



Growth under elevated CO₂ concentration affects the temperature response of photosynthetic rate

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In this study, we tested the hypothesis that an elevated CO₂ concentration leads to a shift of the temperature optimum of the photosynthetic rate in trees. Since the elevated CO₂ treatment usually leads to a significant decrease in stomatal conductance and consequently to decrease in transpiration followed by an increase in leaf temperature, we hypothesized that elevated CO₂ results in the acclimation of photosynthetic apparatus to the higher temperature.

We studied the two most common species in the Czech Republic – European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karsten). The eight-year-old trees were grown in glass domes at the experimental research site Bílý Kříž in the Beskydy Mts. and they were exposed to ambient (AC; 385 μmol CO₂ mol⁻¹) and elevated CO₂ concentrations (EC; 700 μmol CO₂ mol⁻¹). Based on the gas-exchange and fluorescence techniques we determined the basic photosynthetic characteristics in the range of leaf temperatures from 10 to 45 °C. The changes in temperature acclimation of tree species studied were evaluated on the basis of the shift of temperature optima.

EC treatment led indeed to an increase of leaf temperature up to 3.5 °C in both species studied. The temperature optimum of the light-saturated rate of CO₂ assimilation, measured at the growth CO₂ concentration (i.e. 385 for AC and 700 μmol CO₂ mol⁻¹ for EC trees), was higher by 3 °C in both tree species of the EC variant. Although the shift in photosynthetic temperature optimum disappeared when the AC plants were exposed to an elevated CO₂ concentration, an acclimation of Rubisco carboxylation and electron transport to higher temperature was observed.

Keywords: CO₂ assimilation rate, *Fagus sylvatica*, chlorophyll fluorescence, *Picea abies*, Rubisco

Introduction

Global climate models predict that the atmospheric CO₂ concentration ([CO₂]) may be twice as high at the end of this century and global temperature may increase up to 4 °C (IPCC 2007). The temperature may significantly affect plant productivity and species distribution. In general, plants exhibit maximum photosynthesis at growth temperature, but most plant species are able to acclimate to changes in growth temperature (Hikosaka et al. 2006; Sage and Kubien 2007). Also [CO₂] has direct effects on plant

physiology. Exposure to elevated [CO₂] leads to an increase of the CO₂ assimilation rate in C3 plants (Ainsworth and Rogers 2007; Norby and Zak 2011). Rising photorespiration, caused by increasing temperature, can be suppressed by elevated [CO₂]. An increased stimulatory effect of elevated [CO₂] on carbon uptake is thus expected at rising temperature (Crawford and Wolfe 1999). Plants grown under elevated [CO₂] however, often exhibit acclimation changes of the photosynthetic apparatus that can affect plant responses to temperature (Lewis et al. 2001). Plants grown under elevated [CO₂] often

have a higher leaf temperature due to a decrease in stomatal conductance and subsequently reduced dissipation of latent heat via transpiration (Leverenz et al. 1999; Long et al. 2006). Acclimation of the photosynthetic apparatus to elevated $[\text{CO}_2]$ may result in lower photosynthetic capacity due to the reduction in carboxylation activity of Rubisco enzyme and/or the rate of electron transport (Špunda et al. 2005; Ainsworth and Rogers 2007; Urban et al. 2012). These changes are similar to acclimation changes of the photosynthetic apparatus in higher temperature condition (Sage and Kubien 2007; Way and Sage 2008). A shift in temperature optima, similar to those induced by elevated temperatures, are thus expectable under conditions of elevated $[\text{CO}_2]$ (Hikosaka et al. 2006). How growth under elevated $[\text{CO}_2]$ influences the photosynthetic temperature response is not yet clear, although it is an important question in terms of future changes in plant production and distribution.

In this study we examined how plant growth under the condition of elevated $[\text{CO}_2]$ affects the temperature response of photosynthesis in two common tree species of the Czech Republic. We tested the hypothesis that the elevated $[\text{CO}_2]$ condition leads to an increase of the temperature optimum of the photosynthesis.

