Effects of xylem water transport on CO_2 efflux of woody tissue in a tropical tree, Amazonas State, Brazil

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ABSTRACT - (Effects of xylem water transport on CO_2 efflux of woody tissue in a tropical tree, Amazonas State, Brazil). We assessed the effect of xylem sap flux on radial CO_2 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 CO_2 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. CO_2 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 CO_2 efflux compared with a night time temperature relationship. Xylem sap flux appears to be a major influence on CO_2 efflux rates. The reductions in CO_2 efflux will become most distinct during periods with a high evaporative demand and predictions of CO_2 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 CO_2 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 CO_2 radial en tejidos leñosos de una especie de árbol tropical en el centro de Manaos (Amazonas, Brasil). Un sistema de cámara abierta fue usado constantemente para medir cambios diarios en la afluencia del CO_2 durante varios días. Al mismo tiempo, se midió el flujo de la savia del xilema. Encontramos una fuerte relación entre las tazas de temperatura y la respiración del tejido leñoso durante el periodo nocturno. Las tazas de afluencia de CO_2 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 CO_2 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 tazas de afluencia del CO_2. Las reducciones en la afluencia del CO_2 serán más marcadas durante periodos con una alta demanda de evaporación y las predicciones de la afluencia del CO_2 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 CO_2 efflux of wood at the ecosystem scale is by using closed dynamic chambers cinched on tree stems and measuring the increase in CO_2 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 CO_2 respired by the woody tissue enclosed in the chamber diffuses laterally from the stem interior into the chamber. The total CO_2 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 CO_2 efflux rates lower than predicted from bark surface or sap wood temperature during daytime, which suggests an

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inner transport of CO_2 dissolved in the transpiration stream, as maybe ongoing bark photosynthesis could be excluded (Edwards & McLaughlin 1978, Kaipiainen *et al*. 1998, Stockfors & Linder 1998). It is assumed that a portion of the CO_2 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 (Kaipiainen *et al*. 1998) and hence this measured CO_2 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 in increasing concern about the measured values of stem CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 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 CO_2 efflux of 10-50% with the onset of the internal water transport (Gansert & Burgdorf 2005, Negisi 1975, 1982). Regarding on 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 CO_2 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 CO_2 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 [ΔCO_2] as output which is the difference between the alternately measured [CO_2] of the reference air stream from a common air source and the [CO_2] of the airstream flowing through the stem respiration chamber. Ambient air was drawn through an air reservoir of 2 liters to buffer CO_2 and/or H_2O 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 g cm^{-2} 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 CO_2 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 CO_2 efflux we found was around 6.5 (day time) and 4.0 (night time) µmol m^{-2} 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) µmol m^{-2} s^{-1} in a *Combretum micranthum* G. Don shrub in Cameroon, whereas maximum values of 9.9 µmol m^{-2} 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 g cm² h^{-1} was relatively low but within the range found for neotropical tree species (Kunert *et al*. 2010). Stem CO_2 efflux, sap flux density, stem surface temperature and air temperature followed similar diurnal patterns (figures 1a to 1c). CO_2 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 CO_2 efflux with surface temperature, ambient air temperature and a negative correlation with xylem temperature. The positive relationship between surface/air temperature and CO_2 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 CO_2 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 CO_2 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 CO_2 efflux was less clear during the day and significant reduction of CO_2 efflux took place during daytime relative to night-time rates (figure 2).

CO_2 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 CO_2 efflux was normalized to 20 °C (figure 2). Similar results were found in a beech and oak tree, where the temperature adjusted CO_2 efflux showed a very pronounced day time depression (Saveyn *et al*. 2007). CO_2 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 CO_2 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,

