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Effect of stand age on whole ecosystem CO_2 exchange in the Canadian boreal forest

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[1]   One of the key steps to estimating the current and future contribution of boreal forests to the global carbon cycle is quantifying the role recovery from fire plays in stand level carbon dynamics. We used tower-based eddy covariance to measure the CO_2 exchange above five black spruce stands in central Manitoba during the 1999 and 2000 growing seasons (June–September). Fluxes in the four youngest stands (11, 19, 36, and 70 year old burns) were measured using portable eddy flux systems stationed in each burn for 4 to 6 weeks. Fluxes in the oldest stand (~1870 burn) were measured continuously throughout 1999 and 2000, providing a baseline for interpretation of the fluxes measured simultaneously in the younger stands. Light-saturated CO_2 uptake was lowest in the 11 year old stand (-4.1 μmol m^{-2} s^{-1}), high in the 19 year old stand (-8.9 μmol m^{-2} s^{-1}), highest in the 36 year old stand (-10.1 μmol m^{-2} s^{-1}), and moderate in the 70 and 130 year old stands (-6.3 and -7.1 μmol m^{-2} s^{-1}, respectively). Whole-ecosystem respiration was lowest in the youngest burn and consistently increased with stand age. Integrated daily carbon balance changed from a slight sink at the 11 year old stand (-0.20 g C m^{-2} d^{-1}) to a modest sink at the 19 year old stand (-1.9 g C m^{-2} d^{-1}) to a large sink at the 36 year old stand (-3.1 g C m^{-2} d^{-1}) to a modest sink at the 70 year old stand (-0.53 g C m^{-2} d^{-1}) to around zero at the 130 year old stand. The results from any single tower in a boreal region are therefore unlikely to be representative of the entire region. Reliable assessments of regional carbon balance will require an approach that incorporates information on the fractional coverage of stands in different age classes and measurements of ecosystem gas exchange by representative stands within each age class.   *INDEX TERMS:* 0315 Atmospheric Composition and Structure: Biosphere/atmosphere interactions; 1615 Global Change: Biogeochemical processes (4805); 1635 Global Change: Oceans (4203); *KEYWORDS:* boreal forest, ecosystem carbon balance, eddy covariance, chronosequence, stand age, CO_2 exchange

1. Introduction

[2] Boreal forests play an important role in the global carbon cycle, accounting for as much as 25% of the carbon contained in the terrestrial biosphere [*Dixon et al.*, 1994]. The boreal region has experienced considerable warming during the last four decades and is predicted to experience disproportionate warming with climate change [*Chapman and Walsh*, 1993; *Intergovernmental Panel on Climate Change* (*IPCC*), 2001]. The amount of carbon contained in boreal forests, as well as the sensitivity of the boreal region to climate change, make understanding the controls over the storage and principal fluxes of carbon in boreal landscapes crucial to global change research.

[3] Stand replacing wildfires are an integral part of North American boreal ecosystems [*Larsen*, 1980; *Van Cleve et al.*, 1986; *Weber and Stocks*, 1998], occurring at individual locations on average every 40 to 250 years [*Bonan and Shugart*, 1989; *Larsen*, 1998]. These fires are often high in intensity, and large in areal extent, due to the fuel loads that accumulate as stands age [*Stocks*, 1991]. This fire cycle creates a mosaic of large, even-aged patches in various

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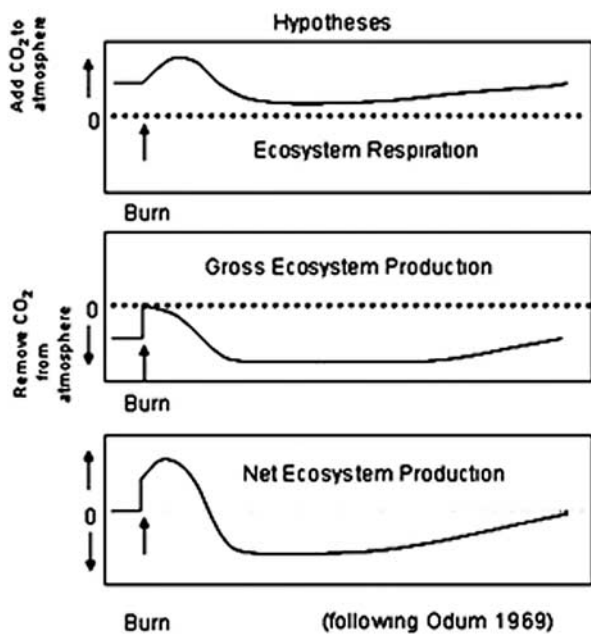
Figure 1. Conceptual model of forest recovery from fire. Curves are drawn by hand based on qualitative field observations in central Manitoba black spruce forests.

stages of succession across the boreal landscape. The frequency of fire, and hence the age distribution of stands across the landscape, may change considerably in the future with either climatic warming or new fire suppression policies [*Li et al.*, 2000; *Kurz and Apps*, 1999; *Weber and Flannigan*, 1997]. One of the key steps to estimating the future contribution of boreal forests to the global carbon cycle is quantification of the role fire recovery plays in stand level carbon dynamics [*Harden et al.*, 2000; *Trumbore and Harden*, 1997].

[4] A range of processes determine the impact of fire and subsequent recovery on the carbon balance of black spruce ecosystems in boreal North America [*Van Cleve et al.*, 1983; *Kasischke*, 2000; *Schulze et al.*, 2000]. Fires in upland, moderately- to well- drained areas typically kill the vegetation while consuming only a fraction of aboveground biomass [*Viereck*, 1983; *Goldammer and Furyaev*, 1996]. This causes a large increase in coarse woody debris, which gradually decomposes over the next century [*Harmon et al.*, 1986; *Hély et al.*, 2000]. Postfire changes in soil temperature, moisture and nutrients control plant and microbial metabolism, which, in turn, drive net primary production and succession [*Kasischke*, 2000; *Landsberg and Gower*, 1997; *Viereck*, 1983; *Van Cleve et al.*, 1983]. Vegetation regenerates with a tendency for more deciduous plants in younger stands before black spruce takes over [*Viereck*, 1983].As vegetation and moss regrow, dead and charred material is protected by burial into colder and wetter ground layers. The trees and moss layer often develop fully within 60 to 80 years following fire, and the stand's biomass may approach steady state [*Gower et al.*, 1997]. The reason for the reduction in biomass increment with maturity is unknown, though it may be related to declines in nutrient availability, hydraulic conductivity, leaf area index and/or increased autotrophic respiration rates [*Gower et al.*, 1996, *Ryan et al.*, 1997].

