficulty of evaluating variations in NEP, ET and energy exchange over the landscape, since the ensemble is a function of stand type, age, and physical and chemical factors.

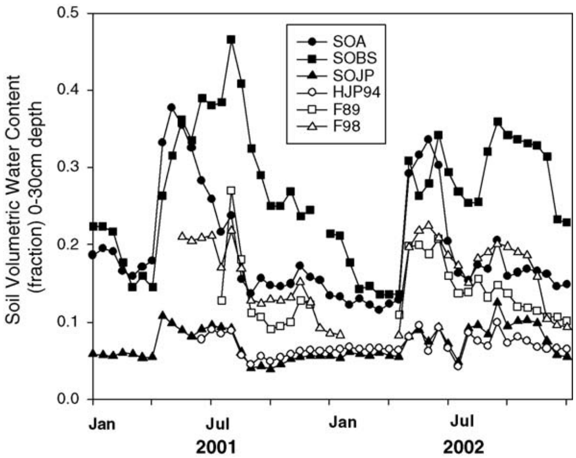

Fig. 6. Mean daily soil volumetric water content at the 0–30 cm depth. Every 15th day is plotted for clarity.

The issue of uncertainty is critical to estimates of NEP (Falge et al., 2001). Morgenstern et al. (2004) calculated annual random variability in NEP of the order of 4 g C m^{-2} y^{-1}, assuming a random error of about 20% for eddy covariance measurements throughout the year (Wesely and Hart, 1985). They also found that biases were largely unaffected by interannual variability, making it possible to quantify differences among years. For multi-day to annual NEP, the greatest uncertainty is caused by choices made in data quality control and gap-filling. Using the BERMS mature site data for 2000, Griffis et al. (2003) estimated that NEP could range from 64 to 142, 18 to 53, and 61 to 91 g C m^{-2} y^{-1} for SOA, SOBS and SOJP, respectively. Similarly, Schmid et al. (2003) estimated that gap-filling uncertainty is of the same magnitude as interannual variability at a mixed hardwood forest, where the forest was a net sink of the order of 80–170 g C m^{-2} y^{-1}. Gaps can create estimates that differ by more than 100 g C m^{-2} y^{-1} (Carrara et al., 2003), or turn estimates of net carbon sinks into sources (Saleska et al., 2003). For our data set, the annual uncertainty for the mature sites is assumed to be controlled by gap filling methods. We estimate this uncertainty as the standard deviation of four methods: (1) our standard network method outlined in Appendix A; (2) a modification of the standard method without the time-dependent parameter, i.e., it only uses the annual logistic relationship between soil temperature and respiration; (3) an annual exponential relationship between soil temperature and respiration; (4) the light-response derivation for respiration following Griffis et al. (2004). This gave us standard deviations in g C m^{-2} y^{-1} for 2001 and 2002 of 24 and 23 for SOA, 23 and 21 for SOBS, and 13 and 19 for SOJP. This indicates that SOA and SOBS were carbon sinks, but SOJP could be a small carbon source or sink in 2002. Uncertainty at HJP94 is estimated based on a similar standard deviation to SOJP of 16 g C m^{-2} y^{-1}.

Both HJP94 and F98 were clearly annual carbon sources. However, F89 and F98 showed periods of both positive and negative NEP during the growing season (Fig. 2). This clearly shows potential problems that could occur when collecting short-term data during field campaigns. For example, early season data at F89 in 2002 showed a sink, whereas, late season data showed a source. Previously, we published field campaign data from post-fire sites measured from towers and aircraft (Amiro et al., 2003). Although we recognized that winter respiration data were needed to estimate annual NEP, some of our conclusions about the potential source strength of early post-fire sites were likely in error. The current study indicates that the sites that are only a few years old are net carbon sources, consistent with carbon budget model predictions, at least in direction (Kurz and Apps, 1999).

Uncertainty at F89 is quite large. We filled the missing winter data using data from each of the mature sites, as well as the mean of these for 2002. This gave annual NEP ranging from 18 g C m^{-2} y^{-1} using respiration from SOA to 106 g C m^{-2} y^{-1} using respiration from SOJP. The standard deviation of these extremes and the mean value is 44 g C m^{-2} y^{-1}. Irrespective of this uncertainty, F89 is estimated to be a carbon sink in 2002 of perhaps half the magnitude of SOA, but greater than SOBS or SOJP. With the same method of estimating uncertainty, the standard deviation for F98 is 22 and 41 g C m^{-2} y^{-1} for 2001 and 2002, respectively.

