Recovery of photosynthesis in 1-year-old needles of unfertilized and fertilized Norway spruce (Picea abies (L.) Karst.) during spring

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Summary Photosynthetic O₂ evolution and chlorophyll a fluorescence were measured in 1-year-old needles of unfertilized and fertilized trees of Norway spruce (Picea abies (L.) Karst.) during recovery of photosynthesis from winter inhibition in northern Sweden. Measurements were made under laboratory conditions at 20 °C. In general, the CO₂-saturated rate of O₂ evolution was higher in needles of fertilized trees than in needles of unfertilized trees over a wide range of incident photon flux densities. Furthermore, the maximum photochemical efficiency of photosystem (PS) II, as indicated by the ratio of variable to maximum fluorescence (Fv/FM) was higher in needles of fertilized trees than in needles of unfertilized trees. The largest differences in Fv/FM between the two treatments occurred before the main recovery of photosynthesis from winter inhibition in late May. The rate of O₂ evolution was higher in needles of north-facing branches than in needles of south-facing branches in the middle of May.

Simultaneous measurements of O₂ exchange and chlorophyll fluorescence indicated that differences in the rate of O₂ evolution between the two treatments were paralleled by differences in the rate of PS II electron transport determined by chlorophyll fluorescence. We suggest that, during recovery of photosynthesis from winter inhibition, the balance between carbon assimilation and PS II electron transport was maintained largely by adjustments in the nonphotochemical dissipation of excitation energy within PS II.

Keywords: chlorophyll fluorescence, fertilization, fluorescence quenching, winter inhibition.

Introduction

The light-saturated rate of photosynthesis at both normal and high intercellular concentrations of CO₂ is often strongly related to leaf nitrogen content (Field and Mooney 1986, Seemann et al. 1987, Evans 1989). This relationship arises because the majority of leaf nitrogen is associated with proteins involved in photosynthesis (Evans 1989, Evans and Seemann 1989). Analyses of gas exchange have indicated that the balance between the capacities of Rubisco and electron transport is maintained in vivo in plants grown at different nitrogen concentrations (e.g., Makino et al. 1992). Furthermore, simultaneous measurements of CO₂ assimilation and chlorophyll a fluorescence in leaves of maize (Zea mays L.) with different nitrogen contents have shown that the lower rate of CO₂ assimilation in nitrogen-deficient leaves at high irradiances was accompanied by an increased nonphotochemical quenching (qN) of chlorophyll fluorescence (Khamis et al. 1990). At high irradiances, qN mainly reflects nonradiative dissipation of excitation energy in photosystem (PS) II (Krause and Weis 1991). Therefore, an increased thermal dissipation of excitation energy in nitrogen-deficient leaves under saturating light conditions provides a mechanism for adjusting the rate of PS II photochemistry to that of CO₂ assimilation (Weis and Berry 1987, Genty et al. 1989, Foyer et al. 1990). Photoinhibitory damage to PS II reaction centers can thereby be minimized (Krause 1988, Baker 1991, Demmig-Adams and Adams 1992). Nevertheless, nitrogen stress has been found to increase susceptibility to photoinhibition in shade-acclimated plants (Ferrar and Osmond 1986, Seemann et al. 1987). An increased sensitivity to excess light has been related to an increased proportion of closed PS II reaction centers, i.e., decreased photochemical quenching (qP) (see Krause and Weis 1991). Because qP (at high irradiances) in nitrogen-deficient leaves of maize was higher than in leaves well supplied with nitrogen, it was suggested that nitrogen stress did not increase susceptibility to photoinhibition in this species (Khamis et al. 1990).

Photoinhibition of PS II is also believed to occur in evergreen conifers during winter (Öquist et al. 1987). It has been suggested that the gradual inhibition of the potential for CO₂ assimilation by low and subfreezing temperatures during autumn and winter predisposes PS II to photoinhibition (Ottander and Öquist 1991). Recovery from winter inhibition of photosynthesis takes place during spring and early summer (Troeng and Linder 1982, Leverenz and Öquist 1987, Lundmark et al. 1988). In boreal forests, nitrogen is often regarded as the mineral nutrient most limiting for growth. Fertilization of conifers resulting in an increased foliar nitrogen content often stimulates photosynthetic capacity (see Linder and Rook 1984). However, the influence of mineral nutrient stress on the photosynthetic performance of conifers during winter and spring does not seem to have been investigated previously. In the present study, the photosynthetic properties of 1-year-old needles of unfertilized and fertilized trees of Norway spruce...
(Picea abies (L.) Karst.) were studied during recovery from winter inhibition. The relationship between PS II activity and carbon assimilation was examined under nonphotorespiratory conditions by simultaneously measuring chlorophyll a fluorescence and O2 exchange.

