Use of modeled photosynthesis and decomposition to describe tree growth at the northern tree line

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Summary Growth of subarctic Scots pine (Pinus sylvestris L.) trees was investigated by a combination of process-based models and dendroecological approaches. Tree ring width indices were strongly autocorrelated and correlated with simulated photosynthetic production of the previous year and with organic matter N mineralization of the current year. An autoregressive model, with photosynthesis and N mineralization as external inputs, explained growth of the trees well. However, relationships for the period 1950–1992 differed significantly from relationships for the period 1876–1949; the slope of the regression of tree ring width index and photosynthesis was lower for the 1950–1992 period. Also, the autocorrelation structure of the data changed. First-order autocorrelation decreased and second-order autocorrelation increased from the earlier to the later period. This means that growth is becoming less sensitive to variations in photosynthesis, whereas the relationships between growth and N mineralization are remaining fairly constant. We postulate that, although photosynthesis has increased in response to increasing [CO2] concentrations, tree growth rate cannot parallel the increase in photosynthesis because potential growth rate is limited directly by temperature.

Keywords: climate change, reduced sensitivity, tree rings.

Introduction

Trees at the timberline are sensitive indicators of climatic variation. However, Briffa et al. (1998a, 1998b) observed that relationships between growth and summer temperatures are changing; growth is less sensitive to variations in temperature nowadays than in the past. Nevertheless, increased growth rates of northern forests have been reported (see Spieler et al. 1996). These increases have been attributed to fertilization by increased atmospheric CO2 concentration ([CO2]) or increased nitrogen deposition from anthropogenic sources (e.g., Lloyd and Farquhar 1996, Berninger and Nikinmaa 1997, Holland et al. 1997). Subarctic trees are supposed to be strongly nutrient-limited (Linder and Axelsson 1982, Tamm 1991, Weih and Karlsson 1999), and annual carbon gains have been attributed to increases in the length of the growing season especially in the spring (Chen et al. 1993, Suni et al. 2003). Process-based models of photosynthetic production and N mineralization could be applied to test these ecological hypotheses.

It is not easy to demonstrate unequivocally that tree growth has been affected directly by increasing [CO2] and other factors. Some authors have attributed increases in the growth rates of trees to increasing [CO2] (Hari and Arvavaara 1988, Kienast and Luxmoore 1988, Graybill and Idso 1993), whereas other authors found no increases in growth rates in response to increasing [CO2] (e.g., Mieliikäinen and Timonen 1996, Mäkinen et al. 2000). In addition to the controversy about changes in growth rates (see discussion between Reams and Van Deusen 1993 and Johnson et al. 1995), it is not known if relationships between growth rates and the environment have remained constant during the most recent decades (LeBlanc 1993). If trees are exposed to increasing [CO2], other limiting growth factors may become more important, thus limiting the ability of trees to increase their growth rates in response to further increases in [CO2]. Also, biogeochemical processes that can be understood at the cellular and leaf levels (e.g., Stitt and Krapp 1999) may be masked at the whole-plant level. Although several authors have concluded that nutrient-stressed plants may be unable to react to increasing [CO2] (e.g., Bazzaz 1990), this view has been questioned (e.g., Lloyd and Farquhar 1996).

Only a few studies have combined ecophysiological approaches with growth information from tree rings (Scuderi et al. 1993, Grote and Erhard 1999, Hogg 1999, Rathgeber et al. 2000). Although such approaches facilitate the investigation of causal relationships between growth and its underlying processes, there are technical difficulties with the use of full-scale process-based models, mostly associated with the large number of parameters and the complexity of these models (Berninger et al. 1992, Vanclay 1994, Korzuhkin et al. 1996).

The objective of our study was to describe short- and medium-term variations in growth rates on the basis of variations in photosynthesis and N mineralization. Specifically, we
tested the hypothesis that the changes in sensitivity of growth observed by Briffa et al. (1998a, 1998b) disappear if growth is analyzed in process-based terms instead of empirical terms. Estimates were calculated with a simple ecophysiological model comprising a hybrid of dendrochronological and ecophysiological models. For the analysis, we used data from five subarctic Scots pine (Pinus sylvestris L.) chronologies.

Methods

Meteorological data

Meteorological data included daily weather data from 1957 to 1992 and monthly temperature data from 1876 to 1992 from Karasjok, Norway (69°28′ N, 25°30′ E, 133 m a.s.l.). Nitrogen deposition in this area is low, < 1 kg N ha−1 year−1 (Airola and Leinonen 1994). Generally, the climate is cold and wet and relatively oceanic (mean yearly temperature of –2.1 °C, mean monthly summer (June–August) temperature of 11.2 °C). Total precipitation is 337 mm year−1, with mean summer (June–August) precipitation of 51 mm month−1.