5.2. Implications of disturbance for the surface energy balance

Estimates of ET at the young sites were sometimes different than one might expect after considering NEP. HJP94 and SOJP had quite similar weekly patterns and annual totals for ET (Fig. 3, Table 2). Bowen ratios were similar between these two sites in 2001, but were higher at SOJP in 2002. This was caused by a 28% lower H at HJP94 ($r^2 = 0.82$), while ET was similar between the sites. The Bowen ratio is clearly less at F98 than at HJP94, especially in 2001. Part of this is an artefact because the F98 measurements in 2001 were made at a height of 10 m within the dead tree canopy. This means that less net radiation was available for turbulent energy dissipation at this height. The instruments were not moved above the dead-tree canopy until 18 August 2002. This should not affect NEP and ET measurements since the dead trees do not contribute much to either. However, there would be a component of H with the interception of radiation by the dead trees. Hence, the within-canopy data cannot be easily compared to above-canopy data at the other sites.

The most surprising site is F89, which has greater ET than all other sites, including SOA. We believe that this is real, since night gap filling is less critical for ET than for NEP, and it seems to be consistent in both years. However, one needs to check where this amount of water could come from (443 mm in 2002). There is clearly variation in precipitation across the BERMS area, ranging at least between 286 and 434 mm in 2002 (Table 2). We do not have good continuous precipitation data at F89, but summer precipitation in 2002 was about 200 mm, similar to that at SOA and at least 100 mm less than SOBS. Spatial variability of precipitation likely plays a large role in the differences in ET among sites. The high ET at F89 results in a low Bowen ratio, similar to SOA in 2001, and lower in 2002. There is another possible explanation for whether the F89 ET values are correct. This site is quite flat with a wetter area to the south that supports regional drainage from west to east. Standing water in fen areas can be found that supports black spruce and tamarack, even in summer. It is possible that this drainage system supported more ET during these 2 years, although we would expect that continuing dry conditions will eventually cause plant stress. This would not be obvious in the soil moisture data in Fig. 6 because it was measured locally near the tower. This landscape is quite different from SOA, which is at a topographic high point. Further investigation is needed to determine whether this successional forest has consistently higher ET than mature forests in the area, although the deciduous post-fire component is expected to have higher ET than the coniferous component (e.g., Meroni et al., 2002).

5.3. Implications for the boreal forest biome

Over the last few years, several research groups have been measuring carbon and energy fluxes over boreal forests that have been recently disturbed by fire or harvesting. Most of these studies report data for field campaigns or for the full growing season. Very young forests are carbon sources with slightly older successional forests being carbon sinks (Meroni et al., 2002; Amiro et al., 2003; Litvak et al., 2003) or close to carbon neutral (Schulze et al., 1999) during the growing season. These studies have been important to help us understand the functioning of younger forests, and how they contribute to the carbon balance in summer. However, it is clear that young forests can be either sources or sinks depending on the period during the growing season (Fig. 2) and we urge caution when interpreting the limited data sets.

Fig. 7 presents annual NEP for the BERMS sites plus the northern old black spruce site (NOBS) near Thompson, Manitoba. There is a large scatter for mature sites depending on stand type, year and age. It also shows that the magnitude of the carbon source from young (<10 years) harvested and burned sites is similar to the range of mature forest sinks. We only have the single point at about 13 years, which although it shows a moderate sink, has much associated uncertainty. We need more sites and years of data in these systems, especially from 20 to 50 years of age, to help support models of carbon balance of the boreal biome. The large interannual variability evident in Fig. 7 highlights the need for continuous data over several years. It is

