

# The concentration and efflux of tree stem CO<sub>2</sub> and the role of xylem sap flow

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**Abstract** The accurate assessment of actual tree stem respiration and its relation with temperature plays a considerable role in investigating the forest carbon cycle. An increasing number of research reports have indicated that tree stem respiration determined with the commonly-applied chamber gas exchange measuring system does not follow expectations regarding temperature relationships. This method is based on the nowadays widely-accepted theory that the respired CO<sub>2</sub> in a tree stem would all diffuse outward into the atmosphere. However, it neglects partial CO<sub>2</sub> that is dissolved in the xylem sap and is carried away by the transpirational stream. Scientists have started to realize that the respired CO<sub>2</sub> measured with the chamber gas exchange method is only a portion of the total stem respiration (CO<sub>2</sub> efflux), while the other portion, which is sometimes very substantial in quantity (thought to occupy maybe 15%–75% of the total stem respiration), is transported to the upper part of the stem and to the canopy by sap flow. This suggests that the CO<sub>2</sub> produced by respiration is re-allocated within the stem. Accordingly, the change in CO<sub>2</sub> efflux could be reflected in the rates of sap flow in addition to its dependence on temperature. Proper methods and instruments are required to quantify the internal and external CO<sub>2</sub> fluxes in the trunk and their interaction with related environmental factors.

**Keywords** sap flow rates, respired CO<sub>2</sub> in the stem, re-translocation of stem respiration

## 1 Stem respiration and forest management

Conventional forest management is mainly for the purpose of maximizing the production of wood or non-wood

products in daily practice and has not paid sufficient attention to the contribution of forest respiration to the atmosphere. Since global warming caused by the ever-increasing atmospheric CO<sub>2</sub> has become a public concern all over the world (Zeng et al., 2006; Zhao et al., 2005), a new thinking that is oriented to buffering atmospheric CO<sub>2</sub> increase, improving the environment and at the same time providing eco-service products by emphasizing carbon management, will be incorporated into future forest plantation and management schemes in addition to producing market-oriented wood products. Therefore, CO<sub>2</sub> release from tree respiration should be taken into consideration in future forest management plans and its measurement might provide an important reference for such. Trees are the most productive plants. They have the most massive support structure due to their canopy foliage, representing a long-term carbon sink capable of removing and storing a large amount of atmospheric carbon on one hand, and on the other hand, consuming large quantities of fixed carbon through respiration due to their increased wood volume. It is estimated that forest autotrophic respiration could consume up to 50% of carbon assimilated through photosynthesis, and is thus a major, even dominant, component of forest ecosystem carbon budgets (Ryan et al., 1994; Damesin et al., 2002; Larcher, 2001). Some studies have shown that the decline in productivity of a mature or an aging forest is mainly due to the increasing volume of the non-assimilating portion (especially the woody tissue of the branch and stem) and to the coinstantaneous gradual stabilization of the biomass of the assimilating tissue (i.e. canopy), and that the consumption of carbon by respiration in woody tissues reduces the forest capability of storing carbon (Zeng et al., 2000, 2007; Yoder et al., 1994; Damesin et al., 2002). More and more studies have demonstrated that stem respiration makes up a large proportion of the forest carbon budget (Janssens et al., 2001); it might be 50% of autotrophic respiration above ground (Janssens et al., 2001; Saveyn et al., 2008), or

10%–25% of the total respiration of a forest (Wang et al., 2006; Xiao et al., 2005; Ryan et al., 1994; Xu et al., 2001; Meir et al., 2002; Chambers et al., 2004; Cavaleri et al., 2006); in some cases it even reaches 42% (Waring et al., 1985; Pruyn et al., 2003). Since respiration is one of the key factors determining whether forest ecosystems will act as net sources or net sinks of carbon, the measurement of stem respiration plays an important role in the investigation of the carbon cycle in a tree or in a forest ecosystem. Despite its importance to tree carbon balance and forest ecosystem carbon cycles, our ability to scale and predict woody tissue respiration is limited. This is, in part, because of an inadequate understanding of the physiological processes within stems in terms of the regulation of CO<sub>2</sub> production. Accurately measuring stem respiration rate and then further up-scaling to total stem respiration at ecosystem level also frequently have limitations and uncertainties, since people's understanding of the origin, possible transfer and efflux of CO<sub>2</sub> in the trunk, and the theoretical assumption from which the measuring methods nowadays are derived are far from complete. The uncertainty in measured values might lead to substantial errors when the investigation of carbon balance of trees is conducted on an even larger scale (Wang, 2004; Wang et al., 2005; Damesin et al., 2002; Bowman et al., 2005).

