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On linking interannual tree ring variability with observations of whole-forest CO₂ flux

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Abstract

We used a 10-year record of the CO₂ flux by an old growth boreal forest in central Manitoba (the Northern Old Black Spruce Site (NOBS)), a ~150-year-old *Picea mariana* [Mill.] stand) to determine whether and how whole-forest CO₂ flux is related to tree ring width. We compared a 37-year ring width chronology collected at NOBS to a second chronology that was collected at a nearby Black Spruce stand with a different disturbance history, and also to three measures of annual whole-forest photosynthesis [gross ecosystem production (GEP)], two measures of annual respiration (R), and one measure of annual carbon balance [net ecosystem production (NEP)]. The year-to-year ring width fluctuations were well correlated between the two sites; increasing our confidence in the NOBS chronology and implying that ring width variation is driven and synchronized by the physical environment. Both chronologies exhibited serial correlation, with a fluctuation in ring width that had an apparent periodicity of ~7 years. Neither chronology was correlated with variation in annual precipitation or temperature. Ring width and NEP increased, while R decreased from 1995 to 2004. GEP either remained constant or decreased from 1995 to 2004, depending on which measure was considered. The lack of relationship between ring width and GEP may indicate that ring growth is controlled almost entirely by something other than carbon uptake. Alternative explanations for the ring width chronologies include the possibility that wood production varies as a result of shifts in respiration, or that an unidentified aspect of the environment, rather than the balance between GEP and respiration, controls wood production. The serial correlation in ring width may be related to increases and decreases in carbohydrate pools, or to gradual changes in nutrient availability, pathogens, herbivores, soil frost or soil water table. The cause or causes of serial correlation, and the controls on the allocation of photosynthate to wood production, emerge as critical uncertainties for efforts in predicting the carbon balance of boreal ecosystems and inferring past climate from tree rings.

Keywords: boreal forest, dendrochronology, ecophysiology, eddy covariance, forest growth, interannual variability, ring width

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Introduction

Both ecology and dendrochronology focus on the relationship between climate variability and plant growth (Briffa *et al.*, 1998; Barford *et al.*, 2001). Ecologists are concerned with the patterns, measurements and implications of temporal variation in net primary production. Dendrochronologists use correlations between growth

(tree ring width) and climate variability to infer past climatic conditions. Ecologists and dendrochronologists approach similar issues from different directions. The two fields focus on contrasting time scales and use different techniques, which can lead to differing conclusions about the response of ecosystems to environmental change. For example, Gu *et al.* (2003) used physiological and meteorological techniques to conclude that increased diffuse radiation from volcanic aerosols increased photosynthesis over 2 years in a temperate deciduous forest. In contrast, Krakauer &

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Randerson (2003) used dendrochronological techniques to conclude that tree growth at latitudes 30–45°N did not increase following historic volcanic eruptions. Only a few studies have attempted to bridge these fields by comparing and reconciling data collected using ecological and dendrochronological approaches (Arneeth *et al.*, 1998; Curtis *et al.*, 2002; Gough *et al.*, 2006).

Most dendrochronologists rely on empirical correlations between ring width and environmental factors rather than a mechanistic physiologically based understanding of plant secondary growth. The reasons for this include uncertainties about what controls plant allocation (Wardlaw, 1990) and how the physical and chemical environment controls plant physiology and biochemistry (Fritts, 1976). The few dendrochronological studies that have explored the mechanistic basis of ring width typically assume that photosynthesis is the primary determinant of ring width (Pietarinen *et al.*, 1982; Gower *et al.*, 1995). However, tree growth involves complex processes such as carbohydrate storage and allocation (Kozlowski *et al.*, 1991; Cannell & Dewar, 1994; Gower *et al.*, 1995). Tree growth is affected by environmental conditions that occurred weeks, months, or years earlier (Arneeth *et al.*, 1998; Sampson *et al.*, 2001; Gough *et al.*, 2006), whereas photosynthesis responds within seconds to current environmental conditions.

Several studies have shown that the relationship between ring width and the physical environment is not always straightforward. Standard dendroclimatological analyses have shown that ring width is nearly insensitive to climatic variability in northeastern North America (Fritts, 1976; Phipps, 1982). The relationship between ring width and temperature has changed markedly over the last 40 years in some boreal forests (Jacoby & D'Arrigo, 1995; Briffa *et al.*, 1998; D'Arrigo *et al.*, 2004; Wilmking *et al.*, 2004). D'Arrigo *et al.* (2004) found that ring width in a Canadian boreal forest responded positively to warm temperatures before 1964 and negatively after 1965. D'Arrigo *et al.* (2004) concluded that the temperature at their site exceeded the optimal temperature for tree growth around 1965, and that further warming suppressed growth by either increasing respiration or decreasing photosynthesis.

The eddy covariance method is a valuable tool for evaluating the fluxes of carbon dioxide between terrestrial ecosystems and the atmosphere (Baldocchi, 2003). Eddy covariance is particularly useful for understanding the responses of ecosystem gas exchange to radiation, temperature, soil moisture, and vapor pressure (Goulden *et al.*, 1997). The eddy covariance method allows for the separate consideration of the factors that control whole ecosystem respiration (carbon loss) and canopy photosynthesis (carbon uptake). Long-term re-

cords (>5 years) of carbon flux are becoming widely available (Barford *et al.*, 2001; Dunn *et al.*, 2006), opening the possibility for studies that compare the interannual variability in carbon dioxide flux with the variability in ring width.

We used a long-term eddy covariance record from an old-growth boreal forest (Goulden *et al.*, 1997; Dunn *et al.*, 2006) to determine the relationship between whole-forest CO₂ flux and tree ring width. Our primary goal was to understand the link between forest metabolism and ring width. We hypothesized that ring width would be correlated with either the current or previous year's integrated photosynthesis. We tested this hypothesis using a 10-year record of CO₂ exchange measured by eddy covariance, a 37-year record of daily weather, and a 37-year chronology of ring width collected at the study site. We compared six measures of annual CO₂ exchange that represented ecosystem carbon gain [gross ecosystem production (GEP)], carbon loss [respiration (R)] or net carbon exchange [net ecosystem production (NEP)] with ring width to determine whether and how the year-to-year fluctuations in ring width were related to the year-to-year patterns of whole-forest CO₂ flux.