Materials and methods

Experimental site and plant material

This investigation took place at the Flakalidhen research area (N 64°07’, E 19°27’, altitude 310 m above sea level) between April and August 1992. The area, which is located about 50 km northwest of Umeå in northern Sweden, was planted with Norway spruce seedlings of local provenance in 1963 after clear-felling. The following treatments were applied to 50 m2 plots: control (C), irrigation (I), solid fertilization (F) and irrigation plus liquid fertilization (IL). In the IL treatment, a complete nutrient solution was injected into the irrigation water during the growing season (see Linder and Flower-Ellis 1992). The treatments commenced in 1987 when the mean height of the trees was 2.6 m. In the present study, only trees from the C and IL treatments were investigated. Air temperature in the stand was measured at 1.7 m above ground in the center of a 15-m diameter opening. The temperature probe was a thermistor with a continuously ventilated radiation shield. Global radiation above the canopy was measured with a solarimeter (CM-5, Kipp and Zonen, Delft, The Netherlands). Sensors were read each minute, and averages were recorded every 10 min by a datalogger (CR-10, Campbell Scientific Inc., Logan, UT, USA).

Second-order shoots were collected from south-facing branches of the seventh whorl down from the tops of five trees in one of the C and one of the IL plots from April 6 to August 11, 1992. In addition, shoots were collected from north-facing branches of the seventh whorl on May 11 and June 1. The same trees were sampled on all occasions. Samples were stored in darkness at 0°C until measurements were made. These were completed within 2 to 3 days. No consistent change in the measured parameters occurred during that time.

Measurements of oxygen exchange

Measurements of O2 exchange by needles at 20°C were made with a leaf-disc oxygen electrode (LD 2, Hansatech Ltd., King’s Lynn, U.K.) described by Delieu and Walker (1983). The cuvette was flushed with humidified 5% CO2 in air before each measurement and whenever the concentration of CO2 decreased to about 3%. Illumination was provided from an array of red light-emitting diodes (LH36U together with control box LS3, Hansatech Ltd., King’s Lynn, U.K.). Photon flux density (PFD) was lowered stepwise to darkness after a pretreatment at 130–160 μmol m-2 s-1 for about 20 min. Subsequently, PFD was raised to near light saturation (780–840 μmol m-2 s-1) for 15–20 min to obtain a steady-state rate of O2 evolution. Measurements of O2 exchange were also made simultaneously with chlorophyll fluorescence (see below) using an adapted top window for the fiber-optic cable of the fluorometer. In this case, white light was provided from a Schott fiber illuminator (FL 101, H. Walz, Effeltrich, Germany). Each sample with a projected leaf area of about 2.7 cm2 was subjected to a range of PFDs in an ascending order. A 15-min exposure was necessary to obtain steady-state rates of O2 evolution at the lowest PFD, whereas 10 min was sufficient at the higher PFDs. Rate of photosynthesis was expressed as gross rate of O2 evolution, i.e., the sum of O2 evolution in light and O2 uptake in darkness. Dark respiration in light was estimated after 5–6 min in darkness. The apparent quantum yield (ϕO2) during combined measurements of O2 exchange and chlorophyll fluorescence was obtained by dividing the gross rate of O2 evolution by the incident PFD. Maximum apparent quantum yield (ϕmax O2) in both red and white light was obtained from the initial slope of the relationship between gross photosynthesis and incident PFD by linear regression. Four to five PFD values below 130 μmol m-2 s-1 were used in red light, whereas three PFD values below 190 μmol m-2 s-1 were used in white light. Photon flux density over the range of 400 to 700 nm was measured with a quantum sensor (LI-190SB, Li-Cor Inc., Lincoln, NE, USA). The projected area of needles was determined with a leaf area meter (Delta-T Devices, Cambridge, U.K.), and needle dry weight was determined after drying for 24 h at 80°C.