Tree ring data

Tree ring data were obtained from five existing chronologies in northern Fennoscandia, each comprising between 10 and 27 trees. The chronologies were located at Karasjok (KJ) (27 trees), Kaaresuvanto (KS) (68°28′ N, 25°30′ E, 350 m a.s.l., 25 trees), Nunas (N) (68°30′ N, 22°30′ E, 350 m a.s.l., 25 trees), Luspa (LU) (68°30′ N, 22°00′ E, 400 m a.s.l., 10 trees) and Leppäjärvi (LJ) (68°30′ N, 22°00′ E, 350 m a.s.l., 10 trees). The trees were dominant and growing in open forests, or open places close to the subarctic tree line. A description of the tree ring series is given in Table 1.

Tree series were detrended using negative exponential functions to remove an age-dependent growth trend, or by a straight line when the exponential function approached a negative asymptote. All ring width measurements of each core (i.e., including data prior to 1876) were detrended using the ARSTAN software package (Cook 1985). Tree ring width measurements were converted to indices by dividing by the series mean. For further analysis, we used both detrended indices (based on data of single trees) as well as robust bi-weighted tree ring indices calculated using ARSTAN (for figures and model identification). A previous dendroclimatological study, based on the same chronologies, showed that negative exponential functions perform better than splines or digital filters in extracting the climate information from these chronologies (Lindholm 1996).

Modeling approach

In classical dendroclimatic research, analyses focus on how tree growth deviates from the mean value as a function of climatic fluctuations (e.g., Mikola 1950, Fritts 1976). Relationships between tree growth and the environment identified by dendroclimatologists have provided empirical descriptions of growth (but see Fritts 1976, Schweingruber 1996) that allow the analysis of growth and its variations by efficient statistical methods. These analyses have indicated high correlations between growth variation and climatic variation.

Ecophysiological modeling, on the other hand, focuses on simulating the general development of stand growth and on providing a conceptual description of the growth process driven by the average environment. Because ecophysiological models are by nature nonlinear dynamic models, a rigorous analysis of growth changes in statistical terms is difficult (see Parysow and Gertner 1999 for some methodological developments). Nevertheless, the few existing tests of process-based models applied to tree rings have shown promising results (Scuderi et al. 1993, Grote and Erhard 1999, Hogg 1999, Rathgeber et al. 2000).

To study changes in the sensitivity of growth to environmental factors and to variations in photosynthesis and mineralization, we combined ecophysiological and dendroclimatological approaches. We simulated time series of photosynthesis and nutrient mineralization. These time series were then correlated to detrended ring width time series. The correlations were calculated with transfer function models that account for the autoregressive features of tree behavior (these systems are also known as linear difference equation systems). The driving variable was simulated photosynthetic production of a standard canopy or N mineralization of standard soil organic matter; i.e., we assumed constant soil organic matter and canopy characteristics, and ignored long-term changes in soil or canopy characteristics. Internal feedbacks of the ecosystem were handled by the autoregressive parts of the model. In dendroclimatological and dendroecological studies, autoregressive models are extensively used with climate variables (instead of photosynthesis and mineralization) as drivers of tree growth.

The photosynthesis model

The photosynthesis model follows Lloyd et al. (1995). All parameter estimates are from Aalto (1999) and are mostly estimated from field photosynthesis data at Värrö, a tree line site in northern Finland (with the exception of $\lambda$ from Berninger et al. (2000)).

Following Farquhar and von Caemmerer (1982), photosynthesis is limited by either light ($A_i$) or Rubisco activity ($A_C$):

$$A = \text{Min}[A_i, A_C]$$

where $A_i$ and $A_C$ are expressed as:

