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BRIEF COMMUNICATION

Stem respiration of Norway spruce trees under elevated CO_2 concentration

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Abstract

Measurements of stem respiration were conducted for a period of four years (1999 - 2002) in 14-year old Norway spruce (*Picea abies* [L.] Karst) trees exposed to ambient (CA) and elevated CO_2 concentration (CE; ambient plus 350 μmol mol^{-1}). Stem respiration measurements of six trees per treatment were carried out 2 - 3 times per month during the growing season. Stem respiration in CE treatment was higher (up to 16 %) than in CA treatment. Temperature response of stem respiration (Q_{10}) for the whole experimental period ranged between 1.65 - 2.57 in CA treatment and 2.24 - 2.56 in CE treatment. The mean stem respiration rate normalized to 10 °C (R_{10}) in CA and CE treatments ranged between 1.67 - 1.95 and 2.19 - 2.72 μmol(CO_2) m^{-2} s^{-1}, respectively. Seasonal variations in stem respiration were related to temperature and tree growth.

Additional key words: glass lamellas domes, R_{10}, tree growth.

Since atmospheric [CO_2] is predicted to reach 700 μmol mol^{-1} by the end of the 21st century (Amthor 1991) if no reduction in anthropogenic carbon emission occurs, it is important to know how plants will react to such a disturbance. Therefore, the effect of elevated [CO_2] on plant respiration, and woody respiration in particular, must be known. Few studies have been done about the long-term effects of elevated [CO_2] on woody tissue. Wullschleger *et al*. (1995) reported no significant effects of elevated [CO_2] on growth and maintenance stem respiration of *Quercus alba* L. trees exposed to elevated CO_2 over 4-year period. On the other hand, Carey *et al.* (1996) showed an increase of stem respiration rate in *Pinus ponderosa* grown under elevated [CO_2]. They also found no difference in growth rate or growth respiration between two treatments, but they assumed an increase in maintenance respiration to be responsible for the increase in total stem respiration. Dvořák and Opuštilová (1997) found lower total stem respiration rates in *Picea abies* trees grown under elevated [CO_2]. In the same experiment Janouš *et al*. (2000) found that elevated [CO_2] prolonged the physiological activity of the stem at the end of the growing season, but the stem maintenance respiration was not affected. Moreover, Gielen *et al.* (2003) reported that stem respiration rates of three *Populus* species (*P. alba, P. nigra, P. euramericana*) were not affected by CO_2 enrichment. Zha *et al.* (2005) suggested that increase in stem respiration of *Pinus sylvestris* trees under elevated [CO_2] for 5 years, was only partly a result of increased growth rate as elevated [CO_2] increased the maintenance component of respiration more than the growth component. Liberloo *et al.* (2008) reported that variation in stem CO_2 efflux of *Populus nigra* grown under elevated [CO_2] could not be satisfactorily explained by changes in temperature. On the base of these results it is still not clear if woody tissue respiration increase or decrease during acclimation to elevated [CO_2] and how long-term elevated [CO_2] influences woody tissue respiration. The aim of this study was to determine the daily course of stem woody tissue respiration under different atmospheric CO_2 concentrations and to elucidate the mechanism of the long-term impact of elevated CO_2 on woody tissue respiration.

The experiment was carried out at the Experimental Ecological Study Site (EESS) Bílý Kříž (49°30' N,

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Abbreviations: CA - ambient CO_2 concentration; CE - elevated CO_2 concentration; Q_{10} - increase in respiration rate per 10 °C; R_{10} - normalized respiration rate to a temperature of 10 °C.

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18°32' E, altitude of 908 m a.s.l.) situated in the Moravian-Silesian Beskydy Mts., Czech Republic. Two identical experimental plots were established in 1996, with 11-year old Norway spruce [*Picea abies* (L.) Karst] trees. Each plot contains 56 trees and it is covered with glass lamellas dome. Glass lamellas dome is a special technology used for studies of elevated CO_2 concentration in juvenile forest, the dome has dimensions of 10 × 10 m in length and 7 m high in the central part (see Urban *et al*. 2001 for more details). The first dome (CA-ambient) contains ambient [CO_2], and the second dome (CE-elevated) contains elevated [CO_2], *i.e.* ambient plus 350 μmol mol^{-1}. Stem CO_2 efflux measurements were carried out during four growing seasons (1999 - 2002) in six trees per variant, using an infrared gas analyser *Li-6250* (*LICOR*, Lincoln, NE, USA) operating in a closed mode. Self-made PVC chambers (cylinder-shaped divided in two parts), sealed by neoprene have been used. Chambers of different sizes were used according to actual stem diameter increment. Stem chambers were always fixed in the same place (about 0.3 m above the soil surface) and only during the measurements of CO_2 efflux, allowing a minimum impact in the woody tissue growth. Measurements were performed 2 - 3 times per month in campaigns of 2 - 3 d, from early morning (06:00) to late evening (21:00) in both variants (CA and CE). The measurements were carried out from early May until late October. Woody tissue respiration rates were expressed per surface area. Because the respiration measurements were realized in woody parts of the trees which contain a large volume of non-photosynthesizing tissues, it was assumed that re-fixation did not occurred during our experiment. Stem temperature was recorded in all investigated trees, using a thermistor (*PT1000*, *HIT*, Uherské Hradiště, Czech Republic) permanently installed in the cambium layer (0.25 m above soil surface) with north orientation and connected to data logger (*Delta-T*, Cambridge, UK). Data analysis was done following the same steps as in Acosta *et al.* (2008). To determine the time-lag response of CO_2 efflux to tissue temperature (Ryan *et al*. 1995), the measured CO_2 efflux were shifted in time against woody tissue temperature recorded in different time relative to the moment of CO_2 efflux measurement. The highest coefficient of determination (r^2) for this relation was accepted.