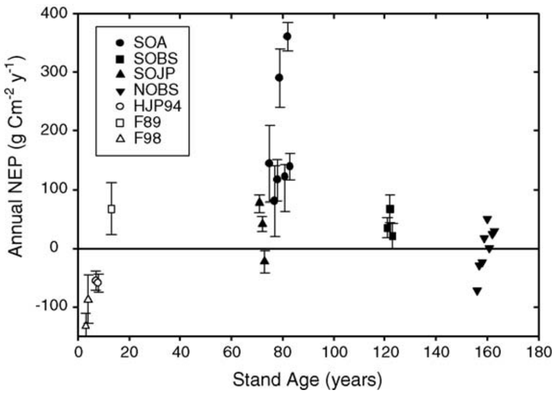

Fig. 7. Annual NEP measurements in the Canadian boreal forest. SOA data are from 1994 to 2002 (Black et al., 2000; Griffis et al., 2003, present study); SOBS and SOJP data are from 2000 to 2002 (Griffis et al., 2003, present study), NOBS (Northern Old Black Spruce) are from 1995 to 2002 (Goulden et al., 1998 updated to 2002 by Dunn and Wofsy, personal communication). Error bars represent estimated uncertainty, when available.

important to note that the general relationship of a carbon source for very young and old boreal forests, with a sink for actively growing forests, is consistent with the stand-age curves used in some carbon budget models (e.g., Kurz and Apps, 1999). As more data become available, this will create an opportunity for comparisons with models.

6. Conclusions

The expansion of flux measurement sites to include forests of various ages is key to estimating net biome production in the boreal forest. In Canada alone, an average of 2–3 million ha are burned by fire annually, with another 1 million ha harvested. The resulting mosaic of stand ages has features that are just starting to be characterized by the flux measurement community, especially on annual scales. We need to expand measurements to reduce the uncertainty in carbon and energy flux estimates, and to allow for scaling up to the ecoregion or biome level using models. The carbon budget model of the Canadian forest sector clearly demonstrates the importance of fire, insect and harvesting disturbances on the overall carbon balance (Kurz and Apps, 1999). However, confidence in these model estimates will be greatly strengthened by direct measurements over several years, incorporating post-disturbance effects.

Projections of future climate suggest that fire will become even more important with possibly a doubling of area burned in Canada by the end of this century (Flannigan et al., 2005). Other boreal areas, such as Siberia, may also see similar increases in fire. This coupled with the potential for more insect infestations (Volney and Fleming, 2000), means that the proportion of younger successional forests could increase. Changes to large expanses of boreal forest would alter energy balance partitioning (e.g., Chambers and Chapin, 2002) and albedo (Betts, 2000; Chapin et al., 2000), which may alter regional and global climates. In addition, more disturbances could increase seasonal amplitudes of atmospheric CO_2 because successional vegetation has higher summer and winter fluxes (Zimov et al., 1999).

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Appendix A. Site-specific issues

A.1. Mature sites (SOA, SOBS, SOJP)

The three mature sites used closed-path LI6262 (LICOR Inc., Lincoln, NE) CO_2/water vapour analysers with air drawn through 4.5 m of heated Decoron 4 mm i.d. tubing at a rate of about 10 L min^{-1}. Both CSAT3 (Campbell Scientific Inc., Logan, UT) and Solent R2 or R3 (Gill Instruments, Lymington, UK) sonic anemometers were used (Table 1). The instruments were mounted on scaffold towers above the canopy, with ac power available. Data were logged at 125 Hz, and block-averaged to 20.833 Hz for eddy covariance calculations. CO_2 storage below the flux measurement height was calculated using a profile of eight measurements taken with a separate LI6262 analyser. Further instrument details are provided by Chen et al. (1999). Additional site information is provided for the SOA site in Chen et al. (1999), the SOBS site in Jarvis et al. (1997) and the SOJP site in Baldocchi et al. (1997). Adequate fetch was available at each of these sites (>1 km). All of these sites originated from fires.

A.2. Harvested site (HJP94)

The HJP94 site used a closed path system with a 5-m long 4 mm i.d. tubing through which air was drawn at 8 L min^{-1}. The tubing was heated and had a 5 μm mesh dust filter. The span of the CO_2 analyser was checked daily using 350 and 430 $\mu L\,L^{-1}$ span gases. Delay times for the tubing were estimated by maximizing the correlation every half hour, and spectral corrections were made using transfer functions (Moore, 1986; Massman, 1991; Moncrieff et al., 1997). Coordinate rotations were not applied since this area is very flat and rotations were negligible for conditions when $u_* > 0.1$ m s^{-1}. Storage below the measurement height was not included since it is very small for this low height and sparse canopy, and has negligible impact on daily totals of NEP. Flux data outside of 3 standard deviations from an 11-day running mean were rejected as outliers.

