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Relationship between temperature and the seasonal course of photosynthesis in Scots pine at northern timberline and in southern boreal zone

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ABSTRACT

In earlier studies the seasonal dynamics of photosynthetic capacity in northern conifers has been explained as a slow response to the ambient temperature. We tested this concept with Scots pine (*Pinus sylvestris* L.). We analysed the seasonal dynamics of photosynthetic efficiency in Scots pine at the timberline in Finnish Lapland, and in a southern boreal forest in Southern Finland. The relationship between the daily photosynthetic efficiency and leaf temperature history was determined from continuous measurements of shoot CO_2 exchange. The shoot CO_2 exchange and photosynthetic efficiency showed similar seasonal patterns in the northern and in the southern locations, following daily mean temperature with a delay. The relationship between the temperature history and photosynthetic efficiency appeared to be near sigmoidal both in the northern and in the southern trees. The relationship was also consistent from year-to-year, thus the seasonal course of photosynthetic efficiency can be predicted accurately from the ambient temperature using a sigmoidal relationship. A rapid decrease of photosynthetic efficiency was observed when daytime temperature dropped below zero or frost had occurred in the previous night. The difference in the rate of acclimation of photosynthetic efficiency between the north and the south was small.

1. Introduction

The clear annual pattern of photosynthetic activity of coniferous trees growing in temperate and boreal zones has been shown in several studies (e.g. Pisek and Winkler, 1958; Pelkonen and Hari, 1980; Bergh and Linder, 1999). The activity increases when the spring progresses, meets the peak in the summer and decreases towards winter. Part of this seasonal variation can be directly attributed to changes in the daily patterns of the environmental driving factors, e.g. increase in light levels and temperature in the spring and a declining trend in autumn, and the direct response of photosynthetic rate to those factors. The instantaneous response of photosynthetic rate to environmental driving factors (or the rate of photosynthesis in standard conditions) also varies within a year. In other words, the internal state of the photosynthetic machinery changes (Pelkonen and Hari, 1980; Bergh et al., 1998).

Several processes govern photosynthetic rate. The energy of solar radiation is captured by pigments in chloroplasts, transported via electron transport chain and transformed into chemical energy as ATP and NADPH. This reaction chain, so called light reactions, is driven by visible light and almost independent on temperature. The chemical energy supplied by the light reactions is utilized in light-independent reactions of Calvin cycle (so called dark reactions) where CO_2 is fixed and photosynthates (sugars) are eventually formed. These latter reactions are temperature-dependent, so their rate is greatly reduced in cold (Sharpe, 1983).

In addition to its direct effects on the photosynthetic processes, temperature may be connected to photosynthetic rate via its effects on the consumption of photosynthates for growth and maintenance of foliage, fine roots and woody tissues. The rates of these respiratory processes are commonly considered to increase exponentially with temperature (e.g. Lloyd and Taylor, 1994; Tjoelker et al., 2000). The reduction in the demand for

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photosynthates taking place in low temperatures is suggested to inhibit photosynthetic production (Savitch et al., 2002; Hjelm and Ögren, 2003). Photosynthates can be stored as starch, but eventually their production must be reduced to match the consumption. The pools and activities of the enzymes involved in CO_2 fixation vary seasonally depending on ambient conditions and the production and consumption of photosynthates. The wintertime reduction in the energy sink of dark reactions is further compensated by reduction of light harvesting capacity and changes in the composition of light harvesting pigments to dissipate excess solar energy as heat (Hansen et al., 1996; Vogg et al., 1998). The minimum photochemical efficiency in boreal evergreens is observed in March and April when intense light exposure of foliage is combined with low temperatures (Öquist and Huner, 2003; Porcar-Castell et al., 2005).

During cold acclimation the evergreen plants also undergo changes in the cell structure and concentrations of soluble compounds in the cytoplasm to develop tolerance for the freezing of extra-cellular water and the associated dehydration stress. There is evidence, however, that the acclimation of photosynthetic machinery and frost hardiness are independent of each other, i.e. photosynthetic capacity at any given value of frost tolerance can vary, or vice versa (Repo et al., 2006).

The time course of the recovery of photosynthetic capacity in spring has been attributed to ambient temperature history (Pelkonen and Hari, 1980; Bergh et al., 1998). Polster and Fuchs (1963) found that short-term frosts can cause a reversal of the recovery of photosynthetic capacity in Scots pine (*Pinus sylvestris* L.). Bergh and Linder (1999) stated that the frequency of severe night frosts and, to a lesser extent, soil thawing and soil temperature are also important factors behind the spring recovery of photosynthesis.

Pelkonen and Hari (1980) suggested that the seasonal changes in the internal state of photosynthetic machinery in boreal evergreen conifers are fully reversible and related to the annual course of ambient temperature through a delayed dynamic response. Suni et al. (2003) demonstrated that the spring recovery of five boreal forest ecosystems could also be explained well by 5-d moving average of air temperature. The model of Pelkonen and Hari (1980) was further developed by Mäkelä et al. (2004) who formulated a simple linear relationship between the ambient temperature history and photosynthetic capacity. The state of acclimation of the photosynthetic apparatus could be described in temperature units as a theoretical variable (S). The reversibility of the annual cycle means that photosynthetic capacity is not pre-determined to grow monotonically in the spring, but during cold spells it can also decrease. In that sense it is conceptually different from accumulated temperature sum, which is traditionally used for predicting phenological events such as budburst, flowering and dormancy (e.g. Sarvas, 1972, 1974; Heikinheimo and Lappalainen, 1997; Linkosalo, 2002; Chuine et al., 2003).