Material and methods

The experiment was carried out at the experimental research site Bílý Kříž in the Beskydy Mountains (49°30' N, 18°32' E, 908 m a.s.l., NE of the Czech Republic). That area has a cool (annual mean air temperature 6.8°C) and humid (annual mean relative air humidity 83%) climate with high annual precipitation (the average for 2000–2009 was 1356 mm). In the present study, we compared the photosynthetic activity in two wide-spread temperate zone tree species – broadleaved European beech (*Fagus sylvatica* L.) and coniferous Norway spruce (*Picea abies* (L.) Karsten). The eight-year old trees were exposed to ambient (385 $\mu\text{mol CO}_2 \text{ mol}^{-1}$; hereafter AC) and elevated CO_2 concentration (700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$; hereafter EC) for five growing seasons using two glass dome facilities. The CO_2 enrichment is continuous from April till November. The environmental air conditions inside the domes are maintained by an air conditioning device together with an adjustable window system. Windows reduced the penetration of photosynthetically active radiation by 26% on average. The air temperature inside and outside the facility differed insignificantly and the relative air humidity was lower inside than outside (by 10%

on average). No statistically significant differences in microclimatic parameters were found between the domes supplied with ambient and elevated $[\text{CO}_2]$. The detailed description of the facility is given in Urban et al. (2001). Plants were grown in their native soil. The geological bedrock was formed by Mesozoic Godula sandstone (flysch type) and is overlain by ferric podzols.

The physiological measurements were carried out on six fully developed beech leaves and current-year spruce shoots in August 2011. Each replicate was represented by an independent plant selected randomly within the glass dome among those trees of average height, stem diameter, and leaf chlorophyll content. Branches with the desired leaves/shoots were cut from the trees. The cut end of each branch was immediately re-cut under water to remove xylem embolisms and kept in the water. Whole branches were placed into the thermostat box Q-cell 60 (Pol-Lab, PL) where, the samples were exposed to different temperatures ranging from 10 to 45°C. Using a gas-exchange system LI-6400 (LI-COR, USA) we measured the temperature response of basic photosynthetic characteristics. Needles were carefully arranged in the assimilation chamber so that it was completely filled. Leaves/shoots were exposed to the saturating irradiance (1400 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) and constant air flow (500 $\mu\text{mol s}^{-1}$) in the assimilation chamber. The wide range of measuring temperature did not allow maintaining a constant vapour pressure deficit (VPD), so it changed naturally ranging from 0.7 kPa at 10°C up to 6 kPa at 40°C. In the assimilation chamber leaves/shoots were acclimated to given condition for 10 minutes and then the light-saturated CO_2 assimilation rate (A_{max}) and stomatal conductance (G_{Smax}) were measured. Measurements were carried out at growth $[\text{CO}_2]$ (i.e. 385 for AC and 700 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ for EC treatment, the long-term effect) and also at $[\text{CO}_2]$ in the second glass dome (i.e. 700 for AC and 385 $\mu\text{mol CO}_2 \text{ mol}^{-1}$ for EC treatment, the short-term effect). The initial linear phase of the relationship between the CO_2 assimilation rate (A) and intercellular CO_2 concentration (C_i) was measured to estimate the rate of *in vivo* Rubisco carboxylation (V_{Cmax}). One of the two LI-6400 was equipped with the leaf chamber fluorometer 6400-40 LCF (LI-COR, USA), which enabled the measurement of chlorophyll fluorescence parameters of light adapted (1400 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) leaves (F_0' , F_V' , F_M' , F_S). These parameters were used to calculate the light-saturated rate of the electron transport (ETR_{max}). Images from the thermal camera Ti55FT Fluke (Fluke, USA) were collected during day in one-hour intervals to

determine the surface temperature of the leaves. In the image five trees of each species were identified and the leaf temperature of 10 leaves/shoots per individual tree was noted.

Two-way analysis of variance (ANOVA) was performed to evaluate the physiological effects of long-term and short-term exposure to different [CO₂]. Significant differences (at $p < 0.05$) among mean values were analysed using Tukey post-hoc test. All statistical tests were performed using SigmaPlot 11 software (Systat Software, Inc., Chicago, IL, USA).

Results

Leaf temperature

In the EC condition the leaf temperature (T_{leaf}) increased by 2 °C on the average as compared to plants cultivated under AC (Fig. 1). The largest differences occurred in the afternoon, when the leaves from EC were up to 3.5 °C warmer than leaves from the AC condition. Beech had a higher T_{leaf} than spruce by approximately 2 °C during the day (10–17 h).

Temperature response of light saturated stomatal conductance

Irrespective of CO₂ treatment, higher temperature optima (T_{opt}) of light-saturated stomatal conductance (G_{Smax}) were found in beech (29–31 °C) as compared with spruce (< 20 °C; Fig. 2). EC treatment resulted in a decrease of G_{Smax} by 21% and 27% at T_{opt} in beech and spruce respectively. The observed changes induced by

EC were not statistically significant. The short-term exposure of leaves to [CO₂] of the second glass dome had no effect on the temperature course of G_{Smax} .