Data and methods

Site description

The study was conducted at two Black Spruce stands in central Manitoba, Canada. Most of the measurements were made at the BOREAS Northern Old Black Spruce Site (NOBS) (55.88°N, 98.48°W) site, which last burned in ~1850. Additional measurements were made at a site ~5 km to the north of NOBS that last burned in ~1930. Both stands were near the northern limit of closed canopy boreal forest and were composed of mid to late successional Black Spruce (*Picea mariana* [Mill.] BSP) with an understorey of Labrador tea (*Ledum groenlandicum* [Oeder]) and feather moss (*Pleurozium* spp. and *Hylocomium* spp.) (Gower *et al.*, 1997; Harden *et al.*, 1997; Wang *et al.*, 2003; Bond-Lamberty *et al.*, 2004). Stand density ± standard error at NOBS in 2001 was 6607 ± 683 trees ha⁻¹, with a basal area of 29.1 ± 2.9 m² ha⁻¹ (Litvak *et al.*, 2003). Canopy height at NOBS was 10.6 m. Stand density at 1930 in 2001 was 7644 ± 1184 trees ha⁻¹, with a basal area of 32.3 ± 4.7 m² ha⁻¹. Canopy height at 1930 was 7.4 m. Both sites were flat and underlain by moderately well drained to poorly drained clays (Harden *et al.*, 1997). Discontinuous permafrost occurred throughout the area, with thin layers occasionally present in veneer bogs and uplands (Veldhuis *et al.*, 2002).

Ring width chronologies

A total of 88 trees located in three 50 m² plots ~300 m west of the eddy covariance tower were cored at NOBS in September 2004. Cores were only taken from healthy mature trees in well-drained stands. Each tree was cored twice (on the north and west aspect of the tree) at breast height (1.3 m) with an increment borer. The cores were air dried, glued onto grooved masonite boards and sanded to enhance ring boundaries. The cores were then scanned at 1200 dpi with a Microtek ScanMaker i900 (Microtek USA, Carson, CA, USA), and the images saved as jpeg files and imported into Lignovision (Rinntech, Heidelberg, Germany) for determination of ring width. Samples were visually cross-dated to identify common marker years and ring width patterns. The diameter of each cored tree was measured with DBH tape (Original Loggers Tape; Spencer Products CO, Seattle, WA, USA). Two cores from each tree were taken from a total of 110 trees at the 1930 site using the methodology described above. The stands at NOBS and 1930 were near monocultures of even-aged Black Spruce, and all cores were from this species. Ring width chronologies for the 37-year period from 1968 to 2004 were calculated for each site as the mean of all cores.

Long-term climate observations

The closest long-term climate record to NOBS is for the airport in Thompson, Manitoba, which is 40 km to the east. Climate data from the Thompson airport were obtained from the Environment Canada Atmospheric Environment Service (<http://www.climate.weatheroffice.ec.gc.ca/>). Data included a nearly continuous record (<1% of data were missing) of daily total precipitation and daily maximum, minimum and average temperature since 1968. Missing temperature data was filled by extrapolating observations from the town of The Pas, Canada, which is ~325 km southwest of Thompson. The Pas maximum, minimum and average temperature correlated well with the Thompson airport record (r^2 for daily average temperature was 0.96). Thompson mean temperature for 1971–2000 was -3.2°C and mean precipitation was 517 mm yr^{-1} .

We used the climate record from the Thompson airport to calculate climatic metrics that were expected to covary with photosynthesis and growth. The maximum potential growing season at NOBS spans the time period from day of year (DOY) 100 to 300. We calculated the potential average growing season temperature as the average temperature from DOY 100 to 300. We calculated the annual growing degree days (GDD) as the integrated daily temperature above 0°C ($\text{GDD} = \sum \text{GDD}_i$, where GDD_i is the (daily average

temperature (T_i)-base temperature (0°C) for $T_i > 0^\circ\text{C}$ and $\text{GDD}_i = 0$ if $T_i < 0$). We calculated the seasonal precipitation (PPT) as the sum of precipitation from the previous September through the current August. Dunn *et al.* (2006) found that soil thaw and water table depth influence carbon exchange at NOBS. Consequently, we calculated the annual climate moisture index (CMI) as PPT minus potential evapotranspiration using a simplified Penman–Monteith equation following Hogg (1997) and the mean CMI from the preceding 3 years (CMI.3) following Dunn *et al.* (2006). Annual CMI was calculated from the previous September through the current August.

Daily incoming solar radiation [insolation ($\text{MJ m}^{-2} \text{ day}^{-1}$)] was estimated using the MTCLIM v.4.3 model (Thornton & Running, 1999). MTCLIM inputs latitude, slope, daily precipitation, and maximum and minimum temperatures to calculate daily average insolation. The output of MTCLIM was checked against insolation measured at ~25 m aboveground level on a secondary tower at NOBS with a pyranometer (CM3, Kipp & Zonen, Bohemia, NY, USA) from 2002 to 2004. Good agreement was found between measured and calculated insolation during the potential growing season (DOY 100–300) ($y = 0.97 \times x$, $r^2: 0.61$, $\text{RSME}: 3.26\text{ MJ m}^{-2} \text{ day}^{-1}$, $P\text{-value} < 0.001$).

Eddy covariance data

The net ecosystem exchange (NEE) of CO_2 was measured continuously from 1995 to 2004 at NOBS (Goulden *et al.*, 1997; Dunn *et al.*, 2006). Instruments at 29 m aboveground recorded the physical conditions at 0.5 Hz. Air temperature was measured with an aspirated thermistor. Photosynthetically active radiation (PAR) was measured with a quantum sensor (PAR, Model LI-190, LI-COR Inc., Lincoln, NE, USA). The storage of CO_2 was calculated from measurements of CO_2 mixing ratio at 0.3, 1.5, 4.6, 8.4, 12.9, and 28.8 m aboveground level. The turbulent flux of CO_2 was calculated as the 30-min covariance of the vertical wind velocity measured with a three-axis sonic anemometer (Applied Technologies Inc., Boulder, CO, USA) and the CO_2 mixing ratio measured with a closed path infrared gas analyzer (IRGA; Model 6262, LI-COR Inc.). NEE was calculated every half hour by adding the turbulent flux of CO_2 to the time derivative of the column storage of CO_2 between 0 and 29 m.