The possibility to use temperature as the primary driving factor for the photosynthetic activity enables us to predict the course of photosynthesis during the year or even under a changed climate. The present understanding of the factors linked to the momentary rate of photosynthetic production allows for extraction of short-term variation in photosynthetic rate from the changes in the physiological state (acclimation). For example, the optimal stomatal control model (Hari et al., 1986; Hari and Mäkelä, 2003) comprises the behaviour of stomatal regulation and the biochemical processes, such as photochemistry (light reactions), CO_2 fixation (dark reactions) and temperature-dependent dark respiration, involved in photosynthesis. Owing to the reasonably small number of parameters, the model can be successfully parameterized with field measurements. At a daily timescale, the model could explain about 95% of the diurnal variation in the instantaneous photosynthetic rate in the shoots of Scots pine in Northern Finland (Hari et al., 1999b; Hari and Mäkelä, 2003). Using the model and measured CO_2 exchange data we can determine the seasonal course of the state of the photosynthetic apparatus.

Mäkelä et al. (2004) explained the seasonal dynamics of photosynthetic efficiency of Scots pine over 1 yr as a slow linear response to the ambient temperature conditions prevailing at the growing site. In this study, we test and refine this concept with extensive datasets of measured shoot CO_2 exchange at two distinct sites, a Scots pine stand growing in the southern boreal zone and another at timberline in the northern boreal zone. The study sites are situated at the SMEAR (station for measuring forest ecosystem—atmosphere relations) field stations, equipped with automated gas exchange measurement systems. This provides a unique comparison of multi-annual time series of shoot gas exchange measured under different climatic regimes.

We also examine the potential differences between two geographical origins of the trees. For phenological events such as bud burst and flowering, northern tree provenances are known to have smaller temperature sum requirements, indicating higher rates of ontogenetic development, than southern provenances (Sarvas, 1967). This phenomenon can be readily observed in common garden experiments where northern provenances burst buds or flower earlier than southern ones (Beuker, 1994). On the basis of these findings one could hypothesize that there could be corresponding differences among provenances also in the case of springtime recovery of photosynthetic efficiency, i.e. that in any given springtime air temperature conditions the recovery is faster in northern than in southern provenances.

2. Material and methods

2.1. Sites and measurements

The measurements were performed at two field stations called SMEAR I and SMEAR II. SMEAR stations are designed to study material and energy flows in the atmosphere–vegetation–soil continuum at different temporal and spatial scales and are operated with versatile and highly automated measurement units in a continuous and long-term manner. Detailed descriptions of the SMEAR study scheme and instrumentation were provided by Vesala et al. (1998) and Hari and Kulmala (2005).

Both study sites are located in the boreal climate zone. The northern site, SMEAR I, is located in Värriö (67°46′N, 29°35′E), Finnish Lapland, 400 m above the sea level at the arctic-alpine timberline. The southern site, SMEAR II, is situated in the southern boreal zone in Hyytiälä (61°51′N, 24°17′E), southern Finland, 180 m above the sea level. The distance between the sites is about 700 kilometres in south-north direction. Both sites are homogeneous 40–50-yr old Scots pine stands, the mean height of the trees being 8 m in Värriö and 15 m in Hyytiälä. In Värriö the mean annual temperature for the climatological normal period (years 1971–2000) was –0.9 °C, mean annual precipitation 592 mm, average end of snow cover period 20 May, and the length of the growing season 114 d. In Hyytiälä the mean annual temperature was +3.3 °C, mean annual precipitation 713 mm, end of snow cover period 30 April and the length of the growing season 162 d (Drebs et al., 2002).

Shoot gas exchange measurements in years 1999 and 2001–2005 were analysed for Värriö and in years 1999–2005 for Hyytiälä. The measuring systems at the two stations were nearly identical. The instrumentation consisted of chambers, sample tubing, gas analysers and a control unit operating the system automatically. The chambers were made of acrylic plastic. In Värriö the chambers were cylindrical with 3.5-dm^3 volume whereas in Hyytiälä the chambers were 1-dm^3 boxes. The chambers were open most of the time exposing the chamber interior to the ambient conditions. For measuring fluxes, the chambers were closed intermittently for one minute. Measurements of CO_2 and water vapour fluxes and concentrations, air temperature inside the chambers and photosynthetically active radiation (PAR) outside of the chambers were done 70–180 times a day. During the chamber closure, gas concentrations and environmental variables were recorded every 5 or 10 seconds. The flux calculation was based on the detection of the gas concentration change in the chambers during the closure (Hari et al., 1999a). More detailed descriptions of the chamber measurements were provided by Hari et al. (1999b) and Altimir et al. (2002).

The experimental Scots pine shoots were located at the top of the canopy. The shoots were debudded prior to chamber installation to prevent new growth inside the chambers. The chambers were installed on the shoots so that they accommodated one age class (1-yr-old) of needles. The needles were gently bent to form a horizontal plane in the same angle as the sensor measuring PAR. The annual data collection covered the period from approximately late April to mid-October in Värriö and the entire year in Hyytiälä. Normally, three or four chambers were in use simultaneously. In Värriö, fresh shoots were taken under monitoring each spring. In Hyytiälä the measurements were sometimes continued for 2yr. After completing the measurements on the shoots, the dimensions of the needles on each shoot were measured and their surface area calculated with Tiren's (1927) equations. The uncertainty of this method is about ±10%, i.e. at least such range of variation in the shoot-specific photosynthetic efficiency can be expected. The all-sided needle areas inside the shoot chambers ranged from 0.02 to 0.06 m^2, specific needle masses being about 130 g m^{-2}.

When chamber measurements were not available, half-hourly averaged climatic data (temperature measured at a height of 9 m in Värriö and at 8 m in Hyytiälä, and radiation measured above the canopy) was used for calculating the temperature history. As the temperature inside the open shoot chambers was up to 2 °C higher than the ambient temperature due to heating by solar radiation, the ambient temperature measurements were converted to correspond to the conditions inside the chamber temperature by adding an empirically determined radiation-dependent term. The mean daily difference varied seasonally depending on light conditions. The maximum of the mean daily difference, 1.1 °C, was observed on the long sunny days of summer and late spring. On cloudy days the difference was typically 0.2–0.5 °C. In winter the chamber temperature was very close to the ambient temperature.

