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Diurnal course of photochemical activity of winter-adapted Scots pine at subzero temperatures

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Abstract

The photochemical activity of native Central Siberian Scots pine trees (*Pinus sylvestris* L) was estimated from the middle of February to the middle of March 2001. We measured chlorophyll (Chl) fluorescence in attached intact needles from trees located approx. 30 km west of the Yenisey river (60°44´N, 89°09´E) near the village of Zotino. In this period, the air temperature varied between –39 °C and +7 °C. At temperatures below –10 °C, *P. sylvestris* needles did not exhibit any variable Chl fluorescence during the daylight period. During the night, however, the effective quantum yield of photosystem 2 (PS2) photochemistry, Φ_2 [$\Phi_2 = (F_m' - F_t)/F_m'$), increased from values near zero to values between 0.05 and 0.20 depending on the needle temperature and sample investigated. The increase started soon after dusk and lasted for 3–6 h depending on the temperature. A faster increase of Φ_2 was found for temperatures around –16 °C, and lower rates occurred at lower temperatures. Irrespective of the temperature, Φ_2 decreased rapidly to near zero values at dawn, when the photosynthetic photon flux density increased to about 1–5 μmol m^{-2} s^{-1}, and remained near zero throughout the day. At temperatures higher than –10 °C, the diurnal decrease and the nocturnal increase of Φ_2 were less distinct or disappeared completely. Hence the winter-adapted Scots pine maintains some photochemical activity of PS2 even at extremely cold temperatures. The capacity of photochemical reactions below –10 °C is, however, very limited and PS2 photochemistry is saturated by an extremely low irradiance (less than 5 μmol m^{-2} s^{-1}).

Additional key words: chlorophyll fluorescence; cold adaptation; diurnal changes; photosystem 2; *Pinus sylvestris* L.; quantum yield.

Introduction

Coniferous evergreens retain their needles for several years and therefore, at the mid-to-high northern latitudes and at high altitudes, their photosynthetic apparatus must survive severe freezing periods often combined with high irradiance in late winter/early spring. To cope with such extreme conditions they have developed complex adaptive mechanisms (for reviews see Alberdi and Corcuera 1991, Körner 1999, Öquist and Huner 2003). These involve also changes in the thylakoid membrane, particularly in the composition of pigments, lipids, fatty acids (Selstam and Öquist 1985, Wellburn 1997), and chlorophyll-protein complexes (Öquist *et al.* 1978, Ottander *et al.* 1995, Vogg *et al.* 1998b). These changes act to protect the photosynthetic apparatus during winter stress.

The content of xanthophylls of the xanthophyll cycle increases, and they are more de-epoxidised during winter as compared to summer (*Pinus ponderosa*, *Pseudotsuga menziesii*, and *Picea pungens*: Adams and Demmig-Adams 1994; *Pinus sylvestris*: Ottander *et al.* 1995). De-epoxidation of these xanthophylls is involved in the mechanism of excitation energy dissipation in pigment antennae, which, in turn, lowers the excitation pressure to

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the reaction centres.

Winter adaptation increases the amount of unsaturated fatty acids (Alberdi and Corcuera 1991, Vogg *et al.* 1998a), thus increasing the fluidity of the thylakoid membrane and the rate of electron transport at low temperature.

Complex winter adaptation is reported for chlorophyll-protein complexes. Ottander *et al.* (1995) found that the photosystem 2 (PS2) complex completely disappeared and the number of light-harvesting complex 2 (LHC2) and photosystem 1 (PS1) complexes decreased in Scots pine needles during winter. Vogg *et al.* (1998b) detected decreases of LHC2, light-harvesting complex 1 (LHC1), and protein CP43 during winter stress of Scots pine. The concentration of D1-protein, which together with D2-protein and cytochrome b_{559} forms the reaction centre (RC) of PS2, was strongly depressed. It is expected that, during winter, light-harvesting complexes are reorganised in a xanthophyll-chlorophyll multi-complex and that PS2 RCs, which had been inactivated by photoinhibition at low temperature, are accumulated. Both of these structures are very efficient in the non-radiative dissipation of excitation energy, thus protecting the remaining active RCs from over-excitation (Ottander *et al.* 1993, 1995).