<table>
<thead>
<tr>
<th>Chronology</th>
<th>Mean segment length (years)</th>
<th>Average width (mm)</th>
<th>Mean correlation between detrended series</th>
<th>Correlation of series with mean chronology</th>
</tr>
</thead>
<tbody>
<tr>
<td>Karasjok</td>
<td>196</td>
<td>0.72</td>
<td>0.42</td>
<td>0.65</td>
</tr>
<tr>
<td>Kaaresuvanto</td>
<td>128</td>
<td>1.15</td>
<td>0.29</td>
<td>0.57</td>
</tr>
<tr>
<td>Nunas</td>
<td>114</td>
<td>1.12</td>
<td>0.41</td>
<td>0.66</td>
</tr>
<tr>
<td>Leppäjärvi</td>
<td>157</td>
<td>0.81</td>
<td>0.46</td>
<td>0.79</td>
</tr>
<tr>
<td>Luspa</td>
<td>165</td>
<td>1.16</td>
<td>0.48</td>
<td>0.69</td>
</tr>
</tbody>
</table>
\[
A_i = J - \frac{K_O C_1 - 0.105 O K_C}{4.5 K_O C_1 + 1.1025 K_C O_i}
\]

\[
A_C = V_{\text{max}} \frac{C_r K_O - 0.105 O K_C}{K_C O_i + K_C K_O + K_C C_1}
\]

where \(C_r\) is substomatal partial pressure of CO\(_2\) (Pa), \(O_i\) is substomatal partial pressure of oxygen (210 Pa), \(J\) is rate of electron transport (\(\mu\)mol m\(^{-2}\) s\(^{-1}\)), \(V_{\text{max}}\) is maximum carboxylation capacity (\(\mu\)mol m\(^{-2}\) s\(^{-1}\)), and \(K_C\) (0.00046 mol mol\(^{-1}\)) and \(K_O\) (0.33 mol mol\(^{-1}\)) are Michaelis-Menten constants for \(\text{CO}_2\) and \(\text{O}_2\) uptake, respectively.

Electron transport rate depends on photosynthetically active radiation as:

\[
J = \frac{I + J_{\text{max}} - \sqrt{(I + J_{\text{max}})^2 - 4 I J_{\text{max}} \Theta}}{2 \Theta}
\]

where \(J_{\text{max}}\) is maximum electron transport capacity, \(I\) is spectrally corrected irradiance (\(\mu\)mol m\(^{-2}\) s\(^{-1}\)) and \(\Theta\) (dimensionless) is the convexity factor of the curve. There is evidence that the light reaction of photosynthesis is inhibited during the winter and recovers rapidly with increasing spring temperature (Hari and Mäkelä 2003, Suni et al. 2003). This limitation was simulated by making \(J_{\text{max}}\) linearly dependent on cumulative growing season temperature sum (the sum of temperatures exceeding 5 °C) for temperature sums between 0 and 100 degree days (DD). Once the growing season temperature sum has surpassed 100 DD, \(J_{\text{max}}\) is kept constant until winter.

The temperature dependencies of \(V_{\text{max}}\) and \(J_{\text{max}}\) are given by:

\[
V_{\text{max}} = V_{\text{max}} e^{H_a (298.15K - 1 - 298.15/T)}
\]

\[
J_{\text{max}} = e^{C - H_a / RT} / (1 + e^{(sT - H_a) / RT})
\]

where \(V_{\text{max}}\) is carboxylation capacity at 25 °C (62 \(\mu\)mol m\(^{-2}\) s\(^{-1}\)), \(C\) is a constant (29.88 dimensionless), \(R\) is the universal gas constant (8.314 J mol\(^{-1}\) K\(^{-1}\)), \(S_t\) is entropy of the denaturation equilibrium (512 J K\(^{-1}\) mol\(^{-1}\)), \(H_a\) and \(H_m\) are activation energies of the light and dark reactions (28,000 J mol\(^{-1}\) and 28,500 J mol\(^{-1}\)), respectively, \(H_a\) is activation energy for the denaturation equilibrium (58,800 J mol\(^{-1}\)), and \(T\) is leaf temperature (K). Leaf temperatures are assumed to equal air temperatures.

Stomatal conductance was simulated as in Berninger et al. (2000) based on the concept of optimization of stomatal conductance (Cowan 1977). It was estimated by numerically maximizing the function:

\[
\max_{g} \left\{ \int_{t_0}^{t_1} \lambda (g, t) - 1/\lambda H(g, t) dt \right\}
\]

Parameter \(\lambda\) has a value of 83.8 mol H\(_2\)O mol\(^{-1}\) CO\(_2\) (Berninger et al. 2000). Stomatal conductance was kept insensitive to CO\(_2\) as in Berninger et al. (2000).

The stomatal component of the photosynthesis model, like that in many other coupled photosynthesis and stomatal conductance models (e.g., Ball Berry model (Ball et al. 1987) or Leuning model (Leuning 1995)), exploits the well-known correlation between photosynthesis and stomatal conductance (Wong et al. 1979). It should therefore result in realistic behavior of stomatal conductance with a low number of parameters.