Following Mäkelä et al. (2004), we estimated leaf temperature T_l from the measured or estimated chamber temperature T_a using a linear relationship between solar radiation I and warming of the leaf in the chamber:

$$T_l = T_a + bI$$

where b is a parameter representing the effect of light on leaf temperature. The value of b was determined by measuring the surface temperature of needles inside an open chamber at different radiation regimes with an infrared sensor.

2.2. Models

Photosynthetic efficiency of the Scots pine shoots was determined daily from the measured CO_2 exchange using the model of optimum stomatal control of photosynthesis formulated by Hari et al. (1986) and Hari and Mäkelä (2003). The model was derived from the hypothesis of Cowan and Farquhar (1977) that plants adjust the stomatal apertures in their leaves in a way that maximizes carbon gain while minimizing transpiration costs in a longer timescale. The model comprises the following equations for photosynthesis, A (mol CO_2 m^{-2} s^{-1}), dark respiration, R (mol CO_2 m^{-2} s^{-1}) and stomatal conductance, g_s (m s^{-1}) as functions of ambient CO_2 concentration, C_a (mol CO_2 m^{-3}), saturation deficit of water vapour at leaf surface, D (mol H_2O m^{-3}) and leaf temperature, T_l (°C):

$$A = C_i f(I) = \frac{(g_s C_a + R) f(I)}{g_s + f(I)}, \tag{1}$$

$$R = Max\left(0, r_0\, Q_{10}^{T_l/10} + r_1\right), \tag{2}$$

$$g = \left(\sqrt{\frac{C_a - R(T_l)/f(I)}{1.6\,\lambda\, D}} - 1\right) f(I). \tag{3}$$

$$g_s = \begin{cases} g_{\min}, & \text{if} \quad g \le g_{\min} \\ g, & \text{if} \quad g_{\min} < g < g_{\max} \\ g_{\max}, & \text{if} \quad g \ge g_{\max} \end{cases}. \tag{4}$$

In eqs. (3) and (4), $g_{\min}$ (m s^{-1}) is cuticular conductance, $g_{\max}$ (m s^{-1}) stomatal conductance when the stomata are fully open, and 1.6 the ratio of diffusivity of water vapour relative to diffusivity of CO_2. The parameter λ (mol CO_2 (mol H_2O)$^{-1}$) is the cost of transpiration, i.e. the carbon required in the long term to sustain transpiration flow. It can also be considered as a measure of water-use efficiency.

The function *f*(*I*) represents the light response of the biochemical reactions of photosynthesis:

$$f(I) = \frac{\beta I}{I + \gamma} \tag{5}$$

where γ (μmol m^{-2} s^{-1}) is a parameter describing the saturation of *f*(*I*), i.e. the shape of the light response. Parameter γ gives the relationship between the light-saturated value and the initial slope of *f*(*I*). The initial slope of *f*(*I*) describes the efficiency of photochemistry, i.e. light harvesting in the chloroplasts (quantum yield per unit internal CO_2 concentration). The key parameter in the annual variation of photosynthesis is photosynthetic efficiency β (m s^{-1}), which is equivalent to the maximum rate of Rubisco-catalysed carboxylation in the Calvin cycle (the light-saturated level of dark reactions). When multiplied by the intercellular CO_2 concentration in the leaf (eq. 1) it equals to the rate of light-saturated photosynthesis.

The parameter estimation method was documented in detail by Hari et al. (1999b) and Hari and Mäkelä (2003). Photosynthetic efficiency β was estimated daily for each shoot by fitting the model to the measured CO_2 exchange. The other parameters were fixed at the values that minimized the sum of squared residuals over the entire year while letting β vary from day to day. Due to the model structure some of the parameters, most notably λ and γ, are intercorrelated and similar behaviour of CO_2 exchange can be achieved with different parameter combinations (Hari and Mäkelä, 2003). Therefore, transpiration measurements were utilized in finding the values of λ, $g_{\min}$ and $g_{\max}$. Respiration parameters were estimated from night-time CO_2 exchange.

The daily mean photosynthetic efficiency of all shoots at each site was used in the further analyses. Because different shoots were monitored each year, there was year-to-year variation in the absolute level of photosynthetic efficiency. This was partly due to real variation in the physiology among the shoots, but also due to varying degree of overlapping of needles and inaccuracy of the measured needle areas inside the chambers. The variation in the absolute level of photosynthetic efficiency between different years was removed using a relative scale for β. For each year, the average of β when $9\,^{\circ}\mathrm{C} < S < 11\,^{\circ}\mathrm{C}$ was used as a reference, denoted as β_{10}.

The method for studying the relationship between β and the leaf temperature history was adopted from Mäkelä et al. (2004). The delayed effect of temperature is described by a theoretical variable, state of acclimation (*S*) that corresponds to the temperature the photosynthetic apparatus is acclimated to. *S* was calculated from the estimated leaf temperature (T_l, °C):

$$\frac{dS}{dt} = \frac{T_l - S}{\tau}, \tag{6}$$

where τ is a time constant, i.e. the slowness of the acclimation of the photosynthetic apparatus. The annual course of *S* was calculated from the needle temperature data in half-hour steps for several values of τ. In each year the initial state of *S* was set equal to the estimated leaf temperature at the beginning of the year. For each day of year, the value of *S* at noon was selected to represent that day.

Mäkelä et al. (2004) proposed a linear relationship between the state of acclimation *S* and photosynthetic efficiency β:

$$\beta = a(S - T_0), \tag{7}$$

where *a* is a scaling factor and T_0 a threshold temperature. The relationship can also be other than linear, and expressed in general form $\beta = f(S)$, *f* being function of arbitrary type. We tested sigmoidal relationship of the form

$$\beta = \frac{\beta_{\max}}{1 + e^{b(S - T_S)}}, \tag{8}$$

where $\beta_{\max}$ is the maximum photosynthetic efficiency. T_s is the inflection point, i.e. the temperature at which β reaches half of $\beta_{\max}$ (and where the β-*S* slope reaches its maximum), and *b* curvature of the function.