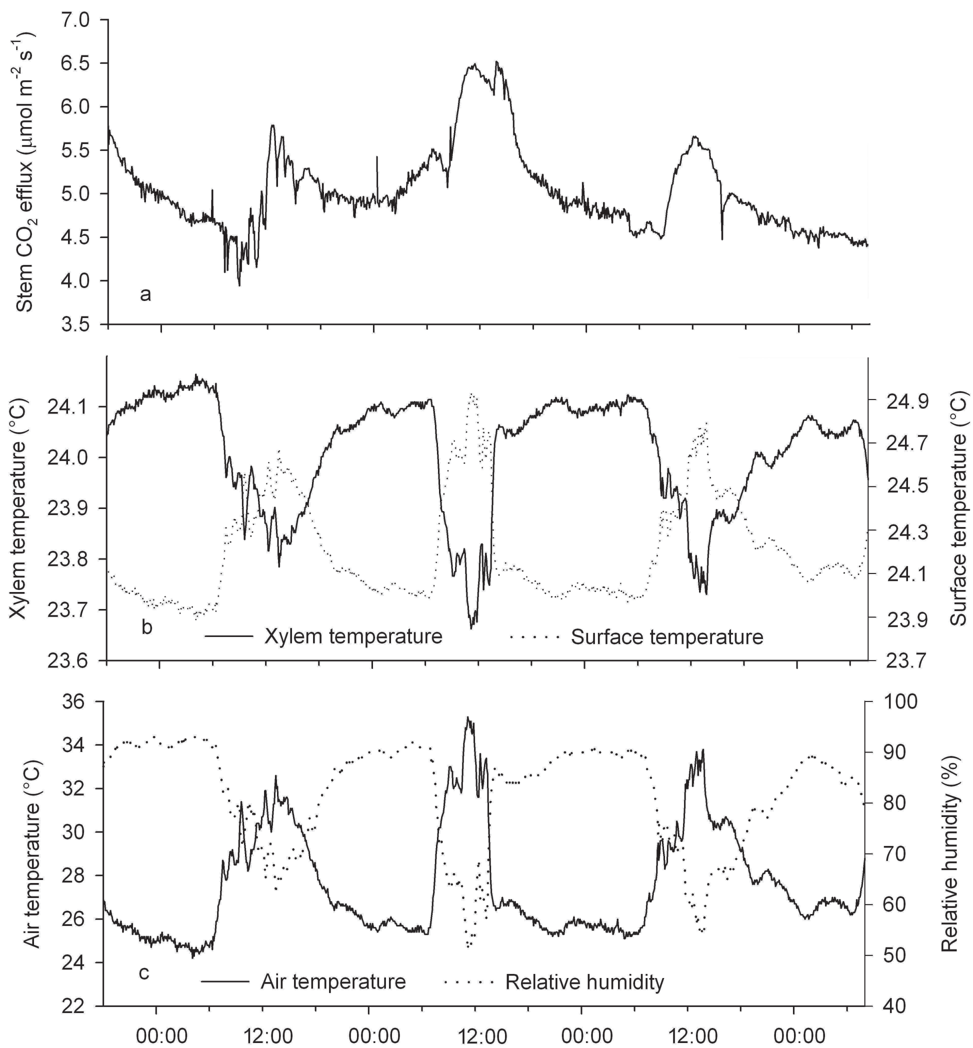

Figure 1. Diurnal course: a. CO_2 efflux; b. xylem temperature; c. air temperature; relative humidity and surface temperature over three entire days.

