

The effect of temperature and PAR on the annual photosynthetic production of Scots pine in northern Finland during 1906–2002

Pertti Hari¹ and Pekka Nöjd^{2,*}

¹ Department of Forest Ecology, P.O. Box 27, FI-00014 University of Helsinki, Finland

² Finnish Forest Research Institute, P.O. Box 18, FI-01301 Vantaa, Finland (corresponding author's e-mail: pekka.nojd@metla.fi)

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The annual photosynthetic production of Scots pine (*Pinus sylvestris*) was simulated for 1906–2002 for a location in northern Finland. We used the PhenPhoto model, which combines two key features of photosynthesis: the response to instantaneous radiation and the acclimation to the annual cycle. The input data for the PhenPhoto model include instantaneous photosynthetically active radiation (PAR) and temperature. The PAR values were generated from existing weather data and the instantaneous temperatures were interpolated from daily maximum and minimum values. The simulated annual photosynthetic production was at a low level during the the first two decades of the 20th century. No trend was observed for 1920–2002. The standard deviation of the annual photosynthetic production was 11.3% of the mean for the period 1906–2002. There were large differences in spring-time recovery of photosynthesis: in 1964 over 30% of annual photosynthetic production had accumulated by 10 June, while at the other extreme (1917) the percentage was only 3.5%. A comparison of the simulated photosynthetic production with tree-ring indices of Scots pine showed a rather similar pattern of high-frequency variation.

Introduction

Over 90% of plant material originates directly from photosynthesis. In addition, respiration also uses considerable amounts of photosynthates. Consequently, fixation of light energy and formation of sugars have a crucial role in understanding growth processes and other metabolism of plants. A long time-series on photosynthetic production would be a valuable tool for analyzing the causal factors behind growth variation and constructing growth models of trees.

The first automatic systems measuring photosynthesis in field conditions were developed about 50 years ago (e.g. Pisek and Winkler 1958). They were typically used for periods of a few days or weeks. Portable systems, also used only for short-term measurements, have dominated the studies on tree photosynthesis in the field since the 1970s. However, as pointed out by Kozłowski and Pallardy (1997), prediction of tree growth from measurements of photosynthesis should be based on both rates and rate-duration aspects. This is problematic when only

short-term measurements are available.

Rather few permanently installed monitoring systems have been in use (e.g. Hari and Luukkanen 1974, Linder and Troeng 1980, Hari *et al.* 1994, Hari and Kulmala 2005). Continuous time series are presently available only for a small number of sites and the measurement periods cover approximately two decades at best. Thus, the time series available from chamber measurements are of limited value for comparisons with data on the annual growth of trees.

Eddy covariance measurements started a new era in the studies of gas exchange of canopies during the late 1980s (e.g. Baldocchi 1988, Valentini *et al.* 2000). Annual photosynthetic production of a plant canopy can be extracted from eddy covariance measurements, although uncertainties involved in the soil CO₂ efflux reduce the accuracy and precision of the result. A rather dense network of measuring stations presently exists, including a number of countries in Europe and North America. However, the short duration of measurement series clearly limits the utilization of eddy covariance measurements in the analysis of tree growth.

Thus, the longest measured series of annual photosynthetic production of trees are rather short for relating annual photosynthetic production to measured annual tree growth. For a meaningful comparison, a data set covering at least 50 years would be needed. As tree growth can be retrospectively measured from tree rings, growth data covering several centuries are frequently available for such analysis.

As the longest continuously measured series of annual photosynthesis cover only a little more than a decade, modeling is the only viable option. For some tree species, accurate models of photosynthetic production are available (e.g. Landsberg and Waring 1997, Thornton *et al.* 2002). Thus, for those species the quality of input data is the main obstacle. Basic weather data are available for over 100 years in most areas of the globe. When the measured weather data and knowledge of photosynthetic process are properly combined, reasonable estimates of annual photosynthetic production can be obtained.

Light is the driving factor of photosynthesis, and therefore necessary for producing accurate

estimates of instantaneous photosynthetic rates, which can be integrated into estimates of annual photosynthetic production. The intensity of radiation, especially photosynthetic active radiation (PAR), is rarely monitored at basic weather stations. Some high standard stations have monitored global radiation since 1956 — international standards for the measurements were established at that time. There are, however, regularities in weather, which can be utilized for generating instantaneous radiation from measured temperature records. Nöjd and Hari (2001a) proposed a method for generating instantaneous light intensities utilizing the fact that the temperature difference between daily maxima and minima is large on clear days and small on cloudy ones.

The photosynthetic rate responds to changes in radiation in a few seconds. The dependence of the photosynthetic rate on light intensity is clearly non-linear. This is the primary reason why instantaneous light intensities and temperatures need to be used in order to link energy fixation with environmental variables. The hyperbolic rectangular and the Michaelis-Menten functions describe the statistical relationship between PAR and the photosynthetic rate (e.g. Thornley 1976). The simple structure of these models makes them easy to use. Models based on physiology, such as those by Farquhar *et al.* (1980) and Laisk and Oja (1998), provide a deeper understanding of the conversion of light energy into chemical form. They, however, include several parameters that can be very difficult to determine for the specific conditions of each site (Hari *et al.* 2008). The optimal stomatal control model (Hari *et al.* 1986, Mäkelä *et al.* 1996) is a compromise between the simplistic statistical approach and the highly detailed models based on physiology. This model includes a straightforward description of the photosynthetic process. Evolutionary arguments were used to derive the model structure.