3. Results and discussion

Shoot CO_2 exchange showed similar seasonal patterns in Hyytiälä and in Värriö, following the daily mean temperature with a delay (Fig. 1). The timing of the start of the spring recovery varied by about two weeks from year to year. The seasonal cycle of photosynthesis can be illustrated by the changes in the apparent light response of shoot CO_2 exchange. In early spring the light-saturated rate of photosynthesis remained low, increased as the spring progressed, levelled off for July and August and declined again in autumn (Fig. 2).

The development of light-saturated photosynthesis and the estimated photosynthetic efficiency β followed very closely the seasonal course of the leaf temperature history indicated by *S* (Fig. 3). Photosynthetic efficiency in early spring remained at stable wintertime level until *S* increased above –4 °C and spring recovery began. The reversibility of photosynthetic efficiency could be observed well in spring 2004 (Fig. 3). In the beginning of May there was a very warm spell with daily mean temperatures about 10 °C above the long-term average, followed by a sudden drop in the temperature. Along with the weather cooling down, photosynthetic efficiency decreased rapidly, in Värriö even lower than to the level predicted by the state of acclimation.

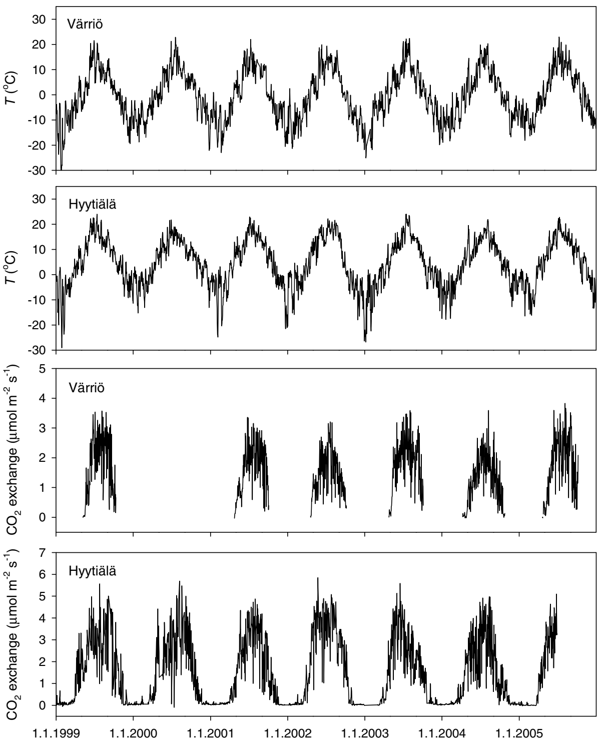

Fig. 1. Time series of daily mean air temperatures in Värriö (SMEAR I) and in Hyytiälä (SMEAR II) in years 1999–2005, and mean mid-day CO_2 exchange of Scots pine shoots in Värriö and in Hyytiälä in years 1999–2005. The CO_2 fluxes were calculated per unit all-sided needle area and averaged between 11:00 and 13:00 solar time.

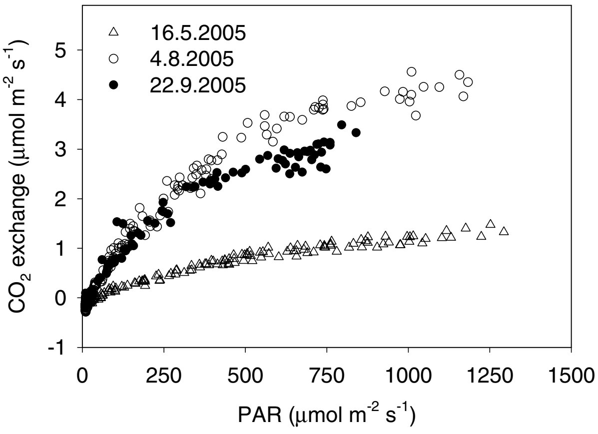

Fig. 2. Relationship between light (photosynthetically active radiation) and shoot CO_2 exchange in Värriö on three randomly selected days in spring, summer and autumn.

In autumn, the measured CO_2 exchange declined along with decreasing light levels and temperature. When photosynthetic efficiency was estimated from the measured gas exchange, the connection of temperature history to the observed decline became clear. In the autumn photosynthetic efficiency remained near the summertime level until the first severe frosts occurred (Fig. 4). This kind of observation emphasizes the central role of temperature in the seasonality of conifer photosynthesis (cf. Lundmark et al., 1998). During the occasional warm spells in December and January, photosynthetic efficiency could still rise fairly high, up to 30%–40% of the summertime level. The minimum values of β were observed in March.

On average the photosynthetic efficiency was similar in the northern and southern trees, with typical summertime values of 0.8–1.0 mm s^{-1} and the range of shoot-to-shoot variation roughly 0.6–1.2 mm s^{-1}. The light saturation parameter γ and the respiration parameters were similar at both sites (Table 1). The cost of transpiration (λ) and maximum stomatal conductance ($g_{\max}$) between the sites showed slightly more conservative water use in the northern shoots, the trees in the north closing their stomata more susceptibly than the trees in the southern site. In Värriö the estimated value of λ was 0.0029 mol CO_2 (mol H_2O)$^{-1}$ while in Hyytiälä it was 0.0021 mol CO_2 (mol H_2O)$^{-1}$. The range of variation in λ and $g_{\max}$ among the shoots was about ±25% of the respective mean values for the site and the difference of λ between Värriö and Hyytiälä was statistically significant (*t*-test, $p = 0.04$). It must be noted, however, that there were systematic errors in the measurements of shoot gas exchange, especially transpiration (Kolari et al., 2004). The inaccuracy in the other parameters of the optimum model is also reflected in the value of λ due to the intercorrelated parameters (Hari and Mäkelä, 2003). A statistical test of the difference cannot give a definitive answer on the origin of the difference.