Measurements of chlorophyll fluorescence

In vivo chlorophyll a fluorescence was measured simultaneously with O2 exchange at 20°C and 5% CO2 with a modulation fluorometer (PAM 101 Chlorophyll Fluorometer with accessory units PAM 102 and PAM 103, H. Walz, Effeltrich, Germany) equipped with a polyfurcated fiber-optic system (101 F, H. Walz, Effeltrich, Germany) as described by Schreiber et al. (1986). The nomenclature of van Kooten and Snel (1990) was adopted. Each sample consisted of needles from shoots stored in darkness at 0°C for at least 2 h. One or two samples from each tree were assessed. Minimal (dark) fluorescence yield (F0) was obtained on excitation with a weak measuring beam from a pulsed light-emitting diode. Maximal fluorescence yield (Fm') was determined after exposure to a 1-s saturating pulse of white light (about 8000 μmol m-2 s-1) from a modified Schott fiber illuminator KL 1500 (FL 103, H. Walz, Effeltrich, Germany) to close all reaction centers. Variable fluorescence (Fv) was calculated by subtracting F0 from Fm'. White actinic light (FL 101, H. Walz, Effeltrich, Germany) was then switched on, and 1-s near saturating pulses (about 8000 μmol m-2 s-1) were applied automatically at 100-s intervals for periodic determination of Fm' during induction. Values of Fm' did not significantly increase when the extrapolation method suggested by Markgraf and Berry (1990) was used. When steady-state conditions were reached, actinic light was switched off to enable determination of Fv. Fluorescence induction kinetics were recorded on a chart recorder (Seconic SS-250 F, Tokyo, Japan). Components of fluorescence quenching at steady state, photochemical quenching (qP) and nonphotochemical quenching (qN) were determined according to van Kooten and Snel (1990). Quenching of Fv (qN) was calculated as described by Bilger and Schreiber (1986). The quantum
yield of PS II electron transport ($\phi_e$) was determined according to Genty et al. (1989).

Statistical analysis

Data were analyzed by analysis of variance (ANOVA) with five trees from each treatment as replicates. Means from each treatment were compared using Fisher’s protected LSD test. Differences were considered significant at $P \leq 0.05$. Paired $t$-tests were used to test differences between north- and south-facing branches of the trees.

Results

The recovery of photosynthesis in 1-year-old needles of fertilized and unfertilized Norway spruce trees was followed from April to August 1992. The main recovery from winter inhibition occurred in late May between Days 132 and 146. This coincided with increasing daily maximum and minimum temperatures (Figure 1A). Values of $F_{V}/F_{M}$ were significantly higher in needles of fertilized (IL) trees than in needles of control (C) trees at all sampling dates (Figure 1B), with the largest differences between the two treatments occurring before the middle of May (Day 132). The highest $F_{V}/F_{M}$ values were reached in August. For samples collected on Days 220 and 224, $F_{V}/F_{M}$ in IL trees was 0.845 (±0.005). Differences in $F_{V}/F_{M}$ between IL trees and C trees were due to differences in $F_0$ (data not shown). Minimal fluorescence yield ($F_0$) was not significantly different between the two treatments on any sampling occasion. Maximum apparent quantum yield of $O_2$ evolution ($\phi_{max}O_2$) was generally higher in needles of IL trees than in needles of C trees (Figure 1C). As expected (see e.g., Evans 1987), values of $\phi_{max}O_2$ measured in white light were lower than those obtained in red light. Furthermore, differences in $\phi_{max}O_2$ between IL trees and C trees generally agreed less well with corresponding differences in $F_{V}/F_{M}$ when white light instead of red light was used. Data on $F_{V}/F_{M}$ and $\phi_{max}O_2$ normalized to maximal values of these parameters for IL trees obtained on Days 220 and 224 indicated that $\phi_{max}O_2$ was inhibited more than $F_{V}/F_{M}$ during spring and early summer (Figure 1D). This was especially evident for measurements in white light. On most occasions, the rate of $O_2$ evolution at near saturating irradiances was significantly higher in needles from IL trees than in needles of C trees, irrespective of whether red or white light was used (Figure 1E). From April to August, the mean difference in photosynthetic capacity between the two treatments was 3.3 (±0.4) µmol m$^{-2}$ s$^{-1}$ on a projected needle area basis and 9.3 (±0.8) nmol g$^{-1}$ s$^{-1}$ on a needle dry weight basis.