Some of these winter adaptations are reflected in changes of chlorophyll (Chl) fluorescence. The ratio of variable and maximal Chl fluorescence (F_V/F_M), which is often used to measure the maximum quantum yield of PS2 photochemistry and which is around 0.8 at 20 °C, decreased already in early autumn (Scots pine: Öquist and Ögren 1985; white spruce: Vidaver *et al.* 1989; Norway spruce: Špunda *et al.* 1997). Winter depression of F_V/F_M also corresponded to the decrease of content of the D1 protein and to the extent of the de-epoxidation of xanthophylls (Adams and Demmig-Adams 1994, Adams *et al.* 1995, Ottander *et al.* 1995). F_V/F_M, however, did not drop below 0.15 even during January through March with the daily temperature varying mainly between 0 and –10 °C, thus indicating that the remaining PS2 RCs were photochemically active during winter. Chl fluorescence yield at the open RCs of PS2, F_0, also decreased during winter. This indicates increased heat dissipation in the pigment antennae.

Conifers growing at mid-to-high northern altitudes are often exposed to temperatures below –10 °C and should survive periods with temperatures as low as –30 to –50 °C. Although the temperature dependence of PS2 photochemistry has been well studied under laboratory conditions covering a broad temperature range, field studies of PS2 functioning performed below –10 °C are rare. Here we present a field winter study of diurnal changes in PS2 functioning for Scots pine grown in natural forest in Central Siberia. During measurements, the leaf temperature ranged from 0 to –30 °C. PS2 photochemistry was tracked by measurement of the effective quantum yield of PS2 photochemistry (Φ_2) using Chl fluorescence *in vivo*. We found that Scots pine keeps PS2 photochemistry functioning even at temperatures close to –30 °C. Below –10 °C, Φ_2 is suppressed to zero during the day, but recovers during the following night to the low winter values.

Materials and methods

Chl fluorescence was measured on native-grown Scots pine (*Pinus sylvestris* L.) in winter. The 30–200-year-old trees were located about 30 km west of the Yenisei river (60°44`N, 89°09`E), near the Zotino village close to the long-term eddy covariance measurement site operated by Max Planck Institute for Biogeochemistry (Jena) and the Institute of Forest (Krasnoyarsk). During the measurement period, *i.e.* from 22 February through 9 March 2001, the ambient air temperature varied between +7 °C and –39 °C. The local temperature extreme for the winter of 2000–2001 was approx. –56 °C.

Diurnal courses of Chl fluorescence were measured with a *PAM-2000* fluorimeter (*Walz*, Germany). Two types of experiments were designed: (*a*) Sequential measurements of effective quantum yield of PS2 photochemistry, Φ_2, on attached needles of nine trees *in situ*. Mean (tree-averaged) diurnal course of Φ_2 was produced for days varying in temperature and irradiance regime. (*b*) Continuous daily measurements of Φ_2 on needles of a single cut branch. Position of needles and fibre optics was fixed during the diurnal measurement.

(*a*): The diurnal courses of Φ_2 of intact attached needles were measured on nine individual trees with *PAM* fluorimeter moving from one tree to another. The fluorimeter is designed to operate at temperatures not lower than –20 °C. Therefore, it was necessary to warm up the *PAM-2000* between series of nine measurements in a hut (at +8 to +15 °C). The outdoor series of nine measurements was as short as possible (~15 min) to prevent the decrease of the instrument temperature below the operation range. The series of measurements on nine branches of different individuals were repeated every 40–120 min, depending on expected changes in the yield, from 06:30 to 24:00 h. Five days with different air temperature and irradiance patterns were selected for the measurements. The temperature and light sensors (parts of the leaf-clip holder accessory) were attached to the fibre optics so as to ensure contact of the temperature sensor with the needles during measurements. The light sensor pointed at an angle of approx. 45° towards the sky during the measurements.

