

Effects of xylem water transport on CO₂ efflux of woody tissue in a tropical tree, Amazonas State, Brazil

Norbert Kunert^{1,2,4} and Alida Mercado Cárdenas³

Received: 1.03.2012; accepted: 13.03.2012

ABSTRACT - (Effects of xylem water transport on CO₂ efflux of woody tissue in a tropical tree, Amazonas State, Brazil). We assessed the effect of xylem sap flux on radial CO₂ efflux of woody tissue of a tropical trees species growing in the Center of Manaus (Amazonas State, Brazil). An open chamber system was used to constantly measure diurnal changes in CO₂ efflux over several days. Xylem sap flux was monitored additionally. We found a strong relationship between temperature and woody tissue respiration rates during night time. CO₂ efflux rates were reduced up to 35% during daytime most probably due to vertical water uptake within the tree trunks. The results suggest a distinct daytime depression of the CO₂ efflux compared with a night time temperature relationship. Xylem sap flux appears to be a major influence on CO₂ efflux rates. The reductions in CO₂ efflux will become most distinct during periods with a high evaporative demand and predictions of CO₂ efflux by the temperature/flux relation are critical during these periods.

Key words: daytime depression, sap flux, temperature dependency, woody tissue respiration

RESUMEN - (Efectos del transporte de agua por el xilema en la afluencia de CO₂ en el tejido leñoso de un árbol tropical, Estado del Amazonas, Brasil). Evaluamos el efecto del flujo de la savia del xilema en la afluencia del CO₂ radial en tejidos leñosos de una especie de árbol tropical en el centro de Manaus (Amazonas, Brasil). Un sistema de cámara abierta fue usado constantemente para medir cambios diarios en la afluencia del CO₂ durante varios días. Al mismo tiempo, se midió el flujo de la savia del xilema. Encontramos una fuerte relación entre las tasas de temperatura y la respiración del tejido leñoso durante el periodo nocturno. Las tasas de afluencia de CO₂ se redujeron hasta un 35% durante el día, probablemente debido a la absorción vertical del agua dentro de los troncos. Los resultados sugieren una depresión de la afluencia del CO₂ específica durante el día comparada con la relación de la temperatura durante la noche. El flujo de la savia del dilema parece tener una influencia más fuerte en las tasas de afluencia del CO₂. Las reducciones en la afluencia del CO₂ serán más marcadas durante periodos con una alta demanda de evaporación y las predicciones de la afluencia del CO₂ dadas por la relación de temperatura/flujo son críticas durante dichos periodos.

Palabras-clave: dependencia en la temperatura, depresión diurna, flujo de savia, respiración de tejido leñoso

Introduction

Woody tissue respiration plays an important role in budgeting ecosystem productivity (Chambers *et al.* 2004). A conventional method to estimate the CO₂ efflux of wood at the ecosystem scale is by using closed dynamic chambers cinched on tree stems and measuring the increase in CO₂ in the closed chamber from the tissue with an infrared gas analyzer (IRGA) over a short time period. This method provides the opportunity to sample a large number of trees within a reasonable time. The common assumption is that

all the CO₂ respired by the woody tissue enclosed in the chamber diffuses laterally from the stem interior into the chamber. The total CO₂ efflux defusing out of the woody tissue is depending strongly on the temperature of the bark surface and/or the temperature of the conductive sap wood so that flux rates are commonly predicted using this temperature relation (Tranquillini & Schütz 1970, Edwards & Hanson 1996, Gansert *et al.* 2002).

