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# Age-dependent response of boreal forest to temperature and rainfall variability

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## Abstract

We used measurements of CO<sub>2</sub> exchange by six Canadian boreal forest stands to determine how sites of contrasting age respond to interannual temperature and precipitation variation. The stands ranged in age (time since last burn) from 4 to 155 years. The study included years that were anomalously cool and moist, warm and dry, cool and dry, and warm and moist. Warmer than average springs accelerated the onset of older stand (>20 years) photosynthesis by as much as 37 days and younger stand (<20 years) photosynthesis by as much as 25 days. The warm-dry year resulted in a marked reduction of mid-summer CO<sub>2</sub> uptake by the younger, but not older, stands. The mid-summer decline in young stand photosynthesis reflected the combination of warmth and drought; similar declines were not observed during the cool-dry or warm-moist years. The annual carbon gain by the oldest stands was greatest during the warm-dry year as a result of the expanded growing season. The annual carbon gain by the youngest stands was consistent from year to year, largely as a result of offsets between increased spring photosynthesis and reduced mid-summer photosynthesis during the warm-dry year. Night-time CO<sub>2</sub> efflux increased by 2–29% during the warm-moist year relative to the warm-dry year. This increase was not systematically related to age. We conclude that the major source of interannual CO<sub>2</sub> exchange variation at the landscape scale is the ability of older, evergreen canopies to respond to warm springs by advancing the onset of photosynthesis. Drought-related reductions in photosynthesis, moisture-driven respiratory losses, and the effects of spring warmth on young-stand photosynthesis are of secondary importance. The advantage conferred on older, evergreen stands during warmer years carries implications for the possible effects of climate change on boreal forest succession. Warmer temperatures may increase the competitive advantage of late successional species relative to early successional species, and also the incidence of fire, thereby accelerating plant succession and shortening the fire-return interval.

*Keywords:* boreal forest, CO<sub>2</sub> exchange, eddy covariance, interannual variability

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## Introduction

Interannual variability is recognized as a 'universal characteristic' of terrestrial ecosystems (Richardson *et al.*, 2007). Multiyear eddy covariance studies have repeatedly found that the fluxes of carbon dioxide, water vapor, and energy vary substantially from year to year (Baldocchi *et al.*, 2001). The major external source of interannual CO<sub>2</sub> exchange variability is thought to be interannual weather variability, though internal sources, such as year-to-year changes in the biotic

response to weather, may be important in some cases (Hui *et al.*, 2003). Understanding how terrestrial ecosystems respond to interannual weather variability is crucial for detecting secular trends in forest functioning and for predicting the effect of projected climate change on forest productivity. In the boreal biome, it is particularly important to assess the biotic response to weather because (a) boreal forests occur at a latitude where projected temperature increases are large (Serreze *et al.*, 2000), (b) boreal forests account for a large portion of terrestrial biomass and their rates of mass and energy exchange have global significance (Sellers *et al.*, 1997), and (c) the temporal and spatial variability of boreal forests is controlled by the effects of wildfire, a process

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that involves several feedbacks to climate (Randerson *et al.*, 2006).

Two climatic features have emerged as important determinants of boreal forest interannual variability: warm springs and hot, dry summers (Welp *et al.*, 2007). Observational studies in mature boreal forests have shown that carbon uptake is generally increased during years with extended growing seasons (Chen *et al.*, 1999; Black *et al.*, 2000; Arain *et al.*, 2002; Barr *et al.*, 2002). When early springs are followed by hot, dry summers, the carbon gains accrued during spring may be offset by a reduction in photosynthesis during summer (Ciais *et al.*, 2005). Angert *et al.* (2005) provide satellite-based evidence for this effect; Barber *et al.* (2000) provide a tree-ring record indicating that the productivity of boreal trees, which had increased from 1900 to 1970, began to decrease around 1970, possibly due to increased drought stress.

The task of characterizing the response of the boreal forest biome to interannual weather variations is challenging, because interannual variability takes place against the backdrop of successional recovery from wildfire, another dominant mode of variability. Forest structure and function change markedly during secondary succession (e.g. McMillan & Goulden, 2008). The boreal landscape is a patchwork of differently aged forests, which range from almost 100% deciduous to almost 100% evergreen. Chronosequence studies have characterized the age dependence of carbon dynamics in boreal forest (Schulze *et al.*, 1999; Litvak *et al.*, 2003; Bond-Lamberty *et al.*, 2004; Goulden *et al.*, 2006), but few have attempted to measure the response to anomalous weather along age transects (Kljun *et al.*, 2006; Welp *et al.*, 2007). Determining the age-dependent response of forests to interannual weather variation requires multiple-year records at multiple sites that differ in age (a chronosequence). Here, we report the interannual variability of net CO<sub>2</sub> exchange at six boreal forest sites that range in age from 4 to 155 years since burn. The study spanned a 4-year period, which included large variability in rainfall and temperature. We compare the sensitivity of photosynthesis and ecosystem respiration to interannual weather variability over the spring and summer, and discuss their combined effect on annual carbon exchange and successional dynamics.

## Materials and methods

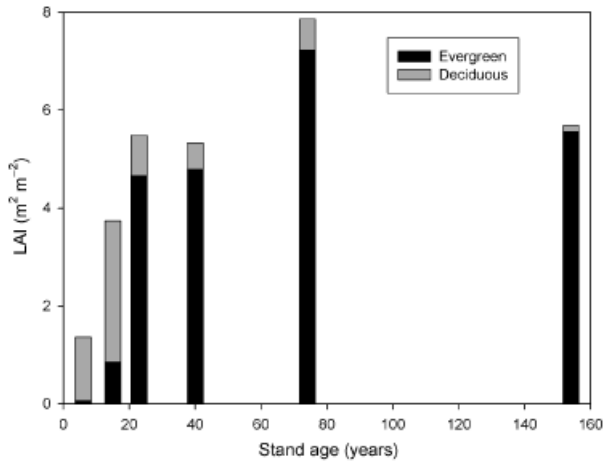
### Site descriptions

The study was conducted in Northern Manitoba, Canada, within 100 km of the BOREAS Northern Study Area (Sellers *et al.*, 1997; Goulden *et al.*, 2006). Our sites comprised a mature black spruce (*Picea mariana* [Mill.]