(*b*): Diurnal changes in relative Chl fluorescence yield were measured on a cut branch using a leaf clip holder (standard accessory of the *PAM-2000*). The analysed branch, the holder, and fibre bundle of the *PAM* fluorimeter were attached to the hut wall. The bundle was

squeezed through a small hole in the wall of the hut. This arrangement allowed the fluorimeter to remain inside the hut (at temperatures from +5 to +10 °C) and maintained the mutual position of the bundle and the analysed needles (detached branch) throughout the continuous whole-day measurements.

Chl fluorescence of dark-adapted pine needles *in situ*, kept below –10 °C, showed a fast increase by about 5 to 20 % to a maximum by switching on the "actinic light", without any further variation on prolonged irradiation. The time resolution of the instruments was not sufficient to record millisecond kinetics of the small Chl fluorescence increase. Therefore, only the Chl fluorescence increase on firing the saturation pulse was measured. Relative Chl fluorescence yield before the saturation pulse, F_t, and maximum Chl fluorescence, F_M', were used to calculate Φ_2 $[(F_M' - F_t)/F_M']$. "Actinic light" varied during the day–night cycles with naturally fluctuating photosynthetically active radiation from sun. No artificial fluorimeter built-in "actinic light" source was used. The effective quantum yield Φ_2 was used instead of the more frequently measured maximum quantum yield of PS2 photochemistry [F_V/F_M ratio, $(F_M - F_0)/F_M$], because darkening of the needles (up to 30 min), which is necessary to take the Chl fluorescence level at a re-oxidised primary quinone (F_0), did not cause a measurable increase of the variable Chl fluorescence (F_V). In the dark-adapted needles during the night, F_t is equivalent to F_0 and F_M' to maximum fluorescence yield F_M. To avoid confusion, we will refer to the diurnally estimated fluorescence parameter with the common name 'effective PS2 yield' Φ_2 hereafter [$\Phi_2 = (F_M' - F_t)/F_M'$] no matter whether it was measured during the light or dark period. (The parameter is referred to as the 'effective quantum yield of photochemical energy conversion in PS2', Φ_2, in Roháček 2002, Eq. 36.) The measuring radiation of the *PAM-2000* (level 3, PAR<0.2 μmol m^{-2} s^{-1}) was switched on 1 s before firing the saturation pulse (level 8, PAR ≈ 3 000 μmol m^{-2} s^{-1}, 800 ms) in the protocol of all measurements. The Chl fluorescence yields F_t and F_M' were taken before and during the saturation flash firing, respectively.

Results

An example of diurnal changes in instantaneous (F_t) and maximum (F_M') Chl fluorescence yield and Φ_2 measured on a detached pine branch [Exp. (*b*)] during a sunny day with max/min temperature of –23/–32 °C is shown in Fig. 1. Effective PS2 yield Φ_2 was depressed to zero already at photon irradiances lower than 5 μmol m^{-2} s^{-1} (*i.e.* at dawn) and was close to zero throughout the day [30–900 μmol(photon) m^{-2} s^{-1}]. The increase in Φ_2 was observed after sunset when the photon irradiance had already decreased well below the detection limit of the leaf clip accessory of the *PAM* fluorimeter (1–2 μmol m^{-2} s^{-1}). Instantaneous and maximum Chl fluorescence yields were also affected by irradiance, decreasing and increasing during early morning and late afternoon, respectively. During the irradiation period, when Φ_2 was close to zero and both F_t and F_M were of similar value, further decreases of about 20 % in both fluorescence intensities were observed. The extent of this decrease closely correlated with the photon irradiance, reaching its maximum under direct sunlight at midday [700–900 μmol(photon) m^{-2} s^{-1}].