## 2 Non-temperature related variation in stem CO<sub>2</sub> efflux

Since the application of infra-red technique to the measurement of gaseous CO<sub>2</sub> concentration began, CO<sub>2</sub> efflux rates have been commonly measured as respiration rates of woody tissues. Many researchers have used the gas exchange method to measure stem respiration rate under the assumption that the only sources of CO<sub>2</sub> efflux are the respiration of local living woody tissues and the respired CO<sub>2</sub> within the stem (including the bark, sapwood and heartwood) moving radially outward from the inner to the outer part and being released via the bark into the ambient atmosphere. This concept has been accepted since the earliest measurements of CO<sub>2</sub> efflux from woody tissue. The measuring system consisting of a gas chamber sealed onto the stem and an infra-red gas analyzer can accurately detect the CO<sub>2</sub> efflux, based on which the respiration rate of the segment covered by the chamber is estimated (Yan et al., 2008; Wang et al., 2006; Damesin et al., 2002; Gansert, 2004). Because the respiratory metabolism is a chemical reaction process of enzyme-degradation in plant cells, temperature is considered to be the most important environmental factor controlling the respiration rate; namely the respiration rate is highly dependent on temperature change (Amthor, 1989; Campbell et al., 1998). Some studies did prove a good exponential correlation between stem respiration rate and temperature (Zeng et al., 2000; Bowman et al., 2005; Maier et al.,

1998); and some have even established the respiration-temperature response relationships in the stem, branch, root and canopy leaves so that this has been scaled up to predict the change in forest respiration rate with time on an even longer temporal scale (Wang et al., 2003; Zhao et al., 2006c; Bowman et al., 2005). However, there has been an increasing number of studies of *in situ* measurements with the chamber gas exchange system reporting obviously diurnal hysteresis between stem respiration rates and temperature. Namely, the so-called stem respiration rates showed evident differences under the same temperature throughout the same day, and the respiration rate and temperature did not comply with the expected functional relationship (Lavigne, 1987; Lavigne et al., 1996; Damesin et al., 2002; Ryan et al., 1995; Bowman et al., 2005). As early as in 1988, Kakubari observed reductions in CO<sub>2</sub> efflux rates from *Fagus sylvatica* L. trees that were unrelated to fluctuations in xylem temperature or air temperature. Gansert (2004) analyzed the diurnal patterns of CO<sub>2</sub> efflux from the stem as well as temperature change and found that the stem respiration rates of *Betula ermanii* and *Betula pendula* during daytime were significantly lower than at nighttime even though the temperatures were the same. This indicated that the respiration did not respond to temperature in the commonly-accepted regular way of exponential function. Saveyn et al. (2008) also observed the non-dependence of CO<sub>2</sub> efflux on temperature in the stems of both European oak and beech. A similar result was found by Wang et al. (2003) that, in the morning, the stem respiration rate had a tight relation with temperature, but such dependence on temperature did not occur in the afternoon, and the respiration even showed an obvious decrease during noontime when the temperature was higher. They attributed this difference of correlation between the stem respiration rate and temperature at different time periods during the same day to water deficit. It is, in this way, very likely that water deficit in the stem tissue may modify the relationship between the stem temperature and CO<sub>2</sub> efflux. Xiao et al. (2005) found that the stem respiration rate of fir showed 2 peaks in the time period between 12:00–16:00 and at 24:00 one after another, during which the temperatures were quite different. On-site monitoring during the rainy season showed that the stem respiration rate of *Pometia tomentosa*, *Barringtonia macrostachya* and *Hevea brasiliensis* reached their first highest values at about 15:00. The stem respiration rates of *P. tomentosa* and *B. macrostachya* had the second peak at about 01:00, while that of *H. brasiliensis* arrived at the second highest value at about 05:00 before daybreak. During dry season, *H. brasiliensis* only shows a one-peak pattern, and the higher stem respiration was observed to occur at 19:00 when the temperature significantly decreased (Yan et al., 2008). Recently, McGuire et al. (2007) reported their new observation that under constant temperature conditions, and thus presumably at a constant stem respiration rate,