[5] Based on observations of recovery in a range of ecosystems, ecologists believe that Net Ecosystem Production (NEP; the net gain or loss of living and dead carbon by an ecosystem) follows an orderly progression through succession (Figure 1) [*Odum*, 1969; *Gorham et al.*, 1979; *Sprugel*, 1985; *Schulze et al.*, 2000]. Net Ecosystem Production represents the difference between Ecosystem Respiration (R_e; decomposition and autotrophic respiration) and Gross Primary Production (GPP; whole ecosystem photosynthesis). Understanding these component fluxes is critical to predicting trends in NEP. In theory, R_e should (1) initially rise following fire due to the decomposition of fire residue, (2) then decline as the fire residue disappears, and (3) finally rise as biomass and autotrophic respiration recover (Figure 1a). Also, in theory, GPP should (1) initially decline following fire due to the loss of leaf area, (2) then recover as leaf area increases, and (3) finally, decline with maturity (Figure 1b). Based on the combination of these responses, we expect that recently disturbed black spruce stands in Canada should be sources of CO_2, middle-aged stands should be sinks of CO_2, and older stands should be in near CO_2 balance with the atmosphere (Figure 1c) [*Odum*, 1969; *Gorham et al.*, 1979; *Sprugel*, 1985; *Schulze et al.*, 2000; *Harden et al.*, 1997; *Schulze et al.*, 1999; *Amiro*, 2001]. Of particular importance is being able to quantify at what age the inflexion points in GPP, R_e, and NEP occur, and how these may vary with both biome and climate.

[6] We tested this conceptual model of how R_e, GPP and NEP change in the Canadian boreal forest by making direct measurements of growing season net ecosystem exchange along an age sequence of five boreal stands in Manitoba, Canada using tower-based eddy covariance. The five sites were in various stages of secondary succession following large stand replacement fires that occurred in 1989, 1981, 1964, ~1930 and ~1870. We then used these data to quantify the influence of stand age on the maximum rates of midday net CO_2 uptake, nocturnal CO_2 efflux, and growing season NEP.

2. Materials and Methods

2.1. Chronosequence Stand Characteristics

[7] The five sites were in various stages of secondary succession following large stand replacement fires that occurred in 1989, 1981, 1964, ~1930 and ~1870. The oldest stand is the BOREAS Northern Study Area Old Black Spruce site (NOBS), located 50 km west of Thompson Manitoba [*Sellers et al.*, 1997].The four younger sites are close enough to NOBS (within 30 km) to experience similar weather over the course of a day (Table 1).

[8] Species composition, basal area, and stem density of canopy dominants, co-dominants, and seedlings were measured in each of the chronosequence sites in September 2001 (Table 2). Short (less than 0.3 m tall) seedlings and herbaceous plants were not included in this inventory. Leaf area index was determined using a LI-COR LAI2000. Because some deciduous plants had already lost their leaves in September, LAI reported in Table 2 is underestimated for the younger stands. Stand characteristics were measured in four 7.5 m × 7.5 m plots per site, one in each ordinal

Table 1. Locations and Measurement Dates of Fluxes in Stands in Age Sequence

	Latitude, Longitude	Measurement Dates
1989 burn	55°54′24″N, 098°58′48″W	23 July to 14 September 2000
1981 burn	55°51′52.8″N, 098°28′37.1″W	23 July to 14 September 2000
1964 burn	55°55′4.8″N, 098°21′59.2″W	28 May to 11 July 2000
1930 burn	55°54′48″N, 098°31′23″W	11 August to 08 September 1999
NOBS	55°2′49″N, 098°28′43″W	continuous

direction from the tower. Plot locations were established using random numbers to generate distances between 0–100 m from the tower. The younger sites (11, 19, and 36 year old stands) were mostly black spruce (*Picea mariana*) prior to burning, as determined by the woody debris that remained from the fire, and are expected to return to black spruce as they mature. The canopy in these young stands was largely a mixture of jack pine (*Pinus banksiana*), aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), willow (*Salix* spp.) and alder (*Alnus crispa*), with a black spruce understory (see Table 2 for stand characteristics). The older stands (70 and 130 year old stands) were dominated by a closed black spruce canopy and a well-developed moss layer (both sphagnum and feathermosses) (Table 2).

2.2. Experimental Design

[9] We used eddy covariance to directly measure the CO$_2$ and energy exchanges above five stands in central Manitoba during the 1999 and 2000 growing seasons (June–September). The forests in central Manitoba are well suited for eddy covariance. The region is generally level and the burns are large, providing ample fetch and increasing confidence in site-to-site comparisons of turbulent flux. Provisional tower locations were selected using Landsat imagery, burn history information from Manitoba Natural Resources, aerial photographs, and topographic maps. Precise tower locations were chosen during site visits to maximize site-to-site consistency in soil drainage (moderate- to well-drained) and fetch from uniform areas. The ages of the older stands were estimated by coring several trees at a height of 0.3 m from the ground and adding 5 years to the number of rings

to account for the approximate age black spruce reaches 0.3-m height. A meteorological station near each tower recorded soil temperature and moisture measurements beginning in summer 1999.

[10] The four youngest sites were remote, without line power and, in some cases, existing access trails. To measure CO$_2$ exchange in these areas we developed a portable eddy flux system that can be transported by helicopter, powered by solar panels, and operated unattended for a month or more. We used one of these systems in summer 1999 and three systems in summer 2000 to measure the above-canopy fluxes for 4–6 weeks of the growing season at the four sites. The first set of measurements were made late in the 1999 growing season above the 70 year old stand (Table 1). The second set of measurements were made early in the 2000 growing season at the 36 year old stand (Table 1). The third set of measurements was made in the second half of the 2000 growing season at both the 11 and 19 year old stands (Table 1). Fluxes and meteorological conditions at the 130 year old stand at NOBS were measured throughout 1999 and 2000 by Harvard University using equipment that has operated there since 1994 (see *Goulden et al.* [1997] for details on this system).

[11] We directly compared the fluxes measured by the portable systems in each of the younger stands with those measured simultaneously at NOBS using a paired tower experimental design [*McFadden et al.*, 1998; *Amiro*, 2001; *Eugster et al.*, 1997]. The long-term observations at NOBS provide a baseline for the interpretation of the data from the younger sites. Fluxes measured at NOBS from 1994 to 1996 show that daytime CO$_2$ uptake at a given temperature and light level is consistent from June through August [*Goulden*

Table 2. Means ± Standard Errors (Unless Otherwise Noted) of Canopy and Seedling Characteristics From the Four Plots Censused in Each Chronosequence Site[a]

