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Acclimation of photosystem 2 function of Norway spruce induced during first season under elevated CO_2 in lamellar domes

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Abstract

Since July 28th, 1997 the two experimental mini-stands of young Norway spruce [*Picea abies* (L.) Karst.] have been grown in lamellar domes at ambient (AC) and elevated concentrations of CO_2 [EC, *i.e.*, ambient + 350 μmol(CO_2) mol^{-1}]. Before the start of exposure to EC (June 1997) the dependencies of photosystem 2 (PS2) quantum yield (Y) on irradiance, estimating the efficiency of PPFD utilisation in PS2 photochemistry, were the same for AC and EC shoots. After one month of EC simulation (August 1997), Y values were higher for EC needles as compared with the AC ones (by 1-42 %), whereas two months later (October 1997) an opposite effect was observed (decrease of Y by from 1 to 33 %). By chlorophyll *a* (Chl *a*) fluorescence induction the effects of EC on PS2 function were further characterised. During the first month a moderate improvement of PS2 function was estimated for EC needles from slightly higher potential yield of PS2 photochemistry (F_V/F_M, by 1 %) and reduced amount of inactive PS2 reaction centres (relative F_{pl} level, by 15 %). However, the prolonged exposure to EC led firstly to a slight but significant decrease of F_V/F_M (by 3 %), secondly to a reduction of half time of fluorescence rise ($t_{1/2}$, by 14 %), and finally to pronounced accumulation of inactive PS2 reaction centres (by 41 %). From the gradual response of individual Chl *a* fluorescence parameters we suggest a probable sequence of events determining the stimulation and subsequent depression of PS2 function for Norway spruce during the first season under EC.

Additional key words: chlorophyll fluorescence induction; dry and fresh matter; *Picea abies*.

Introduction

Higher concentration of atmospheric CO_2 directly influences photosynthesis in higher plants. The stimulation of photosynthetic activities during short-term exposure to EC is a general response of all plant species that have been examined up till now (Eamus and Jarvis 1989, Ceulemans and Mousseau 1994, Saxe *et al.* 1998). However, the long-term effects of EC on photosynthesis vary considerably among plant species. Some species reveal sustainable stimulation of photosynthetic activity, whereas the others, particularly tree species, may exhibit down-regulation of photosynthesis (Marek *et al.* 1995, 1997, Kalina and Ceulemans 1997, Thurnbull *et al.* 1998, Saxe *et al.* 1998). Because trees account for about 70 % of terrestrial atmospheric CO_2 fixation, they may

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Abbreviations: AC and EC = ambient and elevated CO_2 concentration; Chl = chlorophyll; DM/FM = dry mass/fresh mass ratio; F_0, F_M = initial and maximal yield of room temperature Chl *a* fluorescence in dark adapted system; F_P, F_{pl} = other important points determined from the kinetics of Chl *a* fluorescence induction; $(F_P - F_0)/F_V$ = maximum proportion of reduced PQ pool; $(F_{pl} - F_0)/F_V$ = relative proportion of inactive (Q_B nonreducing centres) PS2 reaction centres; $F_V = (F_M - F_0)$ = variable Chl *a* fluorescence; F_V/F_M = potential quantum yield of PS2 photochemistry in the dark-adapted state; LD = lamellar domes; LHC = light-harvesting Chl-protein complex; P_N = net photosynthetic rate; PPFD = photosynthetic photon flux density; PQ = plastoquinone; PS2 = photosystem 2; RC = reaction centre; $t_{1/2}$ = half time of $F_0 - F_P$ fluorescence increase; RuBPC = ribulose-1,5-bisphosphate carboxylase/oxygenase; Y = $(F_M' - F_S)/F_M'$ = quantum yield of PS2 photochemistry in the light-adapted state.

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significantly affect the global carbon budget and mitigate the increase of atmospheric CO_2 (Harmon *et al.* 1990, Vitousek 1991). Therefore, better understanding and description of the opposite response of some abundant tree species such as Norway spruce is important for prediction of the global climate changes scenario.

