Long-term effects of elevated CO_2 on woody tissues respiration of Norway spruce studied in open-top chambers

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Abstract

In an open-top chamber experiment located in a mountain stand of 14-years-old Norway spruce (*Picea abies* [L.] Karst.), trees were continuously exposed to either ambient CO_2 concentration (A), or ambient + 350 μmol mol^{-1} (E) over four growing seasons. Respiration rates of different woody parts (stem, branches, coarse roots) were measured during the last growing season. The calculated increase in the respiration rate related to a 10 °C temperature change (Q_{10}) was different in stem compared to branches and roots. Differences between the E and A variants were statistically significant only for roots in the autumn. Stem maintenance respiration (R_{Ms}) measured in April and November (periods of no growth activity) were not different. The stem respiration values (R_s) were recalculated to a standard temperature of 15 °C to estimate the seasonal course. The obtained R_s differed significantly between used variants during July and August. At the end of the season, R_s in E decreased slower than in A, indicating some prolongation of the physiological activity under the elevated CO_2 concentration. The total stem respiration carbon losses for the investigated growing season (May - September) were higher for A (2.32 kg(C) m^{-2} $season^{-1}$) compared to E (2.12 kg(C) m^{-2} $season^{-1}$). The respiration rates of the whorl branches (R_b) were lower compared with the stem respiration but not significantly different between the used variants. The root respiration rate was increased in E variant.

Additional key words: elevated CO_2 effects, *Picea abies*, Q_{10}.

Introduction

Forest trees respond to an increase of atmospheric CO_2 mainly through changes in photosynthesis. The forest responses are of great importance because of their role in accumulation of atmospheric carbon (Eamus and Jarvis 1989). Besides photosynthesis, respiration is an important physiological process involving conversion of assimilates and storage components to energy and substrate for biosynthesis. Moreover, respiration is regarded as a major component of the annual carbon balance of plants (Ryan 1990). Generally, respiration is divided in two main components, *i.e.* growth and maintenance respiration (McCree 1970, Sprugel and Benecke 1988). The possible effects of the long-term influence of elevated CO_2 are still unknown. For example, Norby (1994) and Rogers *et al.* (1994) results have shown some effects of elevated atmospheric CO_2 on roots, but from some recent reviews (Stulen and den Hertog 1993, Rogers *et al.* 1996) there is still no evidence about unified opinions on elevated CO_2 effects on respiration. Plants grown under elevated CO_2 often exhibit the largest biomass gain below-ground (Rogers *et al.* 1996). Moreover, enhanced root exudation (Rouhier *et al.* 1996) and fine roots turnover rates (Norby *et al.* 1992) were described.

Because of the amount of carbon translocated within the trees (above/below-ground biomass components) and carbon respired, the importance of knowledge on woody parts respiration response to the long-term elevated CO_2 effects is important for the evaluation of elevated CO_2 impacts on biomass production.

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Abbreviations: R_{Ms} - maintenance respiration rate of stems; R_s, R_b, R_r - respiration rate of stems, branches, and coarse roots

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Materials and methods

Plants and experiment design: The long-term influence of elevated concentration of atmospheric CO_2 on young Norway spruce (*Picea abies* [L.] Karst.) trees (14-years-old, average height - 2.5 m) was investigated at the Experimental Research Site of Bílý Kříž in the Moravian-Silesian Beskydy Mts., Czech Republic (49° 30′ N, 18° 32′ E, 943 m a.s.l.). Eight open top chambers (OTCs) were constructed around trees, with one tree per chamber (see Janouš 1996 for detailed description). Four OTCs were supplied with the ambient (natural) CO_2 concentration (A) and four OTCs with air containing ambient plus 350 μmol(CO_2) mol^{-1} (E). The experiments began in May 1992.

Woody tissues respiration measurement: The respiration rate [μmol (CO_2) m^{-2} s^{-1}] from the surfaces of stems, branches and coarse roots was measured during the April - November 1995, *i.e.* during the fourth season of the elevated CO_2 experiments. Measurements in April and November were used to assess maintenance respiration rates. The respiration rate was estimated as the rate of CO_2 efflux in a portable photosynthesis system *LI-6200* (*Li-Cor*, Lincoln, USA). Special respiration chambers constructed for stem, branch, and root respiration measurements were made from opaque PVC plastic and were removable. The used technique for the estimation of woody tissues respiration was close to that published by Martin *et al.* (1994).