changes in sap flow rate caused large differences in CO<sub>2</sub> efflux in *Platanus occidentalis* branches.

The above-mentioned studies demonstrate the asynchronous occurrence of high stem respiration rate and high temperature. Compared to the dark period, significant reductions in CO<sub>2</sub> efflux are observed during the light period. In many instances, the diurnal patterns of the stem respiration rate do not match the diurnal patterns of temperature. Quite often, the stem respiration rate is lower while both the temperature and sap flow rates are higher, therefore giving rise to the speculation that the response of the stem respiration rate to temperature change does not strictly follow the functional correlation, and that the change in sap flow rate might play an important role, something which has been ignored for a long time. If the transport and storage of CO<sub>2</sub> in the xylem strongly affects stem transpiration under normal field conditions, the interpretation of the stem gas exchange measured with the chamber method becomes ambiguous, and a re-assessment of the CO<sub>2</sub> exchange flux between the stem and the atmosphere is essential (Maier et al., 2006). It is now evident that measurements of CO<sub>2</sub> efflux to the atmosphere, which have usually been used to estimate the rate of stem respiration, do not adequately account for the actual carbon balance of trees. Considering the high xylem CO<sub>2</sub> concentration, its transport in the xylem stream represents a potentially large and poorly understood carbon flux in forest ecosystems. Therefore, a new description of internal and external CO<sub>2</sub> fluxes within a tree stem and relevant approaches for accurately measuring the fluxes should be developed to enrich our understanding of the mechanism of stem respiration.

### 3 Concentration and efflux of CO<sub>2</sub> of the stem and its interaction with the xylem sap flow

As for the above-stated phenomena, it is difficult to find a satisfactory and convincing interpretation from the available reports (Martin et al., 1994; Bowman et al., 2005). Indeed, those studies usually paid little attention to or simply overlooked the multi-directional flow of CO<sub>2</sub> in the trunk. As the respired CO<sub>2</sub> from the stem tissue diffuses outward, a portion of the CO<sub>2</sub> is dissolved in the xylem sap flow and is transported upward to the upper part of the stem and the canopy at the same time. In other words, the repartition or re-translocation of CO<sub>2</sub> occurs within the trunk. This is the major reason why there is an obvious hysteresis between temperature change and the stem respiration rate, which is measured based on conventional theory. Although some studies did show an obvious functional relationship between the stem CO<sub>2</sub> efflux and temperature, this was because the measurements were conducted on the excised samples of examined trees (Zeng