Each plant species has characteristic features. At present, estimates of annual photosynthetic production can be produced only for important tree species that have been studied intensively. The species-specific features in the models might be rather few, but nevertheless the model has to be calibrated for each species. We chose Scots

pine (*Pinus sylvestris*) as our study object. It is the dominating tree species in northern Finland (48% of the cubic volume of the Finnish forests). Extensive measured data sets produced by highly detailed monitoring stations are available on the photosynthesis and structure of the species (e.g. Hari and Mäkelä 2003).

In the boreal zone, coniferous trees are dormant in winter, which means that they tolerate very low temperatures and are inactive. In summer they cannot tolerate low temperatures, but are very active. Photosynthesis is strongly inhibited during dormancy and recovers rather slowly during spring (Pelkonen and Hari 1980, Hari and Mäkelä 2003).

As the response of the photosynthetic rate of Scots pine to a certain level of radiation varies continuously during the growing season, the recovery from dormancy has to be described properly if one aims to model the annual photosynthetic production accurately. The optimal stomatal control model was used for studying the development of photosynthesis during the growing season by Hari and Mäkelä (2003). It was discovered that only one of the model parameters changed during the photosynthetically active period, while others remained constant. Mäkelä *et al.* (2004) were able to link the value of the parameter to temperature history of the current season.

The PhenPhoto model combines the two key features: response of photosynthesis to instantaneous radiation and the gradual recovery from wintertime dormancy. After calibration, the model converts light intensity and air temperature to an instantaneous photosynthetic rate. Annual photosynthetic production can thereafter be obtained by integration over the photosynthetically active period.

The aim of our study is to simulate and analyze the effects of radiation and temperature on the annual photosynthetic production of Scots pine near the northern timber line in Finland for the period 1906–2002. We used the PhenPhoto model for simulating the amount of photosynthates produced each year during 1906–2002 by unshaded Scots pine needles with a combined leaf area of 1 m². Factors such as the atmospheric CO₂ concentration, nutrient availability

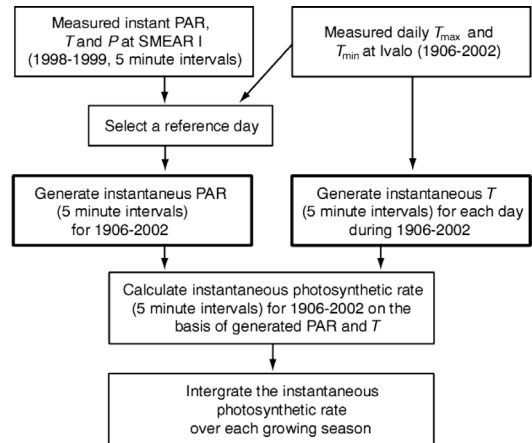


Fig. 1. A flow chart of the steps of estimating the annual photosynthetic production for the period 1906–2002. T = temperature, P = photosynthetic production.

and competition between trees were assumed to be constant and thus excluded from the analysis. Existing daily weather data were used for generating the instantaneous temperature and radiation records needed as model input. To demonstrate that the simulation results could have value for analyzing annual growth variation, the simulated annual photosynthetic production is compared with tree-ring indices describing the radial growth variation of Scots pine during the same period.

Material and methods

Figure 1 shows the steps of simulating annual photosynthetic production for 1906–2002. Two data sets were available: basic meteorological data for the whole period from the meteorological station at Ivalo (68°37'N, 27°13'E) and very intensive measurements of temperature (T), photosynthetically active radiation (PAR) and instantaneous photosynthetic rates for two growing seasons (1998 and 1999) from the measurement station SMEAR I (67°46'N, 29°35'E). Using these data sets, instantaneous temperature and PAR values were generated for the period 1906–2002. These variables were used as input for the PhenPhoto model, which produces estimates of Scots pine (*Pinus sylvestris*) instantaneous photosynthetic rates. Finally, those

photosynthetic rates were integrated over each growing season.

Climatic data

Temperature for 1906–2002 at Ivalo

Daily maximum and minimum temperatures as well as daily rainfall were available from a weather station of the Meteorological Institute of Finland at Ivalo (68°37'N, 27°13'E) for the period 1906–2002. The weather station had been relocated several times. In order to adjust for discontinuities due to the relocations, the standard normal homogeneity test, which utilizes similar data from neighboring meteorological stations (Tuomenvirta 2002), was applied. Additive adjustments, provided by the meteorological Institute of Finland, were applied for correcting both time series of daily maximum and minimum temperatures. Meteorological observations were not available from Ivalo for the growing seasons 1944–1946 due to World War II. The meteorological station was restarted in September 1946. Annual temperature sums for 1906–2002 with a threshold value +5 °C, introduced by Sarvas (1974), were also calculated.

PAR and temperatures for 1998–1999 at SMEAR I

Highly intensive measurements were available from the station SMEAR I, located near the arctic timber line at Värriö (67°46'N, 29°35'E), northern Finland (Hari *et al.* 1994). Photosynthetically active radiation (PAR) was measured using a quantum sensor (LI-190, LI-COR Ltd., NE, USA), which was placed above the tree canopy layer. With the exception of breaks due to technical problems, measurements were done every 5 minutes through the growing seasons of 1998 and 1999.