The temperature response of G_{Smax} was further modified by actual VPD. While beech trees grown in EC revealed lower G_{Smax} as compared to AC ones in the whole VPD interval studied, reducing effect of EC on G_{Smax} declined with increasing VPDs in spruce (data not shown).

Temperature response of light saturated rate of CO₂ assimilation

The light-saturated CO₂ assimilation rate (A_{max}) showed a parabolic temperature relationship (Fig. 3). A_{max} was stimulated by EC treatment; however, the stimulation was negligible at low leaf temperatures below 15 °C and also decreased at temperatures > 35 °C. The maximum values and temperature optima of A_{max} are shown in Tab. 1. Under EC, the maximum of A_{max} was by 75% and 46% higher as compared to AC in beech and spruce, respectively. The temperature optimum of A_{max} ($T_{\text{opt}}(A_{\text{max}})$) was reached in lower temperature under AC as compared to EC condition, on the average by 3 °C in both species studied.

After the short-term exposure of leaves to [CO₂] in the second glass dome, the shift of $T_{\text{opt}}(A_{\text{max}})$ was recorded in similar range as after the long-term exposure to given [CO₂] (Tab. 1). The values of A_{max} were slightly (non-statistically significant) higher in AC plant after short-term exposure to elevated [CO₂] as compared to long-term exposure to EC (Tab. 1).

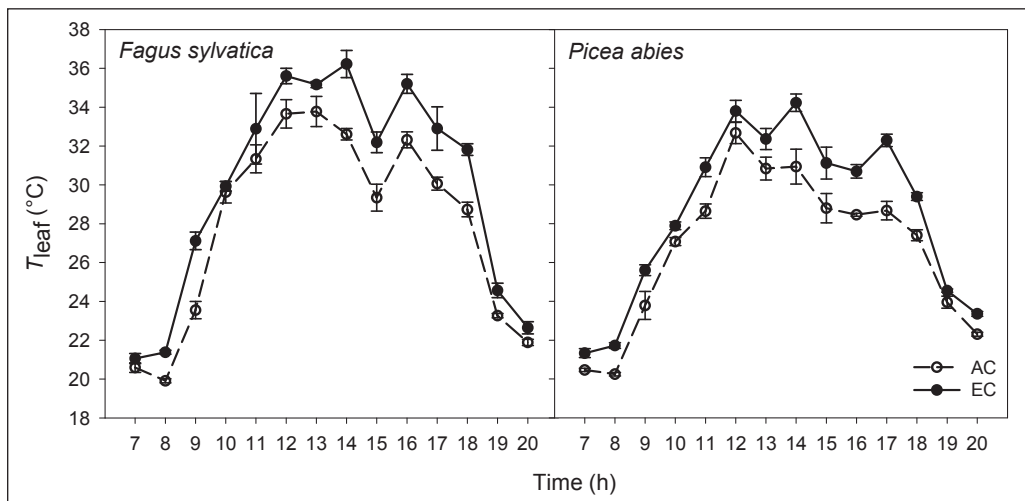


Fig. 1: Daily course of the leaf temperature of *Fagus sylvatica* and *Picea abies* grown at ambient (AC) and elevated atmospheric CO₂ concentration (EC). Means (circles) and standard deviations (bars) are presented ($n = 5$).