BSP) forest, denoted here as UCI-1850, and five younger stands at various stages of succession following stand replacing wildfire (Table 1). All stands were even-aged and resulted from stand-killing wildfires that occurred in ~1850, ~1930, 1964, 1981, 1989, and 1998. The youngest stands (UCI-1989 and UCI-1998) were dominated by herbaceous, ruderal species, including Fireweed (*Epilobium augustifolium*), with tree species present only as seedlings. Medium-aged stands were dominated by jack pine (*Pinus banksiana* Lamb.) and Aspen

**Table 1** Site descriptions

Site	Location	Conditions in summer 2005
UCI-1850	55°52'45"; 98°29'2"	Closed canopy of 14–18 m tall black spruce. Nearly 100% feather moss cover. Open understorey with a few alders, Labrador tea, and willow.
UCI-1930	55°54'21"; 98°31'29"	Closed canopy of 12–20 m tall black spruce, with a few senescent jack pine and aspen. Nearly 100% feather moss cover. Significant shrub layer of alder, willow, and Labrador tea.
UCI-1964	55°54'42"; 98°22'56"	Moderately dense stand of 500–700 cm tall jack pine and aspen, with significant mortality and thinning. Many 200–600 cm tall black spruce. Ground cover of feather moss with sparse grass.
UCI-1981	55°51'47"; 98°29'6"	Dense stand of 500-cm-tall jack pine with scattered 500-cm-tall aspen. Many 100–200 cm tall black spruce. Continuous ground cover of grass, Labrador tea, willow, and wild rose. Mix of sphagnum and feather moss. Most black spruce trees killed by the 1981 fire had fallen before 2000.
UCI-1989	55°55'0"; 98°57'52"	Thick layer of wild rose, grass, Labrador tea, fireweed, alder, and willow. Extensive firemoss with patches of sphagnum ( <i>Sphagnum</i> spp.) and feather ( <i>Ptilium</i> , <i>Pleurozium</i> or <i>Hylocomium</i> spp.) moss. Many 20–100 cm tall black spruce, 100–200 cm tall jack pine, and 50–400 cm tall aspen. Most black spruce trees killed by the 1989 fire fell from 2000 to 2005.
UCI-1998	56°38'9"; 98°12'58"	Thick, patchy layer of fireweed, wild rose, grass, Labrador tea, alder, and patchy firemoss. Many 10–25 cm tall black spruce. Almost all the black spruce trees killed in the 1998 fire were still standing.



**Fig. 1** Leaf area index (LAI;  $\text{m}^2 \text{m}^{-2}$ ) as a function of stand age. Shading indicates the contributions from deciduous and evergreen species.

(*Populus tremuloides* Michx.) saplings at UCI-1981, and a mix of jack pine and black spruce at UCI-1964. Other overstory species at these sites included tamarack (*Larix laricina* [Du Roi] Koch.) and paper birch (*Betula papyrifera*). The older stands (UCI-1850 and UCI-1930) were closed-canopy black spruce forests with a well-developed moss layer, comprising sphagnum (*Sphagnum* spp.) and feather moss (*Pleurozium* or *Hylocomium* spp.). Leaf area index (LAI) increased rapidly with age in the younger stands (Fig. 1). The fraction of LAI composed of evergreen species increased from 5% to 85% in the first 24 years of succession, and then increased to a maximum of 98% with further increases in age. The nearest long-term weather station was at Thompson, MB, 43 km east of UCI-1930. We obtained historical weather data from this site for 1967–2005 from <http://www.climate.weatheroffice.ec.gc.ca>.

### Measurements

We used eddy covariance to measure the  $\text{CO}_2$  and energy exchange by the six stands (Goulden *et al.*, 2006). We used closed-path eddy covariance systems with sonic anemometers (CSAT3, Campbell Scientific, Logan, UT) and air intakes mounted on towers  $\sim 3$  m above the canopies. Air was drawn down the towers to infrared gas analyzers (LI-COR 7000, Lincoln, NE, USA) that measured  $\text{CO}_2$  and water vapor concentration. Net radiation (REBS Q\*7.1, Seattle, WA, USA), incoming and reflected short-wave radiation (CM3, Kipp and Zonen, Delft, the Netherlands), incoming and reflected photosynthetically active photon flux density (PPFD) (SZ-190, LI-COR), air temperature, and relative humid-

ity (HMP45C, Vaisala, Helsinki, Finland) were measured at the tops of the towers.

The turbulent fluxes of  $\text{CO}_2$  and water vapor were calculated from 4-Hz observations, with the following corrections: (1) a trigonometric rotation of the 3-D wind field to force the mean vertical wind to zero (McMillan, 1988), (2) adjustment for the loss of high frequency fluxes due to the transport of  $\text{CO}_2$  and water vapor through the tubing (Shaw *et al.*, 1998), and (3) adjustment for the lack of energy closure (Twine *et al.*, 2000).

We calculated the saturation vapor deficit (SD) and estimated seasonal changes in water balance. The saturation deficit of air was calculated as follows:

$$\text{SD (kPa)} = (1 - \text{RH}) \times 0.611 \exp \left[ \frac{L_v}{R} \times \left( \frac{1}{T_0} - \frac{1}{T_{\text{air}}} \right) \right], \quad (1)$$

where SD is the saturation deficit of air, RH the relative humidity,  $R$  the gas constant for air ( $461 \text{ J K}^{-1} \text{ kg}^{-1}$ ),  $T_0 = 273.2 \text{ K}$ ,  $T_{\text{air}}$  the air temperature (K), and  $L_v$  is the latent heat of vaporization which was calculated as  $L_v = (2.501 - 0.00237 \times T_{\text{air}}) \times 10^6$ .

The cumulative water balance was calculated at each site as follows:

$$W_t = W_{t-1} + \text{MELT} - F_{\text{H}_2\text{O}} + P, \quad (2)$$

where  $W_t$  is the cumulative water balance (cm) at time ( $t$ ),  $W_{t-1}$  the water balance on the previous day, MELT the daily contribution to the water balance from melting snow (cm) based on measurements of snow pack depth and a snow density of  $0.1 \text{ g cm}^{-3}$ ,  $F_{\text{H}_2\text{O}}$  the daily water vapor exchange with the atmosphere (cm), and  $P$  is the daily precipitation (cm). Snow pack depth and precipitation were obtained from the weather record at Thompson Airport, and  $F_{\text{H}_2\text{O}}$  was the eddy covariance flux for each site. Seasonal changes in water balance were similar among sites and we averaged the water balance across the UCI-1850, UCI-1964, and UCI-1989 sites.

Ideally, vertical profiles of  $\text{CO}_2$  would be measured so that the storage term could be accounted for (Goulden *et al.*, 1996). Under atmospherically stable conditions, there is insufficient turbulence to transport air parcels past the sensor, leading to an accumulation of  $\text{CO}_2$  within the canopy that may either be horizontally advected or stored until turbulent conditions return. However, the additional power requirements and logistics necessary for profile measurements were prohibitive for this study. Papale *et al.* (2006) reported that storage had only a small effect on the calculated Net Ecosystem Production (NEP) at eight forest sites in Europe. Papale *et al.*, found that including or neglecting storage changed the annual NEP by just  $-1\%$  to  $8\%$  at sites with developed canopies ( $\text{LAI} > 2$ ). We estimate

that the NEP at UCI-1850 could be as much as  $10\text{--}20\text{ g C m}^{-2}\text{ yr}^{-1}$  more negative if a storage term were included. At younger sites, with shorter, more open canopies,  $\text{CO}_2$  storage would be less important and the error with neglecting storage would be smaller. Our failure to account for  $\text{CO}_2$  storage may have affected the fine details of the age-dependent changes in carbon accumulation with succession, but is unlikely to have altered our main findings.