Air temperatures within canopy at 2.2 m above ground level were also measured every five minutes in 1998–1999. Platinum resistance thermometers (PT-100, T. Pohja, Juupajoki, Finland) were used. The sensors were protected against solar radiation and ventilated by fans.

Measured photosynthesis for 1998–1999 at SMEAR I

Instantaneous photosynthetic rates of Scots pine branches were also measured at SMEAR I during 1998–1999. The station is described in detail by Hari *et al.* (1994). Three trees were chosen from an even-aged Scots pine stand on top of a shallow-sloped hill.

The monitoring system consists of 3 trap-type acrylic chambers (3.6 dm³), a tubing system, infrared gas analyzers for CO₂ and water vapor, sensors for photosynthetically active radiation and temperature and a microcomputer for control and on-line recording of the measurements. The chambers close automatically for measurements for a period of 60 s, approximately 120 times a day. In the cuvette there is an electric fan keeping airflow through the chamber at 0.5 m s⁻¹ when open, and mixing the air when closed. During the 60 s measurement period, a pump draws air into the gas analyzers at a flow rate 0.017 dm³ s⁻¹. The infrared gas analyzers for CO₂ and water vapor measure concentrations at intervals of ten seconds during the closure of the chamber. The measurement system is described in detail in Hari *et al.* (1999), and details of the data have been provided by Hari and Mäkelä (2003).

The measurements of CO₂ exchange were not performed during wintertime because of strong ice formation. In 1998 the measurements continued from late April until late September. In 1999 the period was slightly shorter. Several measurement breaks due to technical problems were encountered in both years. The most notable of them took place in June–July 1998.

Input data for the PhenPhoto model

In order to run the PhenPhoto model for every growing season during 1906–2002, instantaneous temperature and PAR values are needed at sufficiently short intervals. Measured records for either variable are not available for the whole period from northern Finland. Thus, we used available meteorological information for generating the instantaneous values for PAR and air temperature.

Generation of instantaneous temperatures

Instant temperature values at 5-minute intervals were generated for each growing season. Daily minimums and maximums were available for 1906–2002. A highly simplified procedure was applied: we assumed that the daily minimum of each day occurs at 3:00 and the maximum at 15:00. Temperatures for other instants were linear extrapolations between the daily maximum and minimum — a rather crude method. However, the use of commonly applied more sophisticated methods could be also problematic in the conditions of our study area, where the sun does not fall below horizon for a couple of weeks around the summer solstice — a critical period for photosynthetic production.

Generation of instantaneous PAR

Bristow and Campbell (1984) showed that the difference between daily maximum and minimum temperatures correlates with daily PAR that reaches the earth surface. A small difference between daily maximum and minimum indicates a thick cloud cover; a relatively large one usually occurs in clear sky conditions. Nöjd and Hari (2001a) made use of the finding by presenting a method for generating instantaneous PAR. The method only requires data on daily minimum and maximum temperatures for each day. In addition, some PAR data, measured throughout the day with sufficiently short intervals, is needed.

The basic idea for generating instantaneous PAR values was simple: for each day j during 1906–2002 we picked a reference day, for which measured PAR values were available from SMEAR I. Using actual measured radiation data ensures that the generated PAR values follow a realistic pattern. The referenced days were randomly selected from days with the same calendar month and a $T_{\max} - T_{\min}$ within ± 1.0 °C of the day j .

These criteria for selecting a reference day are actually a simplification of the procedure suggested by Nöjd and Hari (2001a). The original method suggested that daily transmission coefficient (ratio of measured daily PAR and the theoretical PAR in clear sky conditions for the

same day) would be used in selecting the reference day, which tends to favor days with average cloudiness. The simplified criteria presented above avoid the problem.

Day length or the solar angle at any given time will not be identical for the day j and its reference day. Therefore, the measured reference day PAR values for each instant were adjusted following guidelines presented by Nöjd and Hari (2001a), which are based on the regular pattern of the position of the sun (e.g. Gates 1980). For each moment throughout the year, PAR under clear sky conditions can be derived accurately. For adjusting the instantaneous reference day PAR values of each instant, we used the ratio of PAR of day j and PAR of the reference day (both under clear sky conditions) for that specific instant. In essence, this means that if the reference day is closer to the summer solstice than day j , the PAR values of the reference day are adjusted downwards, and *vice versa*.

Unlike Nöjd and Hari (2001a), we did not use rainfall as a predictor of instantaneous PAR, because the precipitation measurements during the early 20th century may not be fully comparable with more recent meteorological records.

Generated vs. measured instantaneous PAR values

Generated PAR values may and often will strongly deviate from the true ones for any given instant. Despite this, they can be useful for simulating photosynthetic production over a long time periods, as long as they follow a realistic pattern. A proper mean level and magnitude of variation are both essential. Generated instantaneous PAR values (5-minute intervals) were compared with values measured at SMEAR I over the growing seasons of 1998 and 1999 (for averages and standard deviations *see* Table 1).

Table 1. Generated and measured daily PAR (mean \pm SD) ($\text{mmol m}^{-2} \text{s}^{-1}$) at SMEAR I.

