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Chloroplastic carbon dioxide concentration in Norway spruce (*Picea abies* [L.] Karst.) needles relates to the position within the crown

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Abstract

Differences between sun (E) and shaded (S) foliage were studied in a Norway spruce (*Picea abies* [L.] Karst.) stand. Response curves describing the dependence of the CO_2 assimilation rate (P_N) on the CO_2 concentration at the catalytic site of ribulose-1,5-bisphosphate carboxylase/oxygenase, RuBPCO (P_N-C_c) were estimated using the simultaneous measurements of chlorophyll fluorescence and leaf gas exchange. Higher P_N, higher electron transport (J_a), higher carboxylation capacity (V_c), and higher RuBPCO activity (τ) for sun acclimated needles was found. The S-needles had higher portion of internal limitation and higher CO_2 compensation concentration (Γ) than the E-needles. Because higher degree of limitation of photosynthesis by carboxylation was ascertained, it can be assumed that photosynthesis in shade foliage

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Abbreviations: Chl - chlorophyll; E - sun acclimated needles variant; J_a, J_{aC} - rates of actual electron transport rate and of electron transport rate of carboxylation [μmol m^{-2} s^{-1}]; Jt - electron transport rate from fluorescence measurements [μmol m^{-2} s^{-1}]; LAI - leaf area index; P_{Nsat} - saturated rate of CO_2 assimilation [μmol(CO_2) m^{-2} s^{-1}]; P_0 - potential assimilation rate assuming no stomatal resistance to CO_2 [μmol(CO_2) m^{-2} s^{-1}]; P_p - potential assimilation rate assuming no internal resistance to CO_2 [μmol(CO_2) m^{-2} s^{-1}]; C_a (C_i, C_c) - ambient (internal, chloroplastic) CO_2 concentration [μmol(CO_2) mol^{-1}]; PAR - photosynthetically active radiation [μmol m^{-2} s^{-1}]; PS - photosystem; R_D* - rate of non-photorespiratory CO_2 efflux in the light [μmol(CO_2) m^{-2} s^{-1}]; R_S - rate of CO_2 evolution in the light at zero C_i [μmol(CO_2) m^{-2} s^{-1}]; S - shade acclimated needles variant; RuBPCO - ribulose-1,5-bisphosphate carboxylase/oxygenase; S^* - the apparent specificity factor of RuBPCO *in vivo*; V_c (V_o) - rate of RuBPCO carboxylation (oxygenation) [μmol(CO_2) m^{-2} s^{-1}]; V_{RuBP} - rate of RuBP consumption and formation [μmol(CO_2) m^{-2} s^{-1}]; Γ - compensation CO_2 concentration [μmol(CO_2) mol^{-1}]; Γ^* - compensation CO_2 concentration in absence of photorespiration [μmol(CO_2) mol^{-1}]; Θ - saturation rate [dimensionless]; τ - carboxylation efficiency [mol m^{-2} s^{-1}].
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is limited mainly by lower carboxylation capacity and by low chloroplastic CO_2 concentration.

Additional key words: carboxylation capacity; electron transport rate; net photosynthetic rate; Norway spruce; ribulose-1,5-bisphosphate carboxylase/oxygenase; sun/shade foliage.

Introduction

Radiation supplies energy to plants and controls the distribution of heat, water, and organic compounds in them. There are large vertical differences in distribution of photosynthetically active radiation (PAR) within forest stands (Norman and Jarvis 1975, Eliáš *et al.* 1989, Marek *et al.* 1992). Both the structure and function of the assimilatory apparatus of tree are not fixed during its ontogeny but significantly respond to changing irradiance and its quality. Leaves of upper parts of trees are acclimated to high irradiance (sun leaves) while those of lower parts are acclimated to low PAR (shaded leaves). Impacts of changing radiation conditions and differences in structural organisation of exposed and shaded leaves, chemical composition, and functional characteristics of assimilatory apparatus were documented (Boardman 1977, Anderson *et al.* 1988, Špunda *et al.* 1993, 1997, Pearcy and Sims 1994, Zhang *et al.* 1995).

