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DYNAMICS OF TEMPERATURE NORMALIZED STEM CO_2 EFFLUX IN NORWAY SPRUCE STAND

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Abstract

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Respiration of stems contributes approximately 8 to 13 % to the total respiration of forest ecosystem, which is not negligible, and it has to be included in carbon flux estimates. The aim of this study was to determine dynamics of stem CO_2 efflux during the growing season in Norway spruce stand and factors affecting this efflux. Continuous measurements of stem CO_2 efflux were carried out by an automated system during the growing season in 2006–2009. Further measured characteristics were stem temperature, stem increment and precipitations. Stem CO_2 efflux was in tight relationship with changes in temperature with the mean coefficient of determination of 0.76. This infers that temperature was the main factor driving changes in CO_2 efflux during the season. To eliminate effect of temperature and determine other factors influencing stem CO_2 efflux, CO_2 efflux was normalized for temperature of 10 °C (R_{10}). Basic seasonal course of R_{10} followed the pattern of stem growth rate with its maxima in June and July. The other factor effect, which was possible to determine, was presence of rainfall. Rainfall strong enough caused mostly increase in R_{10}. This effect was the most significant when the R_{10} course had a decreasing trend in the second part of the growing season.

soil CO_2 efflux, R_{10}, *Picea abies*, precipitations, stem growth

Respiration of stems contributes approximately 8 to 13 % to the total respiration of forest ecosystem (Acosta *et al.*, 2008; Tang *et al.*, 2008; Zha *et al.*, 2004, 2007). Within the stem, process of respiration takes place only in living cells which occur in xylem, cambium and inner bark (Ryan, 1990; Stoskfors, 2000; Yoshida *et al.*, 1999). Most of CO_2 within the stem is originated from these respiring stem cells, however, a part of the stem CO_2 is released by rhizosphere respiration and then transported through xylem to the stem in flowing sap (MacGuire and Teskey, 2004; Levy *et al.*, 1999).

CO_2 respired by the stem cells or imported by transpiration stream can diffuse radially to the atmosphere and can be measured as stem CO_2 efflux. The rate of diffusion of CO_2 from the stem to the atmosphere depends on the concentration gradient between stem and atmosphere, barriers to diffusion (Hölttä and Kolari, 2009; Eklund and Lavigne, 1995), and temperature (that affects directly diffusion rate – Fick's law, and also CO_2 solubility in water – Henry's law).

A number of external and internal factors can affect directly the process of respiration or they can affect processes changing concentration of gaseous CO_2 which can diffuse to the atmosphere – e.g. CO_2 solubility in water or sap flow rate (Saveyn *et al.*, 2008; Teskey *et al.*, 2008).

In this study we determined temperature normalized CO_2 efflux rate and its seasonal changes during four growing seasons.

MATERIALS AND METHODS

Site description

Measurements were carried out in Norway spruce (*Picea abies* [L.] Karst) forest at the Ecological Experimental Study Site (EESS) Bily Kriz (49°30´ N, 18°32´ E, 890 m a.s.l., situated in Moravian-Silesian Beskydy Mts., the Czech Republic. EESS Bily Kriz is characterized by mean annual temperature of 5.5 °C and annual precipitation of 1 100–1 400 mm. The Norway spruce stand was planted in 1981 with

4 years old seedlings on the slope (13.5°) with SSW exposure, stand density is 2500 trees per ha. The average tree height was 11.5 to 13 m in the study years.

Measurements

Measurements of CO_2 efflux from tree stems were carried out during the growing season (May–October) in 2006 to 2009. Measurements were done using automatic modified closed gasometrical (non-steady-state through-flow) system SAMTOC (developed at the Institute of Systems Biology and Ecology, the Czech Republic). The system consisted of respiration chambers, pneumatic valves and pistons for chamber closing, eight port distributing manifold, infrared gas analyzer (in years 2006 and 2007 WMA-3, PPsystems, UK; in 2008 and 2009 Li-840, Li-Cor, Lincoln, NE, USA) and personal computer with a control software and an additional hardware. Eight respiration chambers had a half cylinder shape with height of 12 cm and diameter of 6.5 cm. They were installed on the northern surface of stem (to exclude warming caused by the sun radiation) in the height of about 1.3 m. Thermometers (PT 100) were installed approximately 5 cm beside the chambers in cambium layer.

CO_2 efflux and stem temperature were measured in growing season in 2006 to 2009 (Tab. I). In 2009 there was a gap in collected data from 1. 7. to 4. 8. caused by technical difficulties.