Short-term exposure of trees to EC increases rates of net CO_2 fixation (P_N), particularly when other resources are not limiting (Eamus and Jarvis 1989). The enhanced photosynthetic capacity is connected with limited photorespiration and increased activity of ribulose-1,5-bisphosphate carboxylase/oxygenase, RuBPCO (Stitt 1991, Long and Drake 1992). The response of the light reactions of photosynthesis to EC may be easily and rapidly estimated using various parameters of Chl *a* fluorescence which reflect the function of photosystem 2, PS2 (Peterson 1991, Epron *et al.* 1994, Kalina *et al.* 1997, Špunda *et al.* 1998). In *Eucalyptus*, poplar clone Beauprè, and oak the stimulation of photosynthetic CO_2 assimilation is accompanied with increased efficiency of PPFD utilisation in PS2 photochemical reactions (Eamus *et al.* 1995, Scarascia-Mugnozza *et al.* 1996, Kalina and Ceulemans 1997).

However, as mentioned above, the initial stimulation of P_N at EC often declines during longer-term exposure, even under optimal growth conditions (Gunderson and Wullschleger 1994, Vivin *et al.* 1995). The phenomenon of EC-induced photosynthesis depression has been well documented at the level of photosynthetic CO_2 assimilation (Eamus and Jarvis 1989, Ceulemans and Mousseau 1994, Saxe *et al.* 1998, Urban and Marek 1999) and/or activity of RuBPCO (Besford 1990, Stitt 1991, Wilkins *et al.* 1994). On the contrary, the manifestation of the down regulation of photosynthesis under long-term high CO_2 on PS2 functions is poorly characterised (Kalina and Ceulemans 1997, Saxe *et al.* 1998). However, at least a decrease of quantum yield of PS2 was reported for several tree species such as Norway spruce (Marek and Kalina 1996, Marek *et al.* 1997) and poplar clone Robusta (Kalina and Ceulemans 1997). Recently, we have shown that depression of photosynthesis in Norway spruce after four vegetation periods under EC induced the changes in pigment composition and PS2 function similar to the manifestation of high irradiance stress (Špunda *et al.* 1998). It was suggested that decreased capacity of photochemical de-excitation of Chl molecules in spruce needles grown under EC results in enhanced susceptibility of PS2 to the photoinhibition as compared with the needles exposed to the same irradiances under AC. Therefore, the comparison of various parameters of the Kautsky phenomenon represents a rapid tool for monitoring the effects of EC on the photosynthetic apparatus.

The influence of EC on leaf photosynthetic capacity varies during the vegetation period (Epron *et al.* 1996). Therefore, in the present paper we focus on the development of acclimation response of young Norway spruces during the first season under EC in lamellar domes. On the basis of Chl *a* fluorescence parameters we describe the relative changes of PS2 function of needles from the trees exposed to doubled CO_2. We attempt to explain the development of functional changes associated with primary stimulation and later depression of photosynthetic activities.

Materials and methods

Plants: The experiment was conducted on the Experimental Research site Bílý Kříž in the Moravian-Silesian Beskydy mountains (NE Moravia, Czech Republic, 49°30'N, 18°32'E, 943 m a.s.l.). Young Norway spruces [*Picea abies* (L.) Karst., age 10 years, average height 1.5 m] were used. Two lamellar domes (LD, 10×10 m in length, 7 m high) were built around trees *in situ*. In one of them the trees were grown in ambient air (AC, 56 trees, half of them with a high density = 2 trees per m^2, HD; half of them with a low density of 1 tree per m^2, LD). In the LD variant similar mini-stands of Norway spruce were exposed to EC [ambient CO_2 concentration plus 350 $\mu mol(CO_2)\ mol^{-1}$] for one season. The exposure to EC started on 28 July, 1997 and lasted till the middle of November 1997.