Compared to β, the other parameters of the optimum model were found to be rather stable over the year. Parameter γ gives the relationship between photosynthetic efficiency and the initial slope of $f(I)$. Its value did not show systematic changes over the year, i.e. the regulation of light and dark reactions followed the same seasonal patterns. The light reactions must acclimate to the energy consumption by dark reactions to maintain balance between the absorbed light energy and CO_2 fixation (Öquist and Huner, 2003). Therefore, one parameter, photosynthetic efficiency β, is sufficient in characterizing the state of the whole photosynthetic apparatus.

If estimated in time steps shorter than a year, cost of transpiration (λ) showed a slightly decreasing course from the early spring to the beginning of summer and again an increase in the autumn (results not shown). The higher spring and late autumn values of λ correspond to lower values of stomatal conductance and a higher sensitivity of the stomata to respond to air humidity, which can be seen in transpiration measurements (not shown). We used a fixed value for λ instead of letting it vary from day to day. This did not affect the annual pattern of estimated β significantly but it greatly increased the stability in the estimation of the daily values of β.

There is evidence that the temperature response of dark respiration may change seasonally (Law et al., 1999; Atkin et al., 2000). A sensitivity analysis on the respiration parameters with 1 yr of CO_2 exchange data showed that an increase of 50% in

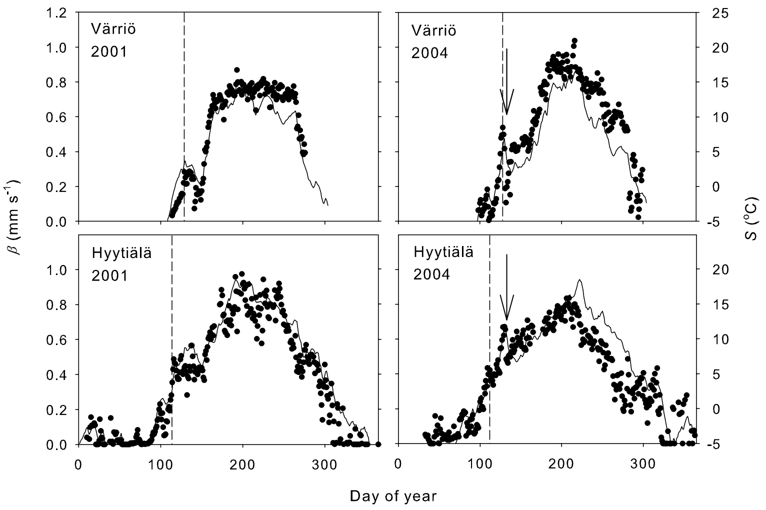

Fig. 3. The annual course of photosynthetic efficiency (β, indicated with dots) estimated daily from the chamber measurements, and state of acclimation (S, indicated with line) derived from leaf temperature in Värriö and in Hyytiälä in years 2001 and 2004. Time constant τ in the calculation of S was 200 h. The arrows are pointing to a day when sudden cooling after a warm spell occurred in spring 2004. The declining temperatures were reflected in the daily values of β. The vertical dash lines indicate the days when the snow had fully melted.

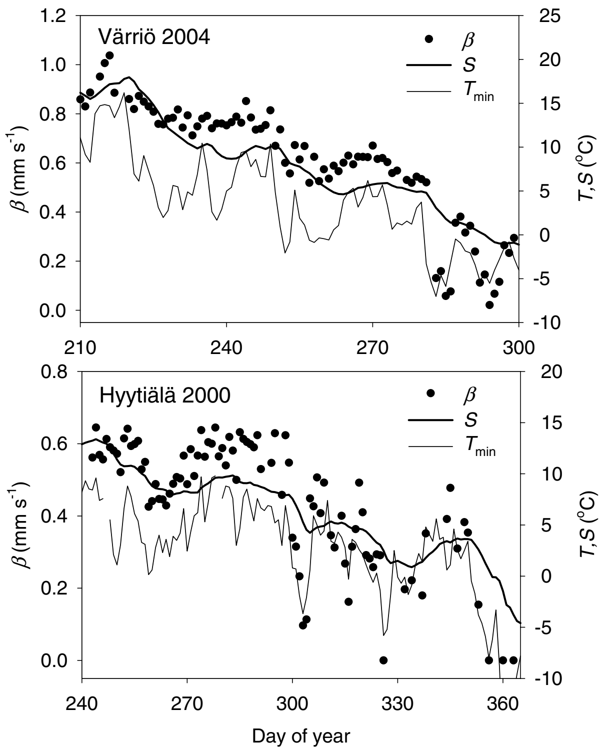

Fig. 4. The courses of daily photosynthetic efficiency (β) of Scots pine shoots, leaf temperature history (S) and daily minimum temperature ($T_{\min}$) in autumn 2000 in Hyytiälä and in autumn 2004 in Värriö. Time constant τ in the calculation of S was 200 h. Note the different scaling of the time axes.

respiration coefficient r_0 in eq. (2) only contributed to 6% increase in photosynthetic efficiency. It did not change the seasonal patterns of β, nor did it noticeably affect the β–S relationship. We ignored the changes in the respiration parameters because they play a minor role compared with the seasonal variation in the photosynthetic parameters. Estimating the temporal variation in the respiration parameters in the north would also be inaccurate, because in midsummer the sun stays above the horizon for a couple of weeks.

The 6-yr pooled data (1645 d for Hyytiälä, 1008 for Värriö) indicated similar behaviour of photosynthetic efficiency β related to the state of acclimation, S, in Hyytiälä and in Värriö (Fig. 5). At the range of 0–10 °C, β was nearly linearly related to ambient temperature history, indicated by S, in both northern and southern trees. In the linear form of β–S relationship (eq. 7), the value of T_0, i.e. the threshold state of acclimation for photosynthesis, got values of about –4 °C. This means that when the temperature has been below zero during the preceding days, there is still a potential for some (up to 15% of typical summertime level) photosynthesis to take place whenever leaf temperature momentarily rises above zero. In Hyytiälä, even at very low values of S in winter, CO_2 uptake that exceeded the measuring noise could be observed, provided that the leaf temperature was momentarily about 0 °C or higher. This observation agrees with the previous findings (Leverenz and Öquist, 1987; Ensminger et al., 2004) that Scots pine is able to opportunistically utilize warm periods throughout the winter. The potential photosynthetic efficiency was in general higher in midwinter than in early spring. In December and January the overall light levels are low and positive temperatures especially are connected to cloudy days whereas later on the light stress becomes more severe. Thus, the need for downregulation of light reactions would also get stronger during the course of winter, as chlorophyll fluorescence measurements on Scots pine in Hyytiälä also indicate (Porcar-Castell et al., 2005).