Burn	Stand Age	Deciduous Component, % of total basal area	BS Diameter, cm	BS Height, m	Dominant Tree Height, m	Total Basal Area (Percent BS), m^2 ha^{-1}	Total Stem Density, N ha^{-1}	Leaf Area Index
				Canopy Characteristics				
1989	11	100	0	0	1	0.4 ± 0.07(0%)	9466 ± 2706	0
1981	19	67	0.7 ± 0.1	2.2 ± 0.05	4–5	5.1 ± 1.3 (2%)	24414 ± 3919	0.95
1964	36	31	2.7 ± 0.4	3.7 ± 0.4	5–6	18.6 ± 2.3 (18%)	20385 ± 5100	1.5
1930	~70	6	7.1 ± 0.4	7.4 ± 2.9	14–16	32.3 ± 4.7 (82%)	7644 ± 1184	2.9
OBS	~130	<1	7.6 ± 0.7	10.6 ± 1.5	17–20	29.1 ± 2.9 (99%)	6607 ± 683	2.4
				Seedling Characteristics				
1989	11	72	0.4 ± 0.05	0.3 ± 0.03		2.79 ± 1.7 (27%)	36700 ± 6053	
1981	19	3.5	0.9 ± 0.1	0.6 ± 0.03		0.59 ± 0.3 (74%)	11781 ± 4484	
1964	36		1.4 ± 0.12	0.8 ± 0.05		0.64 ± 0.23 (84%)	4029 ± 885	
1930	~70	7.2	1.0 ± 0.11	0.5 ± 0.03		0.14 ± 0.06 (93%)	1655 ± 680	
OBS	~130	70	0.9 ± 0.9	0.7 ± 0.08		0.18 ± 0.18 (100%)	2611 ± 412	

[a]The diameter of black spruce (BS) trees provided in canopy section (describes all trees greater than 1.3 m in height) is the measured value at breast height. The diameter of black spruce seedlings (<1.3 m height) given is basal diameter.

et al., 1997]. This implies that daytime observations made at one site in June can be reasonably compared to observations made at another site in August, after accounting for differences in light and temperature.

2.3. Portable Tower Measurements in 1999

[12] The main components of the portable flux system in summer 1999 were a 3-axis sonic anemometer (Solent HS, Gill Instruments) and a closed path CO_2/H_2O infrared gas analyzer (IRGA, Li-Cor model 6262). The measurements were made from a 20 m telescoping aluminum tower (Aluma Tower) and were powered by eight 90-watt solar panels (Siemens SR-90). Net radiation (REBS Q*7.1, Seattle, WA), incoming and reflected short-wave radiation (CM3, Kipp & Zonen), incoming and reflected photosynthetically active photon flux density (SZ-190, LI-COR), air temperature and relative humidity (HMP45C, Vaisala) were measured at the top of the tower.

[13] The IRGA operated in an insulated box at the base of the tower. A diaphragm pump pulled 7 standard liters of air per minute through a Teflon filter located 0.2 m behind the sonic anemometer, down a 25-m length of polyethylene tubing (I.D. 5/32″), and through the IRGA. Pressure was actively controlled in the IRGA's cell at 48 kPa (MKS Instruments). The lag introduced by the transit of air down the tower was 2.5 seconds, and did not change throughout the 6 week measurement period. The attenuation of fluctuations due to flow through the inlet filters, tubing and IRGA was modeled as a linear first-order filter. Time constants for CO_2 (0.41 s) and H_2O (0.44 s) were estimated based on analyses of cospectra (the difference in time response for CO_2 and H_2O was apparently caused by the interaction between water vapor and the tubing) [*Shaw et al.*, 1998]; The loss of CO_2 and H_2O flux at high frequencies was estimated by applying the modeled filter to temperature fluctuations measured by the sonic anemometer ($\overline{W'T'}$, where W' = vertical velocity fluctuations, and T' = temperature fluctuations) and calculating the ratio $F = \overline{W'T'}_{true}/\overline{W'T'}_{filtered}$. We assumed similarity between temperature, CO_2 and H_2O fluctuations and subsequently adjusted measured CO_2 and H_2O fluxes using F [*Goulden et al.*, 1997]. The response time corrections were typically 5% during the day and 15% at night.

[14] The IRGA was calibrated automatically for CO_2 every 6 hours by passing 350 ± 5% ppm of CO_2 (Scott-Marrin, Riverside, CA) in air through the sample cell at 1 standard liter per minute for 2 minutes followed by CO_2-free, dry air for 2 minutes. The H_2O channel was calibrated manually once a month with air of a known dew point (10°) (LI610 dew point generator, Li-Cor), and zero air. Stability of the H_2O channel gain was confirmed by comparison with the Vaisala humidity sensor located on the tower.

[15] The instruments from the portable flux system in 1999 were mounted on the NOBS tower for two weeks in September, 1999 for direct comparison to the long term NOBS flux system. The agreement between CO_2 fluxes calculated by the two systems was good (r^2 = 0.90, y = 1.03x + 0.01), with modest scatter due to timing offsets in the beginning and end of the 30 min blocks of data used to calculate the covariances (Figure 2a). Due to the short duration of the study, and frequent maintenance of closed-path system on NOBS (e.g., inlet filter changes, monitoring
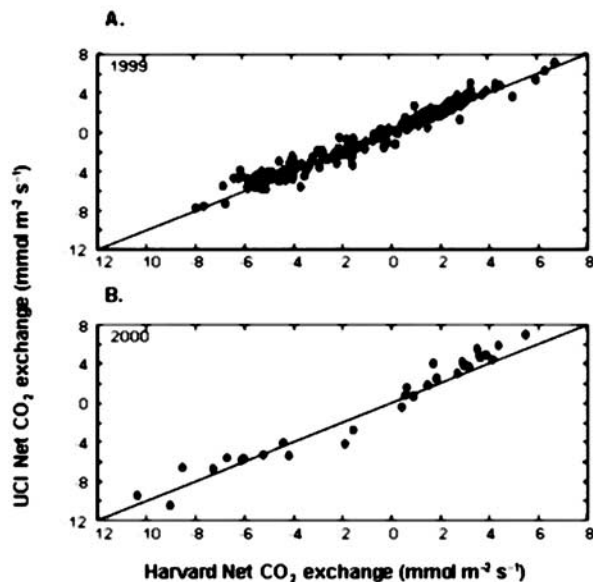

Figure 2. Comparison between 30 min averaged CO_2 fluxes measured by (a) portable system with closed-path IRGA (University of California, Irvine) and fixed tower at NOBS (Harvard) in 1999 and (b) portable system with open-path IRGA (University of California, Irvine) and fixed tower at NOBS (Harvard) in 2000 during system comparisons on NOBS tower. Line in both graphs is 1:1 line.

of pump rate, etc...), we assumed the agreement between the two systems remained constant.

2.4. Portable Tower Measurements in 2000

[16] We replaced the Solent anemometer with a Campbell Scientific 3-axis sonic anemometer (CSAT3) and the closed path IRGA with an open path IRGA (Li-Cor 7500) in 2000. We used three open path systems in 2000, which were compared prior to deployment. One of the portable open path systems was operated at the top of the NOBS tower for comparison to the long term NOBS system in August. The agreement was good during the day, but the closed path fluxes were approximately 25% less than the open path fluxes at night (Figure 2b). This discrepancy may indicate a different capacity of the two types of IRGAs to resolve high frequency fluctuations, and that the correction applied to the NOBS closed path data [*Goulden et al.*, 1997] underestimates high frequency attenuation. To compare fluxes measured by the open path systems with the long-term record at NOBS, we multiplied the open path fluxes at night by 0.75 for subsequent analyses. The open path CO_2 and H_2O channels were calibrated prior to installation on each tower using a span gas of 349 ± 5% ppm CO_2 (Scott Marin, CA) and air with a dew point of 10° (LI610).