These calculations require hourly or daily meteorological data. To overcome the daily weather data missing prior to 1957, we simulated yearly photosynthetic production for the period 1957–1992 at CO\(_2\) concentrations of 280 and 360 ppm. We found that, at each [CO\(_2\)], May and June mean temperatures well explain the variation in photosynthetic production. For the period 1876–1957, we used regressions on monthly temperature to estimate photosynthetic production. These regressions were made for the two CO\(_2\) concentrations and linear interpolation between these values was used to adjust the values for the historical [CO\(_2\)]. For model identification, we used photosynthesis based on monthly values for the period 1876–1957 and daily data from 1957 onward. To test for possible changes in the relationships between growth and its driving variables, we used monthly data for the period 1876–1992 to provide a homogeneous time series of photosynthesis.

The decomposition model

We simulated N mineralization of one parcel of standard soil organic matter in each year, i.e., we assumed no change in substrate quality over time. Instead, we let the autoregressive model account for long-term feedback processes. This approach is analogous to the approach taken for photosynthesis (and similar to the approach usually adopted in dendroclimatological studies).

Northern Scandinavia is humid and soil water effects on organic matter decomposition are probably negligible. During the winter months the soil is covered with thick snow, which decouples soil temperature from air temperature. Therefore, we ignored soil temperature variation during the winter and assumed an exponential increase in N mineralization with summer air temperature:

\[
N = \sum_{\text{May–October}} 2T_{\text{St}}^{10}
\]

where \(N\) is annual N mineralization (relative units), \(T_{\text{St}}\) is mean monthly temperature (°C) and the summing is done over the summer months (May–September). That is, we calculated a variable that is proportional to N mineralization of one unit of litter of a known quality and ignored possible interannual variation in litter quantity and quality (cf. Jenkinson 1990). Previous studies have shown that litter decomposition in the Scandinavian subarctic is temperature controlled and that effects of low soil water contents on decomposition rates in the area are negligible (Johansson et al. 1995).

Time series model building

Because tree ring indices are autocorrelated, standard regres-
Autocorrelation techniques are unsuitable for analyzing tree ring indices. Autocorrelation of growth means that the growth of each year depends on the growth of the previous years. We chose a technique called transfer function modeling to account for the autocorrelation. This technique combines regression models based on external driving variables with autoregressive models; i.e., growth of each year depends, in a linear manner, on growth during the previous years and the values of the input variables (here photosynthesis and N mineralization). These feedbacks are probably caused by fluctuations in foliage area in response to climatic variation and fluctuations in the amount of carbohydrate reserves accumulated during the previous year. The technique differs slightly from response function modeling, which is more commonly used in tree ring analysis, because it allows the simultaneous estimation of autoregressive and regression terms. This should result in more unbiased estimates especially when external input variables are not white noise (i.e., have an autocorrelation structure or change systematically over time).

Time series model building was performed in three steps following the procedures in Box et al. (1994) and Monserud and Marshall (2001). Step 1 is model identification. Most textbooks suggest that model identification should be done using variables where autocorrelation has been removed. Then cross correlations between variables are used to identify probable relationships between inputs and outputs. In Step 2, model parameters are estimated based on the original tree ring indices (i.e., before removal of autocorrelation). In Step 3, model statistics are checked and, if necessary, the model structure is changed.

Figure 1 outlines the model building process we used. The chronology at Karasjok was used to identify and test the model, because the Karasjok forest is located closest to the best long-term meteorological station in the area. Also, the chronology in Karasjok is best replicated. The model was then applied and tested for the single-tree chronologies from all sites.

Model identification was performed with prewhitened, detrended, tree-ring indices and untransformed series of photosynthesis and N mineralization. Prewhitened time series are time series where autocorrelation has been removed. Transfer function models were estimated based on untransformed variables and simplified until the Akaike information criterion (Box et al. 1994) was minimized and all terms in the model were statistically significant ($P < 0.05$). (A reader unfamiliar with time series analysis can consider transfer functions as regression models, where the tree ring index (the independent variable) is explained by the tree ring index of the previous year(s) and independent variables that may (or may not) be lagged.) The model used autoregressive terms and regressions to the driving variables at different short time lags. Significance of the parameters, the residual variance of the model and the Akaike information criterion were used to evaluate different possible models (e.g., Box et al. 1994, Monserud and Marshall 2001).