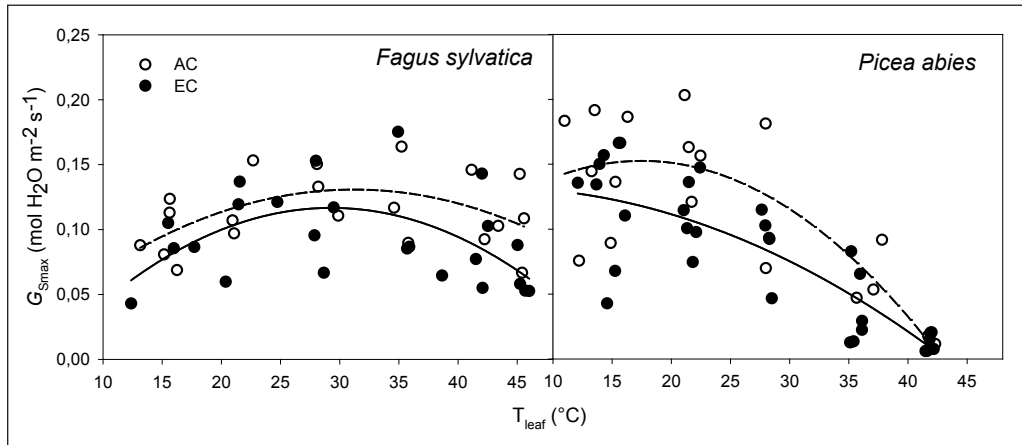


Fig. 2: Temperature response curve of light-saturated stomatal conductance ($G_{S_{max}}$) in *Fagus sylvatica* and *Picea abies* grown at ambient (AC) and elevated atmospheric CO_2 concentration (EC). The parabolic function (dashed line for AC and solid line for EC) was fitted to the data. The individual measured values are shown ($n = 6$), R^2 ranged from 0.40 to 0.62, correlation is significant ($p < 0.05$).

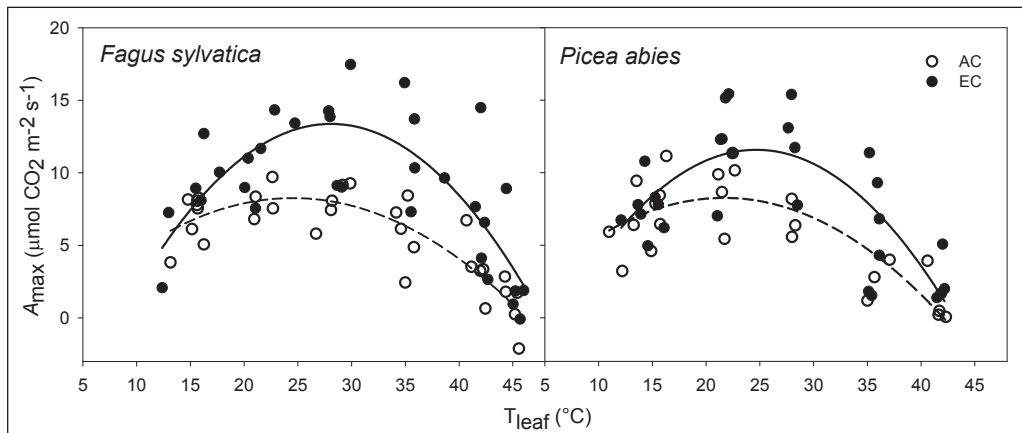


Fig. 3: Temperature response curve of light-saturated rate of CO_2 assimilation (A_{max}) in *Fagus sylvatica* and *Picea abies* grown at ambient (AC) and elevated atmospheric CO_2 concentration (EC). The parabolic function (dashed line for AC and solid line for EC) was fitted to the data. The individual measured values are shown ($n = 6$), R^2 ranged from 0.61 to 0.74, correlation is significant ($p < 0.05$).

Tab. 1: Mean values \pm standard deviations of light-saturated rate of CO_2 assimilation (A_{max}) at its temperature optimum ($T_{opt}(A_{max})$) in *Fagus sylvatica* and *Picea abies* grown at ambient (AC 385) and elevated atmospheric CO_2 (EC 700) and changes of parameters after short-term exposure of leaves to $[CO_2]$ in the second dome (AC 700, EC 385). The identical letters indicate homogeneous groups with statistically non-significant differences ($p > 0.05$) within species and parameter, $n = 6$.

<i>Fagus sylvatica</i>		AC 385	AC 700	EC 385	EC 700
A_{max}	$\mu mol CO_2 m^{-2} s^{-1}$	8.22 ± 1.02^a	14.37 ± 2.62^b	8.35 ± 1.51^a	13.42 ± 2.28^b
$T_{opt}(A_{max})$	$^{\circ}C$	24.5 ± 2.6^a	28.2 ± 1.9^b	25.8 ± 1.8^{ab}	28.1 ± 2.4^b
<i>Picea abies</i>		AC 385	AC 700	EC 385	EC 700
A_{max}	$\mu mol CO_2 m^{-2} s^{-1}$	8.29 ± 1.91^a	12.12 ± 2.80^b	7.12 ± 1.28^a	11.62 ± 2.11^b
$T_{opt}(A_{max})$	$^{\circ}C$	21.5 ± 1.3^{ab}	23.8 ± 2.9^{ab}	20.5 ± 2.3^a	24.6 ± 2.9^b

Temperature response of maximum rate of Rubisco carboxylation

The temperature response curve of maximum rate of Rubisco carboxylation *in vivo* ($V_{C_{max}}$) showed an exponential increase followed by a rapid decline after reaching the maximum (Fig. 4). Under EC conditions, temperature optima of $V_{C_{max}}$ ($T_{opt}(V_{C_{max}})$) were achieved at temperatures higher by 3 °C on average in both tree species as compared with AC conditions (Tab. 2). $V_{C_{max}}$ at its T_{opt} was higher by 21% and 13% under EC as compared to AC in beech and spruce, respectively (Tab. 2).