Because PAR is the limiting factor for shade acclimated leaves, a substantial amount of photosynthetic resources must be invested in the synthesis and maintenance of light-harvesting complexes (LHC) of both photosystems (PS1, PS2) while large amounts of electron transport components, ATP synthase, or the stromal CO_2 fixation enzymes are not so required (Evans 1987, Anderson *et al.* 1988). On the other hand, for sun plants the electron transport steps are limiting factors (Evans 1987, Zhang *et al.* 1995). So high irradiance leads to a higher content of the cytochrome *b/f* complex, plastoquinone, plastocyanin, ferredoxin, and ATP synthase which support faster rates of electron transport and photophosphorylation (Melis 1991, Špunda *et al.* 1993). On the level of thylakoid membrane organisation we can find large shade leaf chloroplasts with a greater area of thylakoid membranes (Melis 1991, Pearcy and Sims 1994). Irregularly orientated grana also have much more thylakoids relative to sun leaf chloroplasts (Chow *et al.* 1988). Shade needle thylakoids have lower Chl *a/b* (Špunda *et al.* 1993, Ilík *et al.* 1997) and xanthophyll/β -carotene ratios (Aro *et al.* 1986). These variations in pigment contents reflect differences in the complement of specific Chl-proteins of PS1 and PS2. Increase in the amount of total Chl associated with LHC2 and decrease in the PS1-LHC1 and PS2 core complexes in low irradiance-adapted plants were found by Leong and Anderson (1984). The adaptation of photosynthetic apparatus of conifers to increased irradiance results in increased capacity of nonradiative dissipation localized within LHC (Špunda *et al.* 1998). The increase of LHC2/PS2 core ratio is typical for shade plants and indicates larger PS2 photosynthetic units (Anderson 1986).

The above mentioned signs of sun foliage are responsible for high values of photosynthetic capacity, respiration rate, stomatal conductance, and transpiration

(Boardman 1977, Zhang *et al.* 1995). Besides the functional differences, there are some structural features such as a larger stomatal density, a thicker layer of cuticle, and an enhanced amount of mesophyll cells in sun leaves compared with the shade ones (Pearcy and Sims 1994).

On the basis of mentioned features of sun/shade acclimated foliage it is possible to expect other differences between them related to P_N at the chloroplast level. The aim of this paper is to estimate the dependence of P_N on the CO_2 concentration at the catalytic site of RuBPCO and to show the differences in limitations to photosynthesis for sun exposed and shaded needles located in a dense canopy of Norway spruce.

Materials and methods

Plants and experimental site: Sixteen-year-old stands of Norway spruces (*Picea abies* [L.] Karst.) were studied on the Experimental Ecological Study Site Bílý Kříž in the Beskydy Mts. (Czech Republic, NE Moravia, 49°30′N, 18°32′E, 943 m a.s.l. - see Kratochvílová *et al.* 1989 for details). The leaf area index (LAI) of the experimental plot was 8.6. The canopy was divided into two crown layers: exposed (E) and shaded (S) (see Marek *et al.* 1998). The main difference between them was the vertical distribution of PAR (Fig. 1). The two different types of needles were used for the estimation of P_N curves, biochemical model parameters, and electron transport rate in one-year-old E and S shoots.

