The relationship between productivity and tree-ring growth in boreal coniferous forests

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Ecosystem productivity estimated with a model calibrated with eddy-covariance data was related to tree-ring growth of two different boreal conifers along a latitudinal gradient. The relationship between ecosystem productivity and growth changed with species and site. Greater photosynthesis in spring and summer increased annual anomalies of radial growth in both species, and the response of growth to productivity was earlier in warmer southern stands particularly for pine. Radial growth of jack pine increased in the long-term with higher productivity, whereas this relationship was more reduced in black spruce. This could express species-specific differences in carbon allocation strategies but likely it is a consequence of the limiting marginal soils where spruce is found in the south. Only tree-rings of jack pine at some sites showed certain potential as direct proxies for ecosystem productivity at the low and high-frequency responses.

Introduction

Climate warming and the increase in atmospheric-CO₂ concentrations cause changes in forest growth and ecosystem productivity. There are reports of contrasting growth responses to warming over recent decades in different types of forests. Although some boreal species show negative growth trends in response to recent climate change (Hoofgaard et al. 1999, D’Arrigo et al. 2004), net ecosystem productivity in boreal and temperate conditions is generally expected to increase with increasing temperatures (Myneni et al. 1997, Boisvenue and Running 2006). Forest growth measurements and models assume that there is a close connection between the stem
growth of a tree and its carbon balance (e.g. Running 1994, Le Roux et al. 2001, Zweifel et al. 2010). Variations in the net ecosystem productivity can be measured and modelled from networks of eddy-covariance towers (Kramer et al. 2002, Baldocchi et al. 2003, Bergeron et al. 2007) which provide useful insights into the carbon balances of ecosystems and their ecological drivers. However, since these towers are expensive to operate they provide limited temporal and spatial coverage of ecosystem carbon balances. Productivity estimates can also be derived from biometric-ecological inventory methods but these methods present similar shortcomings as those for eddy-covariance stations (Ehman et al. 2002, Gough et al. 2008, Ohtsuka et al. 2009).

Tree-ring records obtained using dendrochronological methods (Cook and Kairiukstis 1990) could be a key tool to extend carbon balances or ecosystem productivity to larger time scales and areas. Tree rings would be a useful complement to direct ecosystem productivity estimates since they extend both spatially and temporally beyond the directly measured data of net ecosystem exchange from flux towers. Additionally, a large quality checked archive of tree ring data is readily available from databases such as the International Tree-Ring Data Bank (ITRDB, http://www.ncdc.noaa.gov/paleo/treering.html). They have annual resolution and span many decades of forest growth. Traditionally, empirical models where climatic variables are regressed against tree growth indices were employed to fit the relationship between climate and growth in dendrochronology. Several authors developed mechanistic approaches of annual tree ring formation with more comprehensive process-based models that are also able to take into account the non-linear response of growth to climate (Foster & Leblanc 1993, Berninger et al. 2004, Misson 2004, Vaganov et al. 2006, Drew et al. 2010). These models try to mimic not only the influence of climatic factors, but can also account for phenology, radiation, changes in transpiration and other ecophysiological processes involving carbohydrate synthesis and allocation. The models perform well in explaining annual radial growth but generally not better than the classic, empirical approaches (Anchukaitis et al. 2006, Evans et al. 2006, Shi et al. 2008).

Several authors compared tree-ring growth with estimates of net primary productivity from mechanistic models (Rathgeber et al. 2003, Berninger et al. 2004, Girardin et al. 2008, Hari and Nöjd, 2009). Others studied the relationship between direct carbon flux estimates at eddy-covariance stations and tree-ring growth (Rocha et al. 2006), flux estimates and cambial growth (Zweifel et al. 2010) and flux estimates and biometric measurements of tree growth from permanent plots (Ehman et al. 2002, Gough et al. 2008, Granier et al. 2008, Ohtsuka et al. 2009). If ecosystem carbon fixation and ecosystem productivity could be estimated from tree rings, then dendrochronological data might provide an effective tool for the spatial and temporal extrapolation of micrometerological methods. However, to our knowledge no study has analyzed the variability in the relationship between growth and ecosystem productivity along a climatic gradient, since existing studies are concerned with local relationships between growth of stands around eddy-covariance stations and direct ecosystem flux measurements from the stations. Some agreement between ecosystem productivity and radial growth has been reported, yet these studies suggest that unknown carbon allocation strategies may obscure the growth–carbon relationship (Rocha et al. 2006, Gough et al. 2008, Ohtsuka et al. 2009). We analyzed the relationship between modeled ecosystem productivity and annual radial growth for two coniferous species sampled along a latitudinal (i.e. temperature and precipitation) gradient in eastern Canada. The growth data were originally published in Huang et al. (2010) who analyzed the relationship between the high-frequency of growth and climate using a classical empirical approach. Now we extend this work by using calculated ecosystem productivity as a covariate to investigate whether tree rings can be used as indirect estimates of ecosystem productivity. We split growth into its low- (i.e. to analyze the long-term multidecadal trends) and high-frequency (i.e. to analyze the short-term, annual response) components to analyze this relationship in the short and the long terms.
Material and methods