However, some studies found CO₂ efflux rates lower than predicted from bark surface or sap wood temperature during daytime, which suggests an

1. Max Planck Institute for Biogeochemistry, Department for Biogeochemical Processes, Hans Knöll Str. 10, 07745 Jena, Germany
2. Instituto Nacional de Pesquisas da Amazônia (MCT-INPA), Laboratório de Manejo Florestal, Av. Ephigênio Sales, 2239, 69011-970 Manaus, AM, Brasil
3. McGill University, Department of Natural Resource Sciences, Macdonald Campus, Ste-Anne-de-Bellevue, H9X3V9 Quebec, Canada
4. Corresponding author: nkunert@bgc-jena.mpg.de

inner transport of CO₂ dissolved in the transpiration stream, as maybe ongoing bark photosynthesis could be excluded (Edwards & McLaughlin 1978, Kaipainen *et al.* 1998, Stockfors & Linder 1998). It is assumed that a portion of the CO₂ produced by the living respiring cells might dissolve in the sap and is transported vertically in the xylem along with the transpirational water uptake instead of moving laterally through the stem into the respiration chamber (Kaipainen *et al.* 1998) and hence this measured CO₂ efflux might not be equal to the respiration rate (Saveyn *et al.* 2008). Another recent study also points out the high importance of carbon re-fixation and amount of stem assimilates as significant carbon source for the whole plant carbon budget. Furthermore, bark photosynthesis did not vanish until a long-term exclusion of light (Saveyn *et al.* 2010). Accordingly, there is an increasing concern about the measured values of stem CO₂ efflux and the possible effects caused by other processes rather than by temperature depending respiration (Saveyn *et al.* 2007).

Most studies regarding diurnal changes in CO₂ efflux have been conducted on temperate regions and there is a lack of information dealing with trees growing in the tropics. By comparison, the approach to access the influence of internal water transfer on the CO₂ diffusion out of trees stems has been applied less frequently and successfully in the tropics than in temperate regions. One study using continuous measurements with open dynamic chambers was conducted in a *Schima superba* Gardner & Champ. plantation, in the subtropics of southern China (Zhu *et al.* 2011), and another in a subtropical *Combretum micranthum* G. Don shrub growing in Cameroon (Levy *et al.* 1999). These studies generally found a positive relation between xylem sap flux and CO₂ efflux, but the findings regarding the overall effect of the water transport were quite controversial compared to the results with trees from temperate and boreal forests. There was an increase of CO₂ efflux of up to 9.2 and 12% with the onset of internal water transport in the *Schima* trees and the *Combretum* shrub, respectively. Whereas studies from temperate forests find a reduction of the CO₂ efflux of 10-50% with the onset of the internal water transport (Gansert & Burgdorf 2005, Negisi 1975, 1982). Regarding the difference in environmental settings, the confidence that these controversial findings apply on trees growing in the central tropics is very limited. Hence, conducting a study on a specific tree in the

tropics will give us better insights on the carbon cycle of tropical trees than the existing studies. Therefore, the objectives of the present work were: (1) to assess variations from the nighttime efflux-temperature relation in a tropical tree and (2) to quantify the effect of internal water transfer on the CO₂ efflux rates.

Material and methods

This study was carried out on a specimen of *Hymenolobium pulcherrimum* Ducke (Fabaceae) growing on a private property in the Center of Manaus, Amazonas State, Brazil in May 2011. The sample tree had its full complement of leaves during the study. The studied tree was 30.8 cm in diameter at breast height, 7.5 m high with a crown extension of 185 m². Only one tree was measured, due to limited available equipment and no appropriate replicate of the same tree species in the area. Microclimatic parameters were recorded with a professional weather station (PCE-FWS 20 Weather Station, PCE Inst., Durham, UK) in an open area approximately 6 m away from the sample tree. Microclimate data were stored at 30 s intervals and average was recorded every 5 minutes.