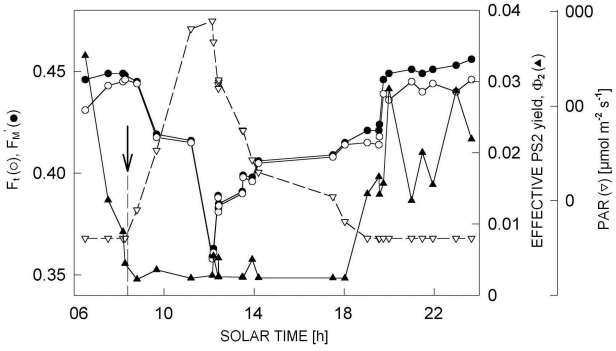

Fig. 1. An example of diurnal chlorophyll (Chl) fluorescence changes in Scots pine needles. The diurnal courses of instantaneous (F_t) and maximal (F_M') Chl fluorescence intensities, effective quantum yield of PS2 photochemistry (Φ_2), and photosynthetically active radiation (PAR) are shown. PAR is plotted on a logarithmic scale. Chl fluorescence changes were measured on a sunny day with maximum/minimum temperatures of –23/–32 °C on a detached pine branch with needles and fibre bundle of the PAM fluorimeter in fixed positions. Sunrise at 08:20 h is marked.

The effective PS2 yield measured in attached needles [Exp. (*a*)] decreased rapidly at dawn, but was recovered in the subsequent night at temperatures below about -10 °C (Fig. 2*A*). The diurnal changes in Φ_2 depended on needle temperature. The trace for 23 February represents a diurnal course of Φ_2 for a sunny day with a minimum needle temperature of –17.5 °C at sunrise. After reaching the maximum of –7.4 °C in the late afternoon, the average needle surface temperature decreased to –16 °C in the evening. The 24 February was a cloudy day with minimum temperature in the morning of –19.6 °C and maximum temperature at midday of –12.6 °C. The temperature in the late evening was –16 °C. On 25 February an extremely cold but sunny day started with –29 °C, reached maximum temperature of –23 °C at 15:00, and finally decreased to –30 °C at midnight. The morning depression of the PS2 yield, which occurred at dawn before the photon irradiance increased to about 5 μmol m^{-2} s^{-1}, had been completed already before sunrise (08:20 h). During the day, Φ_2 remained close to zero for needle temperatures below *ca.* –10 °C. At higher tem-

peratures, an increase of Φ_2 was observed (23 February). On 23 February, the highest Φ_2 during the daylight period corresponded to the highest temperature as well. The fifth pattern (Fig. 2*B*) presented (9 March) is for an unusually warm day with day/night temperatures of +1.7/–7.5 °C. At such temperatures, no depression of Φ_2 was observed during the day, but it did not increase to higher values after sunset even though the night temperature was above –10 °C.