	27.IV–23.IX.1998	9.V–30.IX.1999
Generated	0.244 \pm 0.343	0.259 \pm 0.357
Measured	0.263 \pm 0.360	0.264 \pm 0.361

Measured PAR included a few measurement breaks, which were excluded from the comparison. Both the mean and the standard deviation of predicted instantaneous PAR values were quite close to the observed ones for both years.

The PhenPhoto model

The PhenPhoto model combines two main model components: the optimal stomatal control model of photosynthesis, presented in detail by Hari *et al.* (1986) and Hari and Mäkelä (2003), and a rather simple model describing the annual cycle of photosynthesis, originally presented by Mäkelä *et al.* (2004). Simplifying assumptions were used in order to derive the optimal stomatal control model in accordance with the original hypothesis of optimal stomatal control introduced by Cowan and Farquhar (1977).

The optimal stomatal control model

The solution of the optimal stomatal control problem results in a model of gas exchange, which comprises equations for stomatal conductance g (m s^{-1}), photosynthesis A ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), as functions of PAR I ($\text{mol m}^{-2} \text{ s}^{-1}$), atmospheric carbon-dioxide concentration C_a ($\text{mol CO}_2 \text{ m}^{-3}$), saturation deficit of water vapour D ($\text{mol H}_2\text{O m}^{-3}$), respiration r ($\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and the cost of transpiration λ ($\text{mol CO}_2 (\text{mol H}_2\text{O})^{-1}$);

$$A(t) = \frac{[g(t)C_a + r]f(I(t))}{g(t) + f(I(t))} \quad (1)$$

$$g_s(t) = \left[\sqrt{\frac{C_a - \frac{r}{f(I(t))}}{\lambda a D(t)}} - 1 \right] f(I(t)) \quad (2)$$

$$g = \begin{cases} g_{\min}, & \text{if } g_s \leq g_{\min} \\ g_s, & \text{if } g_{\min} \leq g_s \leq g_{\max}, \\ g_{\max}, & \text{if } g_s \geq g_{\max} \end{cases} \quad (3)$$

where g_{\min} (m s^{-1}) is the cuticular conductance, g_{\max} (m s^{-1}) is stomatal conductance when the stomata are fully open, g_s (m s^{-1}) is the solution

of the optimal control problem, and a is the ratio of diffusivity of water relative to carbon dioxide.

The function f introducing saturation of light reactions is

$$f(I) = \frac{\alpha \gamma I}{\alpha I + \gamma}, \quad (4)$$

where γ (m s^{-1}) is the saturation level of $f(I)$ (m s^{-1}) and α ($\text{m}^3 \text{ mol}^{-1}$) is the initial slope of the function.

Equations 1 and 3 include a respiration term for the CO_2 released in the mesophyll in the metabolism of cells. Consistent with virtually all biochemical reactions, this respiration term is temperature dependent. Exponential dependence is commonly observed to provide a satisfactory fit with measurements. We assume that

$$r(T_1) = r_0 Q_{10}^{T_1/10}, \quad (5)$$

where T_1 ($^{\circ}\text{C}$) is leaf temperature, and r_0 and Q_{10} are parameters (*see* Hari and Mäkelä 2003).

The annual cycle of photosynthesis

Photosynthesis is inhibited during winter; it recovers slowly during spring, though it is enhanced on warm days. The *state of functional substances*, S , is defined as an aggregated measure of the state of those physiological processes of the leaves that determine the current photosynthetic capacity at any moment of time, and assume that its development in time is driven by temperature (Hari *et al.* 2008a). Describing the slow process of annual cycle, we postulate that S follows leaf temperature, T , in a delayed manner: if T is held constant S approaches T , and if T is changed, S will start to move towards the new temperature with a time constant τ . This gives rise to the following dynamic model for S :

$$\frac{dS}{dt} = \frac{1}{\tau} (T_1 - S), \quad (6)$$

where τ (hours) is a time constant and T_1 ($^{\circ}\text{C}$) is leaf temperature.

We assume that there is a linear relationship between α (cf. Eq. 4) and S :

$$\alpha(S) = \max\{c_1(S - S_0), 0\}, \quad (7)$$

where S_0 ($^{\circ}\text{C}$) is a threshold value of the state of functional substances, below which photosynthesis is totally blocked and c_1 is a coefficient of proportionality.

The model defined by Eqs. 1–5 describes the photosynthetic response to prevailing weather, especially to photosynthetically active radiation. Equations 6 and 7 describe the change in the photosynthetic response during the photosynthetically active period. The PhenPhoto model combines these two key features, (i) instantaneous response, and (ii) acclimation to the annual cycle. Thus, it describes the photosynthetic rate during the active period if the values of the parameters, the weather and the weather history are known.

Parameter values

Parameter values, obtained by analyzing chamber measurements made in summer 1997, and presented in detail by Hari and Mäkelä (2003) and Mäkelä *et al.* (2004), were used in the simulations.

As we aimed to analyze the component of variation of photosynthetic production caused by temperature and PAR, the atmospheric CO_2 concentration was assumed to be constant throughout the study period of 1906–2002.