Norway spruce trees had already been exposed to CA and CE for 2 years prior to initiation of stem respiration measurements. Diurnal courses of stem respiration rates are presented as an example for a sunny summer day, July 10th 2001 (Fig. 1). Spruce trees grown at CE manifested higher rates of stem respiration compared to

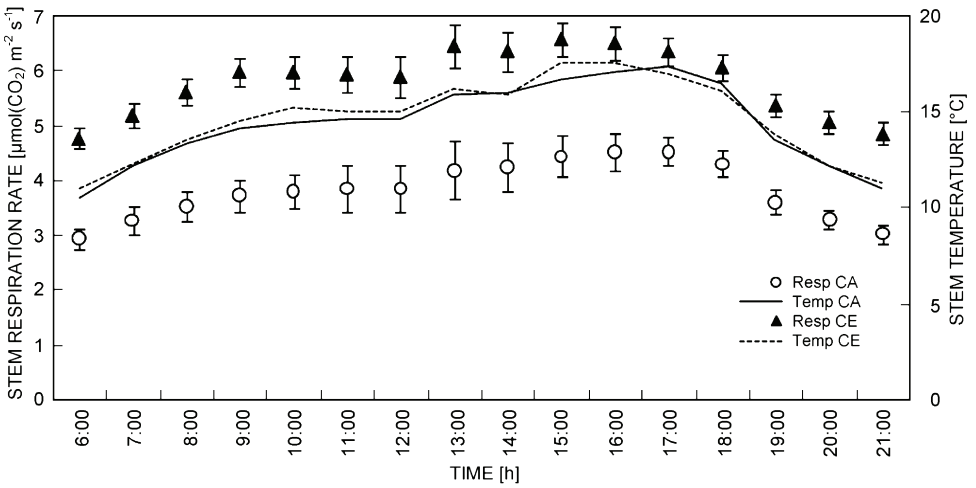

Fig. 1. Mean diurnal courses of stem respiration rate and stem temperature (cambium) in ambient [CO_2] (CA) and elevated [CO_2] (CE) during a summer day (July 10th 2001). Each symbol represents the mean of 6 trees per treatment (12 consecutive measurements were done per tree during the photoperiod). *Error bars* indicate ± SD.

Table 1. Ranges of measured stem respiration rate, stem woody tissue Q_{10} values and normalized stem respiration rate (R_{10}) [μmol(CO_2)$m^{-2}s^{-1}$] at ambient (CA) and elevated (CE) CO_2 concentration in each growing season of the experiment.

Year	Respiration rate		Q_{10}		R_{10}	
	CA	CE	CA	CE	CA	CE
1999	0.41 - 6.32	0.56 - 7.65	2.46	2.43	1.68	2.31
2000	0.29 - 6.39	0.36 - 8.85	1.68	2.49	1.86	2.32
2001	0.68 - 6.57	0.74 - 7.86	2.26	2.29	1.93	2.70
2002	0.46 - 6.62	0.65 - 8.02	2.05	2.33	1.78	2.67

those grown at CA during the main part of the day. Stem respiration rate ranged from 0.29 to 6.57 μmol(CO_2) m^{-2} s^{-1} for CA and from 0.36 to 8.85 μmol(CO_2) m^{-2} s^{-1} for CE (Table 1). The highest stem respiration rates were found in CE at the end of spring and beginning of the summer (June - July). This trend was observed in all four growing seasons. Rates of stem respiration during the autumn were lower than in summer. When integrated over the whole experiment duration (1999 - 2002), stem CO_2 efflux was higher (by 16 %) in CE compared to CA. The mean stem increase in respiration rate per 10 °C (Q_{10}) at CA and CE per each growing season are shown in Table 1. Normalized respiration rate to a temperature of 10 °C (R_{10}) respiration rates were higher in CE compared to CA throughout all the growing seasons (Table 1). The highest respiration rates occurred between the end of spring (June) and in the middle of the summer (August). No statistically significant difference between stem woody tissue temperatures in CA and CE was found. In both CA and CE a clear dependence of respiration to temperature was found. Over the whole course of the experiment a good coefficient of regression (r^2) was found, which indicated tight relation between stem respiration rate and woody tissue stem temperature. The annual coefficients of regression (r^2) per variant were 0.76 in 1999, 0.81 in 2000, 0.82 in 2001, 0.79 in 2002 for CA and 0.80 in 1999, 0.79 in 2000, 0.87 in 2001 and 0.83 in 2002 for CE.

