

DOES LONG-TERM CULTIVATION UNDER ELEVATED CO₂ CONCENTRATION INFLUENCE ACCLIMATION OF ASSIMILATORY PROCESSES TO TEMPERATURE?

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Abstract

The aim of this study was to assess the hypothesis that an elevated (EC) CO₂ concentration [CO₂] leads to the reduction of stomatal conductivity, therefore also to an increase of leaf temperature (T_{leaf}) and thus finally to an acclimation of photosynthesis and other related processes to the higher temperature in selected tree species. The temperature response of photosynthetic characteristics and Chl *a* fluorescence at leaf temperature range 10-45 °C was measured in seedlings of Norway spruce and European beech cultivated at ambient (AC) and elevated [CO₂]. We confirmed that EC can really create conditions of elevated T_{leaf} in the long term acclimated plants compared to AC control. We did not observe temperature acclimation of EC plants in terms of changed temperature optimum of photosynthesis. Instead the acclimation occurred in temperature response of dark respiration and maximum rate of Rubisco carboxylation *in vivo*, thus confirming the initial hypothesis.

Keywords: *acclimation to elevated temperature; elevated CO₂ concentration; photosynthesis; Picea abies [L.] Karst.; Fagus sylvatica L.*

Introduction

As climate gradually changes towards conditions with CO₂ concentration ([CO₂]) as high as 700 ppm and global temperature increase up to 4 °C by year 2100 [1.] it is important to assess the effect of elevated CO₂ (EC) levels, elevated temperatures and their interactions on plants.

Temperature is affecting plants on different time scales. While specie's phylogenetic adaptation to temperature is one of the key determinants of its geographical distribution, during ontogenesis, plants have certain plasticity that allows for acclimation to current growth temperatures. This is often realised by shifting temperature optimum of photosynthesis ($T_{\text{opt}}(A)$) to the average growth temperature and by change in other CO₂ assimilation related processes to maximise plant's productivity [2., 3.].

EC is well known to have stimulating direct effect on net CO₂ assimilation rate (*A*) in C3 plants [4., 5]. It is caused mainly due to present Rubisco non-saturating [CO₂] and inhibition of photorespiration under EC. But this initial increase of carbon uptake can diminish over time [6.].

A is generally limited by one of the three biochemical processes: 1) enzymatic capacity of Rubisco; 2) RuBP regeneration capacity and 3) P_i regeneration capacity with different temperature optima. When the plant is exposed to EC, the equilibrium among these processes can be imbalanced and often leads to an acclimation change consisting of downregulation of non-limiting processes [7.].

EC treatment also generally causes reduction of stomatal conductivity (g_s) or even decrease of stomatal density in leaves in the long term [4.]. This translates into reduced dissipation of

latent heat via transpiration followed by an increase of leaf temperature (T_{leaf}) that is often observed in plants grown at EC [8., 9.].

The way how growth under EC affects temperature response of assimilatory processes is not yet well understood, especially when EC can impose elevated temperature treatment *per se*. In this study we assessed the hypothesis that EC conditions will lead to increase of leaf temperature of selected tree species due to decrease in g_s and transpiration rate and therefore related temperature acclimation of assimilatory processes.

Material and methods

The experiment was carried out at the experimental research station Bílý Kříž in the Beskydy Mountains, Czech Republic. The temperature response of different photosynthetic parameters was measured in T_{leaf} range of c. 10-45 °C using gas exchange analysis (LI-6400, LI-COR, USA). During main campaign in year 2010 (8th-12th, 15th-19th July) *in situ* measurements on sunny shoots/leaves of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* L.) grown at ambient (AC; 385 ppm) and elevated (EC; 700 ppm) CO₂ concentration were performed using daily course of temperatures. In 2011 (17th – 21st August) supplementary campaign was organised. This time we cut selected spruce and beech branches and placed them well watered into thermostat box Q-cell 60 (Pol-Lab, PL) where the measurements were conducted.

Fluorimeter PAM 101–103 (Heinz Walz, Effeltrich, Germany) was used for measurements of Chl *a* fluorescence temperature response. Samples were placed in temperature controlled (thermostat Julabo MC-4, Germany) chamber (Hansatech Instruments, UK) and measured in the dark or under low actinic light intensity (250 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Images from the thermal camera Ti55FT Fluke (Fluke, USA) were collected during day in one-hour intervals to determine the surface T_{leaf} .

Results and discussion

The reduction of g_s values in EC acclimated spruce (35-50%) and beech (40-47%) compared to plants cultivated under AC was documented during different previous experiments at the research site (Kořvancová a kol., 2009). Contrary to these findings we managed to confirm significant reduction of g_s only in beech (26%; $P < 0.05$). The respective value of mean g_s estimated across whole T_{leaf} range for EC grown spruce showed a trend of 13% decrease.

To further demonstrate the differences between T_{leaf} of AC and EC plants we analyzed thermal camera images of leaves taken under both conditions. On average, the EC plants experienced 2 °C higher T_{leaf} compared to AC plants with the highest difference (3.5 °C) in the afternoon. This difference cannot be explained by chamber effect (mean and maximum T_{leaf} increase 1 and 2 °C, respectively) and therefore supports our assumption that EC leads to increase in T_{leaf} in EC compared to AC plants.