#### Data analysis

We prepared two  $\text{CO}_2$  flux datasets for analysis: a discontinuous, nongap-filled set and a continuous, gap-filled set. The two datasets were complimentary. The first provided fluxes that had the minimum processing required for interpretation and were not subject to biases introduced by gap filling. The second set was continuous and could be integrated to longer time scales (for example, to calculate annual fluxes), but may be subject to gap-filling artifacts.

The discontinuous, nongap-filled dataset was created from the 30 min covariances. We calculated the daily average  $F_{\text{CO}_2}$  for periods with incoming PPF  $> 600\ \mu\text{mol m}^{-2}\text{ s}^{-1}$ , and refer to this as the daytime uptake. We calculated the daily average 30 min  $\text{CO}_2$  flux at night (incoming PPF  $< 10\ \mu\text{mol m}^{-2}\text{ s}^{-1}$ ) when the friction velocity ( $u^*$ ) was above  $0.2\ \text{m s}^{-1}$  (Goulden *et al.*, 1996), and refer to this as the night-time efflux.

The continuous, gap-filled dataset accounted for data loss from instrument failure and inadequate turbulence ( $u^*$  correction). We created a modeled respiration dataset based on the relationship between air temperature and night-time efflux (Lloyd & Taylor, 1994) after removing periods with  $u^* < 0.2\ \text{m s}^{-1}$ . We recalculated the temperature sensitivity term in the model at 5-day intervals, because it is known to vary on short (sub-monthly) timescales (Reichstein *et al.*, 2005). Gaps at night were filled with the modeled respiration dataset. Gaps during the day were filled using modeled daytime net uptake calculated from a three parameter hyperbolic fit between existing daytime  $\text{CO}_2$  uptake and incoming photosynthetically active radiation (PAR) (Falge *et al.*, 2001). Two-month time windows were used for the regressions. When regression statistics indicated a poor fit ( $r^2 < 0.1$  for night-time efflux or  $r^2 < 0.4$  for daytime exchange), remaining gaps were filled by diurnal look-up tables and/or linear interpolation. The gap filling for daytime uptake was done over a series of temperature ranges to account for short-term changes to the photosynthetic light response that may occur under fluctuating water or temperature conditions.

## Results

### Weather

The seasonal variation in air temperature at Thompson Airport during the study was extreme (Fig. 2a). Daily averages ranged from below  $-20\ ^\circ\text{C}$  in winter to  $17\ ^\circ\text{C}$  in summer. The year-to-year variation was especially pronounced in April and May ( $12\ ^\circ\text{C}$ ) and comparatively minor in July ( $< 3\ ^\circ\text{C}$ ). Spring was more variable than fall. The years 2003 and 2005 were comparatively warm years, and 2002 and 2004 were comparatively cool years. Degree-day accumulation from April to June was more rapid in 2003 and 2005 than in 2002 and 2004, and the difference persisted throughout the growing season (Fig. 2b).

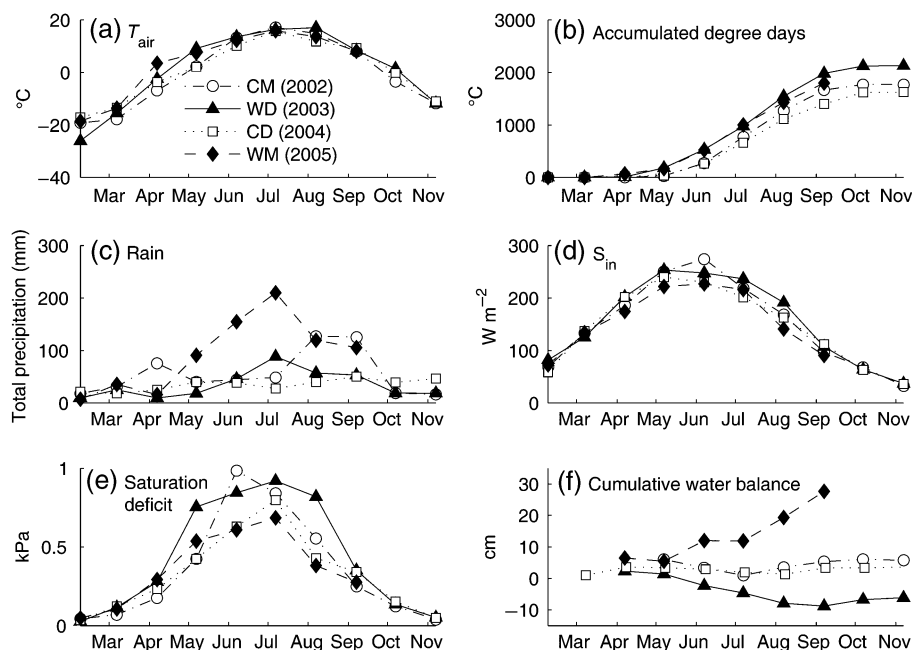
The seasonal distribution and total amount of precipitation over the growing season varied widely from year to year (Fig. 2c). Peak rainfall occurred in mid-summer of the two warm years (2003 and 2005) and in late summer of the two cooler years (2002 and 2004). Total May to September rainfall ranged from 219.9 mm in the driest year (2003) to 716.8 mm in the wettest year (2005). The summer of 2005 was extraordinarily wet, with extensive regional flooding and the highest cumulative rainfall recorded since 1967.

The interannual variability in incident solar radiation was greater during early summer, and the June average varied by  $50\ \text{W m}^{-2}$  from 2002 to 2005 (Fig. 2d). The lowest values occurred in the wettest year (2005), as a result of increased cloud cover.

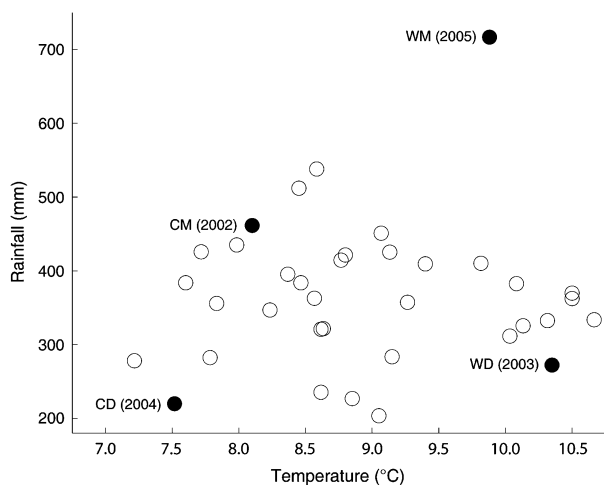
The saturation deficit of air (SD) was strongly seasonal, with peaks at different times in different years, and greater relative variation than air temperature (Fig. 2e). The lowest SD occurred in the wettest year and the highest SD occurred during the warm-dry year (2003) for most months. The largest variation in SD occurred during August.