Tree-ring data: disentangling high- from low-frequency of growth

We analyzed the relationship between annual radial growth and net and gross ecosystem exchange in two boreal species from eastern Canada: black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*). They are dominant post-fire species widely distributed in North America. Jack pine generally occurs at xeric sites with sandy soil, and black spruce generally occurs at sites with poor soil covered by thick moss layers (see Table 1 for further description on the sampled sites). In the south, black spruce stands mostly co-occur with balsam fir (*Abies balsamea*), red pine (*Pinus resinosa*) and white pine (*Pinus strobus*). Jack-pine stands co-occur with black spruce and white birch (*Betula papyrifera*). In the north, monospecific pure stands of both species are frequently found. Samples were collected from dominant trees in dense, mature, un-managed post-fire stands.

Increment cores were collected from 20 trees from nine locations on a latitudinal transect from 46°N to 54°N (Table 1 and Fig. 1). Cores were processed and analyzed to build annual series of individual tree growth increments using standard dendrochronological methods (Cook and Kairiukstis 1990). Detrending methods in dendrochronology can emphasize either the long- or short-term growth response. We therefore split the analysis of the relationship between ecosystem productivity and growth in two: (1) a low-frequency analysis, using a variation of the regional curve standardization (RCS), which fits a single age-growth curve to all sites, and mixed models to study the response of growth to ecosystem productivity in the long-term; (2) a high-frequency analysis of the growth response to ecosystem productivity on each site separately to study how growth at the nine individual sites responded to productivity in the short-term (i.e. to annual growth anomalies). In both analyses, we used mean site chronologies of growth indices instead of individual tree growth series to pool out the influence of individual dendrometric features, thus making the growth indices comparable with estimates of ecosystem productivity.

Low-frequency analysis: $I_{\text{BAI}}$

For the low frequency analysis we used annual, basal area increments (BAI; see Fig. 2) with a

<table>
<thead>
<tr>
<th>Species</th>
<th>Lat. (°N), long. (°W)</th>
<th>Elevation</th>
<th>Stand types (m a.s.l.)</th>
<th>Slopes(°)/aspect</th>
<th>Sample type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black spruce</td>
<td>45°59´, 77°28´</td>
<td>183</td>
<td>Uneven-aged/Mixed</td>
<td>0</td>
<td>Cores</td>
</tr>
<tr>
<td></td>
<td>47°03´, 79°20´</td>
<td>273</td>
<td>Uneven-aged/Mixed</td>
<td>0</td>
<td>Cores</td>
</tr>
<tr>
<td></td>
<td>48°06´, 79°18´</td>
<td>260</td>
<td>Uneven-aged/Mixed</td>
<td>2/N</td>
<td>Cores</td>
</tr>
<tr>
<td></td>
<td>49°09´, 78°32´</td>
<td>440</td>
<td>Uneven-aged/Pure</td>
<td>4/S</td>
<td>Discs</td>
</tr>
<tr>
<td></td>
<td>50°03´, 78°46´</td>
<td>260</td>
<td>Uneven-aged/Mixed</td>
<td>0</td>
<td>Discs</td>
</tr>
<tr>
<td></td>
<td>51°02´, 77°34´</td>
<td>240</td>
<td>Uneven-aged/Mixed</td>
<td>0</td>
<td>Discs</td>
</tr>
<tr>
<td></td>
<td>51°52´, 77°26´</td>
<td>177</td>
<td>Uneven-aged/Mixed</td>
<td>0</td>
<td>Discs</td>
</tr>
<tr>
<td></td>
<td>52°54´, 77°16´</td>
<td>226</td>
<td>Uneven-aged/Mixed</td>
<td>0</td>
<td>Discs</td>
</tr>
<tr>
<td></td>
<td>53°39´, 78°22´</td>
<td>82</td>
<td>Uneven-aged/Pure</td>
<td>5/E</td>
<td>Discs</td>
</tr>
<tr>
<td>Jack pine</td>
<td>46°00´, 77°25´</td>
<td>160</td>
<td>Uneven-aged/Pure</td>
<td>0</td>
<td>Cores</td>
</tr>
<tr>
<td></td>
<td>47°02´, 79°21´</td>
<td>258</td>
<td>Uneven-aged/Mixed</td>
<td>0</td>
<td>Cores</td>
</tr>
<tr>
<td></td>
<td>48°09´, 79°30´</td>
<td>330</td>
<td>Uneven-aged/Mixed</td>
<td>0</td>
<td>Cores</td>
</tr>
<tr>
<td></td>
<td>49°09´, 78°32´</td>
<td>440</td>
<td>Uneven-aged/Mixed</td>
<td>7/N</td>
<td>Cores</td>
</tr>
<tr>
<td></td>
<td>50°09´, 78°49´</td>
<td>245</td>
<td>Uneven-aged/Mixed</td>
<td>10/SE</td>
<td>Discs</td>
</tr>
<tr>
<td></td>
<td>51°12´, 77°27´</td>
<td>215</td>
<td>Uneven-aged/Mixed</td>
<td>4/S</td>
<td>Discs</td>
</tr>
<tr>
<td></td>
<td>51°56´t, 77°22´</td>
<td>200</td>
<td>Uneven-aged/Mixed</td>
<td>0</td>
<td>Discs</td>
</tr>
<tr>
<td></td>
<td>52°54´, 77°16´</td>
<td>226</td>
<td>Uneven-aged/Mixed</td>
<td>0</td>
<td>Discs</td>
</tr>
<tr>
<td></td>
<td>53°42´, 78°04´</td>
<td>125</td>
<td>Uneven-aged/Mixed</td>
<td>3/N</td>
<td>Discs</td>
</tr>
</tbody>
</table>
conservative detrending using the RCS method (Esper et al. 2003). Variance in BAI was first stabilized following Cook and Peters (1997) and then a mean single curve (Fig. 3) was fitted to cambial age aligned BAI series from all sites together to remove population average biological growth. We used a cubic spline with a 50% low-frequency cutoff of 150 years for jack pine and 250 years for black spruce (Fig. 3). These two values were selected to be close to the maximum age encountered in the sample from both species. Annual growth indices ($I_{BAI}$) were calculated using residuals between the fitted mean curve and observed individual BAI (Cook and Kairiukstis 1990). In the low-frequency analysis using $I_{BAI}$, we studied the relationship between growth and ecosystem productivity by analyzing the nine sites together so that we included a broader range in the covariates (calculated ecosystem productivity) to study the existence of non-linear relationships by fitting a single equation relating growth and climate.