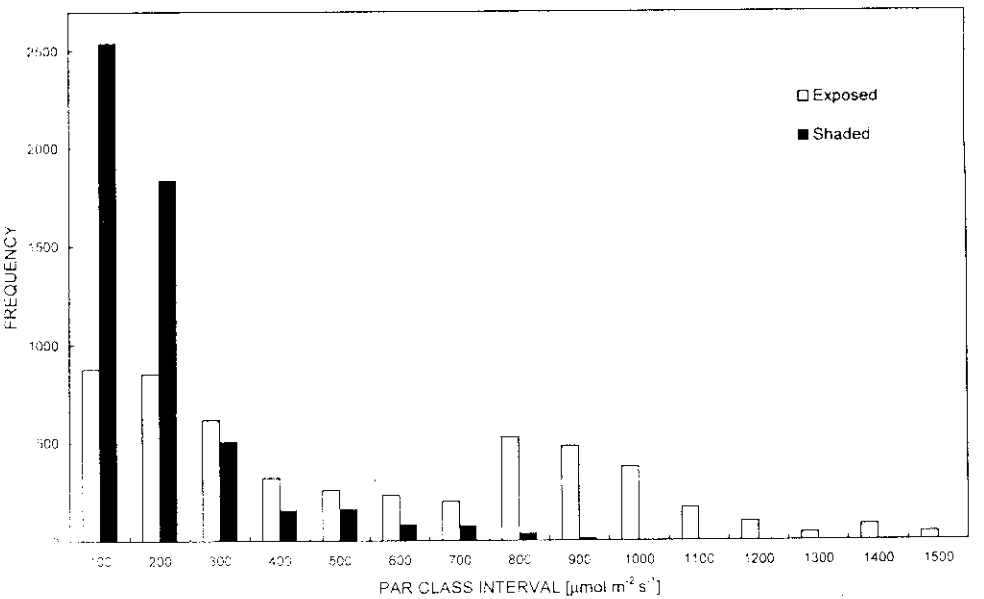

Fig. 1. Daily frequency of incident photosynthetically active radiation in the exposed and shaded crown layer during the period May-September 1996.

Gas exchange measurements: Closed photosynthetic portable system *Li-6250* (*Li-Cor*, Lincoln, Nebraska, USA) based on infra-red gas analysis was used for measurement of the relationship between P_N-C_i and biochemical model parameters. The P_N-C_i relationship was measured under artificial saturating irradiance (1300 μmol m^{-2} s^{-1}) and 7 different ambient CO_2 concentrations of 1100, 700, 500, 340, 150, 100, and 20 μmol mol^{-1} (Marek *et al.* 1995), whereby nine values were taken for each concentration. The P_N-C_i response curves were calculated for the interval of C_i from 0 to 800 μmol mol^{-1}. Microclimatic conditions in the assimilation chamber were kept constant during the measurement (temperature of needles 23±3 °C; relative air humidity 55±5 %).

Measurement of the biochemical model input parameters was based on the estimation of the initial linear part of the P_N-C_i relation curve (Brooks and Farquhar 1985) for two irradiances (about 100 and 250 μmol m^{-2} s^{-1}) and two low C_i concentrations (about 100 and 300 μmol mol^{-1}). Measurements started at low irradiance and high C_i (Marek *et al.* 1995).

Fluorescence of Chl *a* was measured using a pulse amplitude modulation fluorometer *PAM 2000* (*Heinz Walz*, Effeltrich, Germany). Shoots from the E and S parts of crown were kept in the dark for at least 30 min before measurements. Then the sample was situated into the leaf-clip holder *2030-B*, which was connected to the *PAM 2000,* and F_0 was estimated. After 10 min, continuous actinic irradiance (1500 μmol m^{-2} s^{-1} provided by the external halogen lamp *2050-H*) was let down to close all the PS2 reaction centres, and a saturating pulse of "white light" (0.6 s duration, PAR 3500 μmol m^{-2} s^{-1}) was applied for estimation of the F_V/F_M ratio.

The electron transport rate (Jt) was calculated using the equation (Špunda *et al.* 1993):

$$Jt = F_V/F_M \times PAR \times 0.5 \times 0.87$$

In this case (dark-adapted samples) the F_V/F_M is equivalent to the maximum quantum yield of PS2. The value 0.5 expresses that transport of one electron requires absorption of two quanta, as two photosystems are involved. The factor 0.87 expresses 87 % of the incident quanta absorbed by the leaf (Marek 1986).

Estimation of the P_N-C_c response curves that describe the dependence of P_N on C_c was based on simultaneous measurements of Chl fluorescence and leaf gas exchange (Cornic and Briantais 1991). C_c was calculated according to Epron *et al.* (1995):

$$C_c = C_i \times S^*/S$$

where S and S^* are the specificity factor of RuBPCO and the apparent specificity factor *in vivo*, respectively. We used the 2560 mol mol^{-1} value for S (Epron *et al.* 1995). S^* was determined as the initial slope of the regression line going through the origin and passing through points of the J_c/J_o–C_i/O relationship (Cornic and Briantais 1991), where J_c/J_o is the ratio of electron flows devoted to carboxylation and oxygenation, respectively. O_2 mole fraction (O) was 210 mmol mol^{-1}.

Potential assimilation rate (P_p) is defined as the rate of CO_2 assimilation without internal resistances to CO_2 transfer. P_p is the point of intersection of *supply* and

demand function (Farquhar and Sharkey 1982). The demand function is represented by the P_N-C_c response curve, where P_N is the actual assimilation rate for ambient CO_2 concentration (C_a). A potential assimilation rate assuming no stomatal resistance to CO_2 transfer to the leaf (P_0) can be defined when $C_i = C_a$.