The measurements of fluorescence parameters were performed on one-year-old shoots from the S-SW-exposed middle crown parts of individual trees (HD stand) to assure a similar irradiance. The needles for the measurements of room temperature fluorescence induction were taken from similar parts of these trees. All measurements were carried out during the 1997 vegetation period.

Modulated room temperature Chl *a* fluorescence was measured on attached shoots using a fluorometer *PAM 2000* (*H. Walz*, Effeltrich, Germany). The shoots were darkened for 30 min. Afterwards F_0 and F_M were measured at sufficiently weak measuring irradiance and saturating pulse (1 s duration and PPFD of 4000 $\mu mol\ m^{-2}\ s^{-1}$), respectively. The potential quantum yield of PS2 photochemistry was determined as $F_V/F_M = (F_M - F_0)/F_M$. The effective quantum yield of PS2 photochemistry [$Y = (F_M' - F_S)/F_M'$, Genty *et al.* 1989] was monitored in the steady state after 10 min exposure of the shoots to individual incident PPFDs (50, 125, 250, 500, 750, 1 000, and 1 300 $\mu mol\ m^{-2}\ s^{-1}$). Both on AC and EC trees twelve shoots (4 shoots per tree) were measured on 17 June, 6 August, and 9 October 1997.

Kinetics of Chl *a* fluorescence induction at room temperature: Samples containing five one-year-old needles were collected in the morning and were pre-darkened for 60 min. The needles were oriented on the sample holder so that the fluorescence was excited from the upper side of needles. During a 2-s red actinic irradiation (incident PPFD was 130 µmol m^{-2} s^{-1}) the rapid Chl *a* fluorescence induction curve was recorded at 20 °C. Afterwards the samples were darkened for another 60 min and F_0 and F_M were measured with *PAM-2000*. The following parameters were determined from the measured curves: F_0, F_{pl}, F_P, and $t_{1/2}$ (Špunda *et al.* 1998). The ratios F_V/F_M, $(F_{pl} - F_0)/F_V$, and $(F_P - F_0)/F_V$ were calculated. Twelve samples of each variant (4 samples per tree) were measured in July, August, September, and October 1997.

Determination of DM/FM ratio: The sample containing approximately 100 mg fresh mass (FM) of one-year needles was dried for 60 min at 105 °C and afterwards dry mass (DW) was determined. Twelve samples of each variant (4 samples per tree) were measured in June, August, and October 1997.

Statistical analysis: All experimental values were tested for significance by a F-test (a two-sample test for variance), followed by a *t*-test. The result of F-test determined which *t*-test should be used: a two-sample assuming equal variances or a two-sample assuming unequal variances, respectively. The levels of significance $p = 0.05$, $p = 0.01$, and $p = 0.001$ were indicated as *, **, and ***. All calculations and statistical tests were performed using analysis tools from *Microsoft Excel* (version *7.0*).

Results

Photochemical efficiency of PS2 under exposure to EC: The efficiency of photon utilisation in PS2 photochemical reactions was determined from the measured dependencies of steady state quantum yield of PS2 photochemistry (Y) on PPFD for the selected episodes of the vegetation period.

Before the start of EC exposure, the Y did not differ for the shoots of the selected trees in both LD for the entire range of applied irradiances (Fig. 1*A*). After the first month of exposure to EC, the Y of EC shoots compared to AC shoots was slightly higher (by 1 to 5 %) for the lower irradiances (up to 250 µmol m^{-2} s^{-1}) and significantly higher (by 12 to 42 %) for the irradiances of 500 µmol m^{-2} s^{-1} and higher (Fig. 1*B*). However, already after three months under EC a decrease of Y was observed (Fig. 1*C*). This depression was only slight (by 1 to 4 %) at low irradiances (up to 125 µmol m^{-2} s^{-1}) and became significantly pronounced (by 7 to 33 %) at irradiances of 250 µmol m^{-2} s^{-1} and more.