**High-frequency analysis: $I_{rw}$**

In the previous, low-frequency analysis of the relationship between productivity and growth relationships we lose high-frequency site-wise information on the short-term relation of ecosystem productivity and tree growth. Therefore, to perform a parallel analysis with which we could study the site-wise short-term responses of growth we calculated a second set of growth indices after detrending individual ring-width (RW) series with 80-year splines (Cook and
Here, we analyzed the response of growth to ecosystem productivity at each of the nine sites separately.

**Physiological covariates estimated from models calibrated with eddy-covariance data**

We calculated time series of ecosystem productivity for each site using a photosynthesis model fed with local climate data obtained from Natural Resources Canada (Régnière and Saint-Amant 2008) for the nine sites studied. First, to calibrate the model we used integrated eddy-covariance gap-filled half-hourly carbon flux data coming from the four mature black spruce or jack pine forests included in the Fluxnet-Canada Research Network (http://fluxnet.ccrp.ec.gc.ca/e_about.htm) (Table 2 and Fig. 1). Daily flux data from the four forests were calculated from the half-hourly flux measurements and ecosystem carbon data were used to calibrate daily the model from Gea-Izquierdo et al. (2010, Appendix) based on Mäkelä et al. (1996, 2004). In this big-leaf model, stand gross ecosystem exchange (GEE, in mol CO$_2$ m$^{-2}$ day$^{-1}$) was estimated as a function of atmospheric CO$_2$ concentration, photosynthetically active radiation, water vapor pressure deficit and air temperature. In the model, ecosystem respiration ($R_{eco}$) and net ecosystem exchange (NEE) were calculated as

$$\text{NEE} = R_{eco} - \text{GEE}.$$  

The model provided excellent fit to the four individual flux data sets (Efficiency, $EF > 0.94$ see Eq. 1 below for the meaning of EF) and also when fitted to the four sites together (EF = 0.97 for daily GEE and EF = 0.91 for daily respiration). Therefore, we fitted one single model to estimate carbon fluxes for all species and sites (Table 3 and Fig. 4; Gea-Izquierdo et al. 2010).

Throughout the text, negative values of GEE and NEE correspond to a flux from the atmosphere to the land surface, i.e. GEE in all cases and NEE when photosynthesis exceeds respiration.

Once calibrated, the model was used to produce daily estimates of gross and net ecosystem productivity for the nine sites along the climatic gradient and these estimates were included as covariates in the low and high-frequency analyses. From the daily estimates calculated for the nine sites using the model, we obtained time series of monthly, seasonal and annual ecosystem productivity, to compare with growth indices.

The following flux estimates (both year $t$ and year $t - 1$) were evaluated in the $I_{\text{BAI}}$ analyses: (i) annual GEE, NEE, and $R_{eco}$; (ii) spring GEE, NEE, $R_{eco}$ (from April, May, June, which coincides with the annual maximum); (iii) growing
season NEE, GEE and $R_{cco}$ (April–September); (iv) the same for summer (June–August). The model estimates photosynthesis per ground unit area (m²) of closed stands. We assumed that stand conditions (i.e. leaf area index and closed canopies) would remain unchanged along time and among sites. Later in the discussion we describe possible biases which could have arrived had we applied the same analysis to open stands or to stands with variable canopy conditions.