[17] The flux instruments were positioned 3 to 5 m above the local canopy on the portable towers in both 1999 and 2000. Data for the covariance calculation (output from the sonic anemometer and IRGA) were recorded at 4 Hz, while output from air temperature, relative humidity, incident and reflected PPFD, incident and reflected solar radiation and net radiation sensors were recorded at 0.5 Hz. Raw data were stored on a laptop at the site for subsequent processing
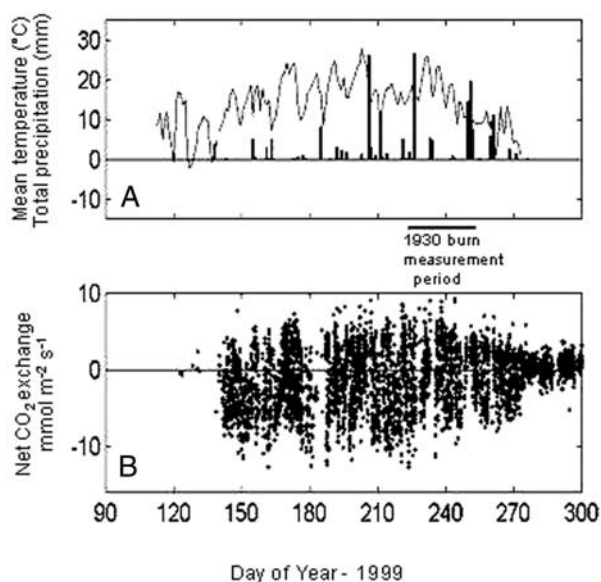
Figure 3. Measurement period in 70 year old stand in relation to (a) mean daily temperature and precipitation totals and (b) net CO_2 exchange at 130 year old NOBS from 1 April to 1 November 1999.

and calculation of 30 min sensible heat, latent heat, CO_2 and momentum fluxes using the Fortran programs developed by *Wofsy et al.* [1993] and *Goulden et al.* [1997].

[18] The open path IRGA measures molar density of CO_2 and H_2O (mol m^{-3}), whereas the turbulent flux is defined as the covariance between fluctuations of vertical velocity (W') and CO_2 (or H_2O) mole fractions in dry air (mol mol^{-1}) (C'). We used two independent ways to remove density fluctuations induced by temperature and water vapor fluctuations: (1) following equations of *Webb et al.* [1980] to correct the 30 min fluxes and (2) using the Ideal Gas Law to calculate the 4 Hz CO_2 and H_2O mole fractions in dry air. The two methods used to correct for density fluctuations differed by less than 3%. Thirty minute fluxes and means were also calculated in the field by the data logger (CR23X, Campbell Scientific). Fluxes calculated by the data logger and the Fortran processing code differed by less than 5%. When laptop failure resulted in the loss of 4 Hz data (as happened in the 1989 burn), fluxes calculated by the data logger were used for subsequent analyses. A subsample of the 30 min fluxes and sensor output means calculated by the data logger were transmitted by GOES satellite at three-hour intervals to confirm operation of the system throughout the study.

[19] We rejected flux data during subsequent analyses for periods with low atmospheric turbulence (friction velocity <0.2 m/s), malfunctioning instruments, and with prevailing wind directions from behind the tower [*Goulden et al.*, 1997]. Gaps in the data record during the periods indicated above were not filled.

3. Results

3.1. Seasonal and Interannual Patterns of Weather and CO_2 Exchange at NOBS

[20] The broad trends in air and soil temperatures at NOBS in April–October 1999 were similar to those in

April–October 2000. Spring warming occurred in mid to late May and autumn cooling occurred in mid-September of both years (Figures 3a and 4a). Periodic, short-term decreases in temperatures in the summer months of both years were associated with weather fronts. A closer look indicates that warmer temperatures in late May, early June and September extended the peak growing season in 1999 somewhat relative to 2000. From June 1 to September 1, total precipitation in the Thompson area was higher in 2000 (254 mm) than in 1999 (122 mm).

[21] The seasonal patterns and absolute rates of CO_2 exchange at NOBS in 2000 were similar to those observed in the previous year (Figures 3b and 4b). Mean midday light-saturated net CO_2 exchange (whole-ecosystem respiration minus whole-ecosystem photosynthesis, with more negative values indicating greater uptake) from June 1 to Sept 1 was similar during the two years (1999: -5.96 ± 0.30 μmol m^{-2} s^{-1}; 2000: -6.2 ± 0.34 μmol m^{-2} s^{-1}). Mean nocturnal CO_2 efflux (whole-ecosystem respiration, with more positive values indicating greater respiration) from June 1 to Sept 1 was slightly higher in 1999 (3.73 ± 0.09 μmol m^{-2} s^{-1}) than 2000 (3.24 ± 0.13 μmol m^{-2} s^{-1}).

[22] The 70 year old, 19 year old and 11 year old burns were studied in late summer, and the meteorological conditions and patterns of CO_2 exchange observed at NOBS during these periods imply that these fluxes can be compared directly (Table 3). In contrast, the fluxes at the 1964 burn were measured early in the summer, a period that the NOBS measurements indicate had lower air and soil temperatures and longer days (Table 3). A comparison of the daily carbon balance at NOBS from early to late summer indicates that NOBS is a carbon sink early in the growing season, but switches to a slight carbon source later in the year (Table 3) [*Goulden et al.*, 1997]. Hence the fluxes measured at the 1930, 1981 and 1989 stands and at NOBS in late summer
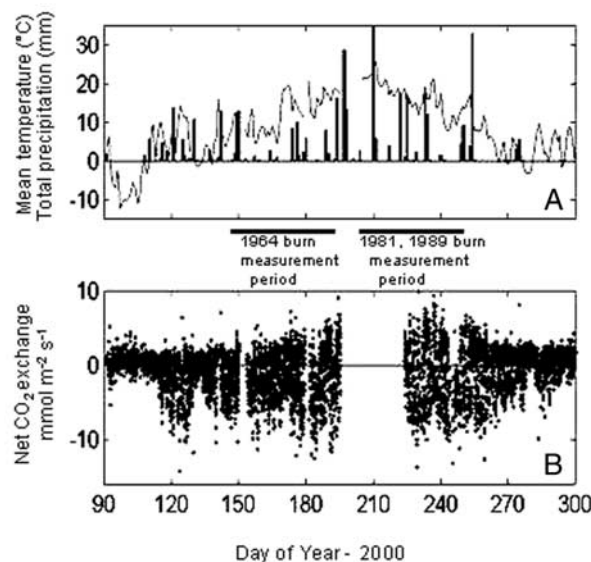

Figure 4. Measurement period in 11, 19, and 36 year old burns in relation to (a) mean daily temperature and precipitation totals and (b) net CO_2 exchange at 130 year old NOBS from 1 April to 1 November 2000.