Chl *a* fluorescence induction: The changes of potential quantum yield of PS2 photochemistry in the dark-adapted state (F_V/F_M, Fig. 2*A*) were monitored during the whole 1997 season. During the first month of simulation of EC we found a slight increase of F_V/F_M (by 1 %) and afterwards the EC needles showed a significant decrease of this parameter (up to 3 %) as compared with AC needles. This parameter reacts very promptly to the effects of EC on the PS2 function. The F_V/F_M differences of the above mentioned magnitude may indicate slight but significant changes in PS2 function. For instance, plants exposed to a moderate high irradiance stress reveal F_V/F_M typically about 3 % lower than in the plants grown under optimal conditions (Bolhàr-Nordenkampf *et al.* 1991, Kurasová *et al.* 2000).

The kinetics of fluorescence induction during several seconds of actinic irradiation (Kautsky phenomenon) is a source of valuable information on the functional state of PS2 (Lichtenthaler and Rinderle 1988, Špunda *et al.* 1998). The half time of fluorescence rise from F_0 to F_P ($t_{1/2}$) is indirectly proportional to the size of LHC2 (Öquist and Wass 1988) and directly proportional to the size and the activity of plastoquinone pool (Bolhàr-Nordenkampf and Öquist 1993). In our case $t_{1/2}$ was nearly the same for EC and AC needles up to August 1997 (Fig. 2*B*). In September and October we estimated a significant decrease of this parameter for EC needles compared to the AC ones (by 9.3 and 14.5 %, respectively).

The first phase of rapid fluorescence increase to the F_{pl} of Kautsky phenomenon corresponds to the closure of inactive (Q_B nonreducing) PS2 reaction centres, RCs (Guenther and Melis 1990, Melis 1991). The proportion of inactive PS2 RC's may be qualitatively assessed as the ratio $(F_{pl} - F_0)/F_V$ (Klinkovský and Nauš 1994). This ratio was lower for EC than AC needles during the whole season (up to 15 %) except the June and October measurements. In October 1997 this ratio was significantly by 41.1 % higher for EC than AC needles (Fig. 2*C*). The large pool of inactive PS2 RC's is a typical feature of plants stressed by high irradiances (Guenther and Melis 1990, Melis 1991).

Discussion

Stimulation of PS2 activity—first phase of response to EC: The responses of PS2 functional activities were studied during the first year of exposure to EC. After two weeks of EC influence we found several changes in PS2 activities which documented a stimulation of PS2 photochemical reactions. The positive effects of EC on P_N are well documented for many plant species (Eamus and Jarvis 1989, Ceulemans and Mousseau 1994, Saxe *et al.* 1998). The energy supply and reducing power (ATP and NADPH) for these processes are formed in light reactions of photosynthesis, which consist of several subsequent steps starting by conversion of absorbed radiant energy in photochemical reactions of both photosystems. Thus, stimulation of NADPH and ATP consumption by the carbon fixation cycle increases the effective quantum yield of PS2 photochemistry together with higher capacity of linear electron transport. The actual photochemical efficiency of PS2 in light-adapted leaves was higher for some species grown in EC (Besford *et al.* 1996, Scarascia-Mugnozza *et al.* 1996, Kalina and Ceulemans 1997). In our experiment, the Y-PPFD responses for EC and AC shoots (Fig. 1*B*) revealed that the EC shoots were in the stage of the primary stimulation of photosynthesis after two weeks under EC. Significantly higher values of Y for irradiances above 500 µmol m^{-2} s^{-1} reflected higher capacities of both PS2 photochemical reactions and linear electron transport.