Statistical analyses

First, to analyze the differences between mean site responses ($I_{BAI}$, low-frequency) to physiological covariates we used linear mixed models including a random intercept for site (Verbeke and Mohlenberghs 2000). We studied the relationship between $I_{BAI}$ as the dependent variable and physiological covariates on a single fit including all sites together. Serial correlation in the time series was taken into account by including a first auto-regressive, AR[1], variance-covariance error structure to each site submatrix. To compare models including GEE as covariate with those including GEE² (quadratic relationship) we used Akaike’s Information Criterion (AIC) and the model minimizing AIC was considered to be the best (Burnham & Anderson 2004). Model performance was evaluated using the model efficiency (EF):

$$EF = 1 - \frac{(n-k-1)^{1/2} \sum(y_i - \hat{\mu})^2}{(n-1)^{1/2} \sum(y_i - \bar{\mu})^2}$$  \hspace{1cm} (1)

where $n$ is the number of observations, $k$ is the number of parameters, $y_i$ is the $i$th value of measured variable $y$, $\hat{\mu}$ is the predicted value, and $\bar{\mu}$ is the mean of the measured variable). We used partitioning of variance to discuss the influence of each covariate (random and fixed) on the final model, which was calculated assuming that total variance equaled the sum of the individual variances of the different covariates within the linear models fitted. Secondly, for the high-frequency analysis, $I_{RW}$ was compared separately for each of the nine sites with monthly estimates of the covariate explaining most varia-

<table>
<thead>
<tr>
<th>No. Station in Canada</th>
<th>Lat. (°N)</th>
<th>long. (°W)</th>
<th>Altitude (m)</th>
<th>Stand height (m)</th>
<th>Dominant tree species</th>
<th>Mean reference period</th>
<th>NEE (mean ± SD) (µmol m⁻² s⁻¹)</th>
<th>T_{mean} (°C)</th>
<th>Period</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 NOBS</td>
<td>55.9, 98.5</td>
<td>10.6</td>
<td>150</td>
<td>259</td>
<td>Pinus banksiana</td>
<td>1999-2005</td>
<td>-0.534 ± 3.163</td>
<td>517.0</td>
<td>2.9</td>
</tr>
<tr>
<td>2 Saskatchewan</td>
<td>54.0, 105.1</td>
<td>14</td>
<td>125</td>
<td>597</td>
<td>Picea mariana</td>
<td>1999-2005</td>
<td>-1.061 ± 3.409</td>
<td>405.6</td>
<td>0.8</td>
</tr>
<tr>
<td>3 old jack pine</td>
<td>53.9, 104.7</td>
<td>14</td>
<td>94</td>
<td>520</td>
<td>Pinus banksiana</td>
<td>1999-2005</td>
<td>-0.677 ± 2.983</td>
<td>430.0</td>
<td>0.1</td>
</tr>
<tr>
<td>4 Quebec old mature</td>
<td>53.9, 104.7</td>
<td>14</td>
<td>4</td>
<td>382</td>
<td>Picea mariana</td>
<td>2003-2005</td>
<td>-0.672 ± 3.574</td>
<td>961.3</td>
<td>0.4</td>
</tr>
</tbody>
</table>

Table 2. Characteristics of eddy-covariance data sets used.
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ance in the $I_{BAI}$ analyses. To study the linear relationship between pair of variables we calculated Pearson’s correlation coefficients ($r_p$) (Cook and Kairiukstis 1990).

Results

Long-term growth and productivity along the latitudinal gradient

NEE and GEE variables decreased with increasing latitude together with mean annual temperature and precipitation (Fig. 5; Huang et al. 2010). The mean BAI of both pine and spruce varied with age, in time along the 1900s and also at different sites (Figs. 2–4). There was a decrease of mean annual growth with latitude in pine (Spearman’s correlation: $r_s = -0.867, p = 0.004$), but not in spruce (Spearman’s correlation: $p = 0.291$; Fig. 5). The ecology and growth response to climate along the gradient differed between species, thus we analyzed the two species separately. Pearson’s correlations between $I_{BAI}$ and annual estimates of components of ecosystem productivity (i.e. NEE, $R_{eco}$, GEE) were slightly higher than those between $I_{BAI}$ and summer or seasonal productivity, and correlations between $I_{BAI}$ and seasonal and annual GEE and NEE were almost identical (Table 4). For this reason, hereafter we only report results using GEE covariates quoted as productivity.

High photosynthetic productivity enhanced tree growth (Table 5) and the relationship

Table 3. Best-fit model results for mean daily GEE model used to calculate ecosystem productivity series (Appendix). EF = efficiency (see Eq. 1 and definition in the text).