The slope of the relationship between β and S decreased markedly especially in Värriö when S increased above 10 °C. The temperature dependence is probably saturating but summertime temperatures in Finland seem to seldom reach saturating level. Light-saturated photosynthesis has an instantaneous response to temperature, which generally rises to a maximum in the range 25–40 °C and falls rapidly to zero at higher

Table 1. Parameters of the optimal stomatal control model of photosynthesis

Symbol	Definition	Unit	Value	
			Hyytiälä	Värriö
$g_{\min}$	Minimum stomatal conductance	mm s^{-1}	0.05	0.03
$g_{\max}$	Maximum stomatal conductance (stomata fully open)	mm s^{-1}	1	0.8
r_0	Respiration parameter	mol CO_2 m^{-2} s^{-1}	0.1 10^{-6}	0.1 10^{-6}
r_1	Respiration parameter	mol CO_2 m^{-2} s^{-1}	–0.13 10^{-6}	–0.13 10^{-6}
Q_{10}	Relative increase of respiration per 10 °C	–	2	2
b	Increase in leaf temperature per unit PAR	°C $mmol^{-1}$ m^2 s^1	1.5	1.5
γ	Half-saturation parameter	μmol m^{-2} s^{-1}	900	1000
λ	Cost of transpiration	mol CO_2 (mol $H_2O)^{-1}$	0.0021	0.0029
β*	Photosynthetic efficiency	m s^{-1}	Variable	Variable

* Parameter estimated by fitting the entire model to measured gas exchange, separate values for each day.

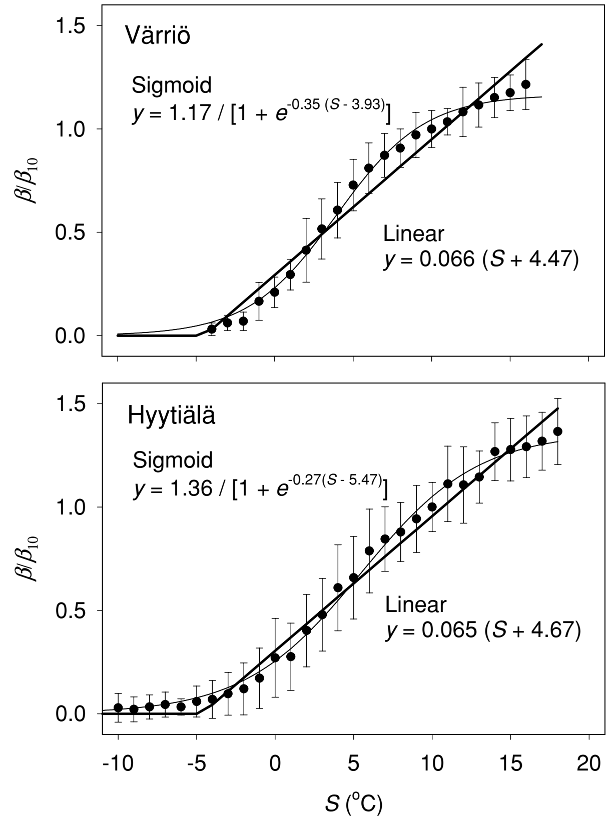

Fig. 5. Relative photosynthetic efficiency (β/β_{10}) of the Scots pine shoots versus state of acclimation (S) derived from leaf temperature with time constant of 200 h in Värriö (top) and in Hyytiälä (bottom). The variation in the absolute level of photosynthetic efficiency among different shoots was removed using a relative scale for β. The average of β when $9\ °C < S < 11\ °C$ was used as a reference, denoted as β_{10}. The data cover years 1999–2005 and was divided to classes of 1 °C. The error bars indicate the standard deviation of β/β_{10} ratio within each class of S. The corresponding parameterisations for the linear and sigmoidal functions are also shown. Only temperature classes that include 5 d or more are shown.

temperatures as protein functioning is impaired (Berry and Björkman, 1980; Krivosheeva et al., 1996). The highest observed values of S, about 19 °C, correspond to daytime highs of 25–30 °C. In those conditions it is quite possible that the photosynthetic machinery adapted to the cool boreal climate is reaching its peak capacity. Due to the non-zero photosynthetic efficiency at low values of S and the decrease of the slope at high temperatures, the overall relationship between β and S exhibited sigmoidal rather than linear behaviour. The parameterisations of linear and sigmoidal functions are summarized in Fig. 5.

When the time constant τ was estimated using a linear dependence of photosynthetic efficiency on S (eq. 7), the value of τ that explained best the measured time series of photosynthetic efficiency varied between 100 and 275 h from year to year. On average the time constant in the north (250 h) was slightly higher than in the south (200 h) suggesting a slower spring recovery of photosynthesis in the north. Year-to-year variation in the estimated τ was, however, greater than the corresponding difference between the two geographical locations. The optimal value of τ was insensitive to the type of the function used, as long as the predicted dependence of β on S was close to linear between 0 °C and 10 °C. In the sigmoidal model the optimal time constant was slightly smaller, 240 h and 180 h in the north and in the south, respectively. The sigmoidal β-S function (eq. 8) explained the day-to-day variation was β slightly better than the linear form. The percentage of explained variance (PEV) in the whole daily β/β_{10} dataset by the sigmoid was 91% in Hyytiälä and in Värriö. The corresponding PEVs for the linear form were 90% and 88%, respectively. The sigmoid did not have a dramatically better fit than the linear function but it is biologically more appropriate because photosynthetic rate tends to saturate at high temperatures. The goodness of the model fit was in general insensitive to the value of τ. In Hyytiälä, values of τ ranging from 120 to 250 h gave PEV of at least 90% for the sigmoidal β-S relationship. The estimated time constants were smaller than those estimated in Värriö for year 1997 by Mäkelä et al. (2004).