We also observed significant ($P < 0.01$) increase in values of water use efficiency at reference temperature 20 °C ($\text{WUE}_{\text{max}}(20)$) in EC grown plants compared to AC and significant ($P < 0.01$) increase of temperature sensitivity of this parameter in beech trees grown in EC compared to AC.

Temperature response of A at saturating irradiance (A_{max}) measured at growth [CO₂] showed significant increase in $T_{\text{opt}}(A_{\text{max}})$ of beech grown in EC compared to AC (3 °C; $P < 0.01$) and spruce grown in EC compared to AC (6 °C; $P < 0.001$). However, after meticulous analysis it was shown that the shift in temperature optimum happened mainly due to the direct effect of EC, i.e. change from one A -limiting process (limitation by enzymatic capacity of Rubisco) to another

(RuBP regeneration capacity limitation) with different temperature optimum [3.]. This was proved by estimating $T_{\text{opt}}(A_{\text{max}})$ at the same $[\text{CO}_2]$ (700 ppm) for both AC and EC grown plants. Under these conditions we observed no change in $T_{\text{opt}}(A_{\text{max}})$ for any plant species and $[\text{CO}_2]$ treatment.

We estimated the response of maximum rate of Rubisco carboxylation *in vivo* (V_{Cmax}) to temperature and the temperature optimum ($T_{\text{opt}}(V_{\text{Cmax}})$) of this biochemical process. The computed $T_{\text{opt}}(V_{\text{Cmax}})$ for EC compared with both AC grown species was significantly ($P < 0.05$) higher (3 °C). This is a temperature acclimation trait consistent with [10.] who observed increase in activation energy of V_{Cmax} in both *Eucalyptus globulus* plants acclimated to elevated temperature only or acclimated to elevated temperature and EC compared with control plants. They discuss that $T_{\text{opt}}(V_{\text{Cmax}})$ shift to higher temperatures in plants acclimated to temperature increase did not occur because the conditions were already at the limit of photosynthetic capacity of *E. globulus*. After decrease of temperatures in winter $T_{\text{opt}}(V_{\text{Cmax}})$ shifted by c. 5 °C towards lower temperatures.

Measurements of dark respiration at reference temperature 20 °C ($R_{\text{D}}(20)$) showed significant ($P < 0.05$) decrease in EC compared to AC grown beech (24%). This is a trait discussed only in relation with acclimation to elevated temperature and cannot be explained simply by $[\text{CO}_2]$ change [11.].

Spruce grown at EC showed slightly higher $F_{\text{V}}/F_{\text{M}}$ values at 46 and 48 °C compared to AC treatment. Although not significant, it could be an indication of PS II temperature acclimation in spruce under EC conditions.

We did not observe any change in temperature optima of ETR after long term acclimation to EC in spruce and beech but we noticed ETR stimulation by EC conditions in beech and decrease of ETR in spruce. This result indicates an improvement in light use capacity in photochemical reactions of beech after acclimation to EC while spruce exhibits a mild acclimation depression of photosynthetic processes related to quantum yield of photochemical reactions of PS II.

Non-photochemical efficiency (D) complements ETR results and shows higher values for spruce after acclimation to EC across whole temperature range in contrast with lower D values of EC acclimated.

Conclusion

In this study we confirmed that EC can really create conditions of elevated T_{leaf} in the long term acclimated plants compared to AC control. Although the shift in $T_{\text{opt}}(A_{\text{max}})$ observed in EC compared to AC plants measured at growth $[\text{CO}_2]$ is probably attributed solely to direct effect of EC, i.e. shift to a A -limiting process with different temperature optimum, we observed traits that exhibit clear acclimation to elevated temperatures. One of them is significant decrease of $R_{\text{D}}(20)$ in beech grown in EC compared to AC. The second is a shift in $T_{\text{opt}}(V_{\text{Cmax}})$ of both spruce and beech grown in EC compared to control by 3 °C towards higher temperatures. The results presented here support the hypothesis that both in Norway spruce and European beech long term acclimation to EC led to temperature acclimation of assimilatory processes.

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Abstrakt

Cílem této studie bylo ověřit hypotézu, že zvýšená (EC) koncentrace CO₂ [CO₂] vede k redukci průduchové vodivosti a tudíž také ke zvýšení teploty listu (T_{leaf}) a tak v konečném důsledku k aklimaci fotosyntézy a dalších souvisejících procesů na zvýšené teploty u vybraných druhů dřevin. Závislost charakteristik fotosyntézy a Chl *a* fluorescence na teplotě listu v rozsahu 10-45 °C byla měřena na sazenicích smrku ztepilého a buku lesního kultivovaných při okolní (AC) a zvýšené [CO₂]. Potvrdili jsme, že EC opravdu může vytvořit podmínky zvýšené T_{leaf} u dlouhodobě aklimovaných rostlin v porovnání s AC kontrolou. Nepozorovali jsme teplotní aklimaci EC rostlin ve smyslu změny teplotního optima fotosyntézy. Místo toho k aklimaci došlo u závislosti temnotní respirace a maximální rychlosti karboxylace *in vivo*, čímž se potvrdila původní hypotéza.