Table 3. Weather Conditions and Net CO_2 Exchange Measured at NOBS During the Three Study Periods

Variable	Coincident With 1930 Burn Measurements (11 Aug. to 8 Sept. 1999)	Coincident With 1964 BURN Measurements (28 May to 11 July 2000)	Coincident With 1981–1989 Burn Measurements (23 July to 14 Sept. 2000)
T_{air} mean, °C	16.45	15.43	17.39
T_{air} max, °C	31.24	24.2	34.27
$T_{soil\ 2\ cm}$ mean, °C	10.2	8.7	11.4
Wind speed, m s^{-1}	3.81	3.2	3.7
Incoming PAR, μmol m^{-2} s^{-1}	333.74	403.3	338.65
Total precip, mm	75	71	185
Mean midday net CO_2 uptake, ●μmol m^{-2} s^{-1} (SE)	−6.65 (0.62)	−9.17 (0.56)	−7.89 (0.38)
Mean nighttime respiration, μmol m^{-2} s^{-1} (SE)	2.84 (0.14)	2.61 (0.09)	3.58 (0.15)
Daily carbon balance, kg C ha^{-1} d^{-1}	1.85	−10.4	1.4

can be compared, and the fluxes measured at the 1964 stand and at NOBS in early summer can be compared. However, caution is needed when comparing the fluxes measured at the 1964 stand to those measured at the other young stands.

3.2. CO₂ Flux at Younger Sites

[23] We compared the day-to-day patterns of CO_2 exchange at the younger stands to those simultaneously measured at NOBS to determine whether all of the sites respond in similar ways to variations in weather. The day-to-day trends in net ecosystem CO_2 exchange in the younger stands closely matched the variation at NOBS (Figures 5, 6, and 7), with the closest agreement between the 70 and 130 year old

stands. On cloudy days, relatively low net CO_2 uptake at NOBS coincided with low uptake in the 1930 burn (e.g., DOY 230–234, 243, Figure 5). Similarly, high nighttime ecosystem respiration at NOBS on warm nights coincided with high respiration in the 70 year old stand (e.g., DOY 238, 244; Figure 5).

[24] We calculated mean diurnal patterns of CO_2 flux for each site by binning the observations into half-hour intervals and averaging over the duration of each data set. This approach reduces sampling error and improves the confidence of comparing diurnal patterns between sites [*Moncrieff et al.*, 1996]. The results demonstrate the advantage of using closely matched measurement systems in nearby
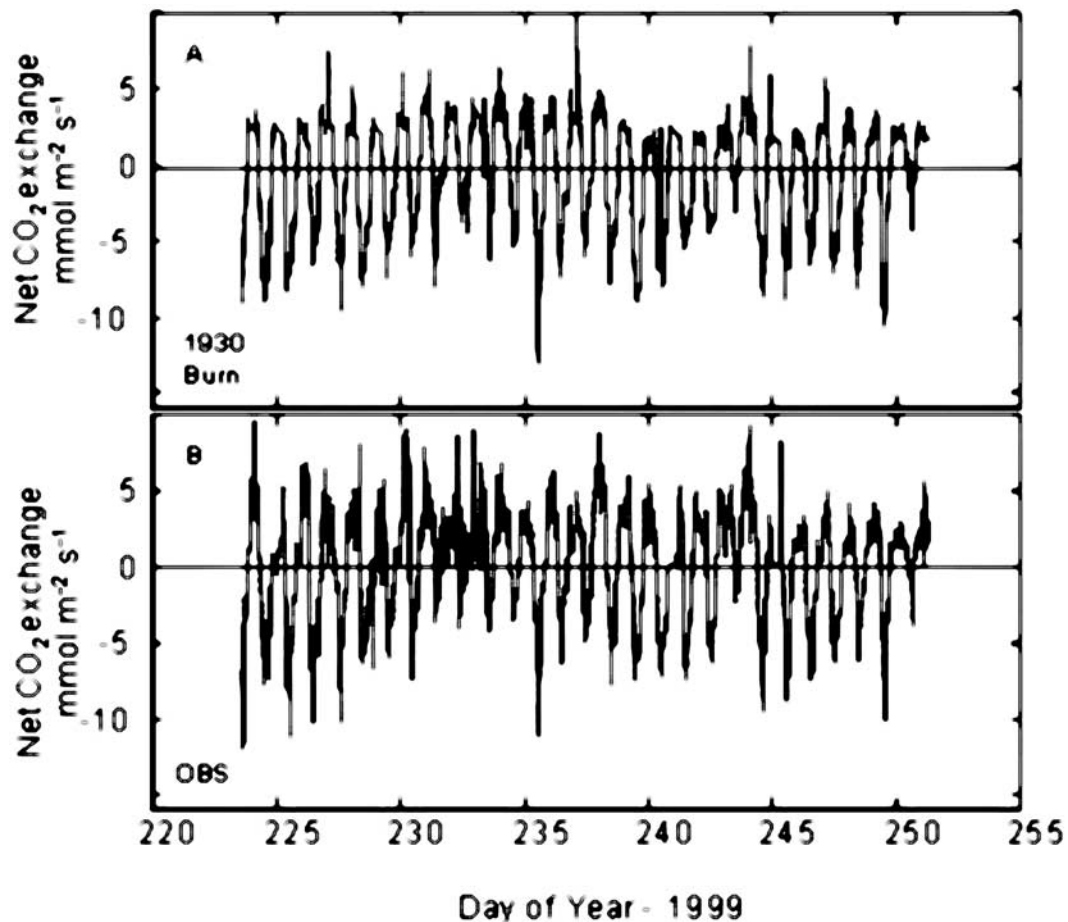