The stem respiration of each tree enclosed in individual OTCs was measured at height 1.3 m above the ground. The plastic stem chamber (very small inner volume) with foam gasket material was simply attached to thin plastic rings permanently sealed around the stem only during the respiration rate assessment. The bark surface temperature inside the chamber was measured with a thermocouple thermometer. The branch respiration was measured on the fourth (from the top of the tree) branch whorl located in the south/south-west section of the crown. The respiration chamber was of the cylindrical shape, and was attached to the branch in the same way as the stem chambers. Similar chambers as for the branches were used for the measurement of coarse root respiration. A root of about 2 - 2.5 cm in diameter was very carefully denuded. The respiration chamber was attached to the root and again covered with the soil. These chambers remained on the roots during the whole growing season and were not ventilated. The reason was a presumption, that the climate (air humidity, temperature and CO_2 concentration) of a chamber without artificial ventilation seemed to be closer to natural soil conditions.

The measurements of the woody tissues respiration during season 1995 were carried out on the basis of a five days sequence at each mentioned month. Respiration rates were related to the actual tissue surface temperature inside the chamber. The respiration rate increase with the temperature increase of 10 °C, the Q_{10} coefficient (Kinerson 1975, Linder and Troeng 1981), for spring (*i.e.* May - June), summer (*i.e.* July - August), and autumn (*i.e.* September - October) was calculated as $Q_{10} = e^{10b}$, where b is the linear slope of the relation between natural logarithm of respiration rate and tissue temperature (Svenson 1989). The obtained Q_{10} values were used for the recalculation of measured respiration rate on a reference temperature (15 °C) and for the seasonal carbon efflux estimation.

Statistical processing of data: Each treatment (*i.e.* A and E) was repeated in four OTCs and each measurement of the respiration rate by the gas exchange system was represented by nine replications. An evaluation of the statistical significance of differences between A and E was based on the *F*-test and *t*-test (the zero assumption was the equality of the mean values. This analysis was carried out using the *EXCEL* programme package.

Results

Stem respiration: All measurements carried out during the selected time period of the growing season (*i.e.* spring, summer, autumn) were used for the calculation of the Q_{10} values but statistically significant differences between A and E variants were not found for the stems and the branches (Table 1). The Q_{10} values of stems were remarkably different compared to branches and roots. Stem maintenance respiration (R_{Ms}) was measured in April and November (in periods of no growth activity). The obtained R_{Ms} values for A and E were not significantly different and also the shape of curve expressing relation of R_{Ms} to the stem surface temperature was similar in both investigated variants (Fig. 1). Values of R_s were recalculated to a standard temperature 15 °C (Martin *et al.* 1994). The obtained R_s differed between the variants used. The significantly higher values of R_s in A (P = 0.05) were obtained in the July and August (Fig. 2). At the end of the season, R_s in E decreased slower in comparison with R_s in the A, indicating some prolongation of the physiological activity under elevated CO_2. The total stem respiration (calculated on the basis of the months integrals) for the investigated growing season (May - September) was higher for A (2.32 kg(C) m^{-2} $season^{-1}$) compared to E (2.12 kg(C) m^{-2} $season^{-1}$).

Table 1. Q_{10} values in different woody tissues of trees cultivated in elevated (E) and in ambient (A) CO_2 concentrations during the growing season 1995.

	Spring		Summer		Autumn	
	A	E	A	E	A	E
Stems	1.95 ± 0.17	1.96 ± 0.12	2.15 ± 0.23	2.15 ± 0.19	2.09 ± 0.14	2.09 ± 0.24
Branches	2.43 ± 0.81	2.90 ± 0.85	2.52 ± 0.41	2.94 ± 0.64	2.15 ± 0.75	2.45 ± 0.85
Roots	2.51 ± 0.60	2.43 ± 0.71	2.55 ± 0.16	2.51 ± 0.09	2.52 ± 0.12	2.29 ± 0.03