et al., 2000) in which no sap flow occurred and the re-translocation of CO<sub>2</sub> was insignificant. Normally stem respiration is higher when it is measured on an excised segment of the wood (Wang et al., 2004). The rapid increase in CO<sub>2</sub> efflux observed after tissues are excised or injured is likely the result of rapid diffusion of CO<sub>2</sub> from the xylem, rather than an actual increase in the rate of respiration of the wounded tissues (Teskey et al., 2005). It was reported that 15%–75% of CO<sub>2</sub> moved upward with the sap flow during daytime, while 100% respired CO<sub>2</sub> was released into the ambient atmosphere via the bark at night when the stem sap flow ceased (McGuire et al., 2004; Bowman et al., 2005; Pruyn et al., 2002; 2003). The site of the xylem in the vicinity of the cambium layer contains a large amount of CO<sub>2</sub> at an evidently higher concentration than the surrounding ambient atmosphere, and sometimes it is even 3 times higher (Eklund, 1990; Levy et al., 1999; McGuire et al., 2004). This portion of CO<sub>2</sub> can easily dissolve in the xylem sap. Either in the bark or in the xylem, the plant cells filled with water objectively constitute great resistance to CO<sub>2</sub> diffusion outward. Inconsistencies between the diurnal patterns of CO<sub>2</sub> efflux and stem temperature have also been noted as a result of a high diffusion resistance of wood and cambium. Therefore, sapwood temperatures measured at the time of CO<sub>2</sub> flux measurement may not coincide with the actual measurements of CO<sub>2</sub> evolution outside the bark (Ryan et al., 1995). A consequence of the buildup and transport of CO<sub>2</sub> in stems is that the respiration of woody tissues can not be accurately estimated by way of measurement of CO<sub>2</sub> efflux to the atmosphere. The increased CO<sub>2</sub> concentration in the stem serves as a source not only being diffused through the stem to the atmosphere, but also being carried away from the lower to higher regions of trees. From this it can be seen that the externally measured values of stem respiration of trees may in large part be only the portion of the rate of CO<sub>2</sub> diffusion from the xylem sap rather than the total output of the respiratory processes. Some of the built-up CO<sub>2</sub> within stems may be fixed by wood photosynthesis because of the chloroplast-containing tissues in the bark and cambium (Pfanzen et al., 2001). For those fractions of CO<sub>2</sub> carried to the canopy, they may take part in carbon fixation by leaves. The utilization of this part of CO<sub>2</sub> by leaves has obvious merits over the CO<sub>2</sub> exchange process through the stomata that normally limits the entrance of external CO<sub>2</sub> into the leaf mesophyll tissue mainly to achieve a trade-off with water loss (Stringer et al., 1993; Larcher, 2001; Teskey et al., 2002). Inevitably, these two processes complicate the investigations on stem respiration and, in the meantime, affect the estimate of the whole tree carbon budget. Naturally, scientists have become increasingly aware that CO<sub>2</sub> efflux has a potential and commonly ignored relationship with the sap flow rate and canopy water use. If the functional relationship between the stem respiration rate and temperature based on conventional

theory were scaled up to calculate forest respiration in different seasons or in a whole year, it might lead to distinct inaccuracies.

Based on the above discussion, it is believed that the respired CO<sub>2</sub> in the trunk is re-allocated due to the sap flow in the xylem. One portion is released into the ambient atmosphere, while the other portion is dissolved in the sap and transported to the upper part of the stem and canopy by transpirational stream. The so-called respiration rate commonly measured using the current gas exchange system with a chamber sealed onto the stem is only the stem CO<sub>2</sub> efflux. If the CO<sub>2</sub> concentration in the xylem ([CO<sub>2</sub>]<sub>x</sub>) changes diurnally and seasonally, the CO<sub>2</sub> efflux from the bark would change accordingly. Since the sap flow rate could alter the xylem CO<sub>2</sub> concentration, the changes in CO<sub>2</sub> efflux would therefore be correlated with the change in sap flux in addition to being dependent on the temperature.

#### 4 Verification and clarification of the tri-relationship of xylem CO<sub>2</sub> concentration, sap flow rate, and CO<sub>2</sub> efflux

Some researchers observed and measured [CO<sub>2</sub>]<sub>x</sub>, while at the same time believing that the change in [CO<sub>2</sub>]<sub>x</sub> would affect the measurement of stem CO<sub>2</sub> efflux (Hari et al., 1991; Levy et al., 1998, 1999; Saveyn et al., 2008). It was also noted that the decrease in the stem CO<sub>2</sub> efflux was in association with the increase in the sap flow rate (Martin et al., 1994; Gansert, 2004). However, direct experimental proof and a satisfying explanation have been lacking. One important reason for this is related to the technical difficulties involved in obtaining reliable measurements reasonably verifying the existence of the multi-directional flow of xylem CO<sub>2</sub>. A relationship among xylem CO<sub>2</sub> concentration, sap flow rate and CO<sub>2</sub> efflux has not been satisfactorily clarified. The following ways and methods are supposed to prove and clarify the tri-relationship among the xylem CO<sub>2</sub> concentration, sap flow rate and stem CO<sub>2</sub> efflux.