Stem respiration rates were measured with an open chamber system to assess diurnal CO₂ effluxes. An infrared gas analyzer (IRGA, LI 6252 with an LI-670 flow control unit; Li-Cor, Lincoln, Nebraska, USA) was configured in differential mode similar to the method to measure leaf photosynthesis (Licor 1992). The IRGA is giving $[\Delta\text{CO}_2]$ as output which is the difference between the alternately measured $[\text{CO}_2]$ of the reference air stream from a common air source and the $[\text{CO}_2]$ of the airstream flowing through the stem respiration chamber. Ambient air was drawn through an air reservoir of 2 liters to buffer CO₂ and/or H₂O fluctuations. We configured the flow control unit to support a constant flow rate of 1.0 L/min. A semicylindric polyvinyl chloride (PVC) chamber (400 mL) was cinched to the trunk facing to the western side of the studied tree at 130 cm (DBH) above the ground using tie down straps. A metal bar was placed under the tie down straps on the opposite site of the chamber to reduce the pressure on the tree trunk by the tie down straps. The respiration chamber was shielded with aluminum foil to exclude thermal effects by direct sunlight or bark photosynthesis. The respiration chamber was equipped with two different thermocouple-temperature sensors. The first sensor measured the xylem temperature approximately

10 mm above the bark surface where a small radially hole (1 mm in diameter) was drilled into the tree trunk and the sensor was inserted. The second sensor was installed above the sealing of the respiration chamber to measure the stem surface temperature. IRGA and thermocouple outputs were stored every 30 seconds and the average recorded in 5 min intervals with a data logger (DL2 datalogger, Delta-T Devices LTD., Cambridge, UK).

The thermal dissipation method according to Granier (1985) was used to measure sap flux density. The sensors consisting of two cylindrical probes were inserted radially (0-20 mm below cambium) into the tree trunk, with one probe placed approximately 10-15 cm vertically above the other. The studied tree was equipped with two Granier sensors, one on the southern and one on the northern side of the trunk at 130 cm (DBH) above the ground. Sap flux sensors were at least 20 cm vertically away from the respiration chamber. After Granier (1985) the thermal influence of the heated probe on surrounding wood tissue is negligible at a distance of 10-15 cm from the source. Sensors were protected from thermal influences and water intrusion by a reflective polyethylene/paperboard box and a plastic cover. Probe output voltage was recorded every 30 seconds, and the average value stored every 5 minutes (DL2 datalogger, Delta-T Devices LTD., Cambridge, UK). Sap flux density (J_s in $\text{g cm}^{-2} \text{h}^{-1}$) was calculated from differences in voltage (ΔV) using the calibration equation determined by Granier (1987). Each night the maximal nighttime voltage (ΔV_{max}) was determined and used as reference voltage for that day. We assumed zero sap fluxes as nighttime vapour pressure deficits were low and the voltage courses of sensors reached equilibrium most nights suggesting refilling of internal reserves was completed. Possible controls of temperature and tree water transport on CO₂ efflux were tested using linear regression analysis. We used SPSS, 15th edition (SPSS Inc., Chicago, IL, USA) for all statistical analyses.

Results and discussion

The maximum and minimum CO₂ efflux we found was around 6.5 (day time) and 4.0 (night time) $\mu\text{mol m}^{-2} \text{s}^{-1}$. These values are corresponding well with results from other studies from various trees. Levy *et al.* (1999) reported efflux rates between 6.0 (day time) and 3.5 (night time) $\mu\text{mol m}^{-2} \text{s}^{-1}$ in a *Combretum micranthum* G. Don shrub in Cameroon,