In both variants, woody tissue stem temperature recorded between 10 to 40 min before stem respiration measurements fitted better ($r^2 \geq 0.67$ in both, CA and CE) the stem surface CO_2 efflux than the current temperature measured in the time of respiration measurements. The largest time-lag response (approx. 40 min) was observed during the summer, the shortest (approx. 10 min) in autumn for both variants. This difference could be explained by the differences of stem growth rates in individual variant or differences of the transpiration stream and slow gas diffusion. Stem diameter values (at 0.3 m above the ground) were significantly higher ($P < 0.05$) for trees exposed to CE compare to trees at CA. No statistically significant differences in stem respiration rate related to a stem surface were found. Amthor (1991) pointed out that trees exposure to elevated [CO_2] altered growth or maintenance-related processes, either by directly inhibiting respiratory enzymes or indirectly by changing tissue chemistry. However, Carey *et al*. (1996) considered that increased stem respiration in response to elevated [CO_2] could be a result of higher cost of maintaining proportionally greater protein content in the cambium or phloem. Moreover, Zha *et al*. (2005) suggested that the increase in stem respiration is partly a result of the increased growth rate and concluded that elevated [CO_2] increases the maintenance component of respiration more than the growth component. We consider that the different stem respiration rates between trees in the elevated and ambient CO_2 treatments are related to growth processes influenced by assimilation. In our experiment, trees grown in CE showed higher growth compared to CA, thus, growth processes at CE required more energy than in CA.

In our results Q_{10} exhibited seasonal variation possibly explained by the evidence that respiratory Q_{10} is not constant and dependent on both the shape of the temperature response curve and the range of measurement temperature used in its determination (Stockfors 2000). Similarly to Gielen *et al.* (2003), enriched CO_2 conditions did not affect the relationship between stem respiration and temperature in our study. However, obtained Q_{10} values in our study were consistent with other values reported in literature (Wullschleger *et al.* 1995, Carey *et al.* 1996, Janouš *et al.* 2000, Gielen *et al.* 2003). From the point of view of the time-lag, our results obtained under elevated [CO_2] are similar to these obtained in field condition (Ryan *et al*. 1995, Acosta and Brossaud 2001, Acosta *et al.* 2008).

Another explanation for the differences in stem respiration rate between CA and CE treatments is related to the transport of CO_2 by the transpiration stream. It has been proposed that a portion of CO_2 respired from sapwood enters the transpiration stream and is carried upward in the xylem sap rather than diffusing outward through the bark (Negisi 1979). This would result in greater underestimation of CO_2 efflux from trees grown in ambient [CO_2] because they are presumably transpiring at a faster rate than the more water conservative trees grown in elevated [CO_2] (Eamus 1991). On the other hand, Kupper *et al*. (2006) found *vice versa* results compared to Eamus (1991), moreover, Bowman *et al*. (2005) in an experiment of sap flow rate related to stem respiration found that 86 to 91 % of woody tissue respired CO_2 diffused to the atmosphere over a 24-h period. Furthermore, Ceulemans and Mousseas (1994) reported that the acclimation process has mainly attributed to source-sink status, when elevated [CO_2] increase the amount of available sugars and the plant responded differently depending on its storage capacity. Thus, the acclimation effect of elevated [CO_2] was partly responsible for differences found in stem respiration at CA and CE. In general, the increase of tree growth in elevated [CO_2] results from an increase in both leaf area and leaf photosynthetic rate, and also frequently from a decrease in shoot respiration rate. Moreover, Li *et al.* (2009) reported that elevated [CO_2] also influenced some endogenous plant growth regulators.

The seasonal differences in woody tissue respiration, together with differences in Q_{10} or R_{10} between years, indicate that year to year changes in respiration were assumed to be related not solely to seasonal temperature and elevated [CO_2] but also to growth, photosynthesis and metabolic activity.

References

Acosta, M., Brossaud, J.: Stem and branch respiration in a Norway spruce forest stand. - J. Forest Sci. **47**: 136-140, 2001.