Adequate turbulent mixing and the possibility of tower obstruction or combustion sources upwind are key factors determining the quality of NEE data (Goulden *et al.*, 1997). The power generator, instrument hut, access trail, and tower were all located east of the sonic anemometer. We rejected data during calm periods

($u^* < 0.20 \text{ m s}^{-1}$) or periods with wind from behind the tower (wind direction: 45–135°), and focused our analysis on the remaining data, which we refer to as the ‘unfilled’ tower data. The eddy covariance instrumentation at NOBS was fully operational for 78% of the time during 1995–2004. The turbulent mixing was inadequate during 18% of the time and the wind direction was inappropriate 16% of the time.

Ecosystem physiology

We used three measures of carbon gain (GEP_{TR} , NEE_{day} , GEP_{EM}), two measures of carbon loss (R_{TR} , $\text{NEE}_{\text{night}}$), and one measure of net CO_2 exchange (NEP_{TR}) to investigate the relationship between ring width and ecosystem physiology (see Table 1 for a summary of these measures). Each measure has strengths and weaknesses, and includes a set of underlying assumptions. We are hesitant to trust any single measure of ecosystem physiology, but feel that the combination of multiple measures of photosynthesis and respiration gives an overall representation of the physiological activity of the site.

We report and discuss our results using an ecological sign convention, where photosynthesis, respiration, and carbon storage are all considered processes with positive signs. Hence, a statement such as ‘photosynthesis increased’ indicates that GEP_{TR} , NEE_{day} or GEP_{EM} became more positive, and the forest assimilated more CO_2 during daytime. A statement such as ‘respiration increased’ indicates that R_{TR} or $\text{NEE}_{\text{night}}$ became more positive, and the forest lost more CO_2 at night. A statement such as ‘NEP increased’ indicates that NEP_{TR} became more positive, and the forest accumulated more carbon over a year.

Tower-based measures of carbon uptake (NEE_{day} , GEP_{TR}).

We used the tower measurements of daytime net CO_2 exchange averaged from DOY 100 to 300 (the maximum potential growing season) for each year from 1995 to 2004 as our first measure of ecosystem carbon gain (NEE_{day}). We calculated NEE_{day} from the unfilled tower observations for daytime periods ($\text{PAR} > 10 \mu\text{mol m}^{-2} \text{ s}^{-1}$) with a suitable wind direction. The advantages of NEE_{day} are that it assumes very little and is sensitive to both growing season length and daytime CO_2 uptake. The disadvantages of NEE_{day} are that it is also influenced by respiration and the year-to-year patterns of NEE_{day} cannot be unambiguously attributed to the year-to-year patterns of photosynthesis. We used the annual sums of gross ecosystem exchange (GEE) derived from the gap-filled data described by Dunn *et al.* (2006) to calculate our second measure of ecosystem carbon gain (GEP_{TR}). The

Table 1 Summary measures of canopy physiology

Measure	Description
<i>Ring width chronologies</i>	
NOBS	Ring width chronology from 88 black spruce trees in the fetch of the NOBS tower. NOBS_{dev} is the annual ring width deviation from the 37 year mean.
1930	Ring width chronology from 110 black spruce trees in a 70-year-old forest. 1930 _d is the chronology after detrending with an exponential fit.
<i>Carbon uptake</i>	
GEP_{EM}	Predictions of annual gross CO_2 uptake by the forest based on an empirical model that was parameterized with eddy covariance data from NOBS and calculated from Thompson climate data using Eqn (1).
GEP_{TR}	Annual sums of gross ecosystem exchange (GEE) from gap filled eddy covariance data (Dunn <i>et al.</i> , 2006).
NEE_{day}	Average daytime ($\text{PAR} > 10 \mu\text{mol m}^{-2} \text{ s}^{-1}$) NEE from Day of Year 100 to 300 (the maximum potential growing season) during well-mixed periods ($u^* > 0.20 \text{ m s}^{-1}$).
<i>Carbon loss</i>	
R_{TR}	Annual sums of respiration (R) from gap filled eddy covariance data (Dunn <i>et al.</i> , 2006).
$\text{NEE}_{\text{night}}$	Average nighttime ($\text{PAR} < 10 \mu\text{mol m}^{-2} \text{ s}^{-1}$) NEE from Day of Year 100 to 300 (the maximum potential growing season) during well-mixed periods ($u^* > 0.20 \text{ m s}^{-1}$).
<i>Carbon accumulation</i>	
NEP_{TR}	Annual sum of NEE from gap-filled eddy covariance data (Dunn <i>et al.</i> , 2006).

NOBS, northern old black spruce site; GEP , gross ecosystem production; NEE, net ecosystem exchange; NEP, net ecosystem production.

advantages of GEP_{TR} are that it is sensitive to both growing season length and daytime CO_2 uptake, and it provides a measure of photosynthesis that is not confounded by respiration. The disadvantage of GEP_{TR} is that its calculation assumes that daytime respiration can be extrapolated from night-time respiration as a simple function of temperature.

Empirical model of GEP (GEP_{EM}). We used an empirical model based on tower measurements of carbon uptake at NOBS to derive a 37-year chronology of GEP for our third measure of ecosystem carbon gain (GEP_{EM}). We estimated annual GEP for NOBS from 1968 to 2004 by first running the empirical gross ecosystem CO_2 exchange (GEE_{hr}) model from Goulden *et al.* (1997) for the 1995–2004 meteorological observations at NOBS and summing these values to daily totals. These calculations generated a partial time series of daily GEP over the last 10 years. We then regressed the daily GEP at NOBS against the simultaneous daily meteorological conditions observed at the Thompson airport and MTCLIM insolation. Finally, we combined these regressions with the complete meteorological record from the Thompson airport to calculate the annual GEP ($g\ C\ m^{-2}\ yr^{-1}$) at NOBS from 1968 to 2004. The final model was in the form:

$$GEP_{EM} = GEP_{light} \times GEP_{temp}, \quad (1)$$

$$GEP_{light} = (\beta \times I) / (\alpha + I), \quad (1a)$$

$$\begin{aligned} \text{if } T < 0 & \quad \text{then } GEP_{temp} = 0, \\ \text{if } 0 < T < 15 & \quad \text{then } GEP_{temp} = T/15, \\ \text{if } T > 15 & \quad \text{then } GEP_{temp} = 1. \end{aligned} \quad (1b)$$