The combined effects of the rainfall seasonality and SD seasonality led to large interannual variations in the seasonal course of cumulative water balance (Fig. 2f). The water balance at all sites became increasingly negative in 2003, with a net deficit beginning in May and continuing until fall. The water balance during 2002 and 2004 was similar, and remained slightly positive, between 0 and 10 cm for the entire growing season. The water balance increased sharply to a maximum of  $\sim 25\ \text{cm}$  by September 2005 (when field measurements ended), indicating pooling or surface run-off of surplus water. Site-to-site variations were minor compared to the seasonal and interannual patterns.

The 4 study years had markedly different weather during the potential growing season (April 1 to September 30), both in comparison with each other and in



**Fig. 2** (a) Air temperature, (b) accumulated degree days, (c) total precipitation at Thompson Airport, (d) mean daily solar radiation at the towers, (e) vapor pressure deficit, and (f) cumulative water balance (average for UCI-1850, UCI-1964, and UCI-1989). The letter codes indicate the growing season weather during the 4 study years: CM, cool-moist (2002); WD, warm-dry (2003); CD, cool-dry (2004); WM, warm-moist (2005).



**Fig. 3** Total rainfall (April–September) as a function of mean daily temperature (April–September) from 1967 to 2005. Data were obtained from Environment Canada (<http://www.climate.weatheroffice.ec.gc.ca>). The letter codes indicate the growing season weather during the 4 study years: CM, cool-moist (2002); WD, warm-dry (2003); CD, cool-dry (2004); WM, warm-moist (2005).

comparison with the 38-year mean (Fig. 3). The years 2003 and 2005 had unusually warm growing seasons (>9.5 °C), and 2002 and 2004 had unusually cool growing seasons (<8.5 °C). The years 2003 and 2004 were

unusually dry (<260 mm), and 2002 and 2005 were unusually moist (>450 mm). We refer to 2002 as the cool-moist (CM) year, 2003 as the warm-dry (WD) year, 2004 as the cool-dry (CD) year, and 2005 as the warm-moist (WM) year.

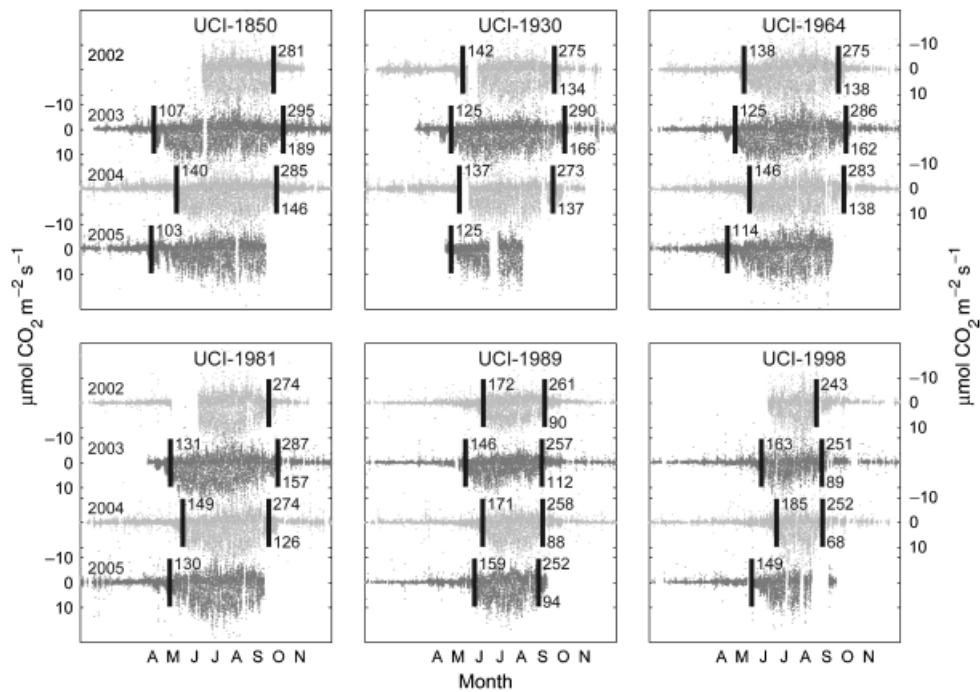
*Growing season: start day, end day, and length*

We defined the growing season as the period when the maximum daily CO<sub>2</sub> uptake was at least 35% of the maximum summer value. We refer to the Day of Growing Season Start as  $D_{GSS}$  and the Day of Growing Season End as  $D_{GSE}$  (Fig. 4).  $D_{GSS}$  ranged from Day of Year (DOY) 103 to DOY 185 (mean ± SD, 140 ± 20,  $n = 21$ ) and  $D_{GSE}$  ranged from DOY 243 to DOY 295 (mean ± SD, 271 ± 15,  $n = 20$ ). The growing season began earlier at old stands (DOY ~124) than young stands (DOY ~164) (Fig. 5a).  $D_{GSS}$  decreased with increasing stand age, following a relationship that was roughly logarithmic:

$$D_{GSS_{av}} = -15.106 \ln(\text{AGE}) + 192.28, \quad r^2 = 0.87, \quad (3)$$

where  $D_{GSS_{av}}$  was the  $D_{GSS}$  averaged across the 4 study years and AGE is the average stand age (years since last burned).

The growing season started ~21 days earlier in warm years (2003, 2005) than in cool years (2002, 2004).  $D_{GSS}$  at old stands occurred in mid-April to early



**Fig. 4** Half hourly rates of NEE from 2002 to 2005. Bars indicate start and end of growing season (defined as the period when the maximum daily uptake was at least 35% of the maximum summer uptake). Numbers to the upper right of the bar indicate the Julian day start of the growing season ( $D_{\text{GSS}}$ ) and end of the growing season ( $D_{\text{GSE}}$ ). Numbers to the lower right of the right bar indicate the length of the growing season in days.

May (DOY 103–125) during warm years, and in mid-May (DOY 137–142) during cool years.  $D_{\text{GSS}}$  at young stands occurred in late May to early June (DOY 146–163) during warm years, and in late June to early July (DOY 171–185) during cool years. Interannual and age-dependent variability in  $D_{\text{GSE}}$  was smaller than in  $D_{\text{GSS}}$  (Fig. 5b).  $D_{\text{GSE}}$  was earlier, and less variable in younger stands than older stands. The growing season ended at the four older stands in late September to mid-October ( $D_{\text{GSE}} = \text{DOY } 273\text{--}295$ ), and in early to mid-September ( $D_{\text{GSE}} = \text{DOY } 243\text{--}261$ ) at the two youngest stands. The smaller variation in  $D_{\text{GSE}}$  relative to  $D_{\text{GSS}}$  may be related to the environmental cues for these events.  $D_{\text{GSS}}$  is triggered by air temperature, whereas  $D_{\text{GSE}}$  is thought to be more sensitive to decreasing day length (Suni *et al.*, 2003), a seasonal cue that is inherently stable from year to year.