Processing of statistical values: The P_N-C_i and P_N-C_c curves were calculated using the *FOTOS* programme (Pirochtová and Marek 1991). For each treatment a set of 6 curves and related parameters, *i.e.*, saturated rate of CO_2 uptake (P_{Nsat}), compensation CO_2 concentration (Γ), carboxylation efficiency (τ), were statistically proceeded. The statistical significance of differences of these parameters between the E and S variants was based on the F- and *t*-tests of mean values. The analysis used analytical tools of the *EXCEL* programme package.

Results

***P_N-C_i* response curves**: There were differences between S and E needles as shown by the measured P_N-C_i response curves (Table 1, Fig. 2). The P_{Nmax} for E-needles was higher by 2.5 % (statistically significant, $p = 0.05$) than that for S-needles. Differences of the rate of CO_2 evolution in the light at zero CO_2 concentration (R_S) between E and S needles were not found. Compensation concentration of CO_2 (Γ) for the E-foliage was 38.7 % lower ($p = 0.01$) than that for the S-foliage. Differences in carboxylation efficiency (τ) between E and S needles (56.0 %) were highly statistically significant ($p = 0.01$).

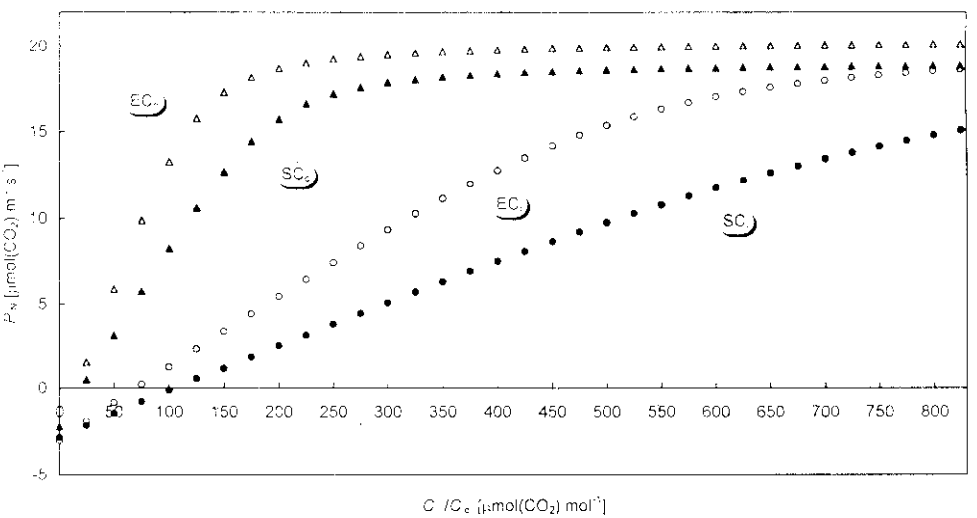

Fig. 2. Relationship between the internal CO_2 concentration (C_i) and CO_2 concentration at the catalytic site of RuBPCO (C_c), respectively, and the net photosynthetic rate (P_N) under saturating irradiance (1300 μmol m^{-2} s^{-1}). EC_i - response curve for sun exposed needles at C_i; SC_i - response curve for shaded needles at C_i; EC_c - response curve for sun exposed needles at C_c; SC_c - response curve for shaded needles at C_c.

Table 1. Parameters of net photosynthetic rate-internal CO_2 concentration response (P_N-C_i) and of P_N-chloroplastic CO_2 concentration response (P_N-C_c) curves: P_{Nsat} - saturated rate of CO_2 uptake [μmol(CO_2) m^{-2} s^{-1}]; Γ - compensation CO_2 concentration [μmol(CO_2) mol^{-1}]; Θ - saturation rate [dimensionless]; R_S - rate of CO_2 evolution in the light at zero C_i [μmol(CO_2) m^{-2} s^{-1}]; τ - carboxylation efficiency [mol m^{-2} s^{-1}] for exposed, E = sun acclimated needles from upper part of tree crown, and shaded, S = shade acclimated needles from lower part of tree crown. Means ± SD; the same letters indicate significant differences (on the level of 95 %); * high statistical difference (on the level of 99 %); $n = 6$.