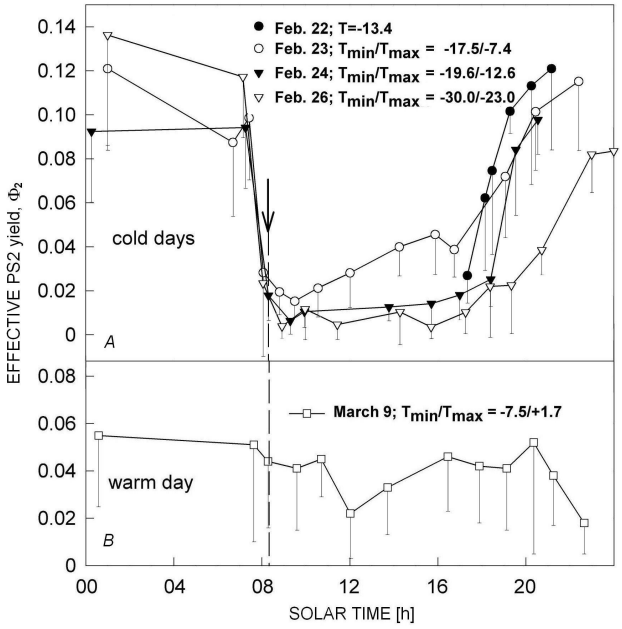

Fig. 2. Diurnal and afternoon courses of effective quantum yield of photosystem 2 (PS2) photochemistry (Φ_2) in Scots pine needles measured during four cold days (*A*, air temperatures lower than –10 °C) and one warm day (*B*, air temperatures higher than –10 °C) differing in irradiance variations. Minima/maxima of needle surface temperature are given. Φ_2 was measured using a routine procedure of a *PAM* fluorimeter. Each value represents the mean of measurements on 9 different trees. Negative SD values are shown. Sunrise at 08:20 h is marked.

The morning temperatures determined the effective PS2 yield depression, and the night temperatures affected the rate of Φ_2-recovery (Fig. 2). At –16 °C, Φ_2 was fully recovered 5 h after sunset; at –30 °C, the recovery of Φ_2 proceeded much slower and did not reach the pre-dawn value observed for the warmer nights (see Fig. 2 for temperatures). The points in Fig. 2 represent the means of nine locations, each taken on a branch oriented differently towards the sun and shaded to a different extent by other trees. Therefore, the mean values highlight neither the daily course of direct sun exposure of the needles nor the variation of needle-surface temperature.

In Fig. 3, all data from both types of experiments are compiled, completed with temperature, and plotted against irradiance and leaf-surface temperature. Below approximately –10 °C, Φ_2 decreased with increasing photon irradiance and decreasing temperature. For temperatures below –20 °C and photon irradiance above 10 µmol m^{-2} s^{-1}, nearly all measurements showed complete depression of Φ_2. Above –10 °C, Φ_2 did not exhibit considerable changes as irradiance increased from 10 to about 300 µmol m^{-2} s^{-1}. Φ_2 tended to increase with decreasing temperature from above zero to –10 °C at irradiances of 0–5 µmol m^{-2} s^{-1}.

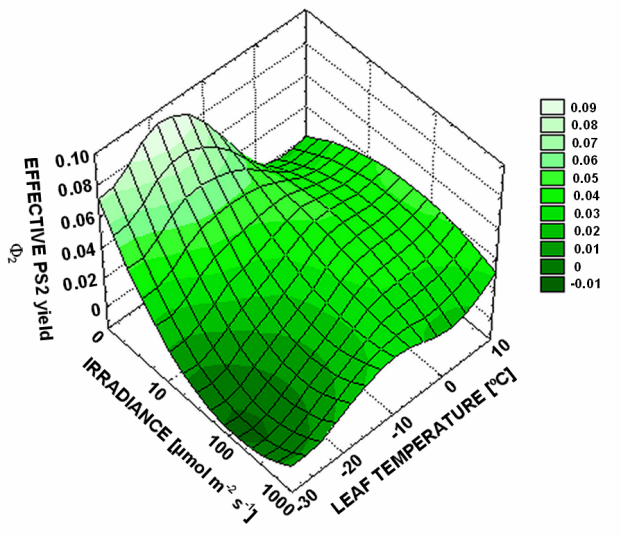

Fig. 3. Dependence of effective quantum yield of PS2 photochemistry (Φ_2) of Scots pine needles on irradiance and needle surface temperature. The surface plot was constructed by pooling all measured 586 points, most of them used in Figs. 1 and 2, completed with the leaf temperature coordinates and by using fitting and smoothing Least squares procedure of *STATISTICA 6*. The surface region with negative values of Φ_2 is an artefact produced by the smoothing procedure. Photosynthetic active irradiance is plotted on a logarithmic scale.