Daily GEP was calculated as the product of GEP_{light} and GEP_{temp} Eqn (1). GEP_{light} Eqn (1a) is a rectangular hyperbola and describes the maximum daily GEP (β) and insolation needed to obtain half saturation (α). GEP_{temp} is a normalized function describing the response of daily GEP to air temperature (T), where GEE_{temp} equals 0 below 0°C , GEE_{temp} increases monotonically between 0 and 15°C , and GEE_{temp} saturates at 1 when air temperature is greater than 15°C Eqn (1b). We found good agreement between GEP_{EM} and summed daily GEE_{hr} ($\beta = 7.8573\ g\ C\ m^{-2}\ day^{-1}$, $\alpha = 144.7563\ W\ m^{-2}$, $y = 0.9344x$, $r^2 = 0.89$, RSME: $1.51\ g\ C\ m^{-2}\ day^{-1}$). The advantage of GEP_{EM} is that it provides a much longer data set for comparison with ring width. The disadvantage of GEP_{EM} is that it is further removed from the actual tower measurements than are NEE_{day} and GEP_{TR} . A second disadvantage of GEP_{EM} is that it assumes forest photosynthesis

responded to the physical environment in a constant way throughout the study.

Tower-based measures of carbon loss (NEE_{night} , R_{TR}). We used the tower measurements of nocturnal CO_2 efflux averaged during the potential growing season for each year as our first measure of carbon loss (NEE_{night}). We calculated NEE_{night} from the unfilled tower observations for well-mixed nocturnal periods with wind from a suitable direction. The advantage of NEE_{night} is that it provides a direct measure of ecosystem respiration that accounts for both changes in growing season length and peak activity within the growing season. The disadvantage of NEE_{night} is that it only provides a measure of nocturnal respiration, and is insensitive to the effects of daytime weather on respiration. We used the annual sums of ecosystem respiration from Dunn *et al.* (2006) to calculate our second measure of ecosystem carbon loss (R_{TR}). The advantage of R_{TR} is that it provides a measure of both daytime and night-time respiration. The disadvantage of R_{TR} is that its calculation assumes daytime respiration can be extrapolated from nocturnal observations as a function of temperature (Goulden *et al.*, 1997; Baldocchi, 2003).

Measures of carbon accumulation (NEP_{TR}). We used the tower-based calculation of NEP for each year from 1995 to 2004 as our measure of carbon accumulation (NEP_{TR}). We calculated NEP as the integral of the half-hourly gap-filled NEE data set prepared by Dunn *et al.* (2006). Periods with missing NEE due to anemometer malfunction, noisy data (e.g., due to precipitation) or inadequate turbulent mixing were filled (57% of the data were filled) to calculate NEP using a parameterized hyperbolic relationship with PAR during the day and a linear relationship with soil temperature at night (see Dunn *et al.*, (2006) for details). The advantage of NEP_{TR} is that it provides an integrated measure of ecosystem metabolism that accounts for changes in growing season length and all other aspects of the environment that affect photosynthesis or respiration. A second advantage of NEP_{TR} is that it provides a measure of carbon accumulation that would be expected to bear some relationship to ring width. A disadvantage of NEP_{TR} is that its calculation includes assumptions related to gap filling and the treatment of atmospherically calm periods (i.e., $u^* < 0.20\ m\ s^{-1}$).

Statistical and spectral analysis

Relationships between ring width and canopy physiology were tested for significance at the 95% confidence level using least squares regression. As it is easier to

biologically interpret relationships between canopy physiology and ring width (Briffa & Osborn, 1999; Barber *et al.*, 2000), we decided to use ring width rather than statistically transformed ring width index values in our analyses. In the results section, we report the Pearson correlation coefficients (r), R^2 , and P -values for the correlation between ring width and canopy physiology and weather. The square of the Pearson correlation coefficient (R^2) indicates the percentage of variance in y (i.e., ring width) that can be explained by x (i.e., canopy physiology or weather). The P -values represent the probability that the slope of the regression (i.e., $y = \beta_0 + \beta_1 x_t$) between two variables equals zero ($\beta_1 = 0$). Lags were introduced into the regressions (i.e., $y = \beta_0 + \beta_1 x_{t-1}$, and $y = \beta_0 + \beta_1 x_{t-2}$) because ring width chronologies are often correlated with weather before the year of ring formation (Fritts, 1976). We analyzed the ring width chronologies for autocorrelation (i.e., correlation of ring width in the current year to ring width during previous years) and report the Pearson's correlation value for a first-order autocorrelation (AR(1)). Statistical analyses were performed using MINITAB V.14.2 (Minitab Inc., State College, PA, USA).

We analyzed ring width chronologies, weather data, and GEP_{EM} at annual time intervals using a fast Fourier transform (FFT) to derive Fourier amplitudes and compare the spectral properties of the climatic and physiologic variables. The FFT separates a signal into a series of sinusoidal functions of different frequencies such that the original signal variance is recovered when all squared amplitudes are summed. FFT analyses were performed in MATLAB using the FFT function, which uses the FFTW library (<http://www.fftw.org>) and the Cooley–Tukey algorithm (Cooley & Tukey, 1965).

Results

Temporal trends in ring width

We developed 37-year chronologies of ring width for the trees at NOBS and 1930 (Fig. 1). The trees at NOBS did not exhibit an age-related growth trend over the last 37 years, whereas the trees at the 1930 site exhibited an exponential decline in growth that accounted for 77% of the variability in ring width (P -value < 0.001). The growth trend at 1930 was removed using an exponential function [detrended 1930 (1930_d)] and compared with the annual ring width deviations at NOBS ($NOBS_{dev}$). The chronologies at NOBS and 1930 displayed similar, well-correlated variations in ring width from 1968 to 2004 ($r^2: 0.58$, P -value < 0.0001) (Fig. 2). The correlation between sites increases our confidence in the NOBS chronology and demonstrates that Black Spruce ring width variation is synchronous across the landscape.

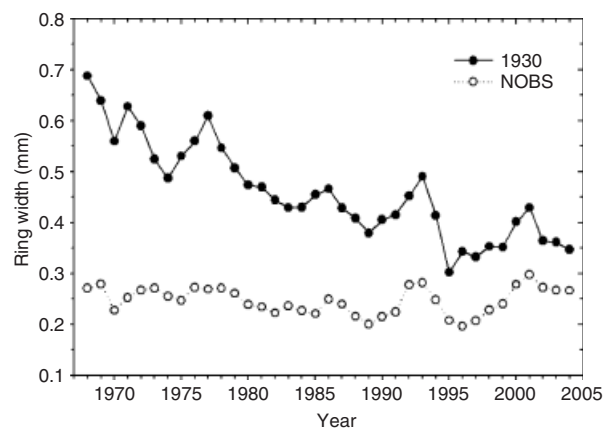


Fig. 1 Ring width chronologies for Northern Old Black Spruce Site (\circ) and 1930 (\bullet) from 1968 to 2004.