		P_{Nsat}	Γ	Θ	R_S	τ
C_i	E	20.34±0.15 a	68.31±7.50 b*	0.936±0.011 c*	2.97±0.47	0.0432±0.0021 d*
	S	20.81±0.25 a	111.37±14.02 b*	0.861±0.025 c*	2.80±0.46	0.0277±0.0015 d*
C_c	E	20.30±0.32	16.21±2.02 e*	0.935±0.019 f	2.98±0.57	0.1822±0.0124 g*
	S	20.19±0.72	23.79±5.41 e*	0.902±0.023 f	2.80±0.49	0.1192±0.0073 g*

P_N-C_c response curves were based on the determination of Jt and S^*. Sun acclimation leads to Jt higher by 35.6 % as well as to S^* higher by 4.9 % compared to S-needles (Table 2). No statistically significant differences were found for P_{Nsat} and R_S between E and S needles. In E-needles, Γ was lower by 31.9 % ($p = 0.01$) than in S-needles. Photosynthetic apparatus of E-needles reached τ higher by 52.0 % ($p = 0.01$) than in S-needles.

P_0, P_p, and C_c at $C_a = 350$ μmol mol^{-1} are shown in Table 4, P_p/P_N as a function of C_a for both types of needles in Fig. 3. For S-needles, P_0 was lower by 39.1 %, P_p by 9.3 %, and C_c by 34.5 % than for E-needles.

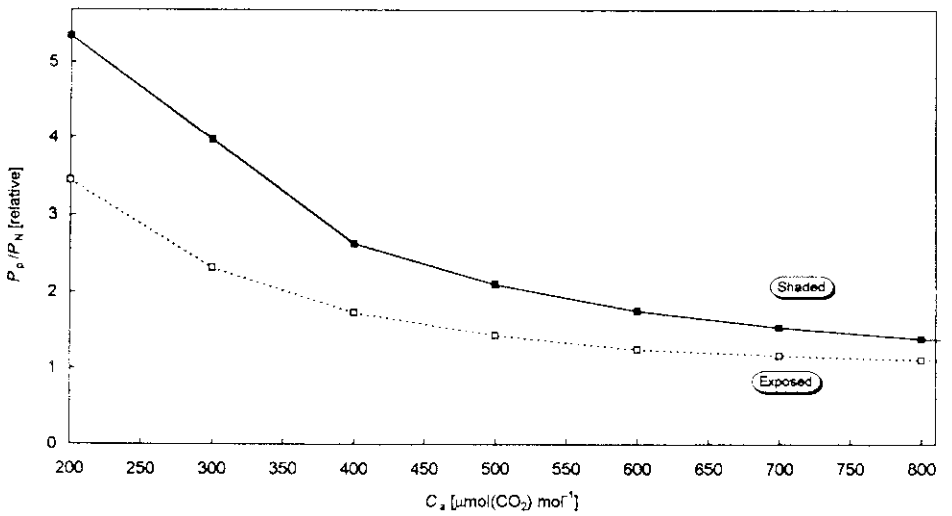

Fig. 3. Relationship between the ambient CO_2 concentration (C_a) and the ratio P_p/P_N, where P_p is the potential assimilation rate at C_a assuming no stomatal resistance to CO_2, and P_N is net photosynthetic rate at C_a under saturating irradiance (1300 μmol m^{-2} s^{-1}) for sun exposed and shaded needles.

Table 2. Input parameters of the biochemical model of RuBPCO activity: Γ^* - compensation CO_2 concentration in absence of photorespiration [μmol(CO_2) mol^{-1}]; R_D^* - rate of non-photorespiratory CO_2 efflux in the light [μmol(CO_2) m^{-2} s^{-1}]; Jt - electron transport rate from fluorescence measurements [μmol m^{-2} s^{-1}]; S^* - the apparent specificity factor of RuBPCO *in vivo* for exposed, E = sun acclimated needles from upper part of tree crown, and shaded, S = shade acclimated needles from lower part of tree crown. Means ± SD; the same letters indicate significant differences (on the level of 95 %); * high statistical difference (on the level of 99 %); $n = 6$.