The trace in the three-dimensional plot, representing the temperature dependence of Φ_2 in the dark, shows an increase from about +5 to –15 °C and a decrease upon further lowering of the temperature to –30 °C. The trace includes the predawn values as well as all measurements performed from dusk (at an irradiance lower than 5 µmol m^{-2} s^{-1}) to midnight and, therefore, reflects both the temperature dependence of the effective PS2 yield at predawn steady state and the dark relaxation rate after dusk. The decrease below –15 °C is related, therefore, to a slower after-dusk PS2 relaxation at lower temperatures. To reduce the influence of the after-dusk relaxation on the temperature dependence of Φ_2, only the data measured after the fast phase PS2 dark relaxation, *i.e.* between 21:30 and 18:00 h of the next day, were extracted. The temperature dependence created from these measurements is presented in Fig. 4 (*closed circles*). It shows that Φ_2 in the dark increased from 0.02 to 0.10, with the temperature decreasing from near zero to about –15 °C, and remained close to 0.10 at further

lowering of temperature. For comparison, temperature dependence of Φ_2 constructed from data obtained at two irradiance intervals (10–100 and 100–340 μmol m^{-2} s^{-1}, respectively) is shown (Fig. 4). In irradiated needles, Φ_2 slightly increased from above zero temperatures to about –8 °C and was reduced to zero magnitudes upon lowering the temperature to –23 °C.

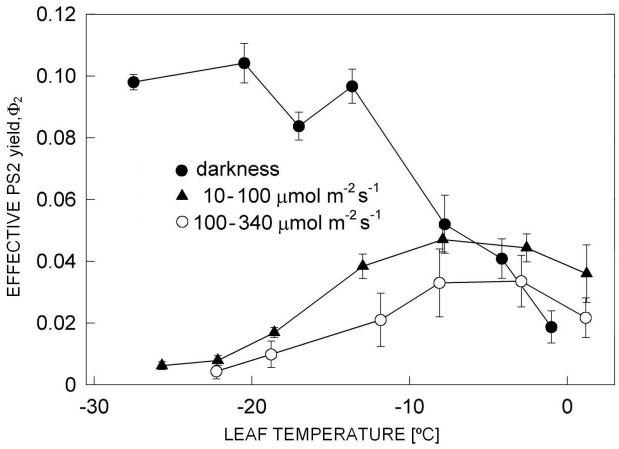

Fig. 4. Dependence of effective quantum yield of PS2 photochemistry (Φ_2) of Scots pine needles on needle surface temperature at different irradiances. The trace with closed circles summarizes Φ_2 measurements in dark adapted needles (measured between 21:30 and 18:30). *Closed triangles* and *open circles* show the measurements performed at irradiances of 10–100 and 100–340 μmol m^{-2} s^{-1}, respectively. Means ± SD (n = 8–22).

F_V is proportional to the reduction state of the primary quinone acceptor, Q_A, of the photosynthetic electron transport chain (Duysens and Sweers 1963), and depends upon non-photochemical quenching, photoinhibition, *etc*. The Chl fluorescence decay after the saturation pulse might reflect the kinetics of Q_A re-oxidation. Fig. 5