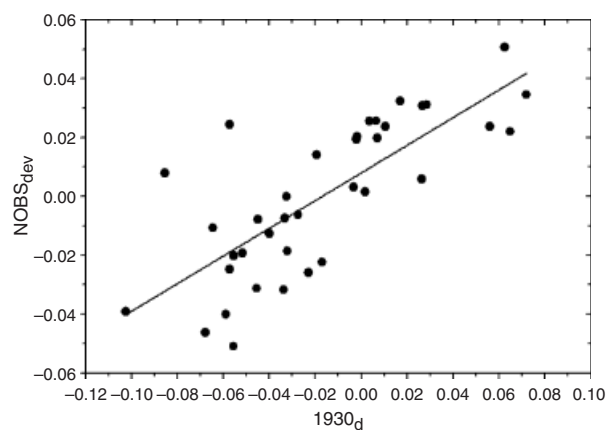


Fig. 2 Relationship between Northern Old Black Spruce Site (NOBS) and 1930 chronologies from 1968 to 2004. 1930 was detrended using an exponential function to remove the growth trend (1930_d). The NOBS chronology was transformed into ring width deviations by subtraction annual ring width from the 1968 to 2004 mean ($NOBS_{dev}$). The least squares fit between the two chronologies was $y = 0.4706x - 0.008$, $r^2: 0.58$, P -value < 0.0001 .

Both chronologies exhibited variability in ring width with peak ring widths occurring with an apparent periodicity of ~ 7 years. Both chronologies had a first-order serial correlation ($AR(1)_{NOBS}: 0.66$; $AR(1)_{1930_d}: 0.46$), indicating that conditions before the growth period influenced growth during the following year.

Relationships between ring width and recent weather

Table 2 summarizes statistical relationships between ring width at NOBS and recent weather. We did not find strong relationships between ring width and weather during the current or previous year, with the exception of a positive relationship between NOBS ring

Table 2 Pearson coefficients (r) and P -values (in brackets) of the correlation between northern old black spruce site (NOBS) ring width and the specified variable during the current (middle column) and previous year (far left column) of NOBS ring width formation

Variable	No lag r (P -value)	1 year lag r (P -value)
Annual temperature	0.107 (0.530)	0.045 (0.794)
Growing season temperature	-0.186 (0.271)	-0.063 (0.716)
Growing degree days	-0.287 (0.086)	-0.148 (0.381)
Annual precipitation (PPT)	0.108 (0.530)	0.298 (0.082)
CMI	0.208 (0.216)	0.363 (0.029)
CMI.3	0.271 (0.105)	0.069 (0.689)

Significant relationships are denoted in bold (P -value < 0.05).

width and CMI during the previous year of ring formation (Table 2).

Temporal trends in ecosystem physiology

Eddy covariance measurements at NOBS revealed a series of surprising long-term trends in ecosystem physiology (see also Dunn *et al.*, 2006). R_{TR} and NEE_{night} decreased during the period of measurement, while ring width and NEP_{TR} increased (Fig. 3). Both R_{TR} and NEE_{night} decreased throughout the period, providing strong evidence for a decline in ecosystem respiration from 1995 to 2004. NEE_{day} or GEP_{EM} remained constant, and GEP_{TR} declined, indicating that ecosystem photosynthesis did not increase from 1995 to 2004 (Figs 3a and 4).

Carbon assimilation and ring width

GEP_{EM} fluctuated from year to year whereas ring width displayed oscillations with an apparent period of ~ 7 years (Fig. 4). Ring width gradually increased after 1996 and reached a maximum in 2001, whereas GEP_{EM} varied markedly from year to year with no apparent long-term trend. GEP_{EM} and ring width are apparently controlled by factors that operate at different timescales, with ring width under the control of mechanisms that operate at comparatively longer time intervals.

NOBS ring width was not correlated with GEP_{EM} for the period from 1968 to 2004 (P -value: 0.241) (Figs 4 and 5a). We investigated the possibility that ring width depends on previous photosynthesis (Arneeth *et al.*, 1998; Kozlowski *et al.*, 1991) and that lagging GEP_{EM} might improve the relationship between ring width and GEP_{EM} . We lagged annual GEP_{EM} up to 10 years and found no statistically significant relationship with ring width for any lag interval (plots not shown). Likewise, monthly sums of GEP_{EM} during any of the 17 months

preceding the end of the growing season demonstrated no relationship with ring width (plot not shown). NOBS ring width was not correlated with GEP_{TR} (P -value: 0.291) or NEE_{day} (P -value: 0.808) (Fig. 5b; Table 3). Lagging GEP_{TR} and NEE_{day} by 1–2 years did not improve the correlation with ring width.

Respiration and ring width

Ring width increased while R_{TR} and NEE_{night} decreased (Fig. 3c) resulting in statistically significant negative relationships between ring width and R_{TR} (r^2 : 0.54; P -value: 0.016), and ring width and NEE_{night} (r^2 : 0.61; P -value: 0.008) (Fig. 5c; Table 3). A 1-year lag decreased the r^2 between R_{TR} and ring width (r^2 : 0.46; P -value_{1-year lag}: 0.043) and decreased the r^2 between NEE_{night} and ring width (r^2 : 0.47; P -value_{1-year lag}: 0.042) (Table 3). The 2-year lags of NEE_{night} and R_{TR} were not correlated with ring width (P -value > 0.05).

Carbon accumulation and ring width

Ring width and NEP_{TR} increased during the period of eddy covariance measurement (Fig. 3b) resulting in a statistically significant positive relationship between ring width and NEP_{TR} (Fig. 5d; Table 3) (r^2 : 0.73; P -value: 0.002). Lagging NEP resulted in a decrease in the variability in ring width explained by NEP ($r^2_{1-year lag}$: 0.70, $r^2_{2-year lag}$: 0.69) (P -value_{1-year lag}: 0.005, P -value_{2-year lag}: 0.010) (Table 3). We calculated the change in woody net primary production (NPP_w) using site-specific allometric equations for Black Spruce (Gower *et al.*, 1997), and found that the change in NPP_w ($18.1 \text{ g C m}^{-2} \text{ yr}^{-1}$) was less than the change in NEP ($82 \text{ g C m}^{-2} \text{ yr}^{-1}$). Assuming that carbon allocation remained constant at the ratio of total NPP to NPP_w reported by Gower *et al.* (2001), the increase in NPP_w indicates an increase in total NPP of $54.1 \text{ g C m}^{-2} \text{ yr}^{-1}$ from 1995 to 2004, which is broadly comparable with the increase in NEP observed during the period.