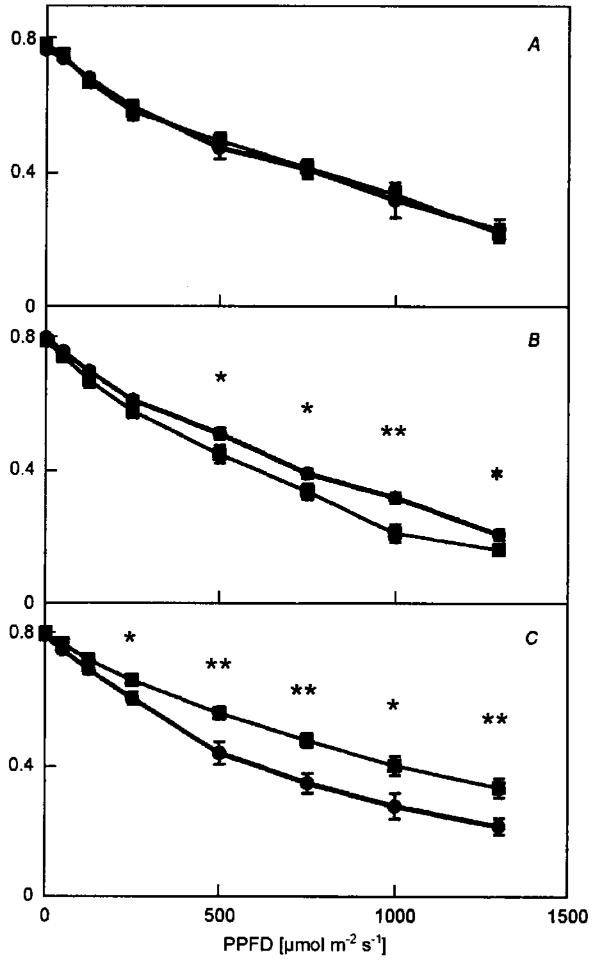

Fig. 1. Photosynthetic photon flux density (PPFD) responses of steady state quantum yield of PS2 photochemistry (Y) in shoots grown in ambient (■) or elevated (●) CO_2. Measurements before (*A* - 17 June), 10 d after (*B* – 6 August), and two and half months after (*C* – 9 October) exposure of trees to elevated CO_2. Means ± SE ($n = 12$). $^*p = 0.05$, $^{**}p = 0.01$.

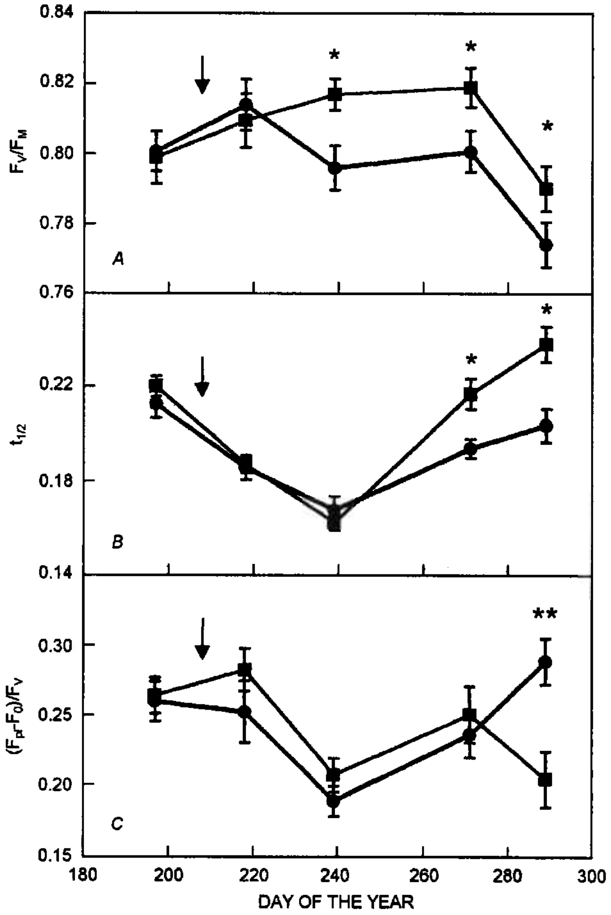

Fig. 2. Potential quantum yield of PS2 photochemistry (F_V/F_M) (*A*), half time Chl *a* fluorescence increase from F_0 to F_P ($t_{1/2}$) (*B*), and relative proportion of inactive (Q_B = non-reducing centres) photosystem 2 reaction centres, (F_{pi} – F_0)/F_V (*C*) for Norway spruces grown in ambient (■) or elevated (●) CO_2 concentration during growing season. The *arrow* denotes the start of elevated CO_2 exposure. Error bars are ± SE ($n = 12$). $^*p = 0.05$, $^{**}p = 0.01$.

