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 &
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 (Arneth 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 (Arneth 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., 2001; Gough et al., 1995). 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 (Arneth et al., 1998; Sampson et al., 2001; Gough et al., 2006), whereas photosynthesis responds within seconds to current environmental conditions.

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 records (> 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 (Pleurozi um 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 (r² 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 (GDD = \sum GDD_o, where GDD, is the (daily average temperature (Tᵢ)-base temperature (0 °C) for Tᵢ>0 °C and GDDᵢ= 0 if Tᵢ<0 °C). 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 (MJ m⁻² day⁻¹)] was estimated using the MTCLIM v4.3 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 × x, r²: 0.61, RSME: 3.26 MJ m⁻² day⁻¹, P-value <0.001).

Eddy covariance data

The net ecosystem exchange (NEE) of CO₂ 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 CO₂ was calculated from measurements of CO₂ mixing ratio at 0.3, 1.5, 4.6, 8.4, 12.9, and 28.8 m aboveground level. The turbulent flux of CO₂ 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 CO₂ 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 CO₂ to the time derivative of the column storage of CO₂ 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.
(\(u^*<0.20\,\text{m}\,\text{s}^{-1}\)) 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 (\(\text{GEP}_{\text{TR}}, \text{NEE}_{\text{day}}, \text{GEP}_{\text{EM}}\)), two measures of carbon loss (\(\text{R}_{\text{TR}}, \text{NEE}_{\text{night}}\)), and one measure of net \(\text{CO}_2\) exchange (\(\text{NEP}_{\text{TR}}\)) 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 \(\text{GEP}_{\text{TR}}, \text{NEE}_{\text{day}}, \text{GEP}_{\text{EM}}\) became more positive, and the forest assimilated more \(\text{CO}_2\) during daytime. A statement such as ‘respiration increased’ indicates that \(\text{R}_{\text{TR}}, \text{NEE}_{\text{night}}\) became more positive, and the forest lost more \(\text{CO}_2\) at night. A statement such as ‘NEP increased’ indicates that \(\text{NEP}_{\text{TR}}\) became more positive, and the forest accumulated more carbon over a year.

**Tower-based measures of carbon uptake (\(\text{NEE}_{\text{day}}, \text{GEP}_{\text{TR}}\)).** We used the tower measurements of daytime net \(\text{CO}_2\) 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 (\(\text{NEE}_{\text{day}}\)). We calculated \(\text{NEE}_{\text{day}}\) from the unfilled tower observations for daytime periods (\(\text{PAR}>10\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}\)) with a suitable wind direction. The advantages of \(\text{NEE}_{\text{day}}\) are that it assumes very little and is sensitive to both growing season length and daytime \(\text{CO}_2\) uptake. The disadvantages of \(\text{NEE}_{\text{day}}\) are that it is also influenced by respiration and the year-to-year patterns of \(\text{NEE}_{\text{day}}\) 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 (\(\text{GEP}_{\text{TR}}\)).

| **Table 1** | Summary measures of canopy physiology
| --- | --- |
| **Measure** | **Description** |
| Ring width chronologies | 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 dev is the chronology after detrending with an exponential fit. |
| Carbon uptake | GEP EM Predictions of annual gross \(\text{CO}_2\) 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 et al., 2006). |
| | NEE day Average daytime (\(\text{PAR}>10\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}\)) \(\text{NEE}\) from Day of Year 100 to 300 (the maximum potential growing season). |
| Carbon loss | R TR Annual sums of respiration (\(\text{R}\)) from gap-filled eddy covariance data (Dunn et al., 2006). |
| | NEE night Average nighttime (\(\text{PAR}<10\,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}\)) \(\text{NEE}\) from Day of Year 100 to 300 (the maximum potential growing season). |
| Carbon accumulation | NEP TR Annual sum of \(\text{NEE}\) from gap-filled eddy covariance data (Dunn et al., 2006). |

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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 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., $y = \beta_0 + \beta_1 x$) 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 GEPEM at annual time intervals using a fast Fourier transform (FFT) to derive Fourier amplitudes and compare the spectral properties of the climatic and physiological 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.

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
displayed oscillations with an apparent period of 3 years (Fig. 4). Ring width gradually increased after 1996
Growing season temperature \( K_{0} \) Growing degree days \( \text{NoBS} \) ring width and the specified variable during the current (middle column) and previous year (far left column) of NOBS ring width formation. We lagged annual GEPEM up to 10 years and might improve the relationship between ring width and long-term trend. GEPEM and ring width are apparently varied markedly from year to year with no apparent GEPEM fluctuated from year to year whereas ring width

| 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)             | \textbf{0.363 (0.029)}        |
| CML3                             | 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 \( \text{NEE}_{\text{night}} \) decreased during the period of measurement, while ring width and \( \text{GEP}_{\text{TR}} \) increased (Fig. 3). Both \( R_{TR} \) and \( \text{NEE}_{\text{night}} \) decreased throughout the period, providing strong evidence for a decline in ecosystem respiration from 1995 to 2004. \( \text{NEE}_{\text{day}} \) or \( \text{GEP}_{\text{EM}} \) remained constant, and \( \text{GEP}_{\text{TR}} \) declined, indicating that ecosystem photosynthesis did not increase from 1995 to 2004 (Figs 3a and 4).

Carbon assimilation and ring width

\( \text{GEP}_{\text{EM}} \) fluctuated from year to year whereas ring width displayed oscillations with an apparent period of \( \sim 7 \) years (Fig. 4). Ring width gradually increased after 1996 and reached a maximum in 2001, whereas \( \text{GEP}_{\text{EM}} \) varied markedly from year to year with no apparent long-term trend. \( \text{GEP}_{\text{EM}} \) 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 \( \text{GEP}_{\text{EM}} \) 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 (Arneth et al., 1998; Kozlowski et al., 1991) and that lagging \( \text{GEP}_{\text{EM}} \) might improve the relationship between ring width and \( \text{GEP}_{\text{EM}} \). We lagged annual \( \text{GEP}_{\text{EM}} \) up to 10 years and found no statistically significant relationship with ring width for any lag interval (plots not shown). Likewise, monthly sums of \( \text{GEP}_{\text{EM}} \) 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 \( \text{GEP}_{\text{TR}} \) (P-value: 0.291) or \( \text{NEE}_{\text{day}} \) (P-value: 0.808) (Fig. 5b; Table 3). Lagging \( \text{GEP}_{\text{TR}} \) and \( \text{NEE}_{\text{day}} \) by 1–2 years did not improve the correlation with ring width.

Respiration and ring width

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

Carbon accumulation and ring width

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

Spectral analysis of ring width, \( \text{GEP}_{\text{EM}} \), and weather

Fourier transforms of the ring width chronologies, \( \text{GEP}_{\text{EM}} \), 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). \( \text{GEP}_{\text{EM}} \), 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.
The correlations between ring width and physiology are summarized in Table 3 and Fig. 5. In general, the measures of carbon uptake (GEPEM, GEPTR, NEEday) were not correlated with ring width, while the measures of respiration (RTR, NEEnight) and carbon accumulation (NEPTR) 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 RTR are not correlated with fluctuations in ring width (Fig. 3c). If there were a strong causal relationship between ring width and RTR, we might expect the residual variation in ring width to be correlated with that in RTR. 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.

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
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 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 $^{14}$C 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 (Arnett 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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