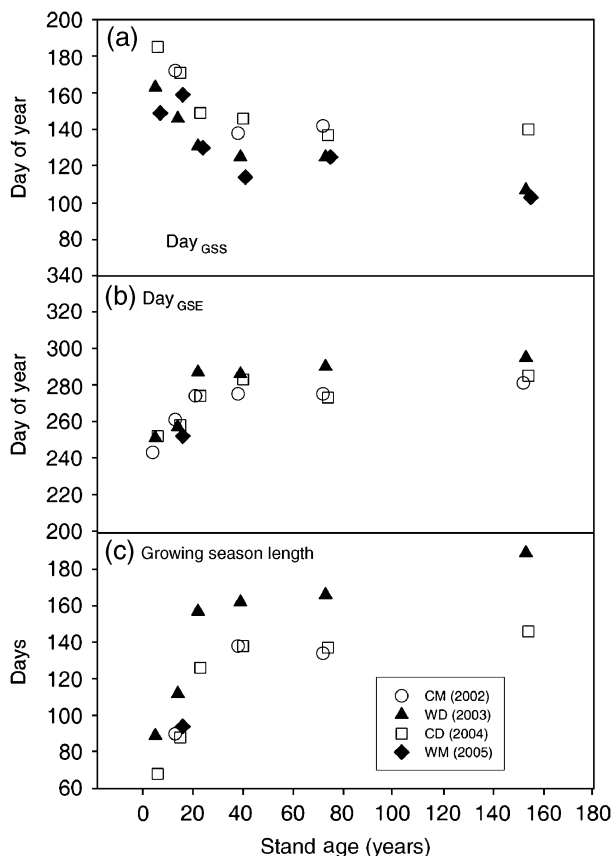
The length of the growing season ranged from 68 days at the youngest stand to 189 days at the oldest stand (Fig. 4). Stand-to-stand variation in growing season length was driven more by  $D_{\text{GSS}}$  than by  $D_{\text{GSE}}$ . The interannual variability in growing season length increased with increasing stand age (Fig. 5c). At the oldest stand, the growing season in the warm-dry year was 43 days longer than in the cool-dry year, whereas at the youngest stand, the growing season in the warm-

dry year was only 21 days longer than in the cool-dry year.

#### *Interannual variability in daytime $\text{CO}_2$ uptake and nighttime $\text{CO}_2$ efflux*

Seasonality and age-dependence were the largest sources of variability in daytime  $\text{CO}_2$  uptake. Interannual variation in the mid-growing-season rates of  $\text{CO}_2$  exchange was a smaller source of variability, though significant year-to-year differences occurred (Fig. 6). The highest rates of daytime  $\text{CO}_2$  uptake occurred at UCI-1981. The lowest rates of daytime  $\text{CO}_2$  uptake occurred during the winter and at the youngest stand. The duration of uptake greater than  $5 \mu\text{mol m}^{-2} \text{ s}^{-1}$  lasted up to 5 months at the older stands ( $>24$  years) (Fig. 6a–d), but only 3 months at the younger stands ( $<24$  years) (Fig. 6e and f).

The greatest interannual variability in daytime  $\text{CO}_2$  uptake occurred during May at the four oldest stands, and in June at the two youngest stands. Months with high interannual variability in mean air temperature also had high interannual variability in daytime  $\text{CO}_2$  uptake. The effect of the early spring and dry summer in the warm-dry year on daytime  $\text{CO}_2$  uptake



**Fig. 5** Variation in the (a) start ( $D_{GSS}$ ), (b) end ( $D_{GSE}$ ), and (c) length of the growing season as a function of stand age. Growing season was defined as the period when the maximum daily uptake was at least 35% of the maximum summer uptake. The letter codes indicate the growing season weather during the 4 study years: CM, cool-moist (2002); WD, warm-dry (2003); CD, cool-dry (2004); WM, warm-moist (2005).

was evident at all sites: daytime  $\text{CO}_2$  uptake in spring was higher than in other years; daytime  $\text{CO}_2$  uptake in summer was lower than in other years. The extra growth conferred by the warm spring was partially offset by a suppression of daytime uptake during July and August. For the two younger sites, the mid-summer reduction in photosynthesis exceeded the extra carbon assimilated due to the earlier growing season start. While significant reductions also occurred at the two oldest sites, more carbon was assimilated over the growing season of the warm-dry year than in other years.

Night-time  $\text{CO}_2$  efflux was lowest during winter ( $< 1 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) and highest in July and August at all sites, with maximum values exceeding  $6.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  (Fig. 7). The greatest interannual variability occurred at UCI-1964 and UCI-1989, due to particularly high night-time  $\text{CO}_2$  efflux in June and July of the warm-moist year.

Over 150 mm rainfall occurred in these two months and we suspect that high respiratory fluxes occurred from the combined effects of high soil moisture and temperature.

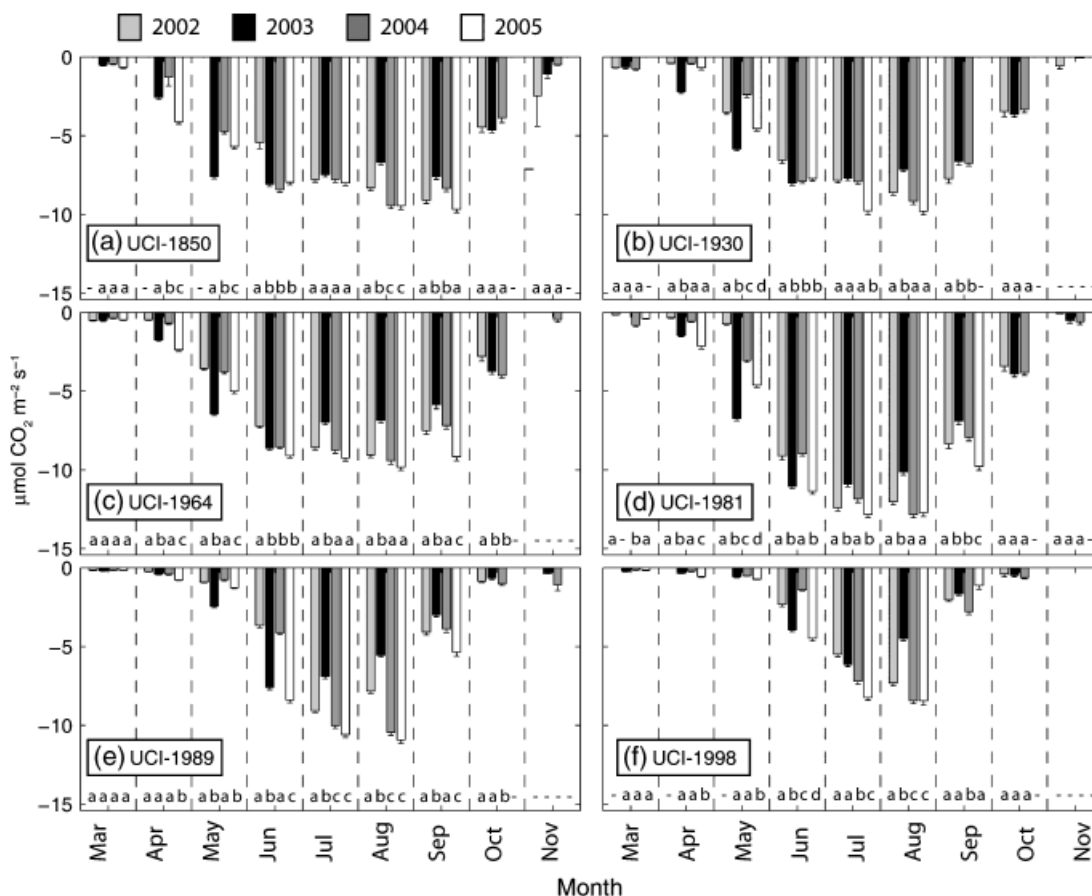
#### *Age-dependent response of $\text{CO}_2$ uptake to interannual weather variation*