This site followed a different gap-filling procedure than the one outlined in Appendix B. Small gaps in NEE of 2 h or less were filled through interpolation. During night conditions when u_* was below the threshold of 0.1 m s^{-1}, respiration was estimated using

$$R = a\exp(bV + c)T_s$$

where a, b and c are coefficients, V is daily mean soil volumetric soil water content, and T_s is daily mean soil temperature at the 5 cm depth. Daily NEP was calculated when at least 50% of the daytime and night-time data were available. Daily total LE and H were calculated when at least 90% of the half-hour values were available for a given day.

A.3. Burned sites (F98, F89)

All systems were battery and solar powered. The F98 site measurements were made at a height of 7.7 m using a closed-path LI6262 sensor and a CSAT3 sonic anemometer on a 30-cm wide triangular tower, until 16 August 2002. The air stream was pulled down a 3-m length of unheated 8-mm i.d. Bevaline-IV tubing at a rate of 5 L min^{-1}, and pushed into the analyser. Corrections were made for lag in the tubing, frequency-response losses, temperature and pressure (Amiro, 2001). The signals were sampled at 4 Hz; a previous comparison with a system operated by the University of British Columbia showed good agreement (Amiro et al., 2003). Starting 18 August 2002, the system used an open-path LI7500 (LICOR, Lincoln, NE) analyser at a height of 20 m on a scaffold tower. The signals were sampled at 10 Hz and fluxes were corrected for density (Webb et al., 1980). The cross-products were retained to allow for post-processing including coordinate rotation. Comparisons between the open-path and closed path systems, mounted at the 7.7 m height indicated that the closed path system needed a further correction of 45% for NEP to account for tubing and frequency losses close to the ground. This correction was applied to all of the closed-path data. The F89 site used the LI7500 open-path system analyser and a CSAT3 anemometer at a height of 5.2 m on a 30-cm wide triangular tower.

The sites had more than 1 km of fetch in all directions, except for the F98 site, where fluxes from between 0° and 90° from north were excluded because of pre-fire harvesting in this direction. Quality control procedures for these sites included using absolute limits of ±30 $\mu mol\,m^{-2}\,s^{-1}$ for NEE, beyond which gaps were created and filled. Another issue occurred in winter with the open-path analysers. There is an apparent downward flux during the day over frozen surfaces where we would expect a slight upward flux. The magnitude increases with greater sensible heat flux, even after doing the density correction. This phenomenon has also been observed by other researchers (Amiro, personal communication), and we have not yet resolved it. Instead, we have excluded the winter open-path data until the issue is resolved.

Appendix B. Gap-filling procedures

We followed the Fluxnet-Canada Research Network gap-filling procedures for all sites except for HJP94.

B.1. Gap filling NEP

The procedure first derived GEP and R from half-hourly NEP values, and then filled gaps in half-hourly GEP, R, and NEP using simple empirical models that were constrained by the measured data. The gap-filling procedure made use of two simple annual empirical relationships determined from measured data. One was between R and soil temperature (T_s) at a shallow depth (usually 5 cm) and the other was between GEP and photosynthetically active radiation (PAR) above the stand. In the first step, parameters were obtained for the annual relationships. In the second step, one additional parameter for each relationship was introduced. In order to account for changes in other environmental variables (e.g., soil moisture, vapour pressure deficit) or phenological stage over a short period of time, this parameter was allowed to vary in time with the other parameters held constant. The time-varying parameter was determined within a moving window as the slope of the linear regression (forced through the origin) between estimates of R (and GEP) obtained from the annual relationships and R (and GEP) from the measurements. The implementation of the moving window used a fixed number of acceptable data points (30 min measurements) rather than a fixed period of time. The window was 100 data points wide, moved in an increment of 20 points at a time. For each window, the obtained value of the time-varying parameter was assigned to the mean time of the 100 data points (i.e., usually near the centre of the window). The values of the time-varying parameters for each individual half-hour period were then estimated by linear interpolation. These adjusted relationships were then used to fill the data gaps. The sensitivity of R and GEP to T_s and PAR, respectively, was largely determined by the annual relationships, but was modified to some extent by the time-varying parameters within each window period.