Acosta, M., Pavelka, M., Pokorný, R., Janouš, D., Marek M.V.: Seasonal variation in CO_2 efflux of stems and branches of Norway spruce trees. - Ann. Bot. **101**: 469-477, 2008.

Amthor, J.S.: Respiration in a future, higher-CO_2 world. - Plant Cell Environ. **14**: 13-20, 1991.

Amthor, J.S.: Plant respiratory responses to the environmental and their effects on the carbon balance. In: Wilkinson, R.E. (ed.): Plant-Environment Interactions. Pp. 501-554. Marcel Dekker, New York 1994.

Bowman, W.P., Barbour, M.M., Turnbull, M.H., Tissue, D.T., Whitehead, D., Griffin, K.L.: Sap flow rates and sapwood density are critical factors in within- and between-tree variation in CO_2 efflux from stems of mature *Dacrydium cupressinum* trees. - New Phytol. **167**: 815-828, 2005.

Carey, E.V., Delucia, E.H., Ball, J.T.: Stem maintenance and construction respiration in *Pinus ponderosa* grown in different concentrations of atmospheric CO_2. - Tree Physiol. **16**: 125-130, 1996.

Ceulemans, R., Mousseus, M.: Effects of elevated atmospheric CO_2 on woody plants. - New Phytol. **127**: 425-446, 1994.

Dvořák, V., Opuštilová, M.: Respiration of woody tissue of Norway spruce in elevated CO_2 concentration. - In: Mohren, G.M.J., Kramer, K., Sabaté, S. (ed.): Impact of Global Change on Tree Physiology and Forest Ecosystems. Pp. 47-51. Kluwer Academic Publisher, Dordrecht 1997.

Eamus, D.: The interaction of rising CO_2 and temperatures with water use efficiency. - Plant Cell Environ. **14**: 843-852, 1991.

Gielen, B., Scarascia-Mugnozza, G., Ceulemans, R.: Stem respiration of *Populus* species in third year of free-air CO_2 enrichment. - Physiol. Plant **117**: 500-507, 2003.

Gonzáles-Meyer, M.A., Siedow, J.N.: Direct inhibition of mitochondrial respiratory enzymes by elevated CO_2: does it matter at the tissue or whole-plant level? - Tree Physiol. **19**: 253-259, 1999.

Janouš, D., Pokorný, R., Brossaud, J., Marek, M.V.: Long-term effect of elevated CO_2 on woody tissue respiration of Norway spruce studied in open-top chambers. - Biol. Plant. **43**: 41-46, 2000.

Kupper, P., Sellin, A., Klimánková, Z., Pokorný, R., Puértolas, J.: Water relations in Norway spruce trees growing at ambient and elevated CO_2 concentrations. - Biol. Plant **50**: 603-609, 2006.

Li, X.-M., He, X.-Y., Zhang, L.-H., Chen, W., Chen, Q.: Influence of elevated CO_2 and O_3 on IAA, IAA oxidase and peroxidise in the leaves of ginkgo trees. - Biol. Plant. **53**: 339-342, 2009.

Liberloo, M., De Angelis, P., Ceulemans, R.: Stem CO_2 efflux of a *Populus nigra* stand: effects of elevated CO_2 fertilization, and shoot size. - Biol. Plant **52**: 299-306, 2008.

Negisi, K.: Bark respiration rate in stems segments detached from young *Pinus densiflora* trees in relation to artificial sap flow. - J. jap. forest. Soc. **61**: 88-93, 1979.

Penning de Vries, F.W.T.: the cost of maintenance processes in plant cells. - Ann. Bot. **39**: 77-92, 1975.

Ryan, M.G., Gower, S.T., Hubbard, RM., Waring, R.H., Gholz, H.L., Cropper, W.P., Running, S.M.: Woody tissue maintenance respiration of four conifers in contrasting climates. - Oecologia **101**: 133-140, 1995.

Stockfors, J.: Temperature variation and distribution of living cells within tree stems: implications for stem respiration modeling and scale up. -Tree Physiol. **20**: 1057-1062, 2000.

Urban, O., Janouš, D., Pokorný, R., Marková, I., Pavelka, M., Fojtik, Z., Šprtová, M., Kalina, J., Marek, M.V: Glass domes with adjustable windows: A novel technique for exposing juvenile forest stands to elevated CO_2 concentration. - Photosynthetica **39**: 395-401, 2001.

Wullschleger, S.D., Norby, J.R., Hanson, J.P.: Growth and maintenance respiration in stems of *Quercus alba* after four year of CO_2 enrichment. - Physiol. Plant **93**: 47-54, 1995.

Zha, T.S., Kellomaki, S., Wang, K.Y., Ryyppo, A.: Respiratory response of Scots pine stems to 5 years of exposure to elevated CO_2 concentration and temperature. - Tree Physiol. **25**: 49-56, 2005.