		Γ^*	R_D^*	Jt	S^*
C_i	E	38.40±2.45 a*	0.45±0.11 b	190.2±5.9 c*	609.5±12.1 d
	S	77.80±3.05 a*	0.36±0.27 b	140.3±7.4 c*	582.6±14.2 d

Biochemical model: Values of input parameters of this model, Γ^* - compensation CO_2 concentration without photorespiration, and R_D^* - rate of non-photorespiratory CO_2 efflux in the light, depended very strongly on the acclimation of photosynthetic apparatus to irradiance (Table 2). The largest difference in the sets of E and S output parameters at C_i = 350 μmol mol^{-1} was noticed for the rate of RuBPCO oxygenation, V_o: for S-needles it was higher by 50.4 % than for E-needles. Lower values were observed in S-needles for the following parameters: V_c (25.5 %), V_{RuBP} (11.8 %), J_a (20.5), and J_{aC} (34.3 %). The J_{max}/V_{cmax} ratio estimated at C_i = 1100 μmol mol^{-1} was higher by 50 % for S-needles than for E-needles.

Table 3. Parameters of the biochemical model of RuBPCO activity calculated for two values of C_i [350 and 1100 μmol(CO_2) mol^{-1}]: V_c - rate of RuBPCO carboxylation [μmol(CO_2) m^{-2} s^{-1}]; V_o - rate of RuBPCO oxygenation [μmol(CO_2) m^{-2} s^{-1}]; V_{RuBP} - rate of ribulose-1,5-bisphosphate (RuBP) consumption and formation [μmol(CO_2) m^{-2} s^{-1}]; J_a, J_{aC} - rates of actual electron transport rate and of electron transport rate of carboxylation [μmol m^{-2} s^{-1}] for exposed, E = sun acclimated needles from upper part of tree crown, and shaded, S = shade acclimated needles from lower part of tree crown.

	C_i	V_c	V_o	V_{RuBP}	J_a	J_{aC}	V_o=%V_c	J_{max}/V_{cmax}
E	350	10.92	2.40	13.31	57.50	10.17	21.98	
	1100	46.31	1.39	21.23	95.42	19,61	3.00	2.06
S	350	8.31	3.61	11.74	45.68	6.68	44.40	
	1100	29.85	2.62	21.12	92.30	17.55	8.78	3.09

Discussion

The vertical gradient of PAR within canopy causes a different photosynthetic capacity of needles (Fig. 1). In accordance with previous papers we noticed differences between E and S needles of Norway spruce in the P_N-C_i and P_N-C_c curves. Characteristic for shade acclimation of Norway spruce needles were a lower Chl *a/b* ratio (values not shown), lower τ, lower electron transport rate and

carboxylation capacity, lower S^*, and generally lower P_{Nsat}. Γ was significantly higher for S-needles than for the E-needles.

Table 4. Values of net photosynthetic rates imposed by stomatal and internal resistances to CO_2 transfer and values of CO_2 concentration at the catalytic site of RuBPCO at the ambient CO_2 concentration (C_a) 350 μmol(CO_2) mol^{-1}. P_N - rate of the actual CO_2 uptake at C_a [μmol(CO_2) m^{-2} s^{-1}]; P_o - potential assimilation rate at C_a assuming no stomatal resistance to CO_2 [μmol(CO_2) m^{-2} s^{-1}]; P_p - potential assimilation rate at C_a assuming no internal resistance to CO_2 [μmol(CO_2) m^{-2} s^{-1}]; C_c - CO_2 concentration at the catalytic site of RuBPCO at C_a = 350 μmol(CO_2) mol^{-1} [μmol(CO_2) mol^{-1}].

	P_N	P_o	P_p	C_c
E	11.2	12.8	19.4	52.0
S	6.7	7.8	17.6	38.0

The lower P_N for S-needles can be caused by a lower electron transport rate, because there are fewer electron transport carriers per unit leaf area, mainly plastoquinone and cytochrome *f* (Boardman 1977, Evans 1987, Anderson *et al.* 1988).