The processing steps to estimate NEP, GEP and R were:

(a) NEE was estimated as the sum of the measured eddy (F_c) and storage fluxes (S_c).
(b) NEP was estimated as −NEE after excluding low u_* data at night (Table 1 thresholds). In applying the low u_* data rejection to night-time periods, S_c was included in the estimate of NEP.
(c) Small gaps in NEP (four half-hour periods or less) were filled by linear interpolation before larger gaps were filled using the procedure outlined below.
(d) Measured R is estimated as $R = -\text{NEP}$ during periods when GEP was known to be zero, i.e., during night and during night and day in the cold season (periods when both air temperature (T_a) and T_s are less than 0 °C).
(e) An empirical logistic $R = f(T_s)$ relationship was fit to the measured R values from (d):

$$R = \frac{r_1}{(1 + \exp[r_2(r_3 - T_3)])} \tag{1}$$

where r_1, r_2, and r_3 are empirical constants.
(f) An additional empirical parameter, $r_w(t)$, was introduced into Eq. (1) resulting in

$$R = f(T_s, t) = \frac{r_w(t) r_1}{(1 + \exp[r_2(r_3 - T_s)])} \tag{2}$$

and $r_w(t)$ was allowed to vary in time (t). It was estimated using a linear regression of the modelled R estimates from (e) versus the R measurements from (d) within a 100-point moving window.
(g) The $R = f(T_s, t)$ model (Eq. (2)) was used to estimate R during the day and to fill gaps in R at night.
(h) GEP was estimated as NEP + R (daytime) or zero (nighttime and during periods when both T_a and T_s were less than 0 °C).
(i) An empirical GEP = f(PAR) model was fit to the non-zero GEP data from (h):

$$\text{GEP} = \frac{\alpha Q P_x}{(\alpha Q + P_x)} \tag{3}$$

where α is the quantum yield, Q is downwelling PAR, and P_x is the photosynthetic capacity (GEP at light saturation). Both parameters were treated as constants.
(j) An additional empirical parameter, $p_w(t)$, was introduced into Eq. (3), resulting in

$$\text{GEP} = f(Q, t) = \frac{p_w(t) \alpha Q P_x}{(\alpha Q + P_x)} \tag{4}$$

and $p_w(t)$ was allowed to vary in time and was derived using a linear regression of the modelled non-zero GEP estimates from (i) versus the non-zero GEP measurements from (h) within a 100-point moving window.
(k) The GEP = $f(Q, t)$ model (Eq. (4)) was used to fill gaps in GEP.
(l) Gaps in NEP were filled using modelled GEP − R.

B.2. Gap filling H and LE

We assume that all convective measurements made by the eddy covariance technique were underestimated during low u_* conditions. Hence both H and LE also needed to be corrected using the same threshold values for u_* used for NEP. This keeps a constant Bowen ratio. Gaps of less than 2 h (i.e., four half-hour periods) were interpolated.

B.2.1. For H

A regression was developed between H and $R_n - G$ for good data periods, based on a 240-point (half-hour period) moving window, moved in an increment of 48 points at a time. The missing H data were then filled with the regression equation output.

B.2.2. For LE

B.2.2.1. Night values of LE

Most gaps in LE occur at night. Although night-time LE can be slightly positive or negative, for the purposes of daily totals, we set the LE gap values to 0.

B.2.2.2. Growing season daytime values of LE

We used the same technique as used for H, based on regression between LE and $R_n - G$ using a 240-point moving window of good daytime measurements.

B.2.2.3. Non-growing season daytime values of LE

LE was not well correlated with $R_n - G$ in winter because it approaches zero. For the non-growing season (T_a and T_s are both <0 °C), we gap-filled using the average value for that half-hour period based on the previous 5 days and following 5 days (i.e., 10 points for the same half-hour period). This is appropriate since there are no real physiological controls over LE in winter.

References

Amiro, B.D., 2001. Paired-tower measurements of carbon and energy fluxes following disturbance in the boreal forest. Global Change Biol. 7, 253–268.