<table>
<thead>
<tr>
<th>Observations</th>
<th>$\tau$ (days)</th>
<th>$\delta$ (µmol m$^{-2}$ s$^{-1}$)</th>
<th>$a_{max}$ (mol m$^{-2}$ day$^{-1}$)</th>
<th>$b$</th>
<th>$T_s$ ($^\circ$C)</th>
<th>Bias</th>
<th>RMSE (mol m$^{-2}$ day$^{-1}$)</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td>10545</td>
<td>2.701</td>
<td>7.603</td>
<td>0.0016</td>
<td>-0.261</td>
<td>8.647</td>
<td>-0.001</td>
<td>0.032</td>
<td>0.967</td>
</tr>
</tbody>
</table>

Fig. 4. Residuals of the fitted flux model expressed as monthly integrals of carbon flux: (A) GEE, (B) ecosystem respiration. Bars correspond to one standard deviation of the mean.
between annual productivity and growth was quadratic for both species (AIC of the model as in Table 5 using GEE as covariate instead of GEE$^2$ was 11.7 units greater for pine and 13.5 units for spruce). However the contribution of random effects in the $I_{BAI}$ model reflected mean differences in radial growth between sites and showed that in the low-frequency analysis the variability of annual growth explained by productivity was reduced for spruce (Fig. 6). The importance of random effects was much greater in the spruce model, where the fixed effects were explaining a very small part of the total variance (Table 5 and Fig. 6). As seen in Table 6 the performance of the $I_{BAI}$ model had not been good if analyzed site-wise because this analysis neglected the high-frequency local responses to ecosystem productivity, which we analyze below.

Table 4. Pearson’s correlations ($r_p$) between growth index from the low-frequency analyses ($I_{BAI}$) and CO$_2$ fluxes (GEE, NEE, $R_{eco}$) for Pinus and Picea.

<table>
<thead>
<tr>
<th></th>
<th>GEE$_{annual}$</th>
<th>GEE$_{annual(t-1)}$</th>
<th>GEE$_{season}$</th>
<th>GEE$_{spring}$</th>
<th>GEE$_{summer}$</th>
<th>NEE$_{annual}$</th>
<th>$R_{eco_annual}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$I_{BAI}$ Pinus</td>
<td>-0.626</td>
<td>-0.614</td>
<td>-0.623</td>
<td>-0.583</td>
<td>-0.623</td>
<td>-0.625</td>
<td>0.624</td>
</tr>
<tr>
<td>$I_{BAI}$ Picea</td>
<td>-0.275</td>
<td>-0.263</td>
<td>-0.250</td>
<td>-0.255</td>
<td>-0.265</td>
<td>-0.274</td>
<td>0.264</td>
</tr>
</tbody>
</table>

Table 5. Model results: the model for site $i$ is: $I_{BAI} = (\mu + a) + \beta$GEE$^2 + \varepsilon_i$, with $a$ being a random site effect, $\varepsilon_i$ the random error; $\mu$ a common intercept for the whole population and $\beta$ a fixed coefficient for GEE$^2$ (the quadratic function of GEE). GEE = annual GEE; EF = efficiency calculated including the fixed and random site effects (Eq. 1); SE = standard error; AR[1] = parameter estimate of first order autoregression used in the variance-covariance structure for the error.

<table>
<thead>
<tr>
<th>GEE model</th>
<th>Parameter (covariate)</th>
<th>Estimate</th>
<th>SE</th>
<th>EF</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Pinus banksiana</strong></td>
<td>Fixed effect estimates</td>
<td>$\mu$</td>
<td>-0.0599</td>
<td>0.0325</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$\beta$ (GEE$^2$)</td>
<td>$5.61 \times 10^{-7}$</td>
<td>$1.01 \times 10^{-10}$</td>
</tr>
<tr>
<td></td>
<td>Covariance estimates</td>
<td>Random intercept (site)</td>
<td>0.0058</td>
<td>0.0041</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AR[1]</td>
<td>0.8931</td>
<td>0.0023</td>
</tr>
<tr>
<td><strong>Picea mariana</strong></td>
<td>Fixed effect estimates</td>
<td>$\mu$</td>
<td>0.03113</td>
<td>0.0171</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$\beta$ (GEE$^2$)</td>
<td>$6.14 \times 10^{-8}$</td>
<td>$1.00 \times 10^{-10}$</td>
</tr>
<tr>
<td></td>
<td>Covariance estimates</td>
<td>Random intercept (site)</td>
<td>0.0018</td>
<td>0.0013</td>
</tr>
<tr>
<td></td>
<td></td>
<td>AR[1]</td>
<td>0.9377</td>
<td>0.0163</td>
</tr>
</tbody>
</table>
Local responses to short-term variations in productivity

Results from the high ($I_{RW}$) frequency analysis were different from those of the low-frequency ($I_{BAI}$) analysis (Fig. 7). Differences between species in correlation values between monthly-simulated productivity and $I_{RW}$ were smaller than those in the low-frequency $I_{BAI}$ analyses (Fig. 7). Yet linear correlation coefficients between covariates and $I_{RW}$ for pine were still generally greater than those for spruce (Fig. 7). In pine, growth of stands located more to the south (latitudes 46°–50°) responded to photosynthesis earlier in spring (particularly at year t) while trees from northern stands responded later in summer (Fig. 7A). The positive response of growth to productivity in black spruce was more homogeneous along the gradient in spring, and the delay in the response with latitude was less evident, particularly in the current year (Fig. 7B). Growth of spruce at low latitudes exhibited a stronger negative response to high productivity in summer of the current year. In contrast, the effect of high productivity in the summer was positive for growth at the highest latitudes for the same period. These effects in summer were detectable for both species also for the previous year. In pine there was a strong relationship between growth and productivity of the previous year, with some differences between latitudes.