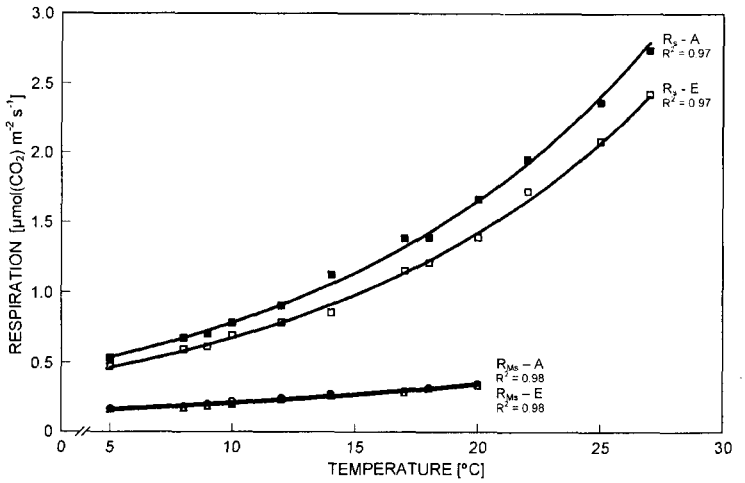

Fig. 1. Relationships between the stem maintenance respiration rate (R_{Ms}) and the stem temperature (values obtained in April and October 1995) and between the stem respiration rate (R_s) and the stem temperature (July 1995). The trees were grown in elevated (ambient + 350 μmol(CO_2) mol^{-1}) CO_2 concentration (E) and in ambient CO_2 concentration (A). Values of the coefficient of determination of used fitted curves are written in the figure.

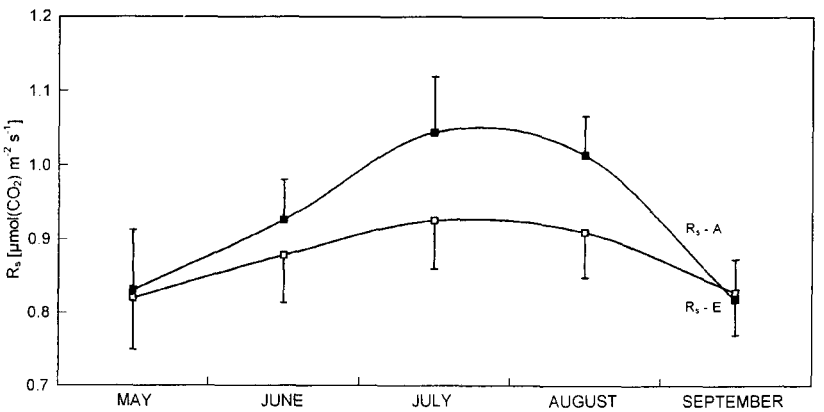

Fig. 2. Seasonal course of the stem respiration rate (R_s) re-calculated to 15 °C. The trees were cultivated in elevated (E) and in ambient (A) CO_2 concentrations. *Vertical bars* represent SE.

Branch respiration: The respiration rates of the whorl branches (R_b) (Fig. 3) were lower compared with the stem respiration (Fig. 1). Likewise, the Q_{10} values (Table 1) were different compared with the stem values. The values of Q_{10} were not significantly different between the variants and investigated periods. However, the significantly different values of R_b between A and E were found at temperatures higher than 25 °C (Fig. 3).

Coarse root respiration: The obtained values of root respiration (R_r) indicate the metabolic activity of this tissue (Fig. 3). Differences in root respiration rate

between the E and A are obvious, especially at temperatures higher than 8 °C. Differences in Q_{10} between the variants and periods of the growing season were found in autumn (Table 1).

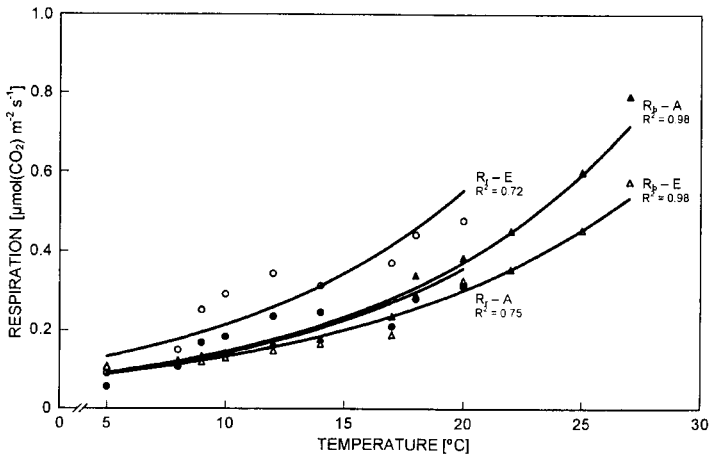

Fig. 3. Relationship between the branch respiration rate (R_b) and the branch temperature, and between the coarse root respiration rate (R_r) and root surface temperature (July 1995). The trees were cultivated in elevated (E) and in ambient (A) CO_2 concentrations. Values of the coefficient of determination of used fitted curves are written in the figure.

Discussion

Literature sources supply very inconsistent results on the effects of elevated CO_2 on woody tissues respiration (Amthor 1991, Bunce 1992, Norby *et al.* 1992). A possible reason for that is the use of different and often insufficiently described methods, and the use of the plants in a very different stages of ontogeny. From this point of view, the method for woody mass growth/maintenance respiration which was used in the presented article seems to be regarded as a standard (Gansert 1994, Ryan *et al.* 1994, 1995, Vivin *et al.* 1995).