Briffa et al. (1998b) found that relationships between tree rings and summer temperatures changed in the second half of the 20th century. We hypothesized that these changes would disappear if we used physiologically based variables, e.g., photosynthetic production, to drive tree growth instead of temperatures. Therefore, changes in parameter values (i.e., the slopes of growth on photosynthetic production and N mineralization) in the recent past were analyzed by splitting the data into two time series (1876–1949 and 1950–1993) (Figure 1). Parameter values were estimated separately for each period. For analysis of changes in parameter value, we used only monthly data. Use of a mixture of daily-weather-based and monthly-weather-based photosynthesis estimates could affect the comparison of pre-1950 parameter values (based on monthly data) and post-1950 parameter values (based mostly on daily data).

Results

Stepwise regression showed that yearly photosynthesis calculated from monthly data depended on May and June temperatures. Effects of temperature and precipitation in other months were not significant. At a constant [CO$_2$], the correlation between photosynthesis estimated on the basis of monthly weather and photosynthesis calculated on the basis of daily weather values was 0.81 (Figure 2).

Model identification was done with prewhitened detrended indices of tree ring width, photosynthesis and N mineralization. Initially, it seemed that the time series could be prewhitened by the third-order autoregressive process, which minimized the Akaike information criterion (Figure 3). The
cross correlation of the prewhitened tree ring series with the time series of photosynthesis and N mineralization revealed significant correlations at Lag 1 for photosynthesis and at Lag 0 and Lag 1 for N mineralization (Figure 4). Decomposition and photosynthesis were correlated ($r = 0.67$). The final model was estimated using detrended rather than prewhitened time series as suggested by Box et al. (1994). When estimating the transfer function model, we found that N mineralization at Lag 1 and the third-order autoregressive process were not significant. Therefore, we deleted these terms. We compared the model with several similar models and found that the selected model minimized the Akaike information criterion.

The model had the form:

$$i_t = \mu + \omega_1 A_t + \omega_2 N_t + \frac{a_t}{1 - \Phi_1 B - \Phi_2 B^2}$$

where $i_t$ is detrended tree ring width index, $\mu$ is the intercept, $\omega_1$ and $\omega_2$ are the regression slopes, $B$ is the lag operator, $\Phi_1$ and $\Phi_2$ are the autoregressive parameters, $a_t$ is a random shock, $A_t$ is simulated photosynthetic production and $N_t$ is simulated N mineralization. A transfer function is similar to a regression model of tree ring index (dependent variable) on the tree ring indices of the two previous years (slopes $\Phi_1$ and $\Phi_2$), the photosynthesis of the previous year (slope $\omega_1$) and the N mineralization of the current year (slope $\omega_2$).

The model described well the variation in tree growth (Figure 5). The proportion of explained variance was similar to that of models describing tree growth as a function of climatic variables (e.g., Lindholm 1996). Photosynthesis and N mineralization varied over time and showed clearly different long-term signals (Figure 6).

We applied the model to detrended single-tree chronologies at all sites (instead of to a chronology that averages many trees). Parameter values for these single trees were usually significant. The parameter values for photosynthesis and N mineralization were positive and the autoregressive processes were stationary. Tree-level values of photosynthesis and N mineralization parameters were not correlated with tree age, but were weakly correlated with each other ($R = 0.31$, $P < 0.01$). This correlation is probably a result of a temperature dependence in both processes. Correlations of all parameters (except for the second-order autoregressive parameter) with age were low ($P > 0.05$), indicating that the parameter values were unrelated to tree age.

There were changes in the sensitivity of the series to the environment over time. We investigated this sensitivity by splitting the data into two periods: 1876–1949 and 1950–1992. The residuals for each period were systematic with respect to photosynthetic production of the previous year and N mineral-
ization of the current year (Figure 7). We then compared the parameter values of the single-tree chronologies before and after 1950 by a two-tailed t-test for paired observations. For this analysis, we estimated photosynthetic values for the whole period based on monthly weather data (using monthly data also after 1957) (cf. Briffa et al. 1998a). We found that parameter values for 1877–1949 and for 1950–1992 differed significantly. The mean slope of the single-tree ring indices on photosynthesis decreased from a mean of 0.046 to 0.025 (P < 0.001 for KJ, N, P < 0.01 for KS, P < 0.05 for LU, and non-significant decrease for LJ). The mean decrease in the slope of photosynthesis was relatively consistent across sites (35–57% of the mean 1872–1949 site value). Changes in the slope of N mineralization were inconsistent across sites (slight decreases for KJ (P < 0.05), KS and N (ns) and increases in LJ (P < 0.001) and LU (ns)). The first-order autocorrelation parameter value decreased from a mean of 0.65 to 0.38 (significant at all sites: P < 0.001 for N, KS; P < 0.01 for LJ, LU; and P < 0.05 for KJ) and the second-order autocorrelation parameter value increased from 0.06 to 0.21 (P < 0.001 for KS, P < 0.01 for KJ, and nonsignificant increases for the other sites). The intercept of the equation increased from –0.26 to 0.003. Increases were inconsistent across sites (significant increases for KJ (P < 0.01), KS and N (P < 0.05) and nonsignificant decreases for LJ and LU) (Figure 8, Table 2). Changes in parameter values were not related to tree age as measured by the maximum number of rings in the core.