Temperature response of light-saturated rate of electron transport

The temperature response curve of light-saturated rate of electron transport (ETR_{max}) had a parabolic course (Fig. 5). EC treatment had no significant effect on the temperature response curve of ETR_{max} , but it tended to reduce ETR_{max} at low temperatures and stimulate at high temperatures. The maximum of ETR_{max} was slightly stimulated by EC in spruce (by 14%), while it remained unchanged in beech. The shift in $T_{opt}(ETR_{max})$ by 3 °C was observed for EC as compared with AC trees (Tab. 3).

After short-term exposure of leaves to [CO₂] in the second dome, ETR_{max} increased by 26% and 13% in AC and declined by 20% and 18% in EC, in beech and spruce, respectively as compared to ETR_{max} at growth CO₂ concentration (Tab. 2). $T_{opt}(ETR_{max})$ was not significantly changed after short-term exposure to [CO₂] in the second glass dome (Tab. 2).

Temperature response of chlorophyll a fluorescence

The actual photochemical efficiency of photosystem (PS) II in fully oxidized state (F_v'/F_m' ; $F_v' = F_m' - F_0'$) decreased with increasing leaf temperature (Fig. 6 a, b). It refers to the increasing need for thermal energy dissipation. The value F_v'/F_m' below 0.3 indicates a damage of PS II, this value was observed at high temperature above 40 °C, especially at AC spruce. Also, the increase in minimum fluorescence yield (F_0') indicates damage on the thylakoid membrane. F_0' started to increase at 22 °C in AC spruce, in EC spruce it was up from 32 °C.

Discussion

In this study, we tested the hypothesis that elevated [CO₂] leads to a shift of the temperature optimum of photosynthetic rate in tree species. Since the elevated CO₂ treatment usually leads to significant decreases in stomatal conductance (Kořvancová et al. 2009), and consequently to decreases in transpiration followed by increases in leaf temperature (Long et al. 2006). In agreement with the initial presumption, we observed a decrease in $G_{s_{max}}$ in EC treatment compared with AC (Fig. 2) and higher leaf temperature in EC plants (Fig. 1).

In this study, VPD increased naturally with increasing temperature. It is assumed that the stimulation effect of EC on A will be higher at higher VPD when EC-induced changes in $G_{s_{max}}$ are relatively low (Barton et al. 2012). We found the highest stimulation of A by EC in the range of VPD 2–4 kPa, which corresponds to T_{leaf}

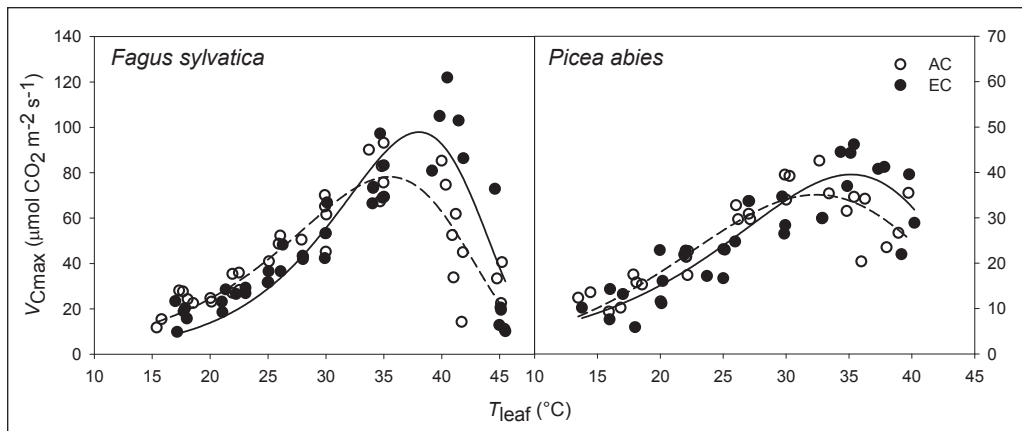


Fig. 4: Temperature response curve of maximum rate of Rubisco carboxylation *in vivo* ($V_{C_{max}}$) in *Fagus sylvatica* and *Picea abies* grown at ambient (AC) and elevated atmospheric CO₂ concentration (EC). The Weibull function (dashed line for AC and solid line for EC) was fitted to the data. The individual measured values are shown ($n = 6$), R^2 ranged from 0.79 to 0.92, correlation is significant ($p < 0.05$).