Simultaneous measurements of $O_2$ evolution and chlorophyll fluorescence revealed that an increased potential for

![Figure 1](image-url)
photosynthesis during recovery was accompanied by substantial changes in chlorophyll fluorescence parameters. Steady-state values of \( q_P \) were lower and steady-state values of \( q_N \) were higher on May 11 than on June 1 and August 11, below an incident PFD of approximately 500 µmol m\(^{-2}\) s\(^{-1}\) (Figures 2A and 2B). A relatively high \( q_N \) at low PFDs was also observed for samples collected on June 26 (Figure 2H). Steady-state values of \( q_0 \) decreased substantially from May 11 to June 1 and then remained relatively constant until August 11 (Figure 2C). Furthermore, steady-state values of \( F'_{V}/F'_{M} \) and \( \phi_e (= q_P \times \)
$F_v/F_M$ were much lower on May 11 than later during the summer (Figures 2D and 2E).

Values of $q_v$ and $q_N$ were very similar in IL trees and C trees over a wide range of PFDs (Figures 2A and 2B), except for samples collected on June 26 (Figures 2G and 2H). In contrast, $q_0$ generally appeared to be lower in IL trees than in C trees during recovery from winter inhibition (Figure 2C), whereas $F_v/F_M$ and $\phi_e$ appeared to be higher in IL trees than in C trees (Figures 2D and 2E). For samples collected on June 26, significant differences in rate of $O_2$ evolution between the two treatments over the range of PFDs tested (Figure 2F) were paralleled by significant differences in $q_0$, $F_v/F_M$ and $\phi_e$ (Figures 2I–K).

The light regime to which the needles were exposed during winter affected the rate of $O_2$ evolution as well as the photochemical efficiency of PS II, at least before the middle of May. For samples collected on May 11, needles from north-facing branches of both treatments had higher rates of $O_2$ evolution than needles from south-facing branches (Figure 3). However, significantly higher values of $\phi_{\text{max}}O_2$ were accompanied by significantly higher ratios of $F_v/F_M$ only in the north-facing branches of IL trees (Table 1). Furthermore, steady-state values of $F_v/F_M$' were higher in north-facing branches than in south-facing branches of IL trees (data not shown). For samples collected on June 1, the rate of $O_2$ evolution at high PFDs was higher in north-facing branches than in south-facing branches of C trees, but not IL trees (Figure 3). Neither $F_v/F_M$ nor $\phi_{\text{max}}O_2$ were significantly affected by branch orientation on June 1 (Table 1).

Mean values of $\phi_e$ had a significant linear correlation to corresponding mean values of $\phi_{\text{max}}$ when needles of C and IL trees collected between May and August were subjected to a wide range of incident PFDs (Figure 4). The relationship between $\phi_e$ and $\phi_{\text{max}}O_2$ was not affected by differences in the light regime to which the needles were exposed in the field. These results suggest that PS II activity was closely linked to the rate of $O_2$ evolution under nonphotorespiratory conditions. However, small deviations from the single curvilinear relationship between $\phi_e$ and $\phi_{\text{max}}O_2$ obtained by Seaton and Walker (1990) for leaves from several species were observed (Figure 4). These deviations were mainly caused by the tendency of the slope of the relationship to decrease from June to August, especially in needles of IL trees (data not shown).

Table 1. Maximum apparent quantum yield ($\phi_{\text{max}}O_2$) and the ratio of variable to maximum fluorescence ($F_v/F_M$) in 1-year-old needles of unfertilized (C) and fertilized (IL) Picea abies collected on May 11 and June 1. The SE is indicated for $n = 4$–5. Significant differences between needles of branches oriented toward south and north are indicated by different letters (paired t-test).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Treatment</th>
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| May 11    | $\phi_{\text{max}}O_2$ | $0.015 \pm 0.002 \pm 0.018 \pm 0.002 b$  
|           | $F_v/F_M$  | $0.022 \pm 0.002 \pm 0.029 \pm 0.001 b$  
|           | $\phi_{\text{max}}O_2$ | $0.046 \pm 0.002 \pm 0.048 \pm 0.002 a$  
| June 1    | $\phi_{\text{max}}O_2$ | $0.049 \pm 0.002 \pm 0.050 \pm 0.001 a$  

Figure 3. Gross rate of oxygen evolution in 1-year-old needles of unfertilized (open symbols) and fertilized (filled symbols) Picea abies as a function of incident photon flux density. Samples were collected on May 11 (circles) and June 1 (squares) from the south-facing (-----) and north-facing (------) sides of the trees. The SE is indicated for $n = 4$–5.