Amiro, B.D., MacPherson, J.I., Desjardins, R.L., 1999. BOREAS flight measurements of forest-fire effects on carbon dioxide and energy fluxes. Agric. For. Meteorol. 96, 199–208.

Amiro, B.D., MacPherson, J.I., Desjardins, R.L., Chen, J.M., Liu, J., 2003. Post-fire carbon dioxide fluxes in the western Canadian boreal forest: evidence from towers, aircraft and remote sensing. Agric. For. Meteorol. 115, 91–107.

Aubinet, M., Grelle, A., Ibrom, A., Rannik, U., Moncrieff, J., Foken, T., Kowalski, A.S., Martin, P.H., Berbigier, P., Bernhofer, C., Clement, R., Elbers, J., Granier, A., Grunwald, T., Morgenstern, K., Pilegaard, K., Rebmann, C., Snijders, W., Valentini, R., Vesala, T., 2000. Estimates of the annual net carbon and water exchange of forests: the Euroflux methodology. Adv. Ecol. Res. 30, 113–175.

Baldocchi, D.D., Vogel, C.A., Hall, B., 1997. Seasonal variation of energy and water vapour exchange rates above and below a boreal jack pine forest canopy. J. Geophys. Res. 102, 28939–28951.

Barr, A.G., Black, T.A., Hogg, E.H., Kljun, N., Morgenstern, K., Nesic, Z., 2004. Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. Agric. For. Meteorol. 126, 237–255.

Betts, R.A., 2000. Offset of the potential carbon sink from boreal forestation by decreases in surface albedo. Nature 408, 187–190.

Black, T.A., Chen, W.J., Barr, A.G., Arain, M.A., Chen, Z., Nesic, Z., Hogg, E.H., Neumann, H.H., Yang, P.C., 2000. Increased carbon sequestration by a boreal deciduous forest in years with a warm spring. Geophys. Res. Lett. 27, 1271–1274.

Carrara, A., Kowalski, A.S., Neirynck, J., Janssens, I.A., Yuste, J.C., Ceulemans, R., 2003. Net ecosystem CO_2 exchange of mixed forest in Belgium over 5 years. Agric. For. Meteorol. 119, 209–227.

Chambers, S.D., Chapin III, F.S., 2002. Fire effects on surface-atmosphere energy exchange in Alaskan black spruce ecosystems: implications for feedbacks to regional climate. J. Geophys. Res. 108, 814510.1029/2001JD000530.

Chapin III, F.S., McGuire, A.D., Randerson, J., Pielke Sr., R., Baldocchi, D., Hobbie, S.E., Roulet, N., Eugster, W., Kasischke, E., Rastetter, E.B., Zimov, S.A., Running, S.W., 2000. Arctic and boreal ecosystems of western North America as components of the climate system. Global Change Biol. 76 (Suppl. 1), 211–223.

Chen, W.J., Black, T.A., Yang, P.C., Barr, A.G., Neumann, H.H., Nesic, Z., Blanken, P.D., Novak, M.D., Eley, J., Ketler, R.J., Cuenca, A., 1999. Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest. Global Change Biol. 5, 41–53.

Environment Canada, 2004. Canadian climate normals 1971–2000. Waskesiu Lake, Saskatchewan. http://www.climate.weatheroffice.ec.gc.ca. Accessed 9 August 2004.

Falge, E., Baldocchi, D., Olson, R., Anthoni, P., Aubinet, M., Bernhofer, C., Burba, G., Ceulemans, R., Clement, R., Dolman, H., Granier, A., Gross, P., Grunwald, T., Hollinger, D., Jensen, N.O., Katul, G., Keronen, P., Kowalski, A., Lai, C.T., Law, B.E., Meyers, T., Moncrieff, H., Moors, E., Munger, J.W., Pilegaard, K., Rannik, U., Rebmann, C., Suyker, A., Tenhunen, J., Tu, K., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. Gap filling strategies for defensible annual sums of net ecosystem exchange. Agric. For. Meteorol. 107, 43–69.

Falge, E., Baldocchi, D., Tenhunen, J., Aubinet, M., Bakwin, P., Berbigier, P., Bernhofer, C., Burba, G., Clement, R., Davis, K.J., 2002. Seasonality of ecosystem respiration and gross primary production as derived from Fluxnet measurements. Agric. For. Meteorol. 113, 53–74.