whereas maximum values of 9.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ are also known for *Schima superba* Gardner & Champ. trees in the subtropics of southern China (Zhu *et al.* 2011). The maximum sap flux density (J_s) of 10 $\text{g cm}^{-2} \text{h}^{-1}$ was relatively low but within the range found for neotropical tree species (Kunert *et al.* 2010). Stem CO₂ efflux, sap flux density, stem surface temperature and air temperature followed similar diurnal patterns (figures 1a to 1c). CO₂ efflux increased with increasing surface temperature, air temperature and sap flux density at day time, but decreased with increasing xylem temperature at night time (figures 1a and 1b). On the first view, this is imposing a positive correlation of CO₂ efflux with surface temperature, ambient air temperature and a negative correlation with xylem temperature. The positive relationship between surface/air temperature and CO₂ efflux would follow the common theory that an increase in temperature causes an increase in cellular respiration and diffusion coefficient and a decrease in the solubility of CO₂ in the xylem water (McGuire *et al.* 2007). On the other hand, the decrease in xylem temperature should have exactly the opposite effect of lower cellular respiration and higher CO₂ solubility during the day. The reduced xylem temperature increases most probably by a cooling effect with the onset of the transpirational water uptake and showed a relatively low amplitude of 0.52 °C difference between night and day time. In contrast, the surface temperature was coupled to the diurnal changes in air temperature and was defined by much higher amplitude between day and night time which was up to 1.19 °C. Thus, we observed that the correlation between surface/air temperature and CO₂ efflux was less clear during the day and significant reduction of CO₂ efflux took place during daytime relative to night-time rates (figure 2).

CO₂ efflux peaked with maximum surface temperature (figure 1a). Despite the higher temperatures during the day than night time, a clear daytime depression was present when CO₂ efflux was normalized to 20 °C (figure 2). Similar results were found in a beech and oak tree, where the temperature adjusted CO₂ efflux showed a very pronounced day time depression (Saveyn *et al.* 2007). CO₂ efflux was significantly reduced with the onset of sap flux in the morning. This effect is more obvious on days with high sap flux rates (*e.g.* second day, figure 2). The increase in CO₂ efflux under high sap flux rates was less temperature related in the morning (figure 3, 6h05min-12h) than the decrease under already lower sap flux rates in the afternoon and evening (figure 3,