The difference evidently originates in the different estimates of needle temperature: we estimated a clearly smaller warming of needles by radiative heating than Mäkelä et al. (2004).

Sarvas (1967) and Beuker et al. (1994) concluded that budburst in the plant specimens of northern origin is occurring earlier than in plants of the same species from southern regions when grown under the same environmental conditions. Considering the recovery of photosynthetic capacity in trees growing at their native sites, our results indicated a slightly slower recovery in the north. Due to the relative insensitivity of the goodness of the model fit to the value of τ, the observed north–south difference cannot be considered statistically significant.

Photosynthetic acclimation showed a small difference between spring and in autumn in Värriö. In autumn, photosynthetic efficiency especially at low values of S was on average higher than in spring (Fig. 6). In Hyytiälä there was no clear difference. The observations of β not declining to the level predicted by S in autumn suggests that the rates of up- and down-regulation in the photosynthetic machinery are slightly different in autumn and spring, i.e. the time constant τ would vary during the year. This assumption does not seem to hold, however, because estimating τ separately for the first and the second half of the year yielded a smaller τ in autumn than in spring. The time constant for the sigmoidal model in Hyytiälä was 200 h in spring and 150 h in autumn. In Värriö the time constant in autumn could only be estimated accurately for 2 yr but it also appeared to be smaller in autumn (200 h versus 250 h in spring). The spring–autumn asymmetry in β-S relationship can be attributed to smaller diurnal variation of temperature in autumn than in spring, i.e. in the autumn nights there are less frequently hard frosts that would affect photosynthetic efficiency on the next days. The decline of photosynthetic efficiency in the autumn was smooth until nighttime frosts became severe.

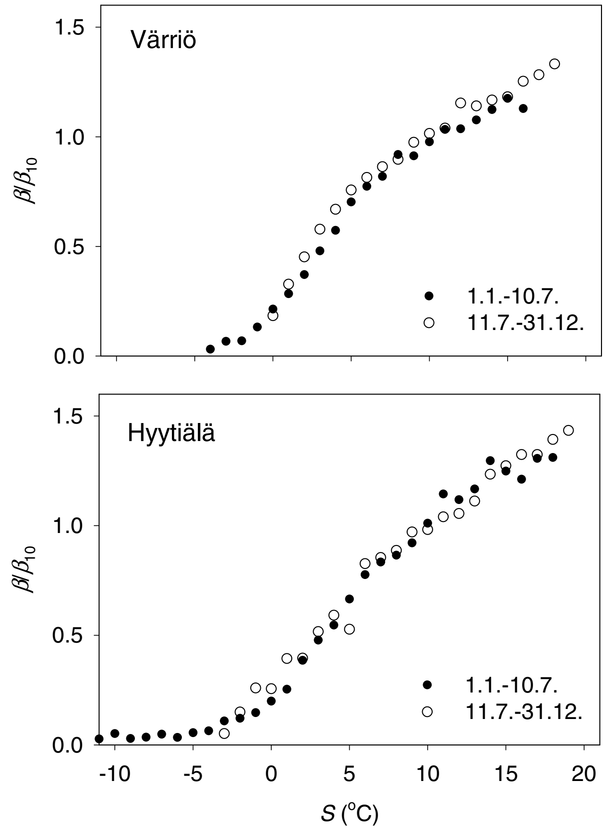

Fig. 6. Relative photosynthetic efficiency (β/β_{10}) of the Scots pine shoots versus state of acclimation (S) derived from leaf temperature with time constant of 200 h in Värriö (top) and in Hyytiälä (bottom). Data from years 1999–2005 were pooled and divided to temperature classes of 1 °C and two time categories: The filled circles represent the days before the average summertime peak in β, the open circles the days after the peak value of β. Only temperature classes that include 5 d or more are shown.

Mäkelä et al. (2004) reported that occasionally, after cold nights, the observed photosynthetic rate stayed at a lower level than the optimum model predicted. In our dataset this rapid temperature response could be seen systematically after freezing nights, most often in spring. In such conditions the shoot CO_2 uptake in the morning increased slower than the model predicted and eventually did not reach the level predicted by the state of acclimation (Fig. 7).

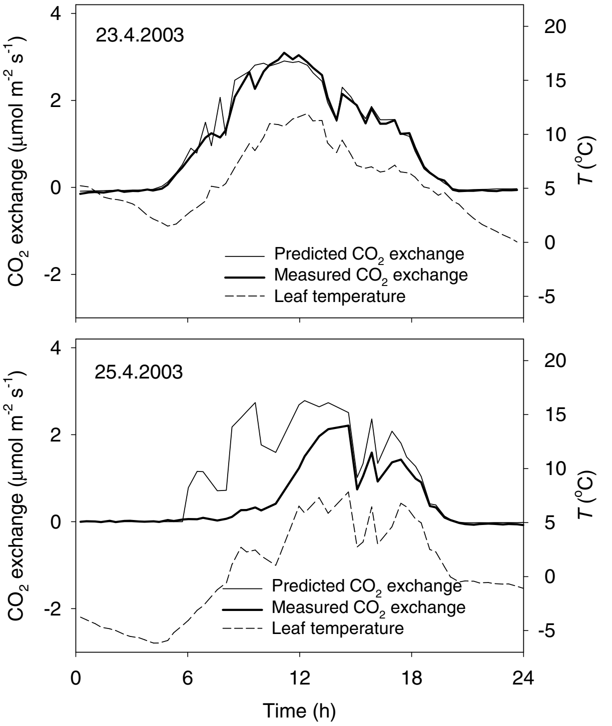

Fig. 7. The effect of cold night on the diurnal course of shoot CO_2 exchange. Predicted and measured daily course of shoot CO_2 exchange in Hyytiälä on a typical bright spring day (top) and on a day when frost occurred in the previous night (bottom). The thin solid line indicates CO_2 exchange predicted with the optimum model and sigmoidal β–S relationship.