Figure 5. Four week record of 30 min averaged net CO_2 fluxes measured simultaneously (a) by portable eddy flux system over 70 year old stand and (b) by fixed tower system at 130 year old NOBS in 1999.
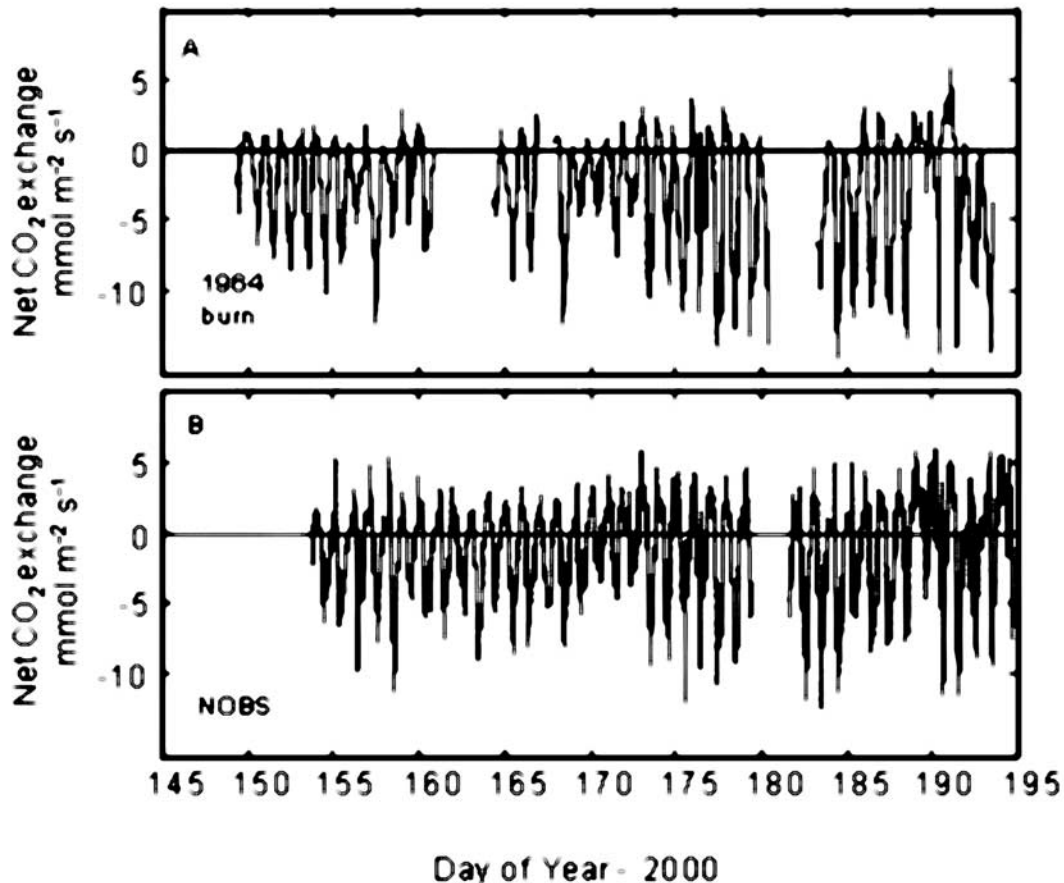
Figure 6. Six week record of 30 min averaged net CO_2 fluxes measured simultaneously (a) by portable eddy flux system over 36 year old burn and (b) by fixed tower system at 130 year old NOBS in 2000.

stands; small differences between sites are readily apparent despite large diurnal fluctuations in exchange within a site. For example, the 30-day records of fluxes measured simultaneously at the 70 and 130 year old stands indicate that light-saturated CO_2 uptake was consistently 1 μmol m^{-2} s^{-1} higher at the younger site, despite no difference in nighttime ecosystem respiration (Figure 8a).

[25] The deciduous foliage at the 36 year old stand began to emerge the last week in May, but peak uptake did not occur until after DOY 175, when mean daily temperatures increased to consistently above 10°C (Figures 4 and 6). Consequently, only the fluxes measured after DOY 175 in the 36 year old stand and NOBS were used for subsequent comparisons. After DOY 175, daytime CO_2 uptake at the 36 year old stand was at least 50% higher than that measured simultaneously at the 130 year old stand, whereas nighttime efflux was 20% lower at the younger stand (Figure 8b).

[26] The CO_2 exchange at both the 1989 and 1981 burns decreased noticeably in the first week of September, coincident with deciduous leaf senescence and a seasonal shift to lower mean daily air temperatures (Figures 4 and 7). For periods before DOY 245, mean midday net CO_2 uptake increased from -3.03 μmol m^{-2} s^{-1} at the 11 year old stand to -5.3 μmol m^{-2} s^{-1} at the 130 year old stand to -6.5 μmol m^{-2} s^{-1} at the 19 year old stand (Figure 8c). Nighttime respiration during this period was highest at the 130 year old

stand (3.6 $\pm$ 0.14 μmol m^{-2} s^{-1}), intermediate at the 19 year old stand (3.09 $\pm$ 0.09 μmol m^{-2} s^{-1}), and lowest at the 11 year old stand (2.35 $\pm$ 0.05 μmol m^{-2} s^{-1}) (Figure 8c).

[27] By combining these observations we see that light-saturated CO_2 uptake was lowest in the 11 year old stand, high in the 19 year old stand, highest in the 36 year old stand, and moderate in the 70 and 130 year old stands (Figure 8d). This trend remained the same when we examined differences in CO_2 fluxes in the younger burns relative to simultaneous measurements made at NOBS (Table 4). Only the 11 year old stand had lower CO_2 uptake during the day than NOBS.

[28] Nocturnal CO_2 efflux increased from the 11 year old stand to the 19 year old stand, but then decreased in the 36 year old stand before peaking at the 70 and 130 year old stands (Figure 8d). Nighttime respiration ranged from a low of 2.5 μmol m^{-2} s^{-1} in the 36 year old stand, to a high of 5.2 μmol m^{-2} s^{-1} in the oldest stand (Figure 9). However, based on the continuous record of fluxes at NOBS, it is likely that the low respiration rates observed in the 36 year old stand are attributable in part to the cooler nights and soil temperatures that occurred early in the growing season. The simultaneous measurements at NOBS were therefore used to normalize the nighttime CO_2 efflux in each burn to reduce the influence of differences in weather. These observations indicate a slightly different pattern of ecosystem respiration along the chronosequence with the youngest burn having the lowest rates of
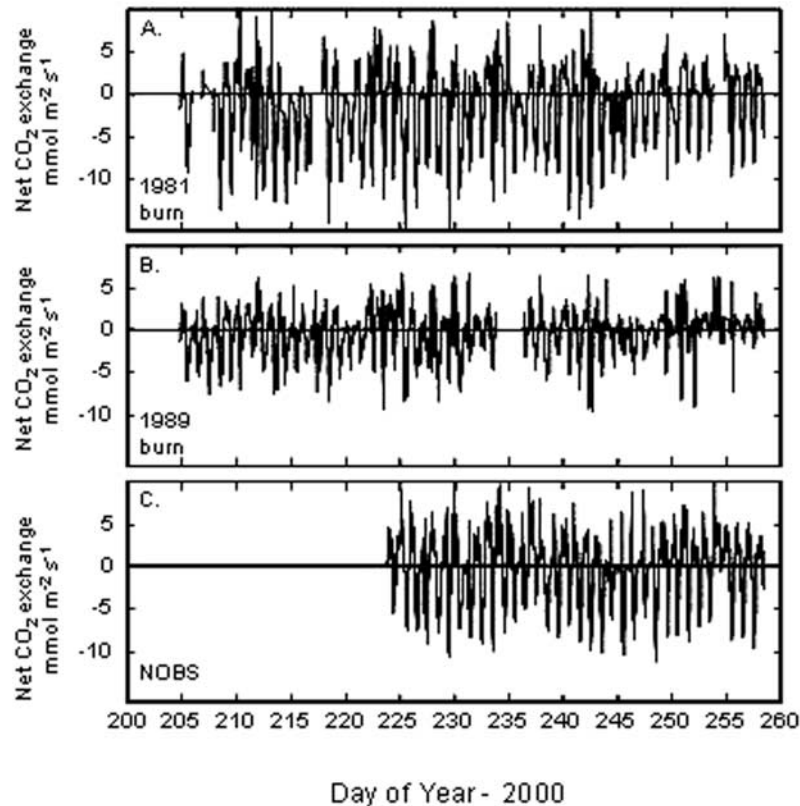
Figure 7. Six week record of 30 min averaged net CO$_2$ fluxes measured simultaneously in (a) 19, (b) 11, and (c) 130 year old stand in 2000.

nighttime CO$_2$ release. The normalized nighttime CO$_2$ effluxes indicate a consistent increase in respiration as the stands mature (Table 4). Respiration in the 11, 19, 36, and 70 year old stands were 32%, 15%, 18%, and 0.5% lower, respectively, than those measured simultaneously at the 130 year old stand.