Tab. 2: Mean values \pm standard deviations of maximum rate of Rubisco carboxylation in vivo ($V_{C_{max}}$) at its temperature optimum ($T_{opt}(V_{C_{max}})$) in *Fagus sylvatica* and *Picea abies* grown at ambient (AC) and elevated atmospheric CO_2 (EC). The identical letters indicate homogeneous groups with statistically non-significant differences ($p > 0.05$) within species and parameter, $n = 6$.

<i>Fagus sylvatica</i>		AC	EC
$V_{C_{max}}$	$\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$	78.4 ± 7.8^a	95.3 ± 9.5^a
$T_{opt}(V_{C_{max}})$	$^{\circ}\text{C}$	35.4 ± 2.1^a	38.1 ± 1.8^a
<i>Picea abies</i>		AC	EC
$V_{C_{max}}$	$\mu\text{mol CO}_2\text{m}^{-2}\text{s}^{-1}$	35.2 ± 4.0^a	39.8 ± 5.3^a
$T_{opt}(V_{C_{max}})$	$^{\circ}\text{C}$	32.6 ± 1.8^a	35.4 ± 1.7^a

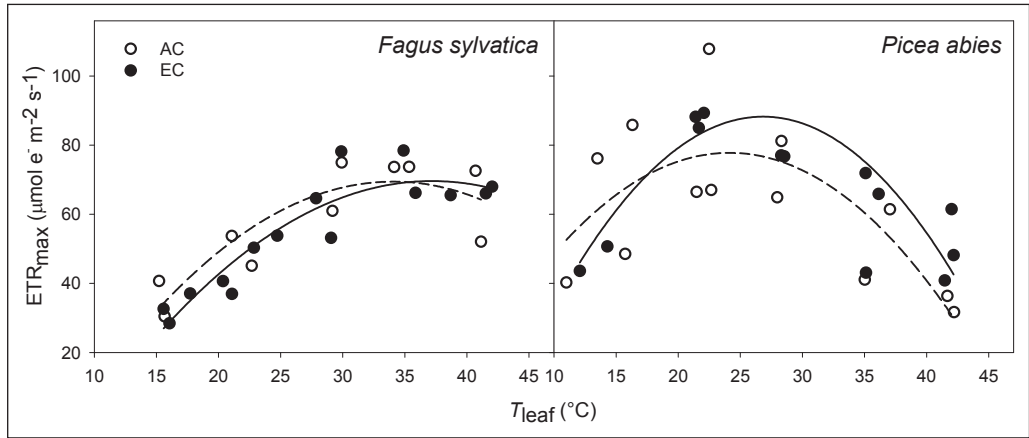


Fig. 5: Temperature response curve of light-saturated rate of electron transport (ETR_{max}) in *Fagus sylvatica* and *Picea abies* grown at ambient (AC) and elevated atmospheric CO_2 concentration (EC). The parabolic function (dashed line for AC and solid line for EC) was fitted to the data. The individual measured values are shown ($n = 3$), R^2 ranged from 0.58 to 0.86, correlation is significant ($p < 0.05$).

Tab. 3: Mean values \pm standard deviations of light-saturated rate of electron transport (ETR_{max}) at its temperature optimum ($T_{opt}(ETR_{max})$) in *Fagus sylvatica* and *Picea abies* grown at ambient (AC 385) and elevated atmospheric CO_2 (EC 700) and changes of parameters after short-term exposure of leaves to $[CO_2]$ in the second glass dome (AC 700, EC 385). The identical letters indicate homogeneous groups with statistically non-significant differences ($p > 0.05$) within species and parameter, $n = 3$.