RuBPCO activity was affected by different position of needles in the tree crown, as shown by the significantly changed value of τ (Table 1). We estimated a higher carboxylation rate and a lower oxygenation rate for E-needles using the biochemical model (Table 3). Activity of RuBPCO is controled by various elements, mainly by nitrogen (Farquhar *et al.* 1980, Lloyd *et al.* 1995). Within monospecific stands, nitrogen tends to be distributed in proportion to absorbed radiant energy, and the concentration of this element decreases with depth in the canopy (Lloyd *et al.* 1995, Hrdlička 1996). We estimated a greater ratio of J_{max}/V_{cmax} for S-needles than E-needles (Table 3). This ratio is not influenced by the age of needles and nitrogen stress (Caemmerer and Farquhar 1981). Lower CO_2 assimilation in shade plants comes more from lower V_{cmax} than from lower capacity for RuBP regeneration (Zhang *et al.* 1995). Correlation between RuBP carboxylase activity and internal RuBP concentration was not found in intact chloroplasts of spinach (Sicher *et al.* 1981). The C_c was calculated from supply and demand functions. For S-needles, we estimated lower C_c at C_a = 350 μmol mol^{-1} by 34.5 % than for E-needles. Low CO_2 concentration in chloroplasts causes deactivation of RuBPCO (Sicher *et al.* 1981).

So we found that P_N of S-tissue is limited by both the electron transport rate and the carboxylation capacity (Table 3). The $J_a(S)/J_a(E)$ was 0.79, and $V_c(S)/V_c(E)$ was 0.74 at C_i = 350 μmol mol^{-1}, while for maximal rates $J_{max}(S)/J_{max}(E)$ = 0.97 and $V_{cmax}(S)/V_{cmax}(E)$ = 0.64. Hence the higher value of J_{max}/V_{cmax} of S-needles than E-needles was caused mainly by the lower carboxylation capacity.

Foliage acclimated to high irradiance is often structurally changed as shown by an increase in number of mesophyll cells per unit leaf area (Pearcy and Sims 1994). The larger internal leaf area of sun acclimated plants facilitates CO_2 diffusion to chloroplast places which leads to lower internal resistances and lower J_{max}/V_{cmax}

ratio (Leverenz 1996). Stomatal limitation share in P_p was 19.5 % and that of internal limitation was 80.5 % for E-needles, while for S-needles these limitations were 10 and 90 %, respectively (Table 4). Nobel (1991) reports for tree species that internal limitation represents about 80 % of the total limitations. These limitations strongly depend on the water potential of plants (Farquhar and Sharkey 1982), and under high soil moisture no significant differences of stomatal limitation and P_{Nsat} are observed (Zhang *et al.* 1995).

We estimated higher R_S and R_D^* for the E-tissue than for the S-tissue. This result, contrasting to the study of Anderson *et al.* (1988) where lower R_S for E-needles of Norway spruce was found, can be explained by a higher energy cost for maintenance (Zhang *et al.* 1995) and greater availability of saccharides due to higher P_N (Pearcy and Sims 1994).

The S-foliage had a larger portion of free assimilation capacity in the whole C_a range than the E-needles (Fig. 2). This portion of free capacity decreased in dependence on increased C_a because diffusion of CO_2 to the RuBPCO active site increased. Beside this fact, we noticed higher values of P_p/P_N (at C_a = 350 μmol mol^{-1}) for both needle types of Norway spruce, similarly to the findings of Epron *et al.* (1995) in beech (*Fagus sylvatica* L.) and sweet chestnut (*Castanea sativa* Mill.) leaves.

The factor of RuBPCO specificity (S) defines relative rates of photosynthesis and photorespiration in plants. Increased plant productivity or larger portion of photosynthesis can occur with increasing S value (Chen and Spreitzer 1992). This value is within the range 2100 to 2950 mol mol^{-1} for C_3 plants (Epron *et al.* 1995). The *in vivo* apparent specificity factor of RuBPCO (S^*) was higher for E-needles compared to the S-ones, and these values were lower than the S values (Table 2). A similar decrease was documented for different tree species such as *F. sylvatica* and *C. sativa* (Epron *et al.* 1995), and it is in contrary to the measurements on *Phaseolus vulgaris* (Cornic and Briantais 1991).

In summary, P_N was higher in E-needles of Norway spruce on both P_N-C_i and P_N-C_c levels of photosynthetic response curves. The depression of photosynthesis is caused by the decline in electron transport rate and mainly by the lower carboxylation capacity of shade foliage. Lower RuBPCO activity of S-needles can be caused by low nitrogen content in the needles as well as by lower chloroplastic CO_2 concentration. We found greater internal limitation of CO_2 diffusion to the chloroplasts for S-foliage. Large free photosynthetic capacity is typical for S-needles of Norway spruce.

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