I: *Seasons when the measurements of stem CO_2 efflux were carried out*

	measurement season
2006	26. 5.–19. 10.
2007	1. 5.–31. 10.
2008	1. 5.–31. 10.
2009	1. 5.–13. 10.

Dendrometer increment gauges DB 20 (EMS Brno, CZ) were fixed on the trees in 1.3 m above the ground (diameter breast height) using stainless tape. We mounted 40 gauges on trees with different strata occupation in the forest. Resolution of used scale is 0.1 mm. The record interval was from 7 to 14 days.

Precipitations were measured by rain gauges HoBo (AMET, CZ) in 2006–2008 and MetOne 386 (Met One Instruments, Inc., Oregon, USA) in 2009.

Data analysis

The natural logarithm of the CO_2 efflux rate and the woody-tissue temperature were regressed using a linear model.

$$\ln(respiration) = \alpha \times T + \beta, \quad [1]$$

where α and β are the regression coefficients. Q_{10} (the proportional change in CO_2 efflux from 10 °C increase in temperature) was calculated (Linder and Troeng, 1981) for each chamber for each growing season from equation:

$$Q_{10} = e^{10\times\alpha}, \quad [2]$$

where α is the regression coefficient obtained from the previous equation. Then, CO_2 efflux was normalized to the temperature of 10 °C according to equation:

$$R_{10} = \frac{R_i}{Q_{10}^{\frac{T_i - 10}{10}}}, \quad [3]$$

where R_i is the measured CO_2 efflux rate at temperature (T) of woody tissue.

The program TableCurve2D (Systat Software, USA) was used for fitting data of R_{10} and stem increment.

RESULTS

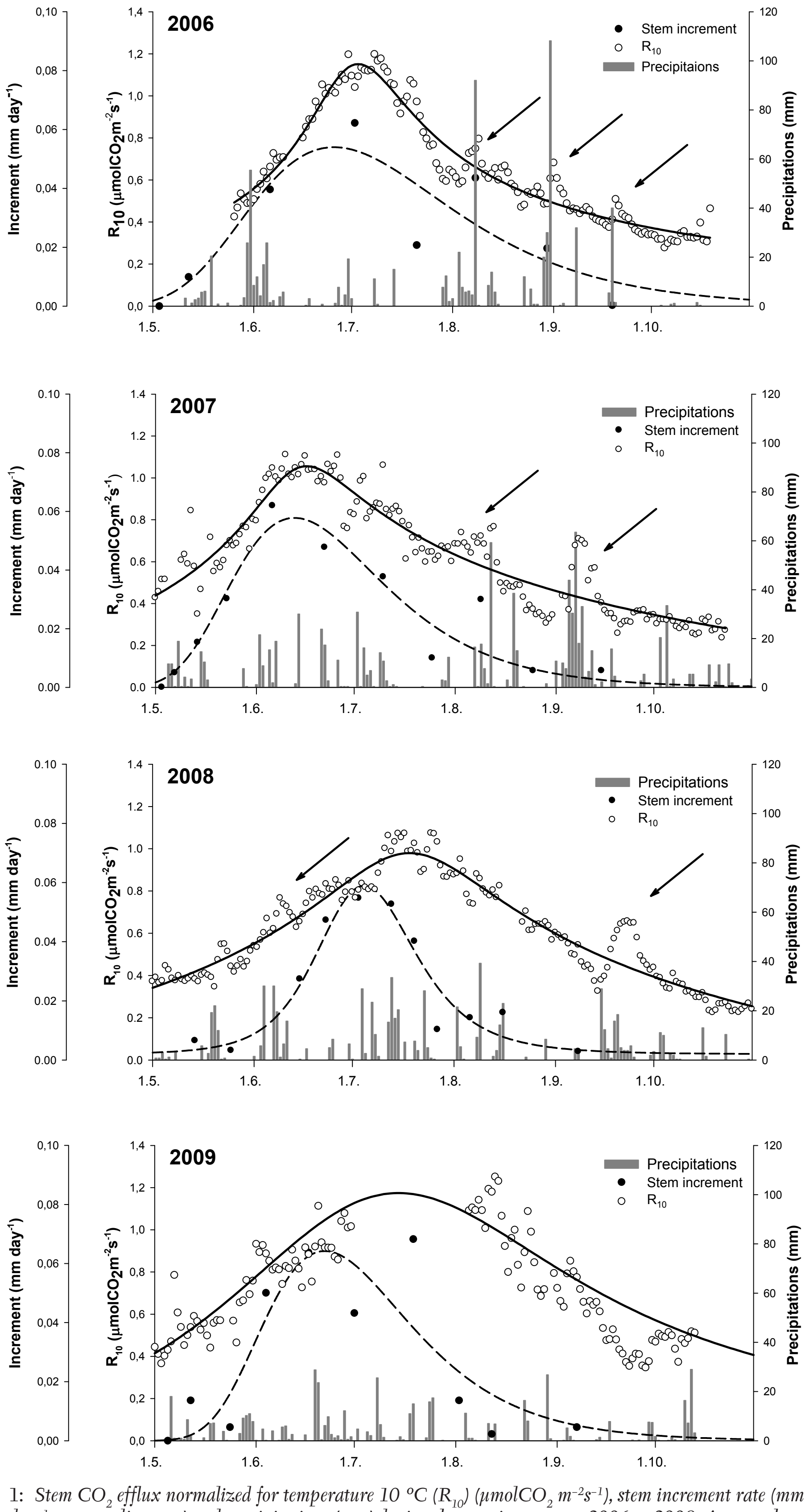
Mean daily air temperature, rainfall amount and stem diameter increment were determined in the experimental forest stand, and mean stem CO_2 efflux and Q_{10} were determined from eight stems in the stand (Tab. II).