Spectral analysis of ring width, GEP_{EM} , and weather

Fourier transforms of the ring width chronologies, GEP_{EM} , and weather demonstrated large differences in the spectral properties of the variables (Fig. 6). Both the NOBS and 1930_d ring width chronologies illustrated a spectral peak at around 7 years with little spectral power at higher frequencies (Fig. 6a). GEP_{EM} , temperature, precipitation, and annual CMI all showed spectral power at higher frequencies (Fig. 6b,c). Annual CMI exhibited a peak at 7 years that had less power than was observed at higher frequencies.

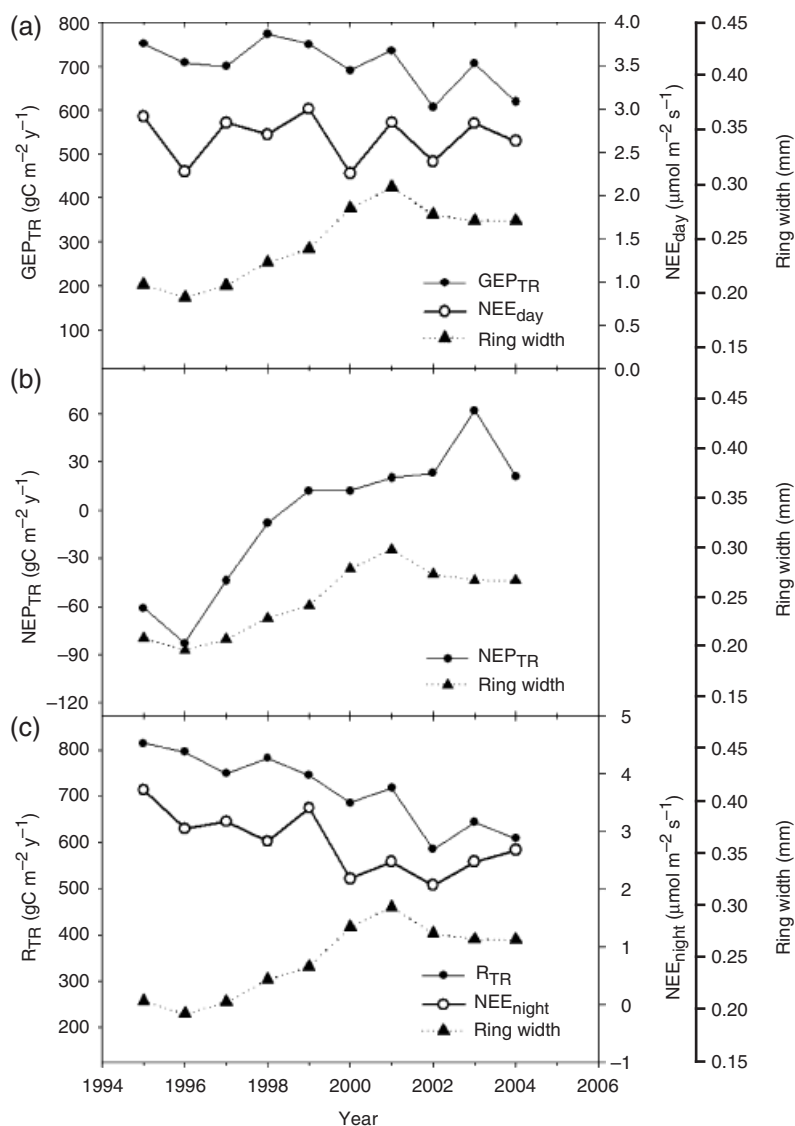


Fig. 3 Time series of measures of photosynthesis (a), carbon accumulation (b), respiration (c) and ring width (a,b,c) from 1995 to 2004. The solid line with \bullet represents the variable on the left axis, while the solid line with \circ represents the variable on the right axis. Ring width is shown on the far right axis and is represented by a dotted line with triangle points.

Summary: ring width and canopy physiology

The correlations between ring width and physiology are summarized in Table 3 and Fig. 5. In general, the measures of carbon uptake (GEP_{EM} , GEP_{TR} , NEE_{day}) were not correlated with ring width, while the measures of respiration (R_{TR} , NEE_{night}) and carbon accumulation (NEP_{TR}) were correlated with ring width during both the current and previous year of ring width formation (Table 3).

The statistical correlation between the trends in respiration and NEP (Fig. 5c,d) may or may not imply causal relationships. The year-to-year fluctuations in R_{TR} are not correlated with fluctuations in ring width

(Fig. 3c). If there were a strong causal relationship between ring width and R_{TR} , we might expect the residual variation in ring width to be correlated with that in R_{TR} . Additionally, the danger of a type II error (acceptance of a false hypothesis) is high given the small sample size and degrees of freedom. A first order serial correlation in ring width and tower data reduces the degrees of freedom from 9 to 2.

Discussion

This is the first study we are aware of that compares a long-term record of whole-forest gas exchange with a

contemporaneous record of tree ring width. The comparison was facilitated by the length and precision of the eddy covariance record (10 years), the simplicity of vegetation at the site (an even-aged, monospecific

stand), and the magnitude of interannual climate variability. Perhaps unsurprisingly, the study raises more questions than it answers.

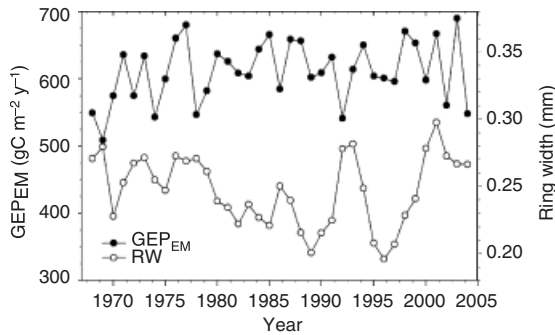


Fig. 4 Time series of gross ecosystem production (GEP_{EM}) (left axis: \bullet) and ring width (right axis: \circ) from 1968 to 2004. There was no significant relationship between ring width and GEP_{EM} (P -value > 0.05).