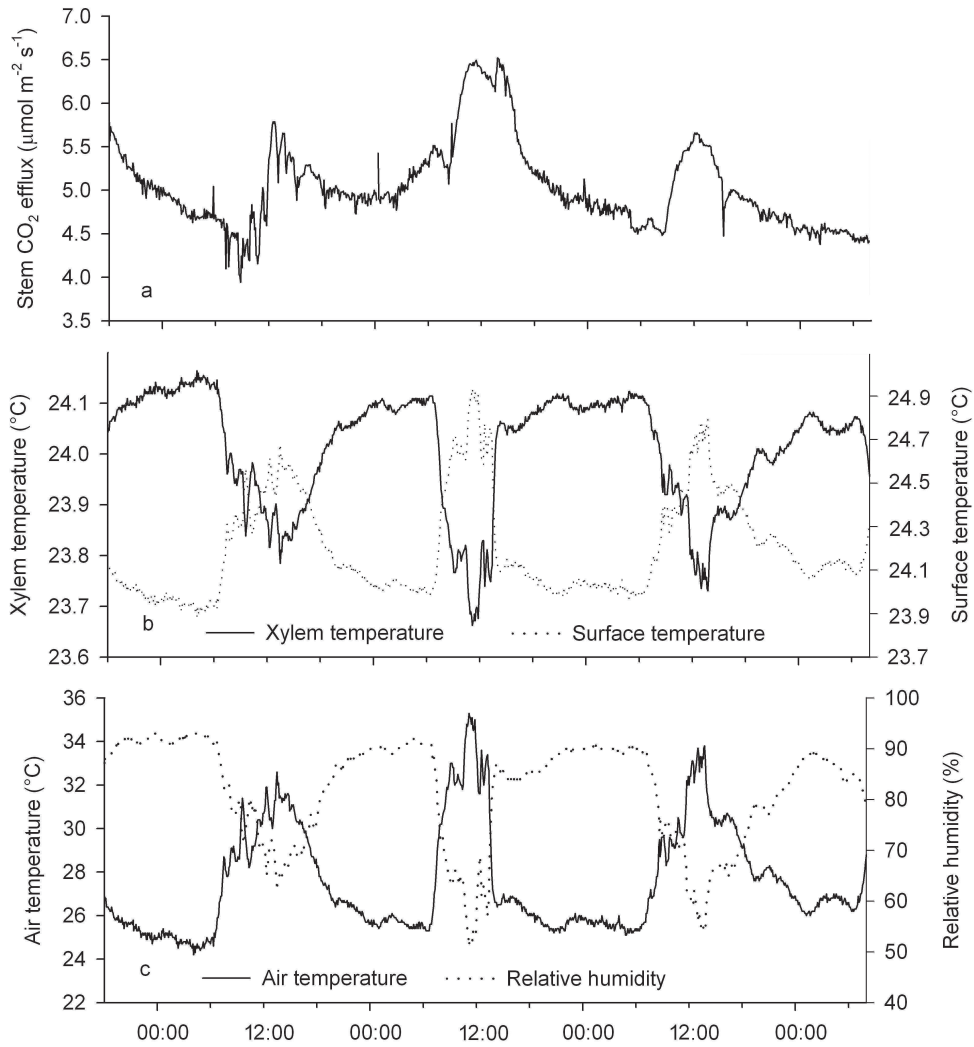


Figure 1. Diurnal course: a. CO₂ efflux; b. xylem temperature; c. air temperature; relative humidity and surface temperature over three entire days.

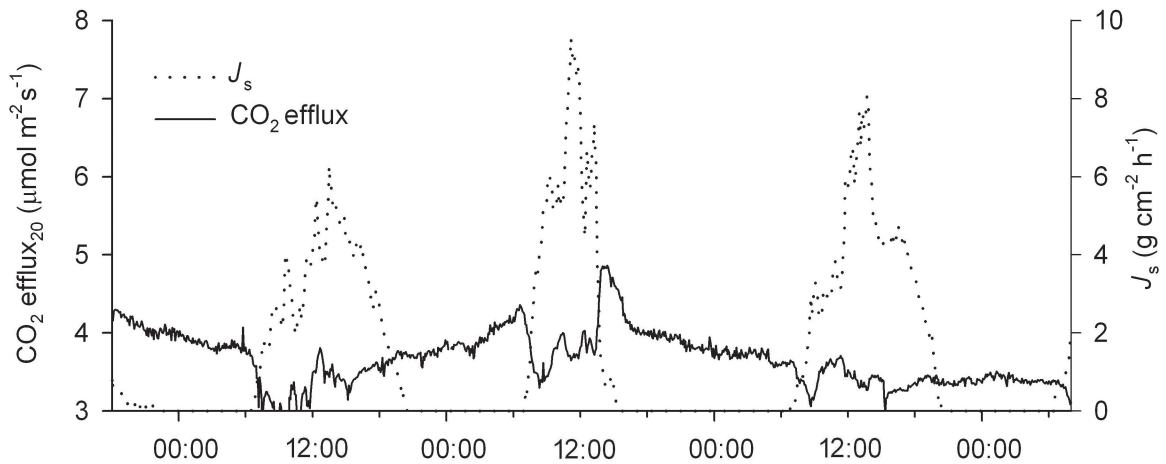


Figure 2. Time course of CO₂ efflux rate, normalized to 20 °C, and sap flux rate for the sample tree over three entire days.

13h-18h). Assuming that the experimental set up could exclude most of the bark photosynthesis, the reduction in CO₂ efflux rate must be caused by the internal water transfer. This reduction was accounting up to a 35% of the CO₂ efflux compared to values predicted by a simple night time temperature relation (figure 4). Similar values were found in beech trees in a temperate forest in Japan, where CO₂ efflux rates were reduced about 10-40% on days with high sap flux rate (Gansert & Burgdorf 2005) and up to 50% in pine and oak trees (Negesi 1975, 1982).