Simulation of annual photosynthetic production

We used the PhenPhoto model for estimating the instantaneous photosynthetic rate with 5-minute time steps during the simulation period of 1906–2002. Annual photosynthetic production for each year was derived by integrating the instantaneous photosynthetic rates over each growing season. Numerical integration was used.

The correlation between the daily difference of T_{max} and T_{min} and atmospheric transmissivity is not especially strong in northern Finland (Nöjd and Hari 2001b). Therefore, estimates of photosynthetic production for an individual day include fairly large random variation due to the method for generating the PAR values: days with a similar difference between daily maximum and

minimum temperatures can actually represent fairly different cloudiness.

To reduce the random variation related to using generated PAR values, we generated 20 different sets of instantaneous PAR data for 1906–2002. A new set of reference days was randomly selected for each of the 20 data sets. Calculation of the estimates of annual photosynthetic production for 1906–2002 was repeated 20 times, each time with a different input data set. Our estimate for annual photosynthetic production during 1906–2002 was calculated as an average of those 20 model runs.

Modeled vs. measured daily photosynthetic production in 1998–1999

We tested the performance of the optimal stomatal control model against measured data on daily photosynthetic production (*see* Fig. 2). Measurements from SMEAR I during the growing seasons of 1998 and 1999 were used.

Instantaneous PAR values were generated for the location of SMEAR I as described above. Actual temperatures, which had been measured at 2 meters above ground level (five minute intervals), were used as model input. Instantaneous photosynthetic rates were calculated using the PhenPhoto model. In the next phase they were integrated into daily photosynthetic production for each day during growing seasons of 1998 and 1999.

In order to reduce random variation related to the use of generated PAR values, the daily photosynthetic production for 1998–1999 was calculated 50 times, each time with different set of generated PAR data. The final estimate of daily photosynthetic production for 1998–1999, which was used for testing against measured photosynthetic production, was an average of those 50 model runs.

Tree-ring data

To demonstrate that our simulation results could be useful for analyzing the growth of Scots pine, the simulated annual photosynthetic production is compared to measured annual ring-widths

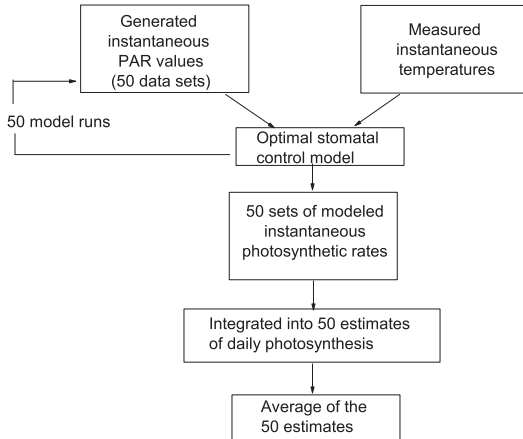


Fig. 2. The procedure for predicting daily photosynthetic production for each day of the growing seasons of 1998 and 1999 on the basis of generated PAR values and measured temperature data.

from northern Finland. A data set collected in 1991 and consisting of 271 Scots pines with the breast-height age varying between 135 and 437 was available (for details see Nöjd and Hari 2001b). The series was extended to cover the period 1991–2002 by coring 22 old Scots pines (93–330 rings at breast height) from sites near the measurement station SMEAR I. The ring-width data was transformed into indices, defined by Fritts (1976) as correction of ring-widths for the changing age and geometry of the tree.

We produced two sets of indices based on profoundly different standardization methods. The first method only aims to remove low-frequency trends. An ordinary least squares model describing the dependence of the radial growth percentage on the tree age was used.

$$\ln(\text{Ir}\%_i) = b_0 + b_1 \ln(n) + e \quad (8)$$

where $\text{Ir}\%_i$ is the radial growth percentage for year i , n denotes n th ring from the pith, b_0 and b_1 are regression coefficients and e the random element.

In contrast, the second standardization method removes also the medium-frequency variation, leaving a stationary time series, which describes the year-to-year variation of Scots pine growth. In the first phase of detrending, a stiff spline with a 50% cut-off in 75 years was fitted to each ring-width series. Radial increment

indices were calculated as the ratio between the observed and estimated values. In the second phase, a flexible spline function with a 50% cutoff frequency in 10 years was fitted the series of indices obtained in the first phase of detrending. Finally, the indices were calculated as a ratio of the indices calculated in the first phase of detrending and the flexible spline. The calculation was performed using the ARSTAN software (Holmes *et al.* 1986). The procedure is similar to that used by Mäkinen *et al.* (2002) for analyzing growth variation of Norway spruce (*Picea abies*) in northern and central Europe.

Results

Modeled vs. measured daily photosynthesis (1998–1999)

Figure 3 shows the results of testing the predicted daily photosynthetic production against the measured one for the growing seasons of 1998 and 1999. In both years, daily photosynthesis reached its peak in late June and remained near the maximum level until the early part of August. The general pattern of the modeled daily photosynthesis is rather similar to the measured one both in 1998 and 1999. The onset of photosynthesis in the spring as well as the gradual reduction in the autumn are described satisfactorily.

The model underestimates photosynthesis on days when measured photosynthesis is especially high for that specific time of the year, i.e. days with clear sky conditions. Similarly, on cloudy days it was generally overestimated. There are some individual days when the modeled photosynthetic production deviates strongly from the measured one. The most obvious example is 12 August 1998.