Discussion

Process-based growth models generally contain sets of equations of photosynthetic production and respiration, as well as rules of how this photosynthetic production is allocated to different plant organs. In the present paper, we estimated tree-ring width at different temporal scales as a direct function of photosynthetic production. The proposed approach is a modification to that in Berninger et al. (2004) who presented relationships between leaf-level photosynthesis and growth of Scots pine and similar to that in Foster and Leblanc (1993) or Federer et al. (1989). Detailed ecophysiological growth models require knowledge of stand structure and its changes over time (Berninger et al. 2004).

This information is, however, rarely available. Permanent sample plots are usually measured only every five years or even less frequently and reconstruction of tree growth with a high temporal resolution depends largely on tree rings. Photosynthetic production depends on the climate and properties of the plant canopy (e.g. Le Roux et al. 2001). The present modeling approach keeps the canopy characteristics fixed and focuses on the estimation of the climatic effects on photosynthesis as e.g. in Mäkelä et al. (2008a) or Gea-Izquierdo et al. (2010). We acknowledge that there are changes in forest productivity associated with changes in the physiological properties of leaves (Kaufmann et al. 2004) and forests in more productive areas or during more productive periods would probably have higher leaf area index (LAI), hence higher photosynthetic production. However, we
The relationship between ecosystem productivity and radial growth is complex. Tree-ring growth reflected both long- and short-term variations in site productivity but not equally for all sites and species. The long-term mean gross ecosystem exchange was well related only to annual radial growth of one boreal evergreen coniferous species along a latitudinal gradient, jack pine, whereas the correlation with black spruce was very weak. In the short-term, annual anomalies of tree growth were well related to simulated productivity at all sites and for both species. The fit of this relationship (absolute maximum correlation values around 0.4; Fig. 7) was similar to that found for empirical dendroecological models using temperature or growing degree days as the

**Time-scale, species-specific relationships between radial growth and productivity**

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**Fig. 7.** Bootstrap correlations between individually detrended RW ($l_w$) data and monthly GEE (from April to November year $t - 1$, and from March to September year $t$): (A) *Pinus banksiana* GEE, (B) *Picea mariana* GEE. White dots indicate significant correlations. Note that high negative GEE values indicate the forest being a carbon sink hence negative correlations between growth and GEE express that greater photosynthesis at a specific period increases growth. The grey scale represents Pearson’s correlations ranging between −0.4 and 0.5.

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main driver (Hofgaard et al. 1999; Huang et al. 2010). Results from tree-ring empirical models are often similar to results from process-based approaches (e.g. Berninger et al. 2004, Anchukaitis et al. 2006, Evans et al. 2006, Shi et al. 2008). The reason for the similar performance of photosynthesis based and climate based empirical models could be that the non-linear relationship between temperature (in our boreal stands) and photosynthetic production converged to linear when analyzed in long time periods.

The differences in the time scale of the relationship between growth and productivity could explain why models of ecosystem productivity and tree growth seem to operate on different processes. Ecosystem productivity in boreal forests where drought is usually not limiting seems to depend largely on the length of the photosynthetically active period (Suni et al. 2003a, 2003b) which usually starts in April or May. Annual tree diameter growth anomalies, on the other hand, seem to depend on summer temperatures (Kirdyanov et al. 2003, D’Arrigo et al. 2004, Vaganov et al. 2006) and growth can correlate quite well with temperatures during short periods (Kirdyanov et al. 2003). Cambial activity is temperature-dependent and varies at different sites and for different species, but higher temperatures are required for xylem cell division than for photosynthesis in the leaves (Körner 1998, Suni et al. 2003b, Rossi et al. 2011). Therefore, time-scale dependent relationships exist between net carbon fixation and growth and the relationship between these two variables is not a fixed ratio (Luysaert et al. 2007, Granier et al. 2008, Zweifel et al. 2010). Trees in boreal forests are considered to use the period of maximum productivity to allocate carbon to the stem for growth, and this period is delayed in summer with increasing latitude (Kirdyanov et al. 2003). After summer, during those months prior to the dormant period, the trees store carbohydrates for next year’s growth (Granier et al. 2008) and year-to-year variations in productivity could be averaged out by changes in carbohydrates reserve or allocation, which results in more diffuse and difficult to detect relationships between GEE and growth.