What mechanisms drive the serial correlation and oscillation in ring width?

The tree ring chronologies at both NOBS and 1930 reveal strong serial correlations and apparent oscillations with periodicities of ~ 7 years (Figs 1, 4, and 6a). The synchronization between sites (Figs 1 and 2) implies that an aspect of the physical environment probably drives the oscillation, causing ring width to be well correlated between the two sites despite differences in disturbance history and seral stage. However, the weather did not show similar serial correlations or oscillations (Fig. 6b, c and Table 2), indicating that the ring width oscillations were not a direct result of weather, and that an ecological or biophysical

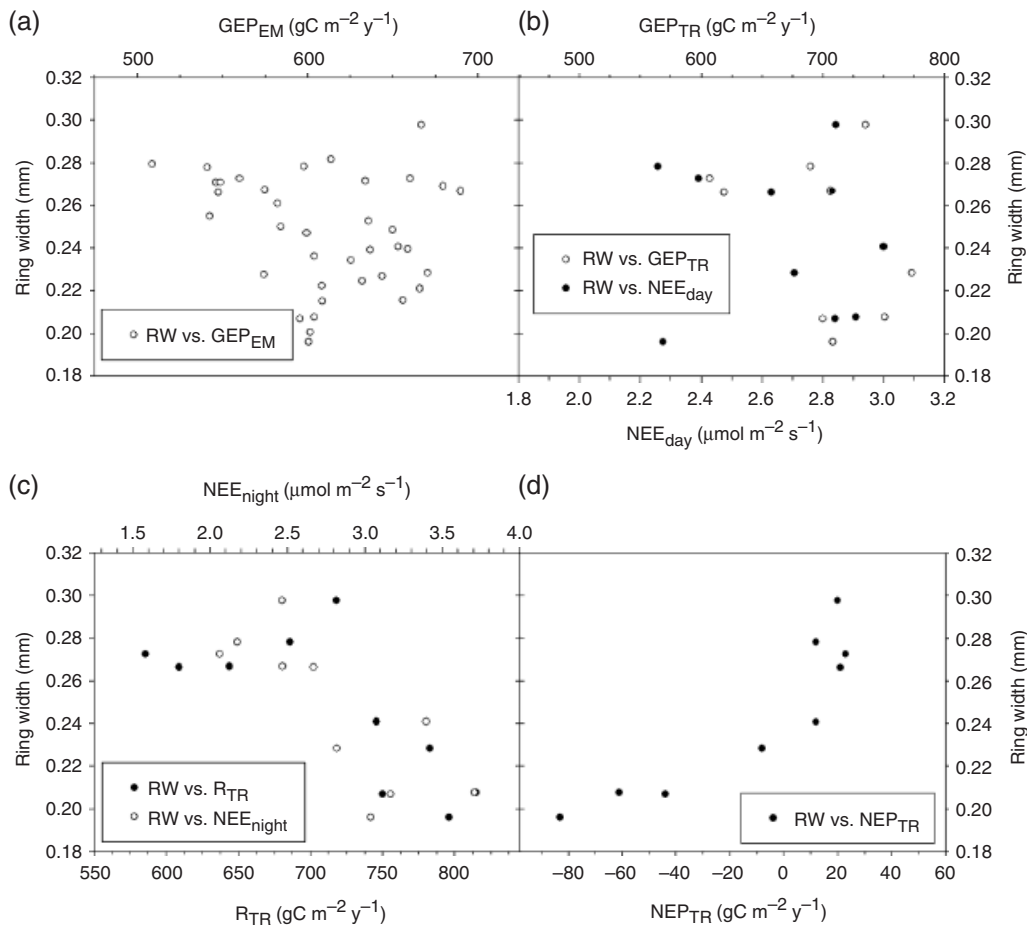


Fig. 5 Ring width (RW) as a function of measures of photosynthesis (a and b), respiration (c), and carbon accumulation (d) during the year of ring formation. Gross ecosystem production GEP_{EM} (a) (\circ), gross ecosystem production GEP_{TR} (b) (\circ), and net ecosystem exchange (NEE) NEE_{day} (b) (\bullet) were uncorrelated with ring width (P -value > 0.05). NEE_{night} (c) (\circ) was negatively related to ring width. R_{TR} (\bullet) was negatively related to ring width. Net ecosystem production (NEP) NEP_{TR} (d) (\bullet) was positively related to ring width.

Table 3 Pearson coefficients (r) and P -values (in brackets) of the correlation between NOBS ring width and the specified physiological variable during the current (middle column) and previous year (far right column) of NOBS ring width formation. Significant relationships are denoted in **bold** (P -value < 0.05)

Variable	No lag r (P -value)	1 year lag r (P -value)
<i>Carbon Uptake</i>		
GEP _{EM}	-0.198 (0.241)	-0.071 (0.681)
GEP _{TR}	-0.371 (0.291)	-0.266 (0.489)
NEE _{day}	-0.089 (0.808)	-0.108 (0.782)
<i>Carbon Loss</i>		
R _{TR}	-0.733 (0.016)	-0.682 (0.043)
NEE _{night}	-0.779 (0.008)	-0.685 (0.042)
<i>Carbon Accumulation</i>		
NEP _{TR}	0.854 (0.002)	0.839 (0.005)

GEP, gross ecosystem production; NEE, net ecosystem exchange; NEP, net ecosystem production.

mechanism that is operating similarly at both sites plays a more proximate role in controlling wood increment. The specific mechanisms behind serial correlation in tree rings are poorly understood (Hughes *et al.*, 1982). Possible causes of autocorrelation include gradual changes in carbohydrate pools within trees, plant allocation to reproduction (masting), nutrient availability, pathogens, herbivores, the extent and duration of soil frost, or the depth of the soil water table. Autocorrelation is a prominent feature in both the tower flux (Dunn *et al.*, 2006) and tree ring data sets. Autocorrelation in tree ring chronologies is poorly understood even though it has clear implications for efforts to model, measure, or understand forest carbon cycling, and to use tree rings to infer past climate.

Why is ring width uncoupled from GEP?