##### 4.1 Re-translocation of stem respiration

The region where the stem respiration takes place includes the bark, the cambium beneath the bark, the xylem, and the parenchyma in the xylem. The cambium layer is mainly composed of meristematic tissues that contain a large amount of division cells, and therefore is known as the most active site where respiration occurs. According to the analyses and discussion above, the respired CO<sub>2</sub> ( $R_s$ ) in the stem can be divided into two portions: one portion ( $E_x$ ) is dissolved in the xylem sap flow in the form of CO<sub>2</sub>, H<sub>2</sub>CO<sub>3</sub> and HCO<sub>3</sub><sup>-1</sup> and transported to the upper part of the stem, canopy branches and leaves during daytime; the other

portion is released into the ambient atmosphere around the stem via the bark, namely the CO<sub>2</sub> efflux ( $E_a$ ) that is usually measured with the conventional chamber gas exchange method *in situ*. Their relationship is then defined as:

$$R_s = E_x + E_a. \quad (1)$$

Equation (1) only formulates the relationship describing the portions of respired CO<sub>2</sub> within the stem. A verification of the re-allocation of respired CO<sub>2</sub> in the stem is necessary.

##### 4.1.1 At the diurnal scale

When the nighttime sap flow approaches zero or finally comes to the end, the xylem sap is saturated with CO<sub>2</sub>, and 100% of respired CO<sub>2</sub> can be considered to be released into the ambient atmosphere. The total stem respiration at this moment equals the CO<sub>2</sub> efflux ( $R_s = E_a$ ). An exponential function between stem respiration and temperature ( $T_s$ ) is then established as:

$$E_a^n = a \cdot e^{bT_s}, \quad (2)$$

where  $E_a^n$  is the nighttime CO<sub>2</sub> efflux measured with the chamber gas exchange method (n refers to nighttime), and  $a$  and  $b$  are regression coefficients. Hereupon, we assume a cessation of sap flow during daytime, and that the respired CO<sub>2</sub> all diffuse out through the bark into the ambient atmosphere. Thus the condition for applying equation (2) is met. We use  $a$  and  $b$  values determined with the nighttime measurement to calculate or predict CO<sub>2</sub> efflux in response to the corresponding stem temperature during daytime:

$$E_p = a \cdot e^{bT_s}, \quad (3)$$

where  $E_p$  is the predicted CO<sub>2</sub> efflux from the stem during daytime, assuming the absence of sap flow activity. Likewise, an *in situ* measurement with the chamber gas exchange system during daytime is conducted to get the actual CO<sub>2</sub> efflux (in  $E_a^d$ , d refers to daytime) and stem temperature. If, under the same stem temperature,  $E_p - E_a^d > 0$ , then the assumption that the respired CO<sub>2</sub> was re-allocated within the stem is proven reasonable at the diurnal scale. In other words, the CO<sub>2</sub> efflux does change with the sap flow in the xylem. The value of  $\Delta E$  ( $E_p - E_a^d$ ) directly reflects the outcome of the carrying away of CO<sub>2</sub> by the sap flow. Whether the diurnal variation of  $\Delta E$  is correlated with the sap flow rate or not would be critical for the above verification. The ratio  $\Delta E/E_p$  (the potential decrease of CO<sub>2</sub> efflux in proportion to the total stem respiration) can be used to analyze and show if such correlation is within an acceptable level of significance or not.

#### 4.1.2 At the seasonal scale

Even though the diurnal experiment might verify the re-translocation of stem respiration, it does not necessarily mean that the relation between the CO<sub>2</sub> efflux and sap flow rate is a causal sequence. An observation on a seasonal scale is necessary to confirm such a relationship. Since the sap flow rate varies with the soil moisture in different seasons obviously (Zhao et al., 2006a, 2006b), such variations should be reflected in the change in  $E_a$  if there was a causal relationship between  $E_a$  and the sap flow rate. Normally, a pronounced hysteresis loop is formed when the measured values of CO<sub>2</sub> efflux are plotted against the stem temperature ( $T_s$ ) (Maier et al., 2006). If the loop radius differs significantly through different seasons with various soil moistures (for example, the loop radius in the wet season is generally larger than that during dry season), and  $E_a$  accordingly shows obvious differences, it means that different soil water supplies cause the difference in  $E_a$  due to the increase or reduction in the sap flow rates, which would further confirm the causal relationship between the change in the sap flow rate and CO<sub>2</sub> efflux.