The potential quantum yield of PS2 photochemistry in the dark-adapted state (F_V/F_M) for plants under optimal conditions is always higher as compared to the stressed ones. During summer the high irradiance stress together with drought may result in long-term decrease of F_V/F_M below the optimum value (*i.e.*, 0.832; Björkman and Demmig 1987). We found slightly higher F_V/F_M for EC needles as compared to AC ones during the first month of exposure to EC (Fig. 2*A*). However, this increase was not stable, but with prolonged exposure to EC a decrease of F_V/F_M was found (*vide infra*).

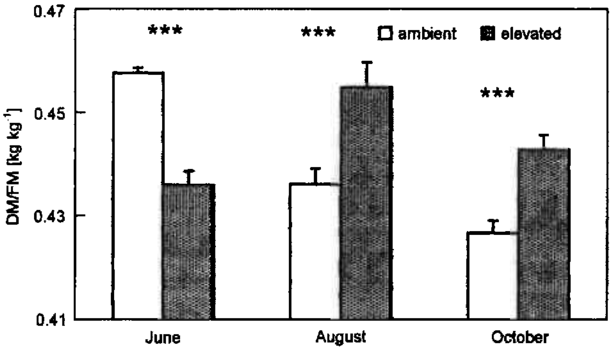

Fig. 3. The dry mass/fresh mass ratio (DM/FM) for needles of Norway spruces grown in ambient or elevated CO_2 during growing season. Means ± SE ($n = 12$). $^{***}p = 0.001$.

Inactive PS2 RC's serve as a reserve pool for the photodamaged ones during high irradiance stress (Guenther and Melis 1990, Melis 1991). Hence, the $(F_{pl} - F_0)/F_V$ ratio can be a useful additional parameter characterising the activity of PS2 RC's (Klinkovský and Nauš 1994, Špunda *et al.* 1998). On the contrary to the situation before EC exposure, after two weeks the proportion of inactive PS2 RC's was by 20.7 % lower for EC needles. Hence, the stimulation of radiant energy utilisation in PS2 photochemistry as mentioned above probably reduced the over-excitation of PS2 for EC needles resulting in consequent reduction of inactive PS2 RC's proportion. This represents a further feature of stimulation of PS2 photochemical activities reflecting a first phase of acclimation of the photosynthetic apparatus to EC.

A gradual depression of PS2 activity—prolonged exposure to EC: We have already proved that prolonged exposure to EC induced a depression of photosynthetic activity in Norway spruce needles (Marek *et al.* 1995, 1997, Špunda *et al.* 1998). Similar results were found for the poplar clone Robusta (Kalina and Ceulemans 1997). However, in our previous experiments the depression of PS2 photochemical efficiency was demonstrated after two or more seasons under EC exposure. In this paper we deal with the possible development of the acclimation depression of photosynthetic reactions during the first year of exposure.

At the end of the season, a pronounced depression of Y at higher irradiances ranging from 22 to 33 % was observed for EC shoots as compared to the AC ones (Fig. 1*C*). This degree of the Y depression after three months under EC in LD was less pronounced than on single Norway spruce tree after two and/or three year exposure to doubled CO_2 (Marek and Kalina 1996, Špunda *et al.* 1998).

In order to obtain more detailed information about manifestation of depression of PS2 function under prolonged exposure to EC, Chl *a* fluorescence induction was tested during the whole season. The potential quantum yield of PS2 photochemistry in the dark-adapted state (F_V/F_M, Fig. 2*A*) was a sensitive parameter for seasonal characterisation of acclimation of the assimilatory apparatus to EC. Already after one month of EC exposure, we observed a slight, but significant decrease of F_V/F_M for EC needles. The lower values of this parameter for EC needles remained till the end of the season. However, the differences of F_V/F_M between EC and AC needles were only up to 3 % (Fig. 2*A*). Hence the second phase of acclimation to EC results in a slight impairment of PS2 photochemistry. However, on the basis of this parameter we cannot explain individual steps of acclimation related to down-regulation of photosynthesis under EC.