Stem CO_2 efflux was in tight relationship with temperature. The exponential regression was determined for each chamber for one whole

II: *Meteorological parameters, tree characteristics growing season in 2006 to 2009 (31. 10.) and stem CO_2 efflux in the experimental stand during experimental periods in 2006 to 2009 (see tab. I)*

	2006	2007	2008	2009
Seasonal mean daily air temperature in 2 m (°C)	15.0	12.9	12.5	12.4
min	–2.4	–0.5	2.8	–2.1
max	28.0	26.1	21.8	24.0
Seasonal rainfall amount (mm)	878.4	888.7	656.7	537.9
Stem diameter increment (mm)	3.26	3.65	3.34	3.69
Mean stem CO_2 efflux (μmol $m^{-2}s^{-1}$)	1.60	1.65	1.77	1.93 *
min	0.20	0.19	0.30	0.30
max	5.37	4.64	4.53	4.96
Mean Q_{10}	2.96	3.44	3.52	3.23

* One month drop-out of CO_2 efflux measurement (1. 7.–4. 8.)



1: *Stem CO_2 efflux normalized for temperature 10 °C (R_{10}) (μmolCO_2 $m^{-2}s^{-1}$), stem increment rate (mm day^{-1} on stem diameter) and precipitations (mm) during the growing seasons 2006 to 2009. Arrows show R_{10} increase caused by rainfall. The full line is a fit curve of stem CO2 efflux, the dashed line is a fit curve of stem increment.*

growing season. The mean value of coefficient of determination (R^2) calculated from these regressions was 0.76 (SD 0.05) for all four growing seasons. This infers that temperature was the main factor affecting changes in CO_2 efflux during the season. To eliminate effect of temperature and determine other factors influencing stem CO_2 efflux, CO_2 efflux was normalized for temperature of 10 °C using equation [3]. The basic seasonal course of R_{10} followed the pattern of the stem increment. Stem growth activity increased in the beginning of the growing season and it had the maximum in June and July (Fig. 1). Then the activity gradually decreased. The curve fitting the stem increment data was rather problematic. In season 2006 and 2007 there was a sudden increase of stem growth the summer caused possibly by a dry period. Nevertheless, we were not able to explain the drop of stem growth in early summer in 2009.

Similarly, R_{10} increased in the beginning of the season up to its maximum in June and July and then it gradually decreased till the end of the season, however, with a little lag of the reached maximum.

During the season we observed significant oscillations around the seasonal course of R10 described above with steep increases and slower decreases of R10 values. As a causal factor, rainfall events were determined. Rainfalls strong enough caused often increase in R_{10} (Fig. 1). Then R10 gradually decreased to the level of the course trend. This effect of rainfall was the most significant when the R_{10} course had a decreasing trend in the second part of the growing season after reaching its maximum. This case was very remarkable especially in 2007 and 2008 when a long rainy period occurred in the autumn (arrows in Fig. 1).

DISCUSSION

Tree stem CO_2 efflux showed a high coefficient of determination of the stem temperature-CO_2 efflux relationship (R^2 = 0.76). Similarly strong correlation was observed also in other studies (e.g. Zha *et al.*, 2004; Saveyn *et al.*, 2008). That infers that stem temperature is a main factor driving CO_2 efflux from stems. Its effect, however, can be decreased or even decoupled by action of other factors, such as water availability (Saveyn *et al.*, 2007). The stem temperature was measured just under the bark in the cambium layer where the most active cells occurs (Lavigne *et al.*, 2004). The temperature there is usually lower than the air temperature and the maxima and minima are lagged. This trend continues further to the stem center where are other living cells (xylem) (Ryan, 1990; Stockfors, 2000). Therefore the measured temperature did not characterize all living cells in the stem.