#### 4.2 Measurement of CO<sub>2</sub> concentration in the stem wood

Due to the high solubility of CO<sub>2</sub> in water, a portion of the respired CO<sub>2</sub> dissolves in the xylem sap. In plant tissues CO<sub>2</sub> presents in both the gaseous as well as aqueous phases. For analysis of the relationship between the sap flow rate and [CO<sub>2</sub>]<sub>x</sub>, one of the important steps is to determine [CO<sub>2</sub>]<sub>x</sub> by using a proper instrument. Because the xylem is a solid structure containing water, the conventional chemical absorption method is unable to accurately measure the xylem CO<sub>2</sub> concentration. Some researchers designed and developed a new method by modifying the medically-applied microelectrode for the determination of stem CO<sub>2</sub> concentration (McGuire et al., 2004). This recently-introduced device for measuring stem internal CO<sub>2</sub> concentrations attracted particular attention no sooner than during its first application in tree physiological research. The microelectrode consists of a pH glass electrode and an Ag-AgCl reference electrode. The reference one is built in a capsule of exchangeable and ventilating teflon film. The capsule is filled with NaHCO<sub>3</sub>/NaCl electrolytes. The microelectrode can produce a measurable voltage in proportion to the CO<sub>2</sub> concentration if it is placed in a liquid medium containing CO<sub>2</sub>. The probe is modified by covering with a plastic pallium that is membrane-permeable and able to generate a moist microclimate. With such modification the probe can be used to directly detect the CO<sub>2</sub> concentration in the stem xylem. In practice, the microelectrode is directly inserted into the xylem, combined together with the sap flow measuring system connected to a data logger to record both the [CO<sub>2</sub>]<sub>x</sub> and sap flux density continuously and synchronously. Because the electrical output of the microelectrode

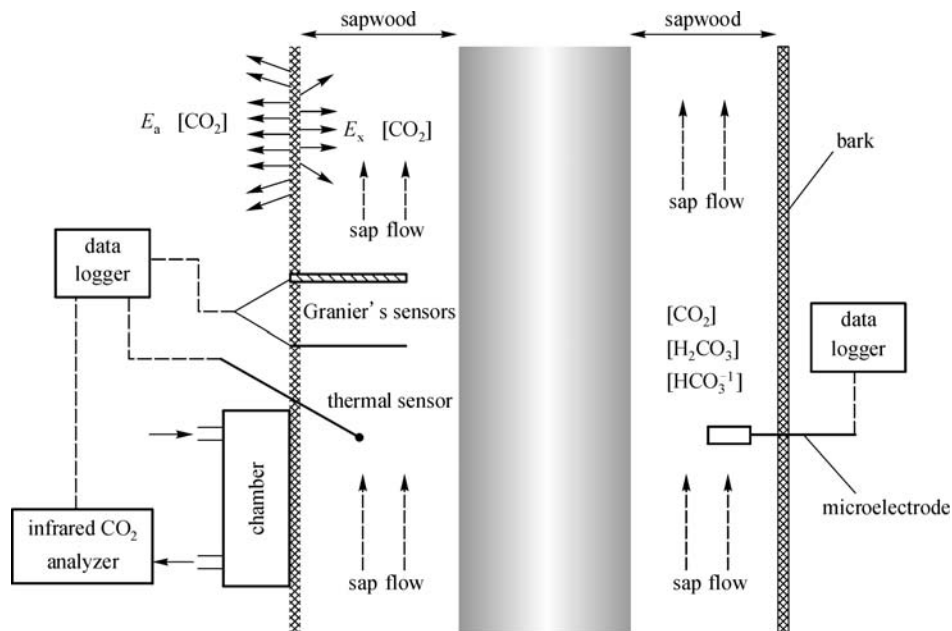
is a weak voltage signal, it needs to be magnified before it is connected to the data logger. The sap flux density ( $J_s$ ), which is usually applied to indicate the change in sap flow rates, can be determined with sap flow sensors (Granier's thermal dissipation probes) (Zhao et al., 2006a, 2006b). Both the  $J_s$  and [CO<sub>2</sub>]<sub>x</sub> change trends are analyzed to clarify the potential relation between the canopy water use and xylem CO<sub>2</sub> concentration. A working scheme for the on-site measurement is shown in Figure 1, indicating monitoring systems on a tree trunk measuring the sap flux density, CO<sub>2</sub> efflux from the stem, CO<sub>2</sub> concentration in the xylem as well as the stem temperature.