<i>Fagus sylvatica</i>		AC 385	AC 700	EC 385	EC 700
ETR_{max}	$\mu\text{mol e}^{-}\text{m}^{-2}\text{s}^{-1}$	69.4 ± 1.2^b	87.5 ± 8.2^c	56.0 ± 5.1^a	69.6 ± 7.1^{bc}
$T_{opt}(ETR_{max})$	$^{\circ}\text{C}$	34.0 ± 1.5^a	33.3 ± 2.3^a	34.1 ± 2.2^a	37.2 ± 1.9^a
<i>Picea abies</i>		AC 385	AC 700	EC 385	EC 700
ETR_{max}	$\mu\text{mol e}^{-}\text{m}^{-2}\text{s}^{-1}$	77.8 ± 16.1^a	88.1 ± 18.8^a	72.3 ± 9.7^a	88.2 ± 11.4^a
$T_{opt}(ETR_{max})$	$^{\circ}\text{C}$	24.2 ± 1.3^a	25.6 ± 1.9^a	26.0 ± 1.4^a	26.8 ± 2.1^a

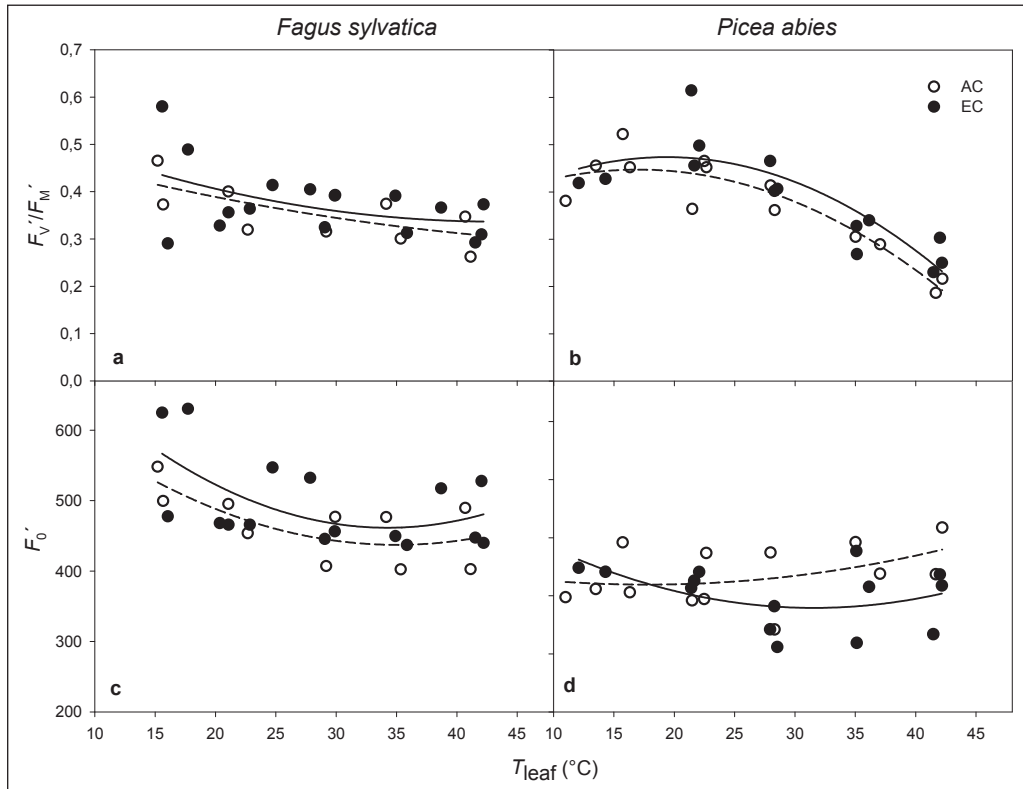


Fig. 6: Temperature response curve of actual photochemical efficiency of PS II in fully oxidized state (F_v'/F_m' ; **a, b**) and minimum fluorescence yield (F_0 ; **c, d**) in *Fagus sylvatica* (**a, c**) and *Picea abies* (**b, d**) grown at ambient (AC) and elevated atmospheric CO₂ concentration (EC). The quadratic function (dashed line for AC and solid line for EC) was fitted to the data. The individual measured values are shown ($n = 3$), R^2 ranged from 0.46 to 0.92, correlation is significant ($p < 0.05$).

of 28–35°C in both species studied (data not shown). Further possible biochemical causes of EC effects on the temperature response of A are discussed.