Seasonal variation in weather caused responses along the age transect that differed between spring and summer (Fig. 8). In May, the greatest uptake rates occurred in the warm-dry year and year-to-year differences were greater at stands older than 20 years (Fig. 8a). Photosynthetic rates were reduced in the warm-moist year relative to the warm-dry year, presumably because of reductions in incoming solar energy associated with increased cloud cover. The effects of heat and/or water stress were evident in August of the warm-dry year, and uptake rates were most severely reduced at the younger sites (Fig. 8b). By contrast, the greatest uptake rates occurred in the warm-moist year due to high rainfall. The sharp reductions of daytime uptake during August in the warm-dry year indicated that the combined effects of high temperature and low rainfall were interactive rather than additive; the combination of heat and drought had a far greater effect than just heat or drought alone.

We examined how daytime uptake responded to the warm spring and hot, dry summer of the warm-dry year relative to other years (Fig. 9). Older stands responded in May to the warm spring whereas the younger stands responded in June. In May, daytime  $\text{CO}_2$  uptake rates increased at the older stands ( $> 20$  years) by  $> 2.5 \mu\text{mol m}^{-2} \text{s}^{-1}$  in the warm-dry year relative to other years, whereas daytime  $\text{CO}_2$  uptake rates remained below  $2.0 \mu\text{mol m}^{-2} \text{s}^{-1}$  at the younger stands ( $< 20$  years). In June, the greatest response to the warm spring in the warm-dry year occurred at the youngest sites, and no further year-to-year differences occurred at the three oldest stands. However, the increased  $\text{CO}_2$  uptake at the old stands in May 2003 (relative to other years) was similar in magnitude to the increased  $\text{CO}_2$  uptake at the younger stands in June 2003 ( $2\text{--}4 \mu\text{mol m}^{-2} \text{s}^{-1}$ ).

The response of late summer (August) daytime uptake to a hot, dry summer was greater at the younger stands than at older stands (Fig. 9). At the four oldest stands ( $> 20$  years), late summer daytime uptake rates were reduced by  $2.1\text{--}2.6 \mu\text{mol m}^{-2} \text{s}^{-1}$  in the warm-dry year relative to the other years. At the two younger stands ( $< 20$  years), late summer daytime uptake rates were reduced by  $3.6\text{--}4.1 \mu\text{mol m}^{-2} \text{s}^{-1}$  in the warm-dry year relative to the other years. In both relative and absolute terms, reductions in daytime  $\text{CO}_2$  uptake were most severe at the younger stands.





**Fig. 6** Monthly time series of daytime net CO<sub>2</sub> uptake (average CO<sub>2</sub> exchange when photosynthetically active radiation exceeded 600  $\mu\text{mol m}^{-2}\text{s}^{-1}$ ). Negative values indicate uptake of CO<sub>2</sub> by the forest. Bars denote different years. Letters below bars indicate significant differences between years: years labeled with similar letters are not significantly different from one another (Tukey's Honest Significant Difference between Means,  $P < 0.01$ ).

## Discussion

### *Age-dependent and interannual variations in carbon accumulation*

The canopy undergoes a rapid increase in leaf area in the early successional stages, followed by a gradual exclusion of deciduous species in the later successional stages (Fig. 1). The initial increase in leaf area was responsible for the rapid recovery in CO<sub>2</sub> exchange during early succession. Carbon accumulation increased rapidly during the first 24 years of succession, and remained broadly constant thereafter (Fig. 10). Variation in carbon accumulation was mostly explained by stand age ( $F = 22.13$ ,  $P < 0.01$ ) in a two-way ANOVA with no interaction and 15 degrees of freedom, with interannual differences also accounting for a significant portion ( $F = 5.73$ ,  $P < 0.05$ ). Interannual variability in carbon accumulation increased with stand age.

Carbon accumulation did not follow an orderly progression with age in later succession, and local peaks in carbon storage rates occurred at UCI-1981 (24 years) and UCI-1930 (75 years), and reduced rates of carbon accumulation occurred at UCI-1964. The lack of an orderly progression in carbon accumulation during succession can be interpreted in two ways. The sites may not represent an ideal successional sequence. For example, UCI-1981 might represent a higher productivity sequence, and UCI-1964 a lower productivity sequence. We previously tested the validity of our 'time-for-space' substitution by comparing the Enhanced Vegetation Index (EVI), a satellite-based measure of productivity, at our tower study sites with EVI at burn scars of corresponding ages (Goulden *et al.*, 2006). The analysis indicated that our time-for-space substitution was valid at most sites, but EVI was somewhat greater at UCI-1981 and somewhat less at UCI-1964 than at other burn scars of the same age, implying that the sites were not perfectly matched.