Nitrogen mineralization was lower in the 1950–1993 period than in the 1876–1949 period, whereas photosynthetic production was slightly higher in the 1950–1993 period. All variables including tree growth were slightly less variable in the 1949–1993 period; however, the change was minor for N mineralization. There was no clear change in mean values of tree ring width indices between periods (Table 3).
Discussion

Our modeling approach described well the growth variation of trees for all sites. Parameter values for photosynthesis and N mineralization were positive and AR processes were stationary. However, despite use of process-based terms, sensitivity of growth to photosynthesis changed, indicating that the findings of Briffa et al. (1998a, 1998b) cannot be explained simply in terms of CO₂ fertilization of trees, but are the result of more profound changes in the ecosystem. These changes were differential, i.e., the response of growth to photosynthesis changed, whereas the response to N mineralization remained virtually unchanged.

We tried to exclude the possibility that the change was a result of the way we analyzed the data. We removed the age-dependent growth trend from our data using a negative exponential, which is a conservative standard method in dendrochronology. We tried two other standardization methods for the Karasjok data and found no qualitative differences between the methods. Also, from a mathematical viewpoint, it is difficult to envisage how the standardization methods could affect our results qualitatively (unless unrealistically tight splines are fit to the data). Our results were not age-dependent, i.e., trees of varying age showed similar results, although parameter changes were larger in younger trees. Removal of autocorrelation before analysis resulted in a significant decrease in the slope of ring width index on N mineralization; however, it also resulted in a change in the slope of ring width index on photosynthesis that was larger than the change for N mineralization (data not shown).

Different studies have found different degrees of autoregressivity in tree ring indices. Meko (1981, cited by Monserud 1986) found that a simple AR(1) (first-order autoregression) model was mostly sufficient, whereas Monserud (1986) suggested that higher-order AR models (up to the order of four) are required. The use of an Auto Regressive Moving Average (1,1) (ARMA(1,1)) process, which worked well with most of Monserud’s data, did not yield good results with our data. Our results were not influenced by insufficient detrending, because our autocorrelation functions died out at reasonable time lags (Monserud 1986, Monserud and Marshall 2001). We do not know why our results differ from those of Monserud (1986), but the discrepancy may be associated with a difference between the drought-stressed conifers from western USA used in Monserud’s analysis and the temperature-limited trees from a humid environment used in our analysis.

Growth analysis showed that N mineralization and photosynthetic production are plausible driving variables of tree growth for our sites. The finding that photosynthesis contains mainly an early season temperature signal agrees with the results of Grace et al. (2002), who found that timing of the onset of photosynthesis in tree-line forests largely determines yearly photosynthetic production. The time lag of photosynthesis might explain why previous authors (Nöjd and Hari 2001) had difficulties finding good relationships between photosynthesis and growth.

The absence of a time lag for N mineralization contrasts with results from several fertilization and soil warming experiments showing that the effect of fertilization or soil heating on growth is delayed (e.g., Hättenschwiler and Körner 1996, Strömberg and Linder 2002). In our case, a step increase in N mineralization would have an immediate effect on growth. However, because of the autoregressive terms in the model, increased growth in the second year would be larger than in the first year. There are two other differences between the results of nutrient fertilization experiments and our work. First, our work considers small random changes in nutrient supply, whereas most nutrient fertilization studies focus on large step changes in nutrient supply. Second, changes in N mineralization are always associated with warmer conditions at these cold and wet sites. Higher temperatures may facilitate cell division and expansion (e.g., Körner 1999), allowing trees to react immediately to improved nutrition with increased growth rates. The correlation between growth and modeled N mineralization at Lag 1 was much weaker than the correlation at Lag 0. Also, correlations of ring indices with photosynthesis at Lag 1 were stronger than the correlations of growth with lagged N mineralization. Lagged N mineralization was not statistically significant in the presence of photosynthetic production in the transfer function model. Our mineralization model is quite simple and reflects the dominant importance of
temperature at this site. However, the long-term responses of decomposition to temperature are poorly understood. Traditional decomposition models (e.g., Jenkinson 1990) have been challenged by the recent observation that long-term decomposition rates are insensitive to temperature (Liski et al. 1999, Giardina and Ryan 2000). This view of decomposition has been criticized (Bosatta and Ågren 1999, Davidson et al. 2000). However, in a long-term soil warming experiment, Melillo et al. (2002) showed that, although soil respiration did not increase in the long term on heated plots, N mineralization increased over the whole 7-year period. This is in agreement with the results of Strömgren and Linder (2002) showing that forest production of a soil-heated Norway spruce forest increases for several years after the onset of soil heating.