Our results agree with those of authors showing a correlation between the high-frequency of growth and photosynthesis (Berninger et al. 2004, Hari and Nöjd, 2009, Zweifel et al. 2010), but different relationships were found for the different sites. Allocation of carbohydrates was the most likely mechanism explaining differences in the growth response between sites and species. Rocha et al. (2006) explained the lack of correlation between measured GEE and ring width on a black spruce site in northern Canada by interannual differences in allocation. Granier et al. (2008) suggested that carbon allocation from photosynthesis is constant during the period when cambium is active in Fagus sylvatica but carbohydrate allocation is a complex phenomenon that is likely to vary with species and also other factors such as climate, soil or even competition (Gough et al. 2002, Rocha et al. 2006). Furthermore, there is evidence for systematic changes in allocation with varying temperature and an interaction of precipitation with temperature along climatic gradients (Vogel et al. 2008). In practice this means that the short-term tree growth may be decoupled from photosynthesis and that trees may modify their growth in response to long-term changes in photosynthetic production (D’Arrigo et al. 2004, Kaufmann et al. 2004). Zweifel et al. (2010) showed the potential complexity of the relationship between growth and photosynthesis and found a strong correlation between cambial activity and GEE which was a function of the time scale, as was also found by Granier et al. (2008). Stronger correlations can be expected at single sites where both flux and growth are measured (e.g. Zweifel et al. 2010) as compared with cases where productivity needs to be simulated along climatic gradients, like we did here.

Other factors precluding a general direct relationship between growth and productivity

Stand-related factors such as stand density, characteristics of tree individuals or microenvironmental variability could also modify the relationship between photosynthesis and growth. To minimize the influence of competition and tree dendrometric features at the different sites we selected mature stands with closed canopies, similar to those used to calibrate the photosynthesis model. However, selection of only
dominant trees, as done classically in many dendrochronological studies, may bias estimated stand growth and its relationship with stand photosynthesis. We believe that the influence of this was minimal at the sampled sites because stands were post-fire, closed and structurally homogeneous. The differences among sites and between species in our results could also be explained by non-climatic factors such as nitrogen availability (Mäkelä et al. 2008b), insect infestation in spruce (Bouchard et al. 2005), different litter decomposition and nitrogen mineralization rates (Bergh et al. 1999, Berninger et al. 2004) or the effect of the humus layer on a differential response to drought (Drobsyhev et al. 2010). Only jack pine decreased its mean radial growth with increasing latitude, hence site temperature and productivity, indicating that climate-controlled most of what foresters call ‘site quality’ for jack pine. For spruce, differences between sites in average growth seemed to be determined by non-climatic factors. Black spruce occupies many different environments in the boreal region of North America, but is not very competitive on eutrophic sites. Those sites occupied by black spruce change along the gradient studied: in the North it is a generalist growing on all types of sites (including good sites), whereas in the south it is restricted to poor sites (Burns and Honkala 1999, Hofgaard et al. 1999). This shift of the realized niche of black spruce could explain its low response to changes in average simulated GEE along the gradient.

NEE was not better correlated with radial growth than GEE probably due to the fact that the fraction of autotrophic to heterotrophic respiration was highly variable between sites (Lloyd and Taylor 1994, Xu et al. 2004). Estimated respiration was closely related to NEE and GEE estimates, but its correlation with growth was weaker than with GEE, contrary to Rocha et al. (2006) but in accordance with Zweifel et al. (2010). However, according to the literature, respiration is only a minor component of interannual variability in carbon fluxes in boreal forests (Suni et al. 2003a, 2003b) while respiration seems to be a major determinant of inter-site variability of net productivity (Valentini et al. 2000, Luysaert et al. 2007). It could be that a varying proportion of GEE is fixed by vegetation in the understory (Knorre et al. 2006).

It could be argued that our GEE model was not applicable given the distance between our sites and three of the flux towers used for the model calibration. The southern stands were in more temperate climate than the eddy-covariance sites, and we found a different response to GEE in summer (particularly of the previous year) for southern sites as compared with that for sites located more to the north. Therefore, it is possible that the photosynthetic production at these sites was more limited by drought than in our calibration data set, and that we overestimated photosynthetic production during summer in the southernmost stands. This would explain the inverse relationship between summer photosynthetic production and growth (expressed as a positive relationship in Fig. 7) for southern sites. Nevertheless in the eddy-covariance-based analysis of Gea-Izquierdo et al. (2010) drought did not appear to affect the estimated GEE at any site with mean temperature below 2.5 °C, like those included in our gradient (Huang et al. 2010). In that paper, the authors tried to incorporate the effects of drought into the model, but concluded that the effect of drought was minor.

Additionally the model had a good fit to coniferous GEE data regardless of species or geographical locations, and the same type of model with small changes in parameters could be used for different sites along a climatic gradient including sites below 46°N (Gea-Izquierdo et al. 2010). The reason for the better fit for jack pine was not in the photosynthesis model since the photosynthesis model was calibrated using mostly black-spruce stands. We therefore believe that using a single GEE model on the geographical gradient studied did not lead to biased results that would compromise our conclusions.

In boreal ecosystems, temperature is generally the strongest driver of photosynthesis and growth and recent decades warming mostly resulted on an increase in photosynthetic activity (Myneni et al. 1997), as reflected by our productivity estimates. Pine growth showed a time trend that we interpreted as an age effect but could also be interpreted as a growth decline reflecting a drought effect in recent years (e.g. Hofgaard et al. 1999, Dulamsuren et al. 2010). However, trees older than 120 years were only found at
53°N (the second northernmost site) and our high-frequency analysis suggests greater water limitations in spruce than in pine. We would expect (if any) water stress limitation to be more widespread in southern stands (Hofgaard et al. 1999) and in any case, any existing age trend did not affect our analysis because growth data were standardized using dendrochronological methods. We analyzed high-frequency and low-frequency responses separately in our paper. The high-frequency is likely to be of secondary importance in long-term growth trends under climate warming and also in terms of productivity. We still do not understand how long-term changes in net productivity and photosynthesis allocation to stem growth will interact. Growth changes in the future may be, therefore, different than just changes in photosynthetic production.