Flannigan, M.D., Logan, K.A., Amiro, B.D., Skinner, W.R., Stocks, B.J., 2005. Future area burned in Canada. Climatic Change. 72, 1–16.

Goulden, M.L., Wofsy, S.C., Harden, J.W., Trumbore, S.E., Crill, P.M., Gower, S.T., Fries, T., Daube, B.C., Fan, S.M., Sutton, D.J., Bazzaz, A., Munger, J.W., 1998. Sensitivity of boreal forest carbon balance to soil thaw. Science 279, 214–217.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., Stow, T.K., 1997. Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. 102, 29029–29041.

Griffis, T.J., Black, T.A., Morgenstern, K., Barr, A.G., Nesic, Z., Drewitt, G.B., Gaumont-Guay, D., McCaughey, J.H., 2003. Ecophysiological controls on the carbon balances of three southern boreal forests. Agric. For. Meteorol. 117, 53–71.

Griffis, T.J., Black, T.A., Gaumont-Guay, D., Drewitt, G.B., Nesic, Z., Barr, A.G., Morgenstern, K., Kljun, N., 2004. Seasonal variation and partitioning of ecosystem respiration in a southern boreal aspen forest. Agric. Forest Meteorol. 125, 207–223.

Gu, L., Baldocchi, D., 2002. Foreward. Agric. For. Meteorol. 113, 1–2.

Jarvis, P.G., Massheder, J.M., Hale, S.E., Moncrieff, J.B., Rayment, M., Scott, S.L., 1997. Seasonal variation of carbon dioxide, water vapour, and energy exchanges of a boreal black spruce forest. J. Geophys. Res. 102, 28953–28966.

Kurz, W.A., Apps, M.J., 1999. A 70-year retrospective analysis of carbon fluxes in the Canadian forest sector. Ecol. Appl. 9, 526–547.

Law, B.E., Falge, E., Gu, L., Baldocchi, D.D., Bakwin, P., Berbigier, P., Davis, K., Dolman, A.J., Falk, M., Fuentes, J.D., 2002. Environmental controls over carbon dioxide and water vapour exchange of terrestrial vegetation. Agric. For. Meteorol. 113, 97–120.

Litvak, M., Miller, S., Wofsy, S.C., Goulden, M., 2003. Effect of stand age on whole ecosystem CO_2 exchange in the Canadian boreal forest. J. Geophys. Res. 108, 822510.1029/2001JD000854.

Massman, W.J., 1991. The attenuation of concentration fluctuations in turbulent flow through a tube. J. Geophys. Res. 96, 15269–15273.

Meroni, M., Mollicone, D., Belelli, L., Manca, G., Rosellini, S., Stivanello, S., Tirone, G., Zompanti, R., Tchebakova, N., Schulze, E.D., Valentini, R., 2002. Carbon and water exchanges of regenerating forests in central Siberia. For. Ecol. Manage. 169, 115–122.

Moncrieff, J.B., Massheder, J.M., deBruin, H., Elbers, J., Friborg, T., Heusinkveld, B., Kabat, P., Scott, E., Soegaard, H., Verhoef, A., 1997. A system to measure surface fluxes of momentum, sensible heat, water vapour and carbon dioxide. J. Hydrol. 188/189, 589–611.

Moore, C.J., 1986. Frequency response corrections for eddy correlation systems. Boundary-Layer Meteorol. 37, 17–35.

Morgenstern, K., Black, T.A., Humphreys, E.R., Griffis, T.J., Drewitt, G.B., Cai, T., Nesic, Z., Spittlehouse, D.L., Livingston, N.J., 2004. Sensitivity and uncertainty of the carbon balance of a Pacific Northwest Douglas-fire forest during an El Nino/La Nina cycle. Agric. For. Meteorol. 123, 201–219.

Saleska, S.R., Miller, S.D., Matross, D.M., Goulden, M.L., Wofsy, S.C., da Rocha, H.R., de Camargo, P.B., Crill, P., Daube, B.C., de Freitas, H.C., Hutyra, L., Keller, M., Kirchhoff, V., Menton, M., Munger, J.W., Pyle, E.H., Rice, A.H., Silva, H., 2003. Carbon in Amazon forests: unexpected seasonal fluxes and disturbance-induced losses. Science 302, 1554–1557.