NOBS ring width was unrelated to all three measures of the previous or current year's carbon uptake (NEE_{day}, GEP_{TR}, and GEP_{EM}; Figs 3a, 4, and 5a, b; Table 3). The lack of a relationship between ring width and GEP may simply indicate that ring growth is controlled almost entirely by something other than carbon uptake. Alternatively, the lack of a relationship between recent GEP and ring width, as well as the strong serial correlation in ring width, may be explained in part if Black Spruce trees possess a large carbohydrate storage pool that integrates several years of net carbon exchange (Chapin *et al.*, 1990; Gower *et al.*, 1995; Hoch & Korner, 2003) and buffers ring width from fluctuations in GEP.

Cannell & Dewar (1994) proposed that inherently slow growing stress-tolerant trees, such as Black Spruce, maintain large storage reserves. Carbohydrate storage presumably increases survival during environmental or

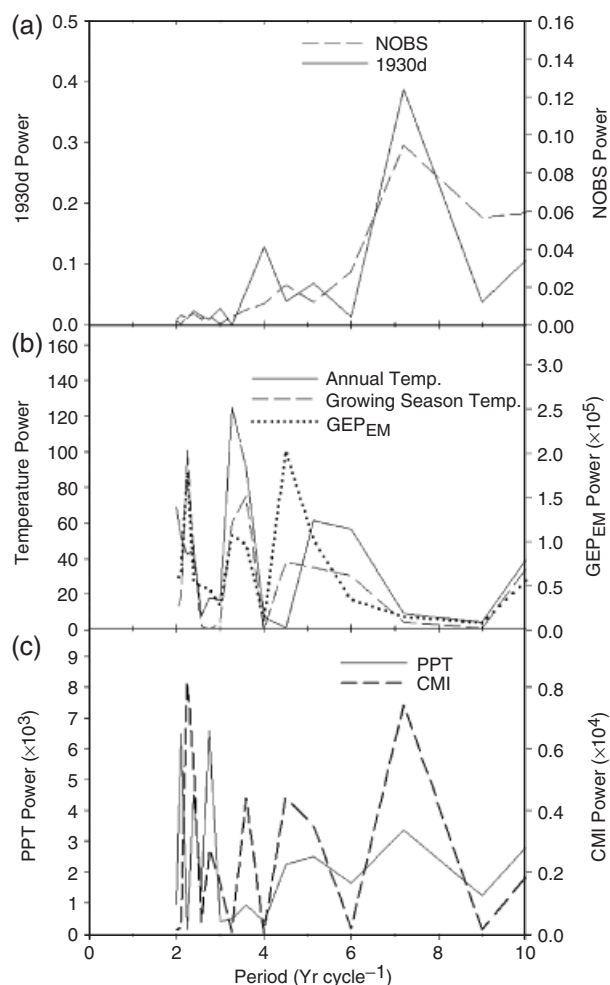


Fig. 6 Fourier Transforms of ring width chronologies, annual empirical model of gross ecosystem production (GEP_{EM}), and climatic conditions from 1968 to 2004. (a) Power spectrum of Northern Old Black Spruce Site (NOBS) (dashed line) and detrended 1930 (1930d) (solid line) ring width chronologies. (b) Power spectrum of average annual (solid line) and growing season (dashed line) (Day of year: 100–300) temperature and GEP_{EM} (dotted line). (c) Power spectrum of precipitation (PPT) (solid line) and annual climate moisture index (CMI) (dashed line). The peaks in the power spectrum indicate the periodicity of the data in years per cycle. NOBS and 1930 ring width data have strong signals at longer periods (>6 years), whereas GEP_{EM}, temperature, precipitation, and CMI have strong signals at shorter periods (<6 years).

biological stress. Wurth *et al.* (2005) found that a tropical forest could replace its canopy after defoliation solely from starch reserves. Czimczik *et al.* (2006) used measurements of the natural abundance of ¹⁴C to demonstrate that the roots at NOBS in July were respiring carbon that had been fixed during a previous year. A large carbohydrate pool might explain the decadal decrease in tree growth in boreal regions following

volcanic eruptions (Krakauer & Randerson, 2003). Cool temperatures following an eruption might decrease photosynthesis and deplete the carbohydrate pool, resulting in a decrease in growth that persists beyond the initial perturbation. A large storage pool is also consistent with the general difficulty of linking short-term biometric measurements of forest growth with contemporaneous eddy covariance measurements of CO₂ exchange (Arneeth *et al.*, 1998; Barford *et al.*, 2001; Sampson *et al.*, 2001; Tschaplinski & Hanson, 2003; Gough *et al.*, 2006).

Is there a causal relationship between the trends in ring width, Respiration, and NEP?

While we are hesitant to fully accept a causal relationship between the trends in respiration, NEP and wood increment from 1995 to 2004 (Figs 3b, c, and 5c, d), the observed correlations are nonetheless intriguing and it is worth speculating whether a common factor could have caused all three patterns. Perhaps an unidentified aspect of the physical environment directly caused the observed decrease in respiration over the study, which, in turn, left more carbon for plant growth and increased ring width and NEP. Alternatively, perhaps an unidentified factor that directly controls plant NPP changed over time, resulting in increased ring width and NEP. Possible factors that might directly control plant growth include nutrient availability or endogenous cycles of plant allocation such as masting. If plant growth is in fact controlled directly by an unidentified factor, and GEP is controlled directly by weather, then respiration may be determined by the difference between GEP and NPP. The decline in respiration from 1995 to 2004 might then have resulted from an increased demand for carbon to support NPP coupled with a relatively constant GEP. This second possibility differs fundamentally from the widely held assumption that NPP is determined by the difference between GEP and respiration (Waring & Schlesinger, 1985; Waring & Running, 1998; Waring *et al.*, 1998).

Conclusions

We are unable to fully explain our observations, although it is clear that wood production and NEP are not simple functions of GEP or annual weather. Alternative drivers of ring width, including the possibility that wood production varies as a result of shifts in respiration, or that wood production is controlled by an unidentified aspect of the environment rather than the balance between GEP and respiration, require further investigation. The physiological mechanisms that determine the timing and quantity of allocation to wood production are poorly understood (Cannell &

Dewar, 1994). Temporal lags, which we suspect are related to increases and decreases in carbohydrate storage pools, appear to be important mechanisms driving interannual variability in growth. Alternative explanations for these lags include gradual changes in nutrient availability, pathogens, herbivores, soil frost, or soil water table. The cause or causes of these lags, and the controls on the allocation of photosynthate to wood production, are critical uncertainties in our understanding of boreal ecosystems.

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