The measured daily photosynthetic production reached a considerably higher level in 1999, but the values are not directly comparable between years: each year different pine branches with a slightly different needle mass were selected for the chamber. Several factors affect the production of the shoot, including position in the chamber, internal shading within the shoot and possible damage of the needles. The leaf area was measured for both years and

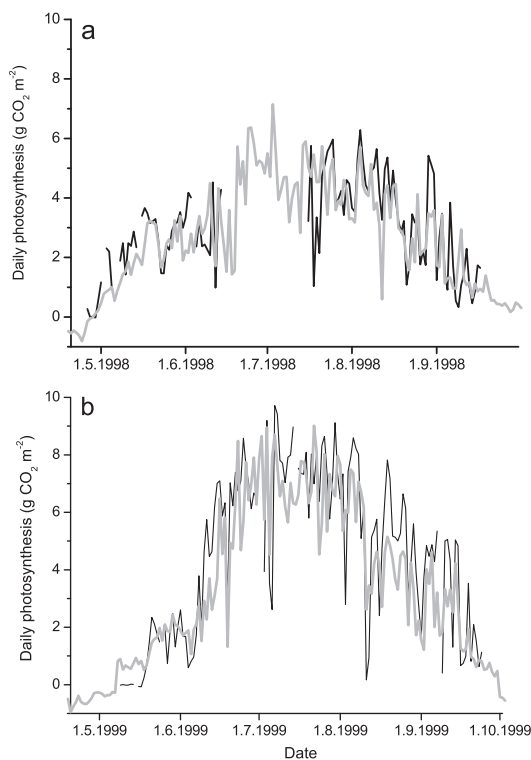


Fig. 3. Measured (black line) and simulated daily photosynthetic production (gray line) at SMEAR I in (a) 1998 and (b) 1999. Measured data include measurement breaks due to technical problems; the most notable occurred in June–July 1998.

used as input for the model, but factors like shading and possible damage were not.

Simulated annual photosynthetic production for 1906–2002

The annual photosynthetic production, simulated using several highly simplifying assumptions, for the period of 1906–2002 is shown in Fig. 4. The standard deviation of the variable was $76.4 \text{ g CO}_2 \text{ m}^{-2}$, which is the equivalent of 11.3% of its mean. During the first two decades of the 20th century, photosynthesis was on a lower level. Thereafter the series shows no trend. The time series shows a relatively strong correlation (0.74) with annual temperature sums, calculated according to Sarvas (1974).

There is much larger proportional variation among years in the springtime recovery of CO_2

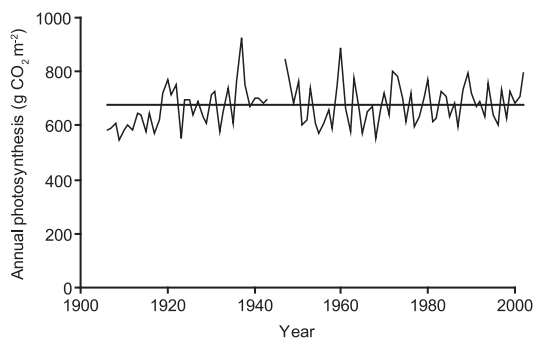


Fig. 4. Annual simulated photosynthetic production of 1 m^2 of unshaded Scots pine needles during 1906–2002. The years 1944–1946 are missing due to incomplete weather data.

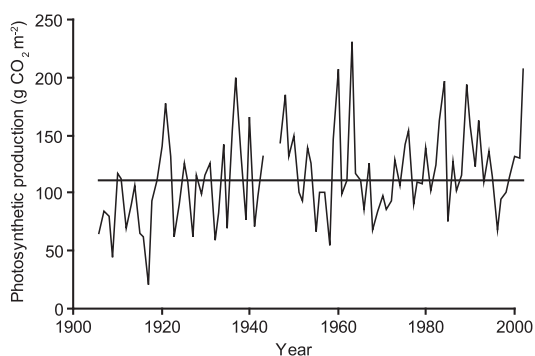


Fig. 5. Simulated photosynthetic production accumulated by 10 June by 1 m^2 of unshaded Scots pine needles with a leaf area of 1 m^2 for the years 1906–2002. The years 1944–1946 are missing due to incomplete weather data.

uptake of Scots pine (Fig. 5). In some years, over 30% of annual photosynthetic production had accumulated by 10 June, while at the other extreme the percentage was about 3%. In 1917 the estimated photosynthetic production accumulated by 10 June was $20 \text{ g CO}_2 \text{ m}^{-2}$, while in 1964 it was $230 \text{ g CO}_2 \text{ m}^{-2}$. During the first two decades of the 20th century, the springtime recovery of CO_2 uptake appears to have been especially slow.

Discussion

We produced an artificial time series of annual photosynthetic production of Scots pine during 1906–2002 in northern Finland. To achieve the aim, several factors, which actually have

a highly significant effect in growth variation of trees, were assumed to be constant. Those include the changing atmospheric CO₂ concentration, nutrient availability, stand dynamics and tree damage. Thus, the variation between years is primarily caused by radiation and temperature, which were the driving factors of the PhenPhoto model. Measured daily minimum and maximum temperatures were used for generating instantaneous temperature and PAR values.