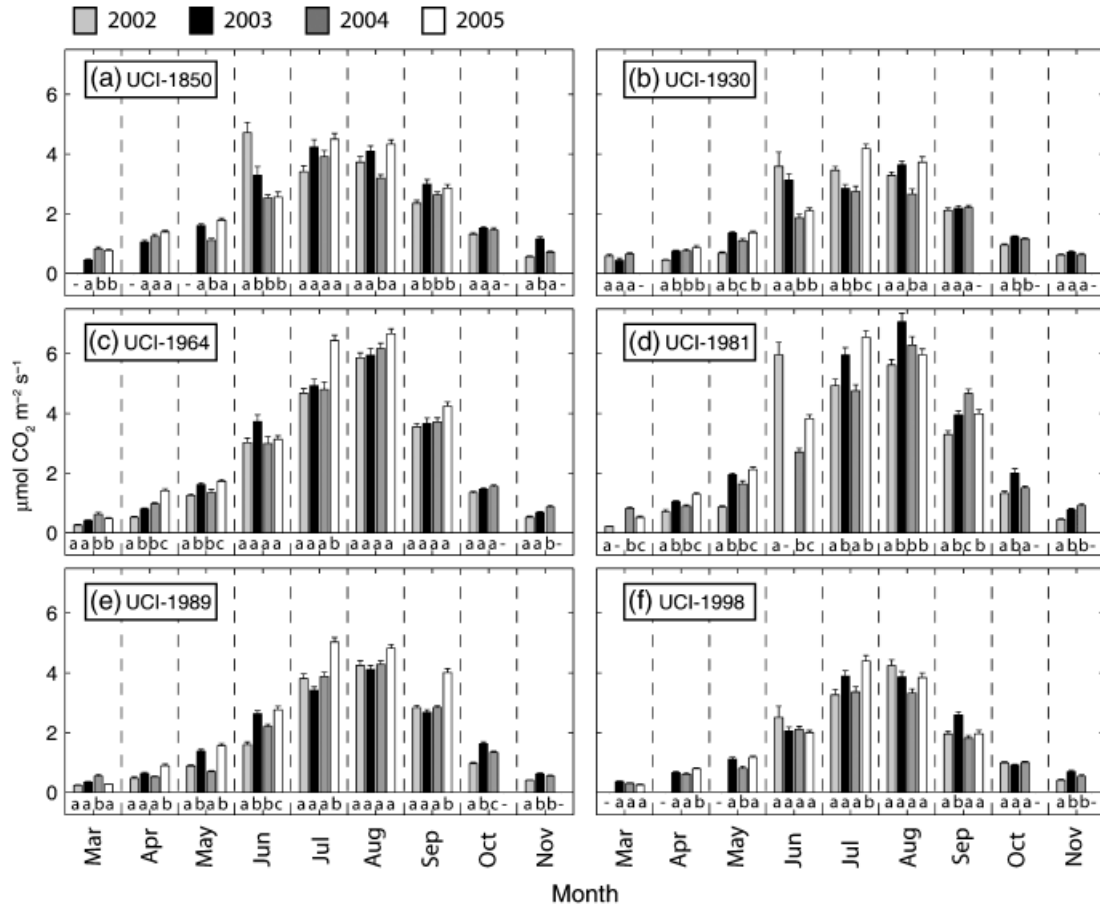


Fig. 7 Monthly time series of respiration (average value of net CO<sub>2</sub> exchange when  $u^* > 0.2 \text{ ms}^{-1}$  and photosynthetically active radiation  $< 10 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ). Bars denote different years. Letters below bars indicate significant differences between years: Years labeled with similar letters are not significantly different from one another (Tukey's Honest Significant Difference between Means,  $P < 0.01$ ).

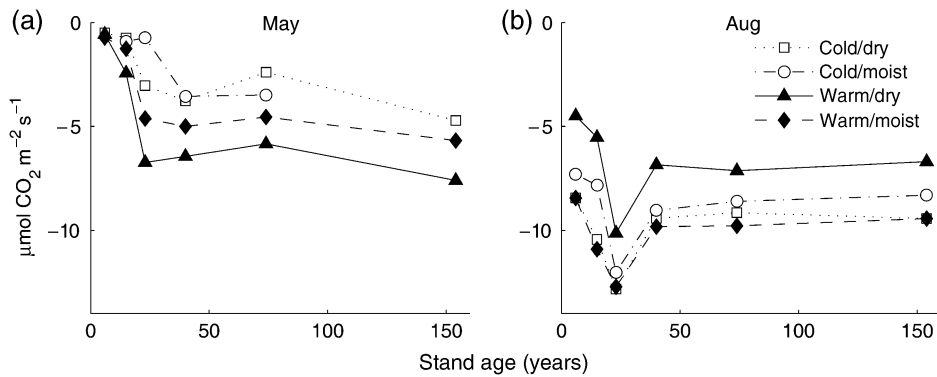
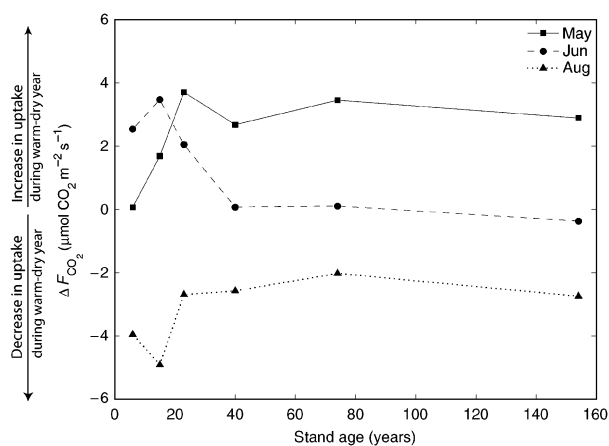


Fig. 8 Average CO<sub>2</sub> flux during bright periods [photosynthetically active photon flux density (PPFD)  $> 600 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ] for each year as a function of stand age in (a) May and (b) August. More negative values indicate greater vegetation CO<sub>2</sub> uptake.

A second interpretation is that the complex relationship between carbon accumulation and stand age represents the sum of the individual species' age-dependent carbon accumulation trajectories. UCI-1981 might have had higher productivity than UCI-1964 because the dominant spe-

cies at UCI-1981, jack pine, was juvenile and at a stage in its life of rapid growth. Similarly, carbon accumulation at UCI-1930 was greater than at UCI-1850, possibly because the dominant species at this site, black spruce, was at a stage in its life of rapid growth.

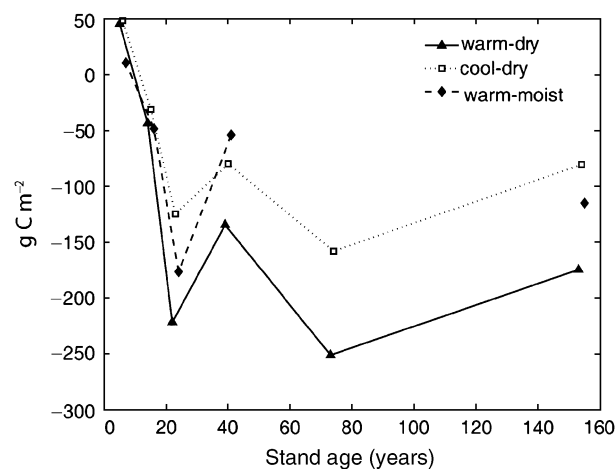


**Fig. 9** Age-dependent response to weather in a year with an early spring and a hot-dry summer (2003). Symbols represent the difference in daytime [photosynthetically active photon flux density (PPFD) > 600  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ]  $\text{CO}_2$  uptake rates ( $\Delta F_{\text{CO}_2}$ ) between the warm-dry year (2003) and the average May, June, and August uptake during the other 3 years (2002, 2004, and 2005).

Annual carbon accumulation rates are limited by LAI in early succession. In mid to late succession, the deciduous component of the canopy is replaced by evergreen species. During this transition, carbon accumulation becomes increasingly driven by the longer-lived, less intense photosynthetic activity of evergreen needle leaf species, rather than more intense, but shorter-lived photosynthetic activity of the deciduous species (Kljun *et al.*, 2006). Further, chronosequence studies are needed to determine whether carbon accumulation follows a smooth progression with age, or alternatively, carbon accumulation exhibits local minima and maxima associated with the growth of individual species.