Conclusions

The relationships between estimated ecosystem productivity and tree-ring width were different for the two species depending on the temporal scale analyzed and along the studied climatic gradient, probably reflecting differences in phenology and species-specific carbon allocation strategies. The year-to-year response of growth (annual anomalies from the site mean) was enhanced by ecosystem productivity in both species whereas the long-term relationship of average tree annual growth with ecosystem productivity showed a good agreement with overall photosynthesis only for jack pine. Probably long-term variations in net photosynthesis change the response of growth to climate, which also depends on non-climatic factors. There is a considerable potential to understand these variations and use tree-ring growth as a proxy for ecosystem productivity but this would require a deeper understanding of the possibly interfering factors, in particular of interannual variations in carbohydrate allocation.

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### Appendix

NEE was modeled using a flux partitioning algorithm where: NEE = R_\text{eco} – GEE, with GEE being gross ecosystem exchange (photosynthetic production) and R_\text{eco} being ecosystem respiration. All C flux estimates are in mol m^{-2} day^{-1}. R_\text{eco} was modeled assuming an Arrhenius type relationship with air temperature, using the expression:

\[ R_{\text{eco}}(t) = R_{\text{\theta}} \exp \left\{ 308.56 \left[ \frac{1}{56.02} - \frac{1}{T_{\text{\theta}}(t) + 46.02} \right] \right\} \]  
(A1)
where $T_{air}(t)$ is the measured temperature (°C) above the canopy and $R_{m}$ is the mean respiration at 10 °C. After comparing different ways of temporal fitting (monthly, every second week, annual), we decided to fit a single expression per site since the differences in the proportion of explained variance were not very large.

In the model, the gross photosynthetic rate per unit ground area $A(t)$ (mol CO$_2$ m$^{-2}$ day$^{-1}$) was modeled as a nonlinear function of stomatal conductance of carbon dioxide $g(t)$ (mol CO$_2$ m$^{-2}$ day$^{-1}$), photosynthetic capacity $\alpha(t)$ (mol CO$_2$ m$^{-2}$ day$^{-1}$), and a saturation function of light intensity $\gamma(t)$ (dimensionless):

$$A(t) = \frac{g(t) C_s \alpha(t) \gamma(t)}{g(t) + \alpha(t) \gamma(t)} \quad (A2)$$

where the stomatal conductance is expressed as:

$$g(t) = \max\{0.00001, \tilde{g}(t)\}, \quad (A3)$$

with

$$\tilde{g}(t) = \left[ \frac{C_s 10^{-\lambda}}{1.6 D(t)} - 1 \right] \alpha(t) \gamma(t) \quad (A4)$$

and the light response of biochemical reactions of photosynthesis:

$$\gamma(t) = \frac{Q(t)}{Q(t) + \delta} \quad (A5)$$

where $C_s$ is the air CO$_2$ concentration in ppm, $Q(t)$ is the incident photosynthetically active radiation ($\mu$mol m$^{-2}$ s$^{-1}$), $D(t)$ is the water vapor pressure deficit (kPa) calculated using temperatures above the tree canopies, $\delta$ is the half saturation parameter of the light function ($\mu$mol m$^{-2}$ s$^{-1}$) and $\lambda$ is a model parameter expressing the carbon required in the long term to sustain transpiration flow (kPa). $\lambda$ was set to 3000 as in Gea-Izquierdo et al. (2010).

Photosynthetic capacity $\alpha(t)$ was modeled as a lagged function of temperature $S(t)$, following:

$$\alpha(t) = \alpha_{max}/\{1 + \exp[b(S(t) - T_s)]\} \quad (A6)$$

and, $S(t)$ from

$$\frac{dS(t)}{dt} = \frac{T_{air}(t) - S(t)}{\tau} \quad (A7)$$

$T_{air}(t)$ is the measured air temperature (°C) at time $t$, and $\alpha_{max}$ (mol m$^{-2}$ day$^{-1}$), $b$ (°C$^{-1}$), $T_s$ (°C) and $\tau$ (days) are the model parameters: $\alpha_{max}$ is the maximum photosynthetic efficiency, which takes into account whole canopy properties; $b$ is the curvature of the sigmoid function and $T_s$ is the inflection point of the sigmoid curve, i.e. the temperature at which $\alpha$ reaches half of $\alpha_{max}$; and $\tau$ is the time constant of photosynthetic acclimation and indicates the time it takes for photosynthetic capacity to acclimate itself to changing temperature. All original references to the different parts of the model and a further explanation on the model can be found in Gea-Izquierdo et al. (2010).