Obtained exponential dependency of the stem maintenance respiration rate (R_{Ms}) on stem surface temperature is in agreement with Kinerson (1975) and Butler and Landsberg (1981). For the Norway spruce located in the vicinity of the experimental site of Bílý Kříž, Janouš (1990) obtained the exponential dependence of R_{Ms} on stem surface temperature in the interval of 8 - 25 °C. Comparable values of R_M for other coniferous species at the same temperature interval were described by Ryan *et al.* (1995). Long-term influence of elevated CO_2 was responsible for the lower values of R_{Ms} (Fig. 1). However, during the period of the maximal growth activity, which is on the Bílý Kříž locality from the middle of June to the middle of July (Janouš *et al.* 1995), the portion of R_{Ms} on the whole stem respiration amounted to 20 and 28 % for A and E, respectively. Higher R_{Ms} portion on the R_s (up to 50 %) was described by Ryan *et al.* (1994) for tropical wet forest species. The R_M is mainly connected with the protein turnover and assimilates translocation (McCree 1970, Sprugel and Benecke 1988). The obtained lower R_{Ms} values in the whole interval of tissue temperatures in E-variant can be a demonstration of the mild nitrogen deficiency in the stem tissue because of its major translocation into needles (Ryan *et al.* 1994, 1995). However, Wulschleger *et al.* (1995) described for young *Quercus alba* seedling cultivated under elevated CO_2 higher values of R_{Ms} and R_s in comparison to the control (ambient) variant.

Commonly described seasonal courses of the R_s (Havranek 1981, Linder and Troeng 1981) were confirmed in the both variants used. Seasonal course of R_s in E-variant demonstrated lower respiration losses, which indicate some changes in the metabolic activity of trees exposed to the long-term influence of elevated CO_2. Respiration rate is strongly related to the metabolic activity of respiring tissue (Ryan 1990) and in E no evidence on increased activity of radial growth was found (Marek 1998). Stem respiration is mainly (up to 70 %) a respiration of xylem and the rest is the respiration of phloem and woody parenchyma cells (Havranek 1981). Thus, woody respiration rate expressed on volume basis [$\mu mol(CO_2)\ m^{-3}\ s^{-1}$] is low in stems which present a low wood density (Ryan 1990). Indeed, the executed analysis of woody tissue quality (Marek 1998) brought evidence of the negative effects of the long-term influence of elevated CO_2 on woody tissue density. It means that lower R_s values in E compared to the A could be interpreted as a possible consequence of the lower portion of live parenchyma cells in wood. Moreover, the stem respiration rate on seasonal basis is connected to the transpiration

rate and stomatal conductance (Ryan 1990). Long-term influence of elevated CO_2 caused decreased stomatal conductance (Marek *et al.* 1995). It means that lower R_s in E can be partly a result of lower sap flow in the stem, because of the connection between the CO_2 efflux and the amount of sap containing dissolved CO_2 (Sprugel and Benecke 1988).

Branch respiration is closely connected to the assimilation activity of leaves carried by branches (Wanner and Tinnin 1986). Because the significant depression of assimilation (down-regulation) was found in E (Marek *et al.* 1995, 1997), obtained lower values of R_b could be interpreted as a result of lower assimilate supply.

Coarse root respiration rate (R_r), *i.e.* respiration of roots with a diameter of 2.0 - 2.5 cm was in E significantly higher compared with the A. The method used for roots respiration and shape of R_r - soil temperature relation was comparable to those published by Gansert (1994) and Vivin *et al.* (1995). Root respiration is not generally related to the soil environmental CO_2 content (Palta and Nobel 1989) and is regarded as a manifestation of the internal metabolic integrity of the tree. Root respiration is mainly related to the active ion uptake (Veen 1981, Lambers *et al.* 1996). Elevated CO_2 is responsible for higher mineral ions uptake (Eamus and Jarvis 1989). This can result in the increased root growth (Marek 1998) and increased sorption activity of roots. Positive effect of long-term elevated CO_2 on root respiration was described by Gifford *et al.* (1985) for wheat, by Vivin *et al.* (1995) for oak, and by Janssens *et al.* (1997) for Scots pine. The next possible explanation of increased root respiration might be the positive effect of elevated CO_2 on carbohydrates exudation by roots and in consequence increased activity of soil microorganisms resulting in an increased availability of mineral ions in soil solution (Davis and Porter 1989, Zak *et al.* 1993).

Despite presented results on long-term influence effects of elevated CO_2 on individual components of woody tissues respiration of Norway spruce, the problem remains still ambiguous and further research on this subject is necessary.

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