Figure 4. The relationship between the quantum yield of PS II electron transport ($\phi_e$) and the apparent quantum yield of $O_2$ evolution ($\phi_{\text{max}}O_2$) in 1-year-old needles of unfertilized (○) and fertilized (●) Picea abies. Measurements were made at incident photon flux densities ranging from 130 to 980 µmol m$^{-2}$ s$^{-1}$. Samples were collected on May 11, June 1, June 26 and August 11. Each point represents a mean steady-state value from 4–5 trees. The regression equation is $y = 11.2x + 0.019 (r^2 = 0.948, P = 0.0001)$. The broken line represents the relationship found in Figure 1B of Seaton and Walker (1990).
Discussion

Winter inhibition of photosynthesis is well known in conifers (for a review, see Öquist and Martin 1986). In addition to low and subfreezing temperatures causing depression of potential photosynthetic activity during winter, the importance of excess light in causing photoinhibition of photosynthesis has been emphasized (Öquist et al. 1987). We observed that winter inhibition was manifested as a depression of the maximal photochemical efficiency of PS II (Fv/FM) and φmaxO₂ (Figures 1B and 1C) as well as of the rate of O₂ evolution at high PFDs (Figure 1E). The main recovery from winter inhibition occurred in late May, although φmaxO₂ tended to increase throughout the study. Similarly, Kull and Koppel (1992) found that the apparent quantum yield of CO₂ uptake in Norway spruce increased steadily from spring to autumn. Recovery coincided with increasing maximum and minimum temperatures during spring (Figure 1A). A strong temperature dependence of recovery has been observed previously (Lundmark et al. 1988).

The increase in Fv/FM in needles from both C and IL trees during recovery was accompanied by an increase in φmaxO₂. Lundmark et al. (1988) found that the apparent quantum yield of CO₂ assimilation was linearly related to Fv/FM during recovery of lodgepole pine (Pinus contorta Doug.) and Scots pine (P. sylvestris L.) under laboratory conditions. Furthermore, seasonal changes in the quantum yield of CO₂ uptake and Fv/FM were linearly related in Scots pine (Leverenz and Öquist 1987). In contrast, Ottander and Öquist (1991) concluded that the recovery of Fv/FM in Scots pine under both field and laboratory conditions was much faster than that of φmaxO₂. When we normalized the Fv/FM and φmaxO₂ data to the maximal values of these parameters obtained in August, we found that inhibition of φmaxO₂, especially in white light, was more severe than that of Fv/FM during spring and early summer (Figure 1D). This may indicate that φmaxO₂ is influenced by factors other than the primary photochemical reactions of PS II (Adams et al. 1990).

Before the main recovery in late May, φmaxO₂ was higher in needles from north-facing branches of both C and IL trees than in needles from the more exposed south-facing branches (Table 1). In addition, the Fv/FM ratio was higher in needles from north-facing branches than in needles from south-facing branches of IL trees. These results are in general agreement with the hypothesis that excessive light constitutes an important stress factor during winter (Öquist et al. 1987). However, there was no difference in φmaxO₂ between exposed and shaded branches of Scots pine during recovery under field conditions (Ottander and Öquist 1991). This was attributed to subfreezing temperatures being the primary factor reducing φmaxO₂. It was previously found that freezing of frost-hardened Scots pine seedlings in darkness at temperatures above those causing permanent damage to the needles increased steady-state qN, whereas steady-state qϕ was only slightly depressed (Strand and Öquist 1988). We observed a similar response in Norway spruce on May 11. At PFDs below approximately 500 μmol m⁻² s⁻¹, the inhibition of O₂ evolution was accompanied by a decrease in qϕ and an increase in qN (Figures 2A and 2B).

In needle samples collected on June 26, qN was elevated at low PFDs (Figure 2H); furthermore, qϕ was suppressed in needles of C trees (Figure 2G), which could promote photoinhibition of PS II (cf. Foyer et al. 1990, Krause and Weis 1991, Ögren 1991). Three major components of qN have been identified in leaves and isolated protoplasts according to their relaxation kinetics on darkening (see Krause and Weis 1991). The fastest phase, referred to as energy-dependent quenching (qE), is assumed to reflect nonradiative dissipation processes within PS II (Krause et al. 1983). Increased qN quenching may serve to minimize an accumulation of reduced primary acceptors (Qₐ) in PS II (Weis and Berry 1987). The slowly relaxing components of qN are commonly attributed to an altered distribution of excitation energy between PS II and PS I (qI) and to photoinhibition (qI) (see Krause and Weis 1991). Both the fast and the slow components of qN can be associated with a quenching of F₀ (Demmig and Winter 1988). Elevated levels of qN on May 11 and June 26 were associated with an increased quenching coefficient for both a fast component (qE) and one (or several) slow component(s), which did not relax in darkness within 5 min (data not shown). It should be noted that the relaxation kinetics of these components were not resolved in detail.