Although the positive shift of the temperature optimum of A_{max} by 3°C was found in both species (Fig. 3), this shift was not observed when the plants were exposed to the same CO₂ concentrations (Tab. 1). These results document a direct effect of elevated [CO₂] on the photosynthetic temperature optimum. The reasons of higher temperature optimum under EC condition may be as follows. A) Photosynthesis under elevated [CO₂] is dominantly limited by RuBP regeneration that has usually higher temperature optima as compared to the photosynthesis limited by Rubisco activity that is usually observed under ambient [CO₂] (Sage, Kubien 2007). B) The Michaelis-Menten kinetic constant for Rubisco carboxylation rises at low intercellular [CO₂] and the photosynthetic rate becomes less sensitive to temperature (Hikosaka et al. 2006). C) Contribution of photorespiration increases

with temperature, but at elevated [CO₂] photorespiration is suppressed allowing an increase in optimal temperature (Borjigidai et al. 2006; Hikosaka et al. 2006). Although the direct effect of EC on the temperature optimum of photosynthesis was observed, our results showed that the photosynthetic apparatus of EC plants were more effective at temperatures above the optimum and less effective at temperature below the optimum in comparison with AC plants as demonstrated by temperature response curves of V_{Cmax} and ETR_{max} (Fig. 4, 5).

Efficiency of Rubisco increases with increase of [CO₂] and temperature. Thus, the reduction of its content is allowed (Woodrow 1994; Hikosaka et al. 2006). A decrease of Rubisco content under EC condition was observed by 25%–42% a 41%–58% at beech and spruce, respectively, on a leaf mass unit (Kořvancová et al. 2009). It can be reasoned that V_{Cmax} is lower for EC plants in comparison to AC plants at sub-optimal leaf temperatures. The shift of $T_{opt}(V_{Cmax})$ can explain the higher activation energy of V_{Cmax} that has

been observed especially at higher temperature and occasionally at EC (Alonso et al. 2008) as well as the suppression of photorespiration under EC (Borjigidai et al. 2006). Higher $V_{C_{max}}$ at above optimal leaf temperatures may be associated with the production of more thermostable Rubisco activase and/or Rubisco itself (Yamori et al. 2005; Sage, Kubien 2007).

A higher activation energy of ETR can cause a decline in ETR and an increase in $T_{opt}(ETR_{max})$ (Hikosaka et al. 2006). ETR is more effective under EC condition because more products of the electron transport (ATP, NADPH) are used for CO_2 assimilation due to the suppression of photorespiration (Logan et al. 2009). Therefore increase in ETR_{max} of AC plants was observed after a short-term exposure to elevated $[CO_2]$. ETR_{max} were the same for AC and EC beech trees measured at growth $[CO_2]$, whereas ETR_{max} of spruce was higher for EC plants. After a short-term exposure of AC plants to elevated $[CO_2]$ they reached the same values. This indicates acclimation changes in EC beech that may result in a decrease of ETR_{max} , e.g. electron transporters content reduction (Špunda et al. 2005; Yamori et al. 2005). Spruce was more sensitive to high temperature than beech; it can be seen in the lower T_{opt} of photosynthetic processes (Fig. 3, 4, 5) and in a rapid stomatal closure at temperatures above 25 °C (Fig. 2). Above 25 °C the actual photochemical efficiency of PS II began to decline at spruce (Fig. 6b). The electron transport through PSII is considered the most labile component of photosynthesis at high temperatures (Sharkey 2005), so the improvement of PS II thermostability is often observed after an increase of growth temperature (Hikosaka et al. 2006). A higher thermostability of PS II was reported also in plants grown under elevated $[CO_2]$ and it is considered a reason for better resistance to higher temperature of EC plants (Taub et al. 2000; Ameye et al. 2012). F_0 started to increase at a higher temperature in EC spruce compared to AC (Fig. 6d), pointing to a better PS II thermostability. One reason may be a higher accumulation of zeaxanthin that was observed in EC plants (Špunda et al. 2005).

The acclimation of the photosynthetic apparatus to EC may protect plants from heat, but on the other hand can cause higher sensitivity to low temperature and frost. It is in agreement with studies on the effect of late spring and early autumn frosts on the CO_2 assimilation of plants grown under elevated $[CO_2]$ (Barker et al. 2005; Loveys et al. 2006; Bertrand et al. 2007). Different models predict that plants will shift their range to the north and to higher altitudes (Hanewinkel

et al. 2013), but if EC conditions leads to acclimation changes of the photosynthetic apparatus analogous to changes caused by a higher growth temperature, the shift of distribution range can be mitigate.

Our results confirmed the hypothesis that EC acclimation leads to an increase of the temperature optimum of the photosynthetic rate. Although a direct effect of elevated $[CO_2]$ on the shift of the photosynthetic temperature optimum was found, acclimation to higher temperatures was observed on the level of Rubisco carboxylation and electron transport.

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