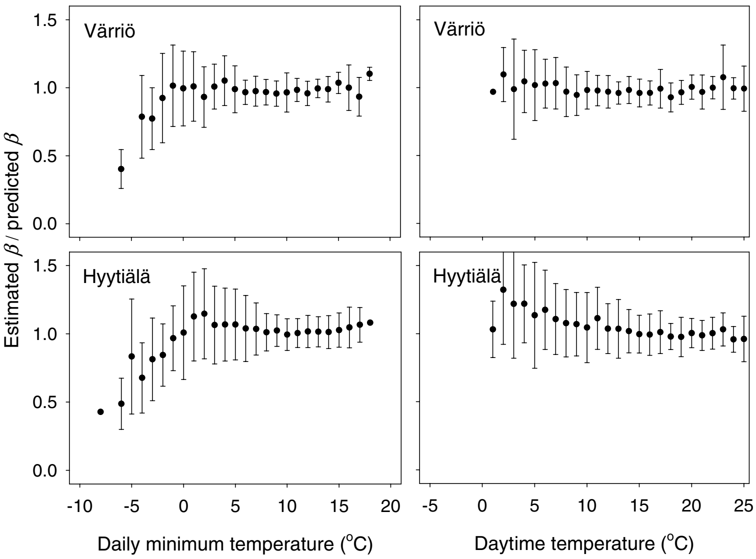

Fig. 8. The short-timescale relationship between leaf temperature and the ratio of the estimated daily photosynthetic efficiency β to the photosynthetic efficiency predicted from the state of acclimation S. The graphs on the left illustrate the relationship between the ratio of estimated to predicted β and the minimum temperature in the previous night. On the right the ratio of estimated to predicted β is plotted as a function of daytime temperature (averaged between 9:00 and 15:00 solar time). The predicted values of β were calculated with the sigmoidal model (eq. 8). Time constant τ in calculating S was 200 h. Data from years 1999–2005 were pooled and divided to temperature classes of 1 °C. The days when the predicted β was less than 10% of β_{10} were excluded. The night-time minimum plots only include the cases when the daytime temperature was above zero, i.e. no instantaneous reduction in the photosynthetic rate was expected.

We examined the deviations of the estimated photosynthetic efficiency from the predicted daily values as a function of daytime temperature and the minimum temperature of the preceding night. If there was frost, the effect of cold night was carried over the whole day, as Polster and Fuchs (1963) already observed. The decline of β was obvious if the temperature in the preceding night fell below zero even when daytime temperature was clearly above zero, i.e. no instantaneous reduction in photosynthetic rate was expected (Fig. 8). In those cases both linear and sigmoidal β-S relationships overestimated β. This behaviour was more pronounced in spring, probably because in autumn the frosts at given value of S were in general milder than in spring. The rate of recovery from a freezing night seemed to be faster than the seasonal acclimation of the entire photosynthetic apparatus. After one day the adverse effect of a single cold night was no more distinguishable unless the frost was severe (<–5 °C).

At daytime temperatures below 0 °C, the photosynthetic efficiency rapidly declined regardless of S. In those cases, however, night-time temperature had also been below zero and the decline in β could be as well attributed to the night frost. We could not see any systematic relationship between the ratio of measured to predicted β and daytime temperature on day 5 when there was no frost in the previous night (Fig. 8). At moderate to high temperatures there was also an apparent lack of temperature sensitivity, which was already reported by Linder and Troeng (1980), although it may be partly due to the difficulty to separate possible temperature effects from VPD and light responses in the field data. Extracting the instantaneous temperature response near zero from the effect of cold nights is also problematic because there are virtually never days when temperature falls below zero after positive night temperature. Measurements in controlled conditions would be needed to overcome this limitation in field data.

The spring recovery of photosynthesis started well before the snow had thawed and the soil started to warm up, which on average occurred around 20 April in Hyytiälä and 2–4 weeks later in Värriö. By that time the photosynthetic efficiency had typically reached 30%–50% of the seasonal maximum (Fig. 3). We inspected the possible effect of cold soil on spring recovery by sorting the data shown in Fig. 8 (the ratio of estimated to predicted β) into two categories: days before and after the disappearing of the snow cover. The effect of cold nights was first eliminated by excluding the days with minimum temperature below zero. In Värriö the average estimated to predicted ratio within the range of $0\ ^\circ\mathrm{C} < S < 4\ ^\circ\mathrm{C}$ was 1.04 before and 1.12 after the snowmelt, i.e. at any given value of S, photosynthetic efficiency was 7% lower before the snowmelt than after it. In Hyytiälä the average ratios before and after the disappearing of the snow were 0.94 and 1.25, respectively. Although Bergh et al. (1998) and Bergh and Linder (1999) emphasized the contribution of cold soil to the spring recovery, the effect in our data was not statistically significant. Moreover, Suni et al. (2003) did not find any close connection between the onset of spring recovery of photosynthesis and soil temperature at five boreal coniferous forest sites. According to the sink limitation hypothesis, low soil temperatures that reduce root growth and maintenance respiration can be considered as a limiting factor for photosynthesis. On the other hand, the share of photosynthetic production that exceeds the demand can be released into the soil as root exudates instead of being consumed by plant respiratory processes (Trumbore, 2006). Therefore, it is not self-evident that low soil temperature and the resulting low root activity would considerably inhibit photosynthetic production in spring.

4. Conclusions

Our measurements indicate that the seasonal pattern of photosynthetic efficiency in Scots pine in the southern boreal zone as well as in the northern boreal timberline consistently follows the state of acclimation derived from the leaf temperature history, exhibiting a saturating response to the temperature history. The deviations of the observed photosynthetic efficiency from the efficiency predicted from the temperature history can be attributed to a more rapid response of photosynthesis to low temperatures and night-time frosts. The differences in the observed relationships between photosynthetic efficiency and state of acclimation were small between the southern boreal and the northern boreal trees.

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