3.3. Carbon Balance Along the Age Sequence

[29] Integrated daily carbon balance varied from a slight sink at the 11 year old stand, to a modest sink at the 19 year old stand, to a large sink at the 36 year old stand, to a modest sink at the 70 year old stand to around zero at the 130 year old stand (Figure 9). This pattern is supported by analyses of the carbon exchange at each of the younger burns relative to the simultaneous exchange at NOBS (Table 4). All of the younger stands gained carbon on a daily basis relative to NOBS during the peak-growing season, with the 36 year old stand sequestering the highest amount (24 kg C ha^{-1} d^{-1} more than NOBS). The amount of carbon sequestered by the 1964 burn relative to NOBS on a daily basis was 66%, a factor of 3, and an order of magnitude more than the sink strength in the 19, 70, and 11 year old stands relative to NOBS, respectively.

4. Discussion

4.1. Absolute Changes in Ecosystem Carbon Balance With Stand Age

[30] The measurements at the four younger sites were limited to 1 to 2 months in the growing season, and annual
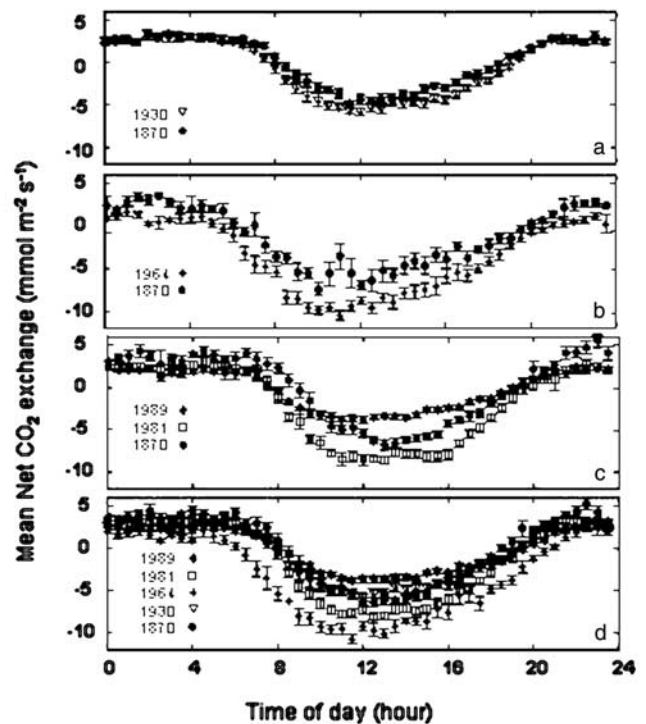

Figure 8. Means and standard errors of diurnal patterns in net CO$_2$ exchange measured simultaneously at (a) NOBS and the 70 year old stand, (b) NOBS and the 36 year old stand, (c) NOBS and the 11 and 19 year old stands, and (d) all chronosequence sites together.

Table 4. Integrated Measures of Daily and Growing Season Carbon Balance Relative to NOBS From Simultaneous Measurements at Burns and NOBS

Burn Year	Mean Daytime Net CO$_2$ Exchange Relative to NOBS, μmol CO$_2$ m^{-2} s^{-1}	Mean Nighttime CO$_2$ Exchange Relative to NOBS, μmol CO$_2$ m^{-2} s^{-1}	Daily Carbon Balance Relative to NOBS, g C m^{-2} day^{-1}	Growing Season Carbon Balance Relative to NOBS,[a] t C ha^{-1}
1989	+2.25	−1.57	−.41	−0.37
1981	−2.6	−1.16	−2.1	−1.9
1964	−2.1	−2.0	−2.5	−2.3
1930	−1.2	−.05	−.73	−0.9

[a]Assume 90 days peak growing season (i.e., summer carbon balance) for 1989, 1981, and 1964 burns and 120 days for the 1930 burn.

measurements at each site will be needed to reliably assess the relationship between stand age and NEP. Nonetheless, we can make a rough estimate of the NEP at each site for comparison to the rates of carbon exchange expected based on the accumulation of biomass. The annually integrated observations at NOBS indicate the 130 year old stand is in approximate carbon balance with the atmosphere [*Goulden et al.*, 1998]. If we do a simple extrapolation assuming all sites lose 0.5 tC in winter [*Goulden et al.*, 1998] and the younger burns with large deciduous components have a 90-day growing season, we estimate that the 11 year old stand is losing 0.25 t C ha^{-1}yr^{-1}, the 19 year old stand is sequestering 0.5 t C ha^{-1}yr^{-1} and the 36 year old stand is sequestering 1.5 t C ha^{-1}yr^{-1}. If we assume the older burns have a 120-day growing season, the 70 year old stand is sequestering 0.5 t C ha^{-1} yr^{-1}.

[31] The biomass of the 130 year old stand at NOBS is about 95 t C ha^{-1}, with half of this mass in trees and the other half in moss [*Goulden et al.*, 1998]. The best estimates for direct combustion losses in this region of the Canadian boreal forest are about 12.5 t C ha^{-1}, with maximum losses up to 23.5 t C ha^{-1} [*Amiro et al.*, 2001]. If we assume the carbon remaining decomposes fully within 130 years of the burn, then the net accumulation of carbon over the regrowth cycle should be about 15–25 t C ha^{-1}. If we extrapolate our tower-based NEP estimates from one age to the next assuming a linear transition, and assume a winter respiratory loss of 0.5 t C ha^{-1} y^{-1} [*Winston et al.*, 1997], the accumulated carbon gain over a 130 year old stand's life should be 55 t C ha^{-1}. While this sum is somewhat higher than that estimated from the biomass analysis, the overall agreement is reasonable given the short duration of the mobile tower observations and uncertainty in the integration, amount of carbon lost in the fire, and respiration losses in the first ten years or winter.

4.2. Relative Changes in CO$_2$ Exchange With Stand Age

[32] The paired tower approach proved well suited to determining the relative changes in CO$_2$ exchange with stand age. Using this approach, we easily resolved differences in CO$_2$ uptake, respiration, and daily carbon balance among the different stands. For example, the 70 year old site stored on average 6 to 10 kg of C ha^{-1} day^{-1} more than OBS. This relatively large difference in NEP was caused by a relatively subtle difference of 10 to 20% in instantaneous daytime uptake. We were able to confidently resolve this difference because the processing code and the instruments at the two sites were either similar or intercalibrated. In addition, by working at sites that were close enough to experience similar weather, we eliminated the confounding

effects of site-to-site differences in climate and were able to focus on the effects of stand structure, species composition, forest physiology, and phenology.