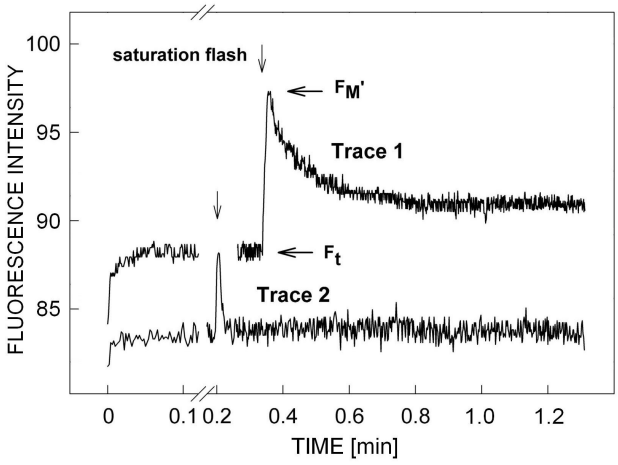

Fig. 5. An example of chlorophyll fluorescence responses of Scots pine needles to the measuring irradiance and saturation pulse. Trace *1* was measured *in situ* with a pine branch at –16 °C at late night. Trace *2* corresponds to the detached branch that had been transferred into the hut (4–6 °C) one hour before the measurement. The warm-adapted needles were darkened for 30 min before the measurement. Saturation pulses (800 ms, 3 000 μmol m^{-2} s^{-1}) were fired using the halogen lamp of the *PAM* fluorimeter. The values of F_M' and F_t of Trace *1* are indicated.

(trace *1*) shows an example of the Chl fluorescence decay kinetics measured on attached dark-adapted needles at –16 °C. The Chl fluorescence decayed with a half-life of 20–30 s after the 800 ms saturation pulse. Afterwards, the analysed needles were warmed in the hut in the dark for 1 h to 4–6 °C. The fluorescence decay kinetics of warmed needles were faster than the time resolution of the instrument used, *i.e*. about 100 ms (Fig. 5, trace *2*). This shows that the temperature decrease from about +5 °C to –16 °C depressed the rate of Q_A re-oxidation by two to three orders of magnitude.

Discussion

The effective quantum yield of energy conversion in PS2, Φ_2, in pine needles when measured at temperatures below –10 °C responded very sensitively to natural (sun) irradiance, rising after dusk and reaching a maximum after midnight but before early dawn. Already at very low photon irradiances (less than 1–5 μmol m^{-2} s^{-1}), it was fully depressed and increased again after dusk only (Figs. 1 and 2). The decrease of Φ_2 during the light period likely results from a small capacity of electron transport through PS2 at low temperature, and thus leading to saturation occurring at very low irradiances. In potato the low temperature inhibits both the electron transport through PS2 and electron flow from PS2 to PS1 (Havaux 1998). As a result, the re-oxidation rate of Q_A and plastoquinones is low, and reduced quinones accumulate on irradiance below –10 °C (Velthuys and Amesz 1975). Accumulation of reduced plastoquinones at low temperatures may result from a different temperature dependence of the electron transport rate on the donor and acceptor sides of PS2. Although the water oxidising complex is capable to donate electrons to $P680^+$ at temperatures as low as –30 or –40 °C (Styring and Rutherford 1988, Gleiter *et al.* 1993), electron flow from Q_A is limited at much higher temperatures (Öquist *et al.* 1993).

Electron flow through PS2 is also reduced in winter-adapted evergreen plants (Martin *et al.* 1978, Öquist and Huner 2003). This reduction is caused by the complex adaptations in PS2 components, including RC (Ottander *et al.* 1995, Vogg *et al.* 1998a,b), electron transport between Q_A and Q_B, and the plastoquinone pool (Öquist and Martin 1980, Ivanov *et al.* 2001, 2002). The rate of Q_A^- re-oxidation in winter-adapted Scots pine was

monitored using the variable Chl fluorescence decay after a saturation flash at 5 °C. The major decay component had a half-life of about 4.5 ms (Ivanov *et al.* 2001). This is in line with our rough estimate in needless warmed to 4 through 6 °C for one hour. A temperature decrease to –16 °C in winter-adapted natural stands in Siberia slowed down the Chl fluorescence decay to about 20 s, *i.e.* by about three orders of magnitude (Fig. 5). This indicates that the low temperature itself rather than a gradual winter acclimation process was the major reason for the decrease of the Q_A^- re-oxidation rate at temperatures below –10 °C.