Schmid, H.P., Su, H.-B., Vogel, C.S., Curtis, P.S., 2003. Ecosystem-atmosphere exchange of carbon dioxide over a mixed hardwood forest in northern lower Michigan. J. Geophys. Res. 108, 441710.1029/2002JD003011.

Schulze, E.D., Lloyd, J., Kelliher, F.M., Wirth, C., Rebmann, C., Luhker, B., Mund, M., Knohl, A., Milyukova, I.M., Schulze, W., Ziegler, W., Varlagin, A.B., Sogachev, A.F., Valentini, R., Dore, S., Grigoriev, S., Kolle, O., Panfyorov, M.I., Tchebakova, N., Vygodskaya, N.N., 1999. Productivity of forests in the Eurosiberian boreal region and their potential to act as a carbon sink—a synthesis. Global Change Biol. 5, 703–722.

Sellers, P.J., Hall, F.G., Kelly, R.D., Black, A., Baldocchi, D., Berry, J., Ryan, M., Ranson, K.J., Crill, P.M., Lettenmaier, D.P., Margolis, H., Cihlar, J., Newcomer, J., Fitzjarrald, D., Jarvis, P.G., Gower, S.T., Halliwell, D., Williams, D., Goodison, B., Wickland, D.E., Guertin, F.E., 1997. BOREAS in 1997: experiment overview, scientific results, and future directions. J. Geophys. Res. 102, 28731–28769.

Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., Flannigan, M.D., Hirsch, K.G., Logan, K.A., Martell, D.L., Skinner, W.R., 2003. Large forest fires in Canada, 1959–1997. J. Geophys. Res. 108, 814910.1029/2001JD000484.

SYSTAT 1997. SYSTAT software. SPSS Inc., Chicago, IL, USA.

Tanner, C.B., Thurtell, G.W., 1969. Sensible Heat Flux Measurements with a Yaw Sphere and Thermometer. TR Ecom 66-G22-F. Department of Soil Science, University of Wisconsin, Madison, Wisconsin.

Twine, T.E., Kustas, W.P., Norman, J.M., Cook, D.R., Houser, P.R., Meyers, T.P., Prueger, J.H., Starks, P.J., Wesely, M.L., 2000. Correcting eddy-covariance flux underestimates over a grassland. Agric. For. Meteorol. 103, 279–300.

Volney, W.J.A., Fleming, R.A., 2000. Climate change and impacts of boreal forest insects. Agric. Ecosys. Environ. 82, 283–294.

Webb, E.K., Pearman, G.I., Leuning, R., 1980. Correction of flux measurements for density effects due to heat and water vapour transfer. Quart. J. Roy. Meteorol. Soc. 106, 85–100.

Wesely, M.L., Hart, R.L., 1985. Variability of short-term eddy-correlation estimates of mass exchange. In: Hutchinson, B.A., Hicks, B.B. (Eds.), The Forest-Atmosphere Interaction. D. Reidel, Dordrecht, pp. 591–612.

Wilson, K., Baldocchi, D., Falge, E., Aubinet, M., Berbigier, P., Bernhofer, C., Dolman, H., Field, C., Goldstein, A., Granier, A., Hollinger, D., Katul, G., Law, B.E., Meyers, T., Moncrieff, J., Monson, R., Tenhunen, J., Valentini, R., Verma, S., Wofsy, S., 2003. The diurnal centroid of ecosystem energy and carbon fluxes at Fluxnet sites. J. Geophys. Res. 108, 466410.1029/2001JD001349.

Wilson, K., Goldstein, A., Falge, E., Aubinet, M., Baldocchi, D., Berbigier, P., Bernhofer, C., Ceulemans, R., Dolman, H., Field, C., 2002. Energy balance closure at Fluxnet sites. Agric. For. Meteorol. 113, 223–243.

Zimov, S.A., Davidov, S.P., Zimova, G.M., Davidova, A.I., Chapin III, F.S., Chapin, M.C., Reynolds, J.F., 1999. Contribution of disturbance to increasing seasonal amplitude of atmospheric CO_2. Science 284, 1973–1976.