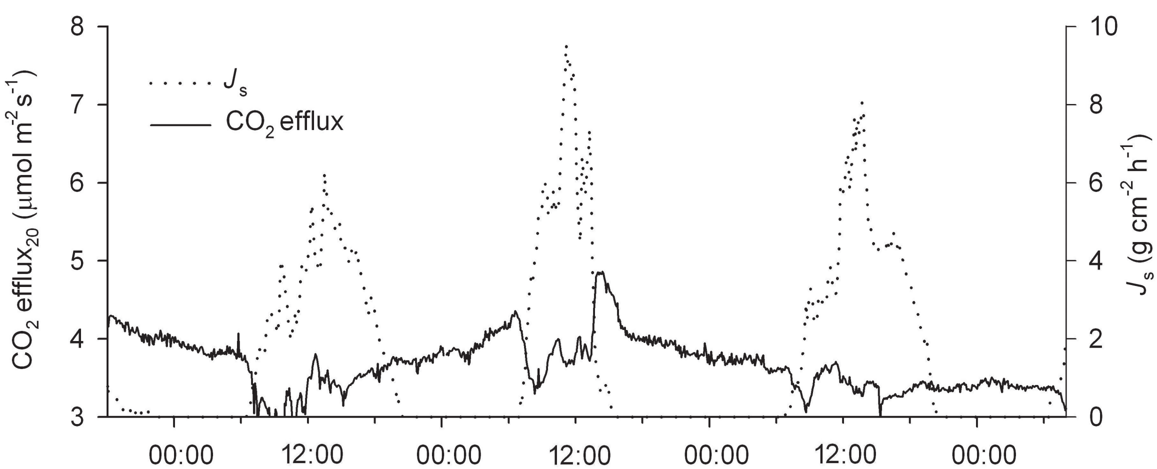

Figure 2. Time course of CO_2 efflux rate, normalized to 20 °C, and sap flux rate for the sample tree over three entire days.

13h-18h). Assuming that the experimental set up could exclude most of the bark photosynthesis, the reduction in CO_2 efflux rate must be caused by the internal water transfer. This reduction was accounting up to a 35% of the CO_2 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 CO_2 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 CO_2 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 CO_2 efflux compared with a night time temperature relationship. Xylem sap flux density appears to be a major influence on CO_2 efflux rates. The reductions in CO_2 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.

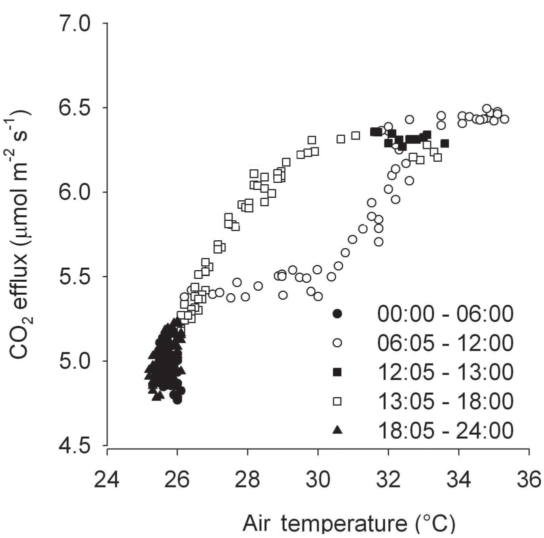

Figure 3. Comparison between daytime and night-time CO_2 efflux at a given temperature on a day with relatively high xylem sap flux rates. The different symbols indicate the time course of measurements.

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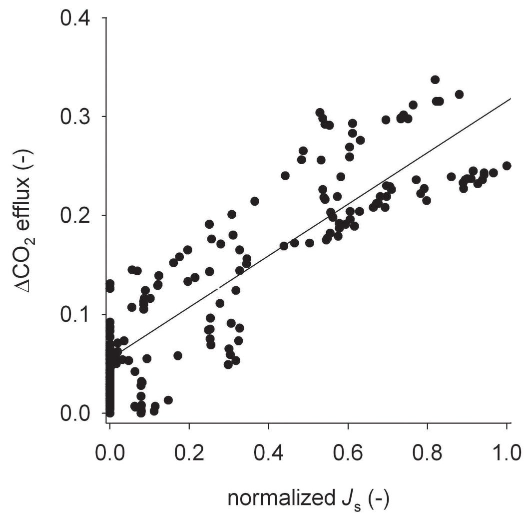

Figure 4. Correlation of daytime reduction of CO_2 efflux (ΔCO_2 efflux) with normalized xylem sap flux ($R^2 = 0.63$, $p < 0.001$). ΔCO_2 efflux given as percentage of the gross temperature dependent CO_2 efflux. A considerable reduction of the CO_2 efflux up to 35% is indicated when high sap flux rates occur.

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