The method was tested by comparing simulated daily photosynthetic production against the measured one for the years 1998 and 1999. The simulated and measured daily photosynthetic production followed a similar seasonal pattern (Fig. 3). However, photosynthetic production was systematically underestimated for days when the measured one was exceptionally high. Similarly, photosynthetic production was overestimated on days when measured photosynthetic production was lower than what is typical for that time of year.

Days with exceptionally high photosynthetic production are invariably days with clear sky conditions, while very thick cloudiness is typical for the other extreme. However, the potential reference days may actually represent quite varying cloudiness. Our estimate of photosynthetic production was produced as an average of 50 model runs, each one using a separate set of generated PAR data. Thus, for clear days some reference days with partial cloudiness will be selected, which causes underestimation. Similarly, generated PAR values for days with heavy cloudiness will tend to be higher than the actual ones.

Modeled instantaneous photosynthesis obviously cannot be accurate when generated PAR data is used. When daily values of simulated photosynthetic production were compared with actual measured ones, considerable differences were still frequently observed (Fig. 3). However, the seasonal pattern of daily photosynthetic production was very similar to the measured one for both 1998 and 1999 (Fig. 3). Over the long term, such as a growing season, disturbances due to random errors caused by generated PAR values should be reduced, as long as the generated instantaneous PAR values have a proper mean level, and their pattern of variation is realistic. The latter is important, because of the non-linear

response of instantaneous photosynthetic rate to radiation. For the growing seasons of 1998 and 1999, both the mean and the standard deviation of the generated PAR values were very close to those of measured PAR (Table 1). As an attempt to reduce the variation related to generated PAR values, we calculated annual photosynthetic production for the years 1906–2002 using 20 different sets of generated PAR data. The standard deviation of the 20 estimates of annual photosynthetic production was small: 3% of the mean.

The range of the estimated annual photosynthetic production, calculated for the period 1906–2002 under a set of simplifying assumptions, is quite narrow. The standard deviation was 11.3% of the mean. There are only two individual years, 1937 and 1960 (both above average), that do not fit within $\pm 20\%$ of the mean. The proportional variation of radial growth of Scots pine in northern Scandinavia — studied with tree-ring analysis — is typically much larger (e.g. Erlandsson 1936, Siren 1961, Nöjd *et al.* 1996, Briffa *et al.* 2008). There is no trend in the estimated annual photosynthetic production for 1906–2002.

In order to demonstrate that the simulated annual photosynthetic production could be useful for analyzing causal factors behind the annual variation of Scots pine growth, two sets of tree-ring indices are shown together with the annual photosynthetic production in (Fig. 6).

While the low- and medium-frequency variation in tree-ring indices is highly sensitive to the chosen standardization option, the method used for producing the indices for Fig. 6a retains those patterns efficiently. Nöjd and Hari (2001b) in fig. 1 show similarly calculated indices based on the same data set for 1906–1990, together with averaged raw ring-widths.

The patterns of year-to-year variation resemble each other rather closely during 1946–2002. Thereagainst, the most notable low-frequency (decadal) pattern in the indices, the fast growth during the 1920s and 1930s, also found in many other studies (e.g. Siren 1961, Nöjd *et al.* 1996, Briffa *et al.* 2008), is not matched at all by the simulated annual photosynthetic production.

The beginning of the 20th century was cold and the 1920s and 1930s rather warm (Briffa *et al.* 2008). Trees react to such a sequence of unfa-

vourable and favourable conditions. There are two possible explanations for the slow growth during 1906–1916 and the subsequent period of above-average growth level: (i) autoregression in tree rings, and (ii) nitrogen dynamics in the soil. The autoregressive explanation assumes that the needle mass as well as sugar and nitrogen pools were reduced during the cold period in the beginning of the 20th century. A tree cannot produce wide annual rings immediately after such unfavourable period even if a climatically favourable growing season occurs: the recovery is bound to be more gradual. During 1917–1938 successive favourable growing seasons resulted in accumulation of needles, photosynthates and nitrogen in trees, which is reflected in growth.

The starting point of the nitrogen-dynamic explanation is that release of ammonium ions from proteins in the soil organic matter is an enzymatic process (Pihlatie *et al.* 2008). Because the rate of all enzymatic reactions depends on temperature, a cold period slows down and a warm period accelerates the release of ammonium ions from proteins in the soil. As nitrogen generally is a key factor limiting tree growth in boreal forest ecosystems, trees react strongly to changes in its availability. Translocation and reuse of nitrogen from senescing needles amplifies the effect of successive favourable and unfavourable years (Bäck *et al.* 2008), which could explain patterns such as slow growth of Scots pine during 1906–1916 and the subsequent long period of fast growth during the 1920s and 1930s.

In Fig. 6b the annual photosynthetic production is shown together with ring width indices produced by standardizing the ring width series with a flexible spline. Again, the year-to-year pattern of variation shows obvious similarities. Prior to the year 1917, when raw ring-width values were very low, the two series are less similar than later in the century.