Additional information was obtained from parameters of Chl *a* fluorescence induction. The half time of the fluorescence increase from F_0 to F_P ($t_{1/2}$, Fig. 2*B*) is the second parameter, which documented a progressive depression of PS2 function during prolonged exposure to EC. There were no differences in $t_{1/2}$ values between EC and AC needles after one month under EC (Fig. 2*B*). Decrease of $t_{1/2}$ after two and three months of exposure to EC (by 9.3 and 14.5 %) indicates either the increased size of LHC2 or diminished size of PQ pool in needles exposed to long-term EC. However, the pigment content and composition did not reveal a trend of changes suggesting an increase amount of LHC (values not shown). Hence, in agreement with the above mentioned depression of Y (Fig. 1) we suggest that the decrease of $t_{1/2}$ is related mainly to the reduced electron transport rate through PQ pool. The gradual character of changes in PS2 function is documented at the end of vegetation season by the increase of the $(F_{pl} - F_0)/F_V$ ratio in EC needles by 41.1 % (Fig. 2*C*). The accumulation of inactive PS2 RC's represents a last but most pronounced sign of depression of PS2 photochemical activities under prolonged exposure to EC. At the end of the first season under EC all the above mentioned Chl *a* fluorescence parameters revealed qualitatively similar differences between EC and AC needles as observed previously for Norway spruce grown in open-top chambers (Špunda *et al.* 1998). This supports the relation of the depression of PS2 photochemical activities to the general depression of photosynthesis under prolonged EC exposure. In previous work we have shown that for Norway spruce the capacity to utilise absorbed photons within PS2 (based on irradiance responses of Y, Fig. 1) is related directly to the irradiance saturated P_N (Špunda *et al.* 1998).

The results supporting the feed-back down-regulation of photosynthetic activities were obtained from the DM/FM ratio (Fig. 3). Exposure to EC induced an increase of biomass accumulation expressed as DM/FM, which was approximately by 4 % higher for EC needles compared to AC ones already after two weeks under EC. Because we found the same difference of DM/FM between EC and AC needles also at the end of the season, we suppose that sink limitation in EC needles may gradually induce down regulation of photosynthesis (Stitt 1991).

We conclude that during the first two weeks the improved utilisation of PPFD within PS2 photochemical reactions reflects stimulation of the photosynthetic reactions under EC. However, already during the first season of EC treatment gradually increasing signs of feedback limitation of PS2 activities developed. From the trends of changes of individual Chl *a* fluorescence the following scenario of the events related to the EC induced depression of photosynthetic reactions can be summarised:

After one month of EC treatment a slightly reduced capacity of utilisation of PPFD induced a moderate decrease of F_V/F_M. The following step after two months under EC led to the gradual limitation of the electron transport through PQ pool. Finally, the consequent PS2 over-excitation was related to the pronounced accumulation of inactive PS2 RC's observed after three months. We are aware that the observed changes in PS2 photochemical activities under prolonged exposure to EC were influenced also by other climatic parameters (such as temperature and irradiance). Particularly, the synergetic effect of excess irradiances and EC could contribute to the above mentioned accumulation of inactive PS2 RC's. This is in agreement with our previous results showing that prolonged exposure of Norway spruce to EC increases the sensitivity of PS2 to high irradiances (Špunda *et al.* 1998). This is to our best knowledge the first report describing the rapid induction of depression of photosynthetic activities for Norway spruce under EC. The physiological relevance of this finding is supported by the fact that these results were obtained for the Norway spruces in the LD, where other climatic factors (*i.e.*, temperature, PPFD, humidity) were only slightly affected.

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