After the sudden drop of Φ_2 at the first photons during morning dawn, the Chl fluorescence yields of the needles F_t and F_M' were depressed in proportion to the irradiance during the light period (Fig. 1). F_t and F_M' were nearly identical and Φ_2 was close to zero throughout the day. The daily course of the Chl fluorescence yield between sunrise and sunset was nearly the inverted image of the daily course of photon irradiance, when plotted on a logarithmic scale. A similar light-induced fluorescence decrease was observed even at cryogenic temperatures. The decrease is stable at the temperature of liquid nitrogen but reversible above –90 °C (Kyle *et al.* 1983). The mechanism of this light-induced Chl fluorescence decrease at low temperatures is not yet completely clear. The Chl fluorescence quenching might result from the accumulation of Chl_Z (Schweitzer and Brudvig 1997, Stewart and Brudvig 1998) and/or from charge accumulation on a non-pigment molecule (Šiffel *et al.* 2000).

Effective PS2 yield Φ_2 measured on dark-adapted needles surprisingly increased with decreasing temperatures (Fig. 4). This "dark" PS2 yield is often used to reflect the potential (maximal) quantum yield of PS2 photochemistry, and is usually taken as a measure of the concentration of active PS2 centres. Obviously, such an interpretation is not applicable to the temperature dependence of the "dark" PS2 yield presented here: the temperature lowering can not increase the concentration of active PS2 centres. It is more likely that the increase in "dark" PS2 yield with lowering temperature reflects a decrease in the rate of non-photochemical processes competing with the photochemical reactions in PS2 centres. With temperatures falling to –15 °C, this non-photochemical dissipation of excitation energy can be limited and the PS2 yield may rise. With rising temperatures, in turn, the dissipation process could become more efficient and suppress the PS2 yield. The mechanism involved in this temperature dependent quenching of absorbed photon energy is not known. Because the maximal Chl fluorescence is quenched, the mechanism should compete for excitations with the process of the charge stabilisation on the primary quinone acceptor. Excitation energy can be dissipated directly in RCs, before being captured on Q_A, *via* cyclic electron transport around PS2 (Buser *et al.* 1992, Barber and de las Rivas 1993, Poulson *et al.* 1995, Havaux 1998, Ivanov *et al.* 2002) and/or on the oxidized primary donor, $P680^+$ (Krieger *et al.* 1992). Inactivation of oxygen evolving complex may also be one possibility (Küpper *et al.* 2004). A decrease in leaf temperature minimised excitation energy trapped by closed RCs by modulation of a non-photochemical dissipation factor (Kornyeyev *et al.* 2004).

The sustained winter quenching of the Chl fluorescence state as governed by the de-epoxidized state of the xanthophyll cycle carotenoids provides considerable protection of winter adapted conifers. The epoxidation state of xanthophylls also shows some correspondence with the F_V/F_M ratio (Adams *et al.* 1995, Ottander *et al.* 1995). However, the xanthophyll cycle operation can hardly account for the variation of effective PS2 yield, Φ_2, reported in this contribution for temperatures below –10 °C because conversion of violaxanthin to antheraxanthin is strongly suppressed by reduced fluidity of thylakoid membranes even at chilling temperatures (Latowski *et al.* 2002, Ji *et al.* 2003).

In this paper we showed that the light-induced depression of the effective quantum yield of PS2, Φ_2, occurring in needles of winter-adapted Scots pine during frosty days, was fully relaxed during the next frosty night. It shows that, even at full sunlight and temperatures close to –30 °C, when most of the electron transport events are inhibited, permanent damage to winter-adapted needles does not occur. This demonstrates a high efficiency of the dissipation of absorbed solar energy in winter-adapted conifers, allowing them to survive in areas with extremely low winter temperatures. The diurnal switching between the light-inhibited and photochemically competent states in fraction of PS2 RCs, continuous through the whole winter, might represent an adaptive advantage increasing the time-integrated PS2 yield and carbon gain in the early spring period. Surprisingly, the effective quantum yield of PS2 photochemistry measured in darkness increased with decreasing temperature. We explain this increase by the temperature dependence of the non-photochemical dissipation of excitation energy, which competes with photochemical reactions in PS2 RCs.

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