Our statistical approach differs from classical dendrochronological approaches because it is based on single trees.
instead of chronologies (i.e., the mean of many trees), and we used transfer functions instead of response functions. We argue that the use of single trees is, in our case, more appropriate. Even within a stand, trees grow on different microsites and experience different soil conditions (and to a minor extent different micrometeorological environments). This means that the relative limitations by carbon and nitrogen differ among the trees. The use of single trees, although computationally less efficient, is a more realistic reconstruction of the relationships between growth and environmental driving forces.

Our modeling approach is a hybrid between the dendrochronological and ecological modeling approaches. Use of ARIMA (Auto-Regressive-Integrated Moving Average) statistical models detected changes in the response of tree growth to the environment. Feedback responses of tree growth to the environment are described empirically. Similarly structured models based on simple relationships between climate and tree growth have been in use for decades in tree ring research (e.g., Fritts 1976, Schweingruber 1996). In contrast, full-scale ecophysiological models, with larger numbers of parameters and feedback cycles, are nonlinear difference (or differential) equation systems. Nonlinear time series are complex and statistical tests for model outcomes and their changes are not readily available (e.g., Priestley 1988). Furthermore, initialization of these full-scale ecophysiological models usually requires detailed knowledge of stand structure (and possibly its history) as well as a detailed description of the soil environment (e.g., Berninger and Nikinmaa 1997, Nissinen and Hari 1998). Also, the large number of parameters in full-scale process-based models causes overparameterization and difficulties with model fitting. Our approach allows the use of efficient mathematical techniques and the analysis of tree growth in cases where there is relatively little information about stand structure and stand conditions.

It is known that trees close to the timberline are sensitive to climate, whereas trees in less extreme environments tend to be less sensitive (Fritts 1976). Mean sensitivity, a common measure of variability of tree rings with respect to the environment (Fritts 1976), of the series was smaller for the 1950–1993 period than for the 1876–1949 period, perhaps because of the enhancement of photosynthesis in response to increased atmospheric [CO$_2$]. The increase in simulated photosynthesis compared with that in a preindustrial atmosphere was 2.4% in 1950 and 6.5% in 1992. Summer temperatures in northern Scandinavia were slightly less in the period 1950–1992 than in the period 1876–1949. Therefore, the trees had higher photosynthetic production at a similar nutrient availability rate.

Estimates of the absolute values of photosynthesis are uncertain because trees might react to increasing [CO$_2$] by downscaling photosynthesis, i.e., a decrease in photosynthetic capacity (mainly carboxylation capacity, $V_{\text{cmax}}$). The extent of downscaling of photosynthetic capacity in response to elevated [CO$_2$] remains controversial. In a recent review, Curtis and Wang (1998) found no evidence for downscaling of photosynthetic capacity in response to elevated [CO$_2$]. In contrast, a meta-analysis by Medlyn et al. (1999) indicated that photosynthetic capacity is reduced at high [CO$_2$], in particular at low nitrogen concentrations. Our estimated 30% decline in the slope in photosynthesis for a 20% increase in [CO$_2$] is larger than almost all published observations of downscaling of photosynthetic capacity in response to elevated [CO$_2$]. It is unlikely that downscaling of photosynthetic capacity in response to lower N mineralization rates explains our results because Scots pine trees grow naturally in infertile sandy and boggy soils, and their photosynthetic capacity seems to be relatively independent of nitrogen concentration for the range of values observed in nature (Vapaavuori et al. 1995). Differences in allocation between foliage and fine roots seem to explain most of the productivity differences in Scots pine forests (e.g., Berninger and Nikinmaa 1997, Vanninen and Mäkelä 1999). We note that Arneth et al. (2002) found an increase in stomatal conductance in response to increasing [CO$_2$]. The reason for the discrepancy between our data and the finding of Arneth et al. (2002) might be that their Siberian Scots pines were drought-stressed, whereas our trees were from a humid environment. Furthermore, Berninger et al. (2000) found no improvement of model fit when a soil water balance model was incorporated into the model.