We conclude that the prediction of CO₂ efflux of wood tissue by the temperature/flux relation is critical and that simple temperature functions are insufficient to predict stem respiration on ecosystem scales. The results suggest a distinct daytime depression of the CO₂ efflux compared with a night time temperature relationship. Xylem sap flux density appears to be a major influence on CO₂ efflux rates. The reductions in CO₂ efflux will become most distinct during periods with a high evaporative demand. Values based on day or night time measurements will be either under- or overestimated, respectively, especially on days with high evaporative demand.

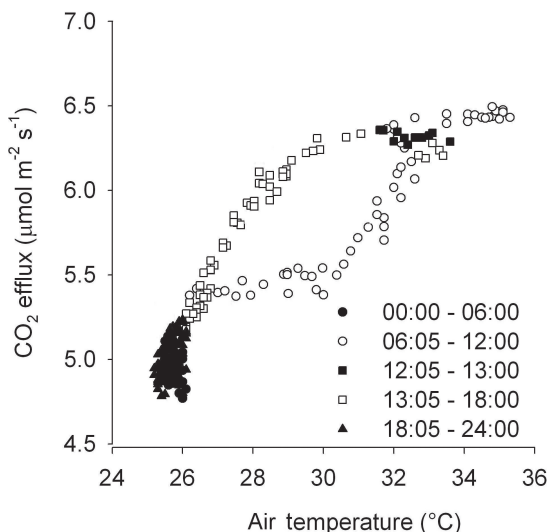


Figure 3. Comparison between daytime and night-time CO₂ efflux at a given temperature on a day with relatively high xylem sap flux rates. The different symbols indicate the time course of measurements.

Acknowledgements

We want to thank Susanne Trumbore for a valuable discussion on the design of this study. We would also like to thank two anonymous reviewers for their valuable comments on an earlier version of the manuscript.

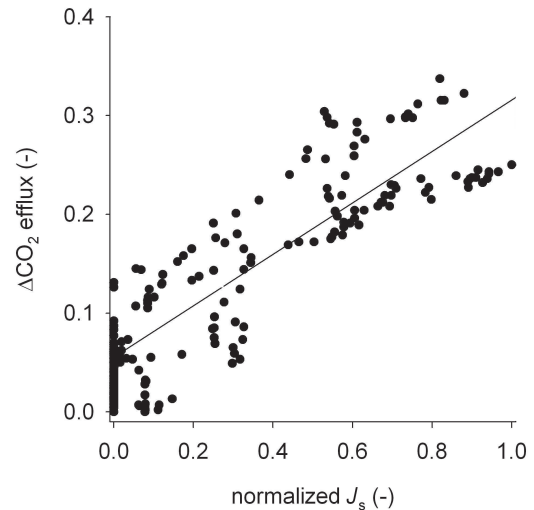


Figure 4. Correlation of daytime reduction of CO₂ efflux (Δ CO₂ efflux) with normalized xylem sap flux ($R^2 = 0.63$, $p < 0.001$). Δ CO₂ efflux given as percentage of the gross temperature dependent CO₂ efflux. A considerable reduction of the CO₂ efflux up to 35% is indicated when high sap flux rates occur.

Literature cited

- Chambers, J.Q., Tribuzy, E.S., Toledo, L.C., Crispim, B.F., Higuchi, N., dos Santos, J., Araújo, A.C., Kruijt, B., Nobre, A.D. & Trumbore, S.E. 2004. Respiration from a tropical forest ecosystem: Partitioning of sources and low carbon use efficiency. *Ecological Applications* 14: 72-88.
- Edwards, N.T. & Hanson, P.J. 1996. Stem respiration in a closed-canopy upland oak forest. *Tree Physiology* 16: 433-439.
- Edwards, N.T. & McLaughlin, S.B. 1978. Temperature-independent diel variations of respiration rates in *Quercus alba* and *Liriodendron tulipifera*. *Oikos* 31: 200-206.
- Gansert, D., Backes, K., Ozaki, T. & Kakubari, Y. 2002. Seasonal variation of branch respiration of a treeline forming (*Betula ermanii* Cham.) and a montane (*Fagus crenata* Blume) deciduous broad-leaved tree species on Mt. Fuji, Japan. *Flora - Morphology, Distribution, Functional Ecology of Plants* 197: 186-202.
- Gansert, D. & Burgdorf, M. 2005. Effects of xylem sap flow on carbon dioxide efflux from stems of birch (*Betula pendula* Roth). *Flora - Morphology, Distribution, Functional Ecology of Plants* 200: 444-455.
- Granier, A. 1985. A new method of sap flow measurement in tree stems. *Annals of Forest Science* 42: 193-200.
- Granier, A. 1987. Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements. *Tree Physiology* 3: 309-320.