[33] Ecosystem respiration was lowest in the youngest stands and highest in the oldest stands. We did not observe the high rates of respiration in the youngest stands that we expected (Figure 1a) [*Richter et al.*, 2000; *Schulze et al.*, 2000]. Instead, our tower-based results imply that fire residue takes a long time to decompose and is not lost in the first decades after fire. This pattern is consistent with field observations of decomposing logs still present in the 1930 burn, buried beneath the moss. The 1981 and 1989 burns had large amounts of woody debris that easily supported the weight of a person and that had not yet fully contacted the ground. Since decomposition increases once the organic debris has full contact with moisture at the ground surface [*Harmon et al.*, 1986], this is consistent with the relatively low respiration we observed at the 1989 stand. The increase in nocturnal CO$_2$ flux with stand age we observed may be explained by higher autotrophic respiration rates in older stands required to maintain accumulating biomass [*Ryan and Waring*, 1992].

[34] The site-to-site differences in daytime uptake were consistent with those expected based on the conceptual model of secondary succession (Figure 1b) [*Odum*, 1969; *Gorham et al.*, 1979; *Sprugel*, 1985]. Canopy photosyn-
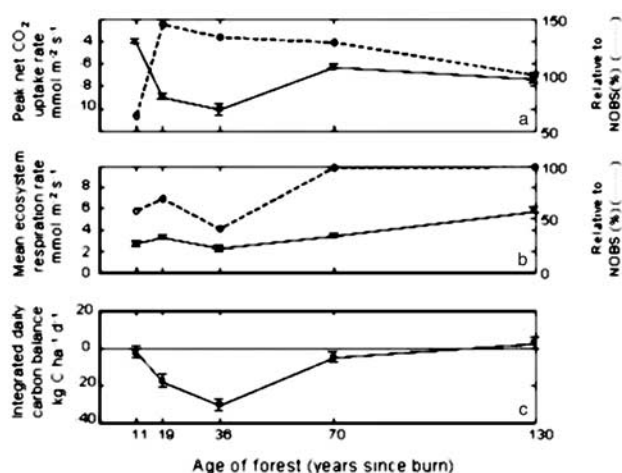

Figure 9. Patterns in measured (a) peak net CO$_2$ uptake, (b) mean nighttime respiration, and (c) daily carbon balance along chronosequence (solid lines). Error bars are standard errors. Dashed lines in Figures 9a and 9b are percent of measured values in younger burns relative to simultaneous measurements made at NOBS.

thesis was low in the most recent burn, highest in the 18 and 36 year old stands, and moderate in the older sites. This age-dependent pattern of canopy photosynthesis is likely due to coincident changes in leaf area and species composition in chronosequence sites (Table 2). Canopy composition shifted from co-dominant deciduous species (primarily aspen), jack pine and black spruce in the 36 year old stand to closed-canopy black spruce in the 70 and 130 year old stands. Thus the decrease in daytime CO$_2$ uptake from the 36 to the 70 year old stand is likely a consequence of the lower leaf-level photosynthetic rates observed in black spruce compared to aspen and jack pine [*Middleton et al.*, 1997; *Dang et al.*, 1997; *Flanagan et al.*, 1997]. The small decrease in daytime CO$_2$ uptake from the 70 to 130 year old stand is consistent with age-related declines in NPP observed in other ecosystems, and may reflect a change in LAI, leaf photosynthesis, hydraulic restriction, or canopy architecture [*Gower et al.*, 1996; *Ryan et al.*, 1997].

[35] The pattern of NEP we observed in the chronosequence sites is similar to predictions of the conceptual model (Figure 1c) and limited observations in forested ecosystems. We found that carbon uptake offsets decomposition between 11 and 19 years after a burn. *Rapalee et al.* [1998] suggest that this transition occurs about 30 years after fire in central Manitoba. Estimates for the carbon balance compensation point in other ecosystems are around 10 years for regenerating logged Siberian pine stands [*Schulze et al.*, 1999], and 20 years for regenerating coniferous forests in the Pacific Northwest [*Cohen et al.*, 1996]. The age-related pattern of NEP we observed differs somewhat from that reported by *Schulze et al.* [2000] for Siberian pine. Compared with *Schulze et al.* [2000], we found a smaller initial respiration peak, a much shorter period of peak carbon accumulation, and a larger decline in carbon accumulation by older stands.

4.3.   Implications for Boreal Regional Carbon Balance

[36] It is clear that stand age is critical to understanding the carbon balance of boreal forests on a regional basis. Most of the net biomass accumulation appears to take place from 20 to 70 years after a fire, with the highest rates of accumulation in a relatively brief 30-year period. Stands younger than 20 years appear to lack sufficient leaf area for rapid carbon accumulation and stands older than 70 years appear to be in near zero carbon balance with the atmosphere.

[37] The brief period of rapid carbon accumulation increases the likelihood that a change in fire frequency will cause a large shift in regional C balance. For example, an increase in fire suppression should initially cause the region to become a carbon sink since CO$_2$ released during combustion would be reduced while some of the stands across the landscape would be in their prime carbon-gaining period. If fire suppression continued, the landscape should approach steady state with the atmosphere within about a half-century, as most of the stands reach maturity and are no longer carbon sinks. If fire suppression were then decreased, depending on which stands burned, burn frequency and severity, the region could become a large source of CO$_2$ for at least 20 years, the time required for the burned stands to begin actively accumulating carbon. Hence an increase in fire suppression could initially increase C storage, but the

effect would be transient, and a subsequent decrease in fire suppression could cause the region to lose carbon for an extended period of time.

[38] Approximately 53% of the land cover in the 733 km^2 around OBS was classified as black spruce in 1994 [*Rapalee et al.*, 1998]. Of this 53%, approximately 23% last burned in 1981, 9% in 1952 to 1965, 57% in 1904 to 1949 and 11% before 1904. (The area burned in 1989 was not considered by *Rapalee et al.* [1998]). Only a small proportion of the black spruce forest in the region is accumulating carbon at high rates (the 9%, which includes our 36 year old stand). The large spatial heterogeneity in CO$_2$ exchange that occurs with ecosystem recovery has implications for efforts to use eddy covariance to assess regional carbon balance. The results from any single tower are unlikely to be representative of the entire region, and a large number of randomly placed towers will be required to accurately measure regional exchange. Hence assessments of regional carbon balance, at least in boreal regions, will require a more sophisticated approach that incorporates information on (1) the fractional coverage of stands in different age classes, and (2) measurements of ecosystem gas exchange by representative stands within each age class. It is not possible to predict the CO$_2$ balance of boreal regions without understanding how CO$_2$ exchange changes as stands mature.

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