Normalization of stem CO_2 efflux (R_{10}) allowed to exclude the temperature effect. Average daily R_{10} of tree stems increased in the beginning of the experimental growing seasons and reached maximum in June and July. After that R_{10} values had gradually decreasing trend till the end of the season. The similar course was observed also in other studies (Shibistova *et al.*, 2002; Stockfors and Linder, 1998). In the beginning of the growing season R_{10} started increasing as well as stem growth. That is assumed as a result of extra respiratory requirements of activated dividing cells of cambium and consequent cell differentiation – growth respiration (Lavigne and Ryan, 1997; Stockfors and Linder, 1998; Gruber *et al.*, 2009b). In the period of stem growth, the growth respiration is the biggest portion of total stem respiration as it exceeds maintain respiration (Lavigne *et al.*, 2004).

The maximum of R_{10} rate occurred later than maximum of stem growth. The reason is that the measured stem growth records cambium cell division and cell prolongation (Gruber *et al.*, 2009b). That is followed by further development and cell wall thickening (Gricar *et al.*, 2008) that is also highly energy consuming. Gruber *et al.* (2009a) observed that maximum of the amount of the wall thickening cells occurred about one month later than maximum of the amount of enlarging cells.

In 2009 there was one month drop-out of our CO_2 efflux measurement (1. 7.–4. 8.) around the expected maximum of R_{10} values so this maximum could not be determined accurately.

We observed a significant increase in R_{10} after some rain events and consequent return to the level of the course trend. This increase was the most remarkable after heavy rains and especially during the second half of the growing season when R_{10} course had a decreasing trend. In several studies (e.g. Maier and Clinton, 2006; Teskey and McGuire, 2005) the relationship between CO_2 efflux and CO_2 concentration in xylem was observed. Saveyn *et al.* (2008) observed a significant increase in stem CO_2 concentration during rain. He explained that as a result of an increase in cell respiration and stopping sap flow which would transport the CO_2 off. The restored sap flow after rain can take off xylem CO_2 and decline xylem CO_2 concentration (Gansert and Burdorf, 2005). However, restoring of the sap flow depends on evaporation rate after rain (Zeppel *et al.*, 2008). The increase in stem CO_2 concentration during and after rain can be caused also by an increased xylem transport of CO_2 originating from root and soil microbial metabolism (MacGuire and Teskey, 2004; Levy *et al.*, 1999) which is highly sensitive to enhanced water availability (Huxman *et al.*, 2004). That can mitigate the effect of CO_2 transport from the stem segment by the restored sap flow.

The response of stem CO_2 concentration to the enhanced water availability during or after rain is also influenced by other conditions. Zeppel *et al.* (2008) found that rainfall amounts less than 20 mm were unavailable to the roots and they had no effect on tree water use of mature evergreen trees, which shows that there can be a rainfall amount threshold of the tree response. Also antecedent soil moisture had the effect on tree water use when changes in tree water use were more significant when the antecedent moisture was low. Nevertheless, it is difficult to determine all these factors *in situ* because they usually action together and of variable power, therefore, it is not easy to recognize them individually.

Contribution of stem respiration to total ecosystem respiration is not high but it is not negligible. This study helped to understand dynamics of stem CO_2 efflux during the growing season and its responses to changes of some external conditions – temperature and presence of rainfall events. The results of this study will contribute to modeling of the forest production and carbon flow.

SUMMARY

The aim of this study was to determine dynamics of stem CO_2 efflux during the growing season in Norway spruce stand and factors affecting this dynamics. Continuous measurements of stem CO_2 efflux were carried out using an automated system during the growing season in 2006 to 2009. Further measured characteristics were stem temperature, stem increment and precipitations. The main factor driving the dynamics of stem CO_2 efflux is temperature. To eliminate effect of temperature as a main factor and determine other factors influencing stem CO_2 efflux, the efflux was normalized for temperature of 10 °C (R_{10}). Basic seasonal course of R_{10} followed the pattern of stem growth rate with its maxima in June and July. However maximum of R_{10} occurred with a lag after the measured maximum of stem growth rate and it is shifted to the period of cell wall thickening. The other factor effect, which was possible to determine, was presence or absence of rainfall. Rainfall strong enough caused a fast increase in R_{10}. Then R_{10} gradually decreased to the level of the course trend. This effect of rainfall was the most significant when the R_{10} course had a decreasing trend in the second part of the growing season. The results of this study will contribute to improving estimates of the forest production and carbon flow to and from the forest ecosystem and modeling these processes.

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