The similar patterns of variation seen in Fig. 6a and b suggest that annual photosynthetic production could have potential as an explaining variable in traditional statistical growth models. However, we realize that the links between these two require more detailed studies. The two methods used for standardizing the tree ring series for Fig. 6 are both somewhat extreme, and neither is

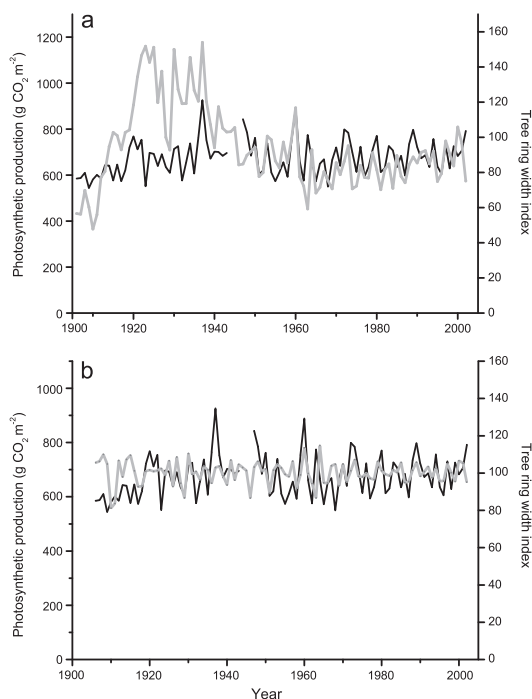


Fig. 6. Annual simulated photosynthetic production of 1 m² of unshaded Scots pine needles during 1906–2002 (black line) shown together with two sets of Scots pine tree-ring indices for the same period. The indices in **a** (gray line) were produced by a method which removes only low-frequency trends from the data. The indices in **b** (gray line) were calculated by standardizing the ring-width chronologies with a flexible spline. The method retains only the high-frequency signal in tree-rings.

probably optimal. Also, an autoregressive term, accounting for the lagged effects of factors such as the availability of nitrogen, could be a vital component of such models.

Dynamic carbon balance forest growth models, which are based on photosynthesis (e.g. Hari *et al.* 2008b), could open a natural way to introduce a time series of photosynthetic production as an input for tree growth models. In addition, hybrid models combining the features of statistical and dynamic models can be constructed. The use of photosynthetic production as explaining factor improves the biological basis of analyzing the causes of growth variation of trees.

Another aspect requiring more detailed analysis is that photosynthetic production for a full calendar year is unlikely to be an ideal explana-

tory variable for predicting ring-width of the same year. Radial growth of Scots pine typically ends in mid-August in northern Finland (Schmitt *et al.* 2004, Mäkinen *et al.* 2008), while considerable amounts of photosynthates are still produced in late August and September (*see* Fig. 3). Those are either stored or allocated to other components of the tree. Also, the results of Berninger *et al.* (2004), indicating a link between radial growth of Scots pine and the photosynthetic production of the previous year, suggest that the proper selection of the period is crucial.

There were sizable differences in photosynthetic production during spring and early summer. The photosynthetic production accumulated by 10 June varied from 3.5% of the annual photosynthetic production in 1917 to 34.1% of the respective figure in 1964.

During 1906–1917, the photosynthetic production accumulated by 10 June was considerably lower than in subsequent years. As Scots pine growth was markedly slow in northern Finland at that time (Fig. 6), the finding is in accordance with that of Nöjd and Hari (2001b), who also found indications of a link between low spring temperatures and below average Scots pine growth in northern Finland. Also, Tuomenvirta (2004) discovered that specifically spring temperatures have shown a statistically significant warming trend in Finland during 1888–2002. However, apart from the early decades of our study period, photosynthesis accumulated by 10 June shows no clear trend.

Some uncertainty is related to the comparability of temperature measurements from Ivalo during 1906–2002. The location of the weather station changed several times. Homogeneity adjustments were made in order to reduce possible bias caused by the location changes by using techniques that utilize temperature records from neighboring weather stations (Tuomenvirta 2001). However, very few weather stations were operating in northern Scandinavia during the early 20th century and the distance between Ivalo and the nearest stations was very large. In such conditions the methods used for correcting the discontinuity of the temperature series are less reliable. These type of problems occur frequently, when long records of meteorological data are used.

We estimated the annual photosynthetic production of unshaded Scots pine needles with a leaf area of 1 m² for northern Finland. As a set of simplifying assumptions was used, the concept is theoretical, reflecting the component of variation caused by variation in temperature and PAR. In practice, the needle mass of forest trees varies from year to year. In climatically extreme conditions, such as those near the northern timber line in Scandinavia, the natural variation of needle mass can be especially high (Pensa *et al.* 2006). If tree foliage is damaged, photosynthetic production estimated using climate and radiation as input variables may strongly deviate from the true one. After a catastrophic event, several growing seasons are required before the needle mass of a tree fully recovers.

We analyzed the effect of temperature and PAR on the annual photosynthetic production of Scots pine using available meteorological data and a model that has been shown to be accurate by intensive field measurements. Testing the results against measured daily photosynthetic production over two growing seasons produced a reasonable fit. The estimated annual photosynthetic production for 1906–2002 showed a rather similar pattern of annual ring width indices. Modeling the annual photosynthetic production could also be applied to analyzing the growth variation of other tree species for which accurate models on photosynthetic production exist. The approach could even be utilized in analyzing the variation of agricultural crops: long time series on annual crops exist for many important species.

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