- Kaipiainen, L.K., Sofronova, G.I., Hari, P. & Yalynskaya, E.E.** 1998. The role of xylem in CO₂ exchange in *Pinus sylvestris* woody stems. *Russian Journal of Plant Physiology* 45: 500-505.
- Kunert, N., Schwendenmann, L. & Hölscher, D.** 2010. Seasonal dynamics of tree sap flux and water use in nine species in Panamanian forest plantations. *Agricultural and Forest Meteorology* 150: 411-419.
- Levy, P.E., Meir, P., Allen, S.J. & Jarvis, P.G.** 1999. The effect of aqueous transport of CO₂ in xylem sap on gas exchange in woody plants. *Tree Physiology* 19: 53-58.
- Licor.** 1992. LI-670 flow control unit instruction manual, LI-COR Inc., Lincoln, Nebraska, USA.
- McGuire, M.A., Cerasoli, S. & Teskey, R.O.** 2007. CO₂ fluxes and respiration of branch segments of sycamore (*Platanus occidentalis* L.) examined at different sap velocities, branch diameters, and temperatures. *Journal of Experimental Botany* 58: 2159-2168.
- Negisi, K.** 1975. Diurnal fluctuation of CO₂ release from the stem bark of standing young *Pinus densiflora* trees. *Journal of the Japanese Forestry Society* 57: 375-383.
- Negisi, K.** 1982. Diurnal fluctuations of the stem bark respiration in relationship to the wood temperature in standing young *Pinus densiflora*, *Chamaecyparis obtusa* and *Quercus myrsinaefolia* trees. *Journal of the Japanese Forestry Society* 64: 315-319.
- Saveyn, A., Steppe, K. & Lemeur, R.** 2007. Daytime depression in tree stem CO₂ efflux rates: is it caused by low stem turgor pressure? *Annals of Botany* 99: 477-485.
- Saveyn, A., Steppe, K., McGuire, M.A., Lemeur, R. & Teskey, R.O.** 2008. Stem respiration and carbon dioxide efflux of young *Populus deltoids* trees in relation to temperature and xylem carbon dioxide concentration. *Oecologia*, 154: 637-649.
- Saveyn, A., Steppe, K., Umbierna, N. & Dawson, T.E.** 2010. Woody tissue photosynthesis and its contribution to trunk growth and bud development in young plants. *Plant, Cell and Environment* 33: 1949-1958.
- Stockfors, J. & Linder, S.** 1998. Effect of nitrogen on the seasonal course of growth and maintenance respiration in stems of Norway spruce trees. *Tree Physiology* 18: 155-166.
- Tranquillini, W. & Schütz, W.** 1970. Über die Rindenatmung einiger Bäume an der Waldgrenze. *Centralblatt für das Gesamte Forstwesen* 87: 42-60.
- Zhu, L.W., Zhao P., Cai, X.A., Zeng, X.P., Ni, G.Y., Zhang, J.Y., Zou, L.L., Mei, T.T. & Yu, M.H.** 2011. Effects of sap velocity on the daytime increase of stem CO₂ efflux from stems of *Schima superba* trees. *Trees* 26: 535-542.