Increased nitrogen deposition may provide an explanation for our results. Nitrogen deposition in the area has been low (<1 kg N ha$^{-1}$ year$^{-1}$) (Airola and Leinonen 1994). However, there is floristic evidence that adjacent areas in northern Sweden may have become more fertile as a result of fertilization (Tybirk et al. 2000). The observation that the slope of photosynthesis is changing, whereas the slope of ring width indices on N deposition is virtually unchanged, does not support this explanation. However, the removal of the age-dependent growth trend or the autocorrelation could have affected our results. The dynamics of these open stands close to the northern limit of the species are not well known. A structural analysis of similar stands showed that, during the past few decades, the age structure of Scots pine stands was probably relatively constant (Stöcklin and Körner 1999), although Scots pine seems to have regenerated well during the 1930s (Hustich 1958).

Another factor that may have affected tree growth is the change in reindeer management during the past centuries (Starck et al. 2000). In northern Finland, reindeer numbers

<table>
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<tbody>
<tr>
<td>Mean ring width index</td>
<td>Mean sensitivity</td>
<td>Mean ring width index</td>
</tr>
<tr>
<td>Karasjok</td>
<td>1.06</td>
<td>0.23</td>
</tr>
<tr>
<td>Kaaresvanto</td>
<td>1.029</td>
<td>0.23</td>
</tr>
<tr>
<td>Nunas</td>
<td>1.066</td>
<td>0.21</td>
</tr>
<tr>
<td>Luspa</td>
<td>0.98</td>
<td>0.21</td>
</tr>
<tr>
<td>Leppäjärvi</td>
<td>0.912</td>
<td>0.34</td>
</tr>
<tr>
<td>Photosynthesis</td>
<td>13.37</td>
<td>1.28 (sd)</td>
</tr>
<tr>
<td>N mineralization</td>
<td>9.35</td>
<td>0.77 (sd)</td>
</tr>
</tbody>
</table>
have increased since World War II (Wahlström et al. 1996), affecting the nutrient cycle of forest ecosystems and other belowground processes. The direct effects of reindeer on Scots pine are restricted to young trees. From an ecological viewpoint, however, it is difficult to understand why trees should become less sensitive to carbon supply when they are fertilized, because carbon limitations should increase when nutrient availability increases.

Our results are also difficult to explain directly in terms of changes in limitations. We note that the second important change during the period has been a change in the autocorrelation structure of the data. A decrease in the first-order autocorrelation coefficient with increases in higher-order autocorrelation coefficients could indicate tree growth will be less sensitive to short-term climatic fluctuations. The decreased mean sensitivity supports this suggestion (e.g., Mikola 1950). It is possible that an increase in carbohydrate storage in the trees equilibrates interannual variation in growth.

Vaganov et al. (1999) claimed that loss of sensitivity in tree ring indices to summer temperature is linked to higher snowpack during winter and a later start of the growing season. Although we observed a decrease in sensitivity of tree ring indices to temperature (data not shown), spring temperatures have increased over the past 100 years in our study area and there is circumstantial evidence that snow melt has been earlier in recent years, e.g., earlier ice break up in the Tornio river flowing through the area (Kajander 1993).

A more likely explanation of our data is an increase in a sink limitation, i.e., the capacity of trees to utilize carbohydrates for growth has not increased even though photosynthetic production has increased. Rates of diameter and shoot extension growth (on an hourly or daily time scale) are temperature-dependent (e.g., Pietarinen et al. 1982). In cold climates, the ability of a tree to grow may be critical. Kö rner (1998) has argued that tree lines are usually limited by their capacity to form new tissues. If photosynthesis has increased, but carbon utilization has not because the potential growth rate is limited by temperature, these limitations should increase. A natural transient response of trees would be an increase in carbohydrate storage, which would probably result in growth that depends less on current-year production, because carbohydrate reserves even out interannual variation in production. The decrease in the slope of growth on photosynthesis, the decrease in the value of the first-term autoregressive coefficient, increases in higher-order autoregressive terms and the increase in the intercept indicate that trees in northern Finland are less dependent on the current carbon supply and rely more on reserves. This will make tree lines in a CO2-rich world more resilient to climatic variation. However, the lower slope indicates that trees become gradually carbon saturated, i.e., trees will not respond to increased [CO2] unless the increase is matched by increased nutrient availability or more favorable temperatures for rapid growth during the growing season.

References


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