The lower rate of photosynthesis in needles of C trees than in needles of IL trees at high PFDs (Figures 1E, 2F and 3) is consistent with results obtained in a similar experiment with Scots pine in central Sweden (Linder and Troeng 1980, Linder and Rook 1984). Invariably, a lower photosynthetic capacity in needles of C trees than in needles of IL trees was accompanied by a lower Fv/FM ratio, which seems to support the hypothesis that nitrogen deficiency increases susceptibility to photoinhibition (Ferrar and Osmond 1986, Seemann et al. 1987). However, a depression of Fv/FM may also be viewed as a protective mechanism of thermal energy dissipation (Demmig and Björkman 1987, Krause 1988). The largest differences in Fv/FM between the two treatments were observed before the middle of May (Figure 1B). Differences in φmaxO₂ obtained in red light were also most pronounced during that period (Figure 1C). The utilization of excitation energy in carbon metabolism was obviously much lower during winter and spring than during summer, inter alia, as a result of low temperatures (Figure 1A; cf. Troeng and Linder 1982). Thus, a protective adjustment or down-regulation of PS II photochemistry may be essential to reduce photoinhibitory damage to PS II (cf. Ottander and Öquist 1991). The less pronounced increase in thermal energy dissipation for IL trees indicates that other mechanisms for photoprotection (see Demmig-Adams and Adams 1992) may be involved during winter.

The marked increase in Fv/FM during recovery was associated with large increases in Fv/FM and φN (Figures 2D and 2E), and a substantial decrease in qN occurred concomitantly (Figure 2C). In the model of Genty et al. (1989), Fv/FM represents the efficiency of excitation capture by open PS II reaction centers, which is assumed to depend on nonradiative processes in the antennae. In the present study, the increase in Fv/FM and the decrease in qN during recovery was related to an increase in Fv/FM rather than to a decrease in qN. However,
the decreased nonphotochemical quenching associated with an increase in \( F_{V}/F_{M} \) can be very similar to a decrease in \( q_{E} \) (often the major component of \( q_{E} \)) in terms of energy dissipation (Krause 1988, Krause and Weis 1991). Differences in thermal energy dissipation associated with \( F_{V}/F_{M} \) may also largely explain the differences in \( F_{V}/F_{M}' \) and \( q_{0} \) between the two treatments (Figures 2C–D and 21–J). These were most obvious for samples collected on June 26. Despite the increased proportion of closed reaction centers observed at low to moderate PFDs on May 11 (Figure 2A), the increase in \( q_{E} \) during recovery (Figure 2E) was predominantly determined by an increase in \( F_{V}/F_{M}' \). Differences in \( q_{E} \) between the two treatments (Figures 2E and 2K) could also be largely attributed to differences in \( F_{V}/F_{M}' \).

In Norway spruce needles collected between May and August, \( q_{E} \) was linearly related to \( \phi_{O_{2}} \) (Figure 4). The relationship between \( \phi_{E} \) and \( \phi_{O_{2}} \) over a range in incident PFD is nearly identical for a wide variety of species grown under favorable conditions (Seaton and Walker 1990). However, the slope of the relationship between \( q_{E} \) and \( \phi_{O_{2}} \) especially in IL trees, tended to decrease from June to August (data not shown). This may be explained by a decrease in whole-plant electron flow to \( O_{2} \). In addition, several factors can modify the relationship between \( \phi_{E} \) and \( \phi_{O_{2}} \) (see Genty et al. 1989; Harbinson et al. 1990, Öquist and Chow 1992). Nevertheless, it is suggested that a proportionality between \( \phi_{E} \) and \( \phi_{O_{2}} \) during recovery was largely achieved by adjustments in thermal energy dissipation, as indicated by changes in \( F_{V}/F_{M}' \).

We conclude that the balance between \( CO_{2} \) assimilation and PS II electron transport in unfertilized and fertilized trees of Norway spruce was maintained during recovery from winter inhibition largely by adjustments in the nonphotochemical dissipation of excitation energy in PS II. However, measurements were made under nonphotosynthetic or otherwise favorable conditions in the laboratory. Therefore, further studies on the relationship between \( CO_{2} \) assimilation and PS II activity should be performed under conditions more similar to those prevailing in the field.

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References