#### *What causes the age-dependent response to anomalous weather?*

Interannual variations in weather caused a greater response in daytime uptake than in night-time efflux (Figs 6 and 7). The response of photosynthesis to weather was age-dependent (Fig. 8); the response of respiration was age-independent. Early springs increased photosynthesis whereas hot, dry summers decreased photosynthesis (Figs 8 and 9). In relative terms, the response to the early spring was greatest at the older stands, whereas the response to the hot, dry summer and high rainfall was greatest at the younger stands (Fig. 9). In absolute terms (quantity of C per unit area), the greatest variability in carbon uptake occurred at the older stands, mostly as a result of variation in the growing season length (Fig. 10). Growing season length was also important for determining carbon uptake at



**Fig. 10** Net Ecosystem Production (NEP) as a function of stand age. Negative values indicate carbon uptake from the atmosphere to the forest. Fluxes are summed from October 1, 2002 to September 30, 2003 (warm-dry); October 1, 2003 to September 30, 2004 (cool-dry); and October 1, 2004 to September 30, 2005 (warm-moist).

the younger stands (Fig. 5), but reductions caused by the hot, dry summer cancelled the extra carbon accrued during the early spring (Fig. 10).

*Warmer springs.* The main factor determining annual carbon accumulation was the length of the growing season. For all site-years combined, carbon accumulation increased by  $2.2 \text{ g C m}^{-2} \text{ yr}^{-1}$  for each additional day of the growing season ( $r^2 = 0.75$ ). Warm springs advanced the growing season by up to 37 days at the older stands and by up to 25 days at the younger stands (Fig. 5). The greater ability of older forests to capitalize on warmer springs can be explained by their greater evergreen component (Fig. 1). In deciduous canopies, photosynthesis begins only after bud break; in evergreen canopies, photosynthesis begins as soon as the nocturnal temperatures remain above freezing (Goulden *et al.*, 1997). The onset of photosynthesis in evergreen stands is reversible if there is a sudden 'cold snap' (Suni *et al.*, 2003). Bud break is a nonreversible process, and deciduous species may use environmental cues that are more conservative, such as accumulated degree-days, to avoid frost damage. Finally, shorter winters confer an additional benefit to evergreen species by decreasing the metabolic cost of maintaining leaves throughout the winter.

*Hotter/drier summers.* The younger stands were more susceptible to water or heat stress during the warm-dry year (Fig. 9). Rooting depth in the species at the younger stands is shallower (Manies *et al.*, 2006). It is also probable that the greater water vapor fluxes that occurred during the high spring growth in 2003

depleted the soil moisture reservoir (Fig. 2f). The lower photosynthetic rates during hot and dry summers in young stands (Fig. 9), and delayed growing season start (Fig. 5a), resulted in equal or lower carbon accumulation rates in warm years (Fig. 10).

**Greater rainfall.** Moisture deficits are known to affect the dependence of respiration on soil or air temperature (Xu *et al.*, 2004), and we found that respiratory fluxes were greatest during the years with high rainfall (Fig. 6). Stimulation of respiration with greater rainfall was not age-dependent (Fig. 7), and was associated with higher rates of photosynthesis, suggesting that the majority of respiration was autotrophic. Measurements of belowground radiocarbon fluxes at these sites indicated that respiration is predominantly autotrophic (Czimeczik *et al.*, 2006). Mosses and lichens, which lack vascular tissue, respond rapidly to transitory increases in water availability, and may be responsible for the observed moisture-driven increases in respiration. The contribution of the moss surface layer can account for 50–80% of whole forest respiration (while only accounting for 10–50% of whole forest photosynthesis) (Goulden & Crill, 1997).

An alternative explanation for the control of NEP in mature black spruce stands was proposed by Dunn *et al.* (2007). At the Harvard NOBS Tower site, which was within 500 m of the UCI-1850 stand, a secular year-to-year trend in NEP was observed and hypothesized to be caused by a suppression of respiration associated with a rising water table. Our site was situated at a slightly more upland location, and we found that wetter conditions stimulated, rather than suppressed, respiratory fluxes. The contrasting response of respiratory flux to moisture highlights the potential importance of soil drainage in controlling soil carbon balance.

#### *Will climate change accelerate boreal forest succession?*

Regional climate models agree that temperature will increase during summer and winter in Northern Manitoba (Christensen *et al.*, 2007). Summer precipitation may also increase, though less agreement exists among models. The response to the temperature anomalies we observed during the warm years may serve as an analog for the response of boreal forest to climate change. We found that the response to weather was age-dependent, which raises the possibility that successional dynamics may change with climate.

The greater incidence of early springs and stress tolerance might confer a competitive advantage to mid- and late-successional evergreens over early-successional herbs and shrubs, resulting in a contrac-

tion of the period in which ruderals dominate. Older (>20 years) stands accumulated more carbon than younger stands (<20 years) in warm years and uptake rates were less severely reduced when subjected to summer drought (Fig. 10). The combined effects of increased competitive ability of conifers, higher fuel accumulation in warm years, and temperature-driven increases in forest fire frequency might accelerate succession. Moreover, the more rapid accumulation of biomass in evergreen canopies results in a higher concentration of combustible material (fuel), increasing the potential for stand-replacing wild fire. Dry years will lead to reductions in fuel moisture and substantially increase the chance of wildfire. Decreased fuel moisture will further increase the chance of large, crown fires during drought years. The areal and temporal extent of stand-replacing wild fire is highly episodic, with the great majority of area burned resulting from a few large fires (Stocks *et al.*, 2002). The number of large fire years per decade has increased over the last four decades (Kasischke & Turetsky, 2006), a trend attributed to recent warming (Gillett *et al.*, 2004). Inspection of Landsat images within our study area acquired during the course of the study (2002–2005) revealed that wildfires occurred only in the warm-dry year (2003). The area within Manitoba burned in 2003 was almost a factor of 10 higher than in 2002 or 2004 (Table 2).

Regionally, the final age distribution of boreal forests will depend on the balance between two opposing forces. First, the competitive advantage of conifer stands under warmer conditions may tend to displace deciduous stands at earlier stages, and reduce the area occupied by deciduous vegetation. However, with increased fire frequency and severity, more successional resets will occur, and increase the area occupied by deciduous vegetation. A change in the age distribution of forests caused by acceleration of succession, and reduced fire return interval, would change the land-

**Table 2** Wildfire areas burned within a Landsat image that encompasses the study sites (Path 33/Row 21), and within the Canadian province of Manitoba (obtained from <http://www.gov.mb.ca/conservation/fire/Fire-Historical/firestatistic.html>)

Year	Area within Landsat image burned		Area burned in Manitoba (km <sup>2</sup> )
	km <sup>2</sup>	% area	
2002	0	0	946
2003	484	1.4	9188
2004	0	0	260
2005	0	0	Not available

atmosphere exchange of both carbon and energy. For instance, one study found that when fire return intervals are greater than 80 years, cooling effects due to the increased albedo of young boreal forests exceeded warming effects due to emissions from the fire (black carbon and greenhouse gases) and the lower CO<sub>2</sub> uptake rates of the early successional vegetation (Randerson *et al.*, 2006). However, at fire-return intervals less than 80 years, boreal forest fires had a net warming effect. This study suggests that the effect of future warming on successional dynamics and fire regimes needs to be considered alongside the physiological response to warming.

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