#### 4.3 Effect of the sap flow on stem CO<sub>2</sub> efflux

As discussed above, the sap flow rate, as a major determinant, significantly affects stem CO<sub>2</sub> efflux rates, and thus a reduction in CO<sub>2</sub> release would become most distinct during periods of high transpiration. At the present time, the commonly-measured  $E_a$  would underestimate the rate of respiration of the stem tissue due to the transport of CO<sub>2</sub> in the transpiration stream. It raises the question of how CO<sub>2</sub> efflux rates relate to tree transpiration. A negative relationship between the stem CO<sub>2</sub> efflux and sap flow rate has been reported (Bowman et al., 2005). The studies of Gansert et al. (2005) on *Betula pendula* also confirm the existence of a negative correlation between the sap flow and radial CO<sub>2</sub> efflux from tree stems. Even though there have been many findings showing that a considerable amount of respiration-evolved CO<sub>2</sub> is dissolved in the xylem sap and transported toward the canopy leaves by the transpirational stream, only a few quantitative or convincing evidence for an interaction between aqueous CO<sub>2</sub> transport and CO<sub>2</sub> release from woody plant stems have been reported (Levy et al., 1999; Teskey et al., 2002). For the purpose of assessing and determining to what extent the sap flow rate is linked to daily variations in the stem CO<sub>2</sub> efflux rates, a direct way has been proposed to try to establish and test the relationship between the internal sap flow rate and CO<sub>2</sub> efflux through manipulation of the whole-tree transpiration, for example, by reducing transpiration through stepwise removal of the foliage (Maier et al., 2006). If the respired CO<sub>2</sub> is re-allocated within the stem as suggested above, the sap flow will, as an important factor, alter the CO<sub>2</sub> efflux, and the difference between  $E_p$  and  $E_a^d$  should have a relationship with the sap flow rate correspondingly. The effect of the sap flow on CO<sub>2</sub> efflux could be determined and explained by using the functional relation between ( $E_p - E_a^d$ ) and the sap flow rate.

#### 4.4 Influence of the tree morphological features on CO<sub>2</sub> efflux

CO<sub>2</sub> efflux measurements have been reported as stem respiration in hundreds of publications. Although there



**Fig. 1** Scheme for monitoring systems on a tree stem measuring sap flow, CO<sub>2</sub> efflux from the stem, CO<sub>2</sub> concentration in xylem, as well as the stem temperature

have been records of these measurements for a long time, finding consistent relationships between rates of woody tissue CO<sub>2</sub> efflux and tissue sizes and types, tree age, species, and environmental conditions has been difficult (Lavigne et al., 1996). Quite a few researchers observed the large variability in stem CO<sub>2</sub> efflux rates encountered among and within trees and across stands (Lavigne et al., 1996; Damesin et al., 2002). Tree form features are important factors influencing the sap flow rate (Barbour et al., 2003; Zhao et al., 2006b). Bowman et al. (2005) demonstrated that differences in the sap flow rates and xylem anatomy were critically important for explaining within- and between-tree variations in CO<sub>2</sub> efflux from stems, because the slope of the regression relationship between CO<sub>2</sub> efflux and sap flux density differed substantially from tree to tree. They concluded that the transport of respiratory CO<sub>2</sub> produced within stems and branches in the xylem stream may influence CO<sub>2</sub> efflux from stems or branches, and such influence caused by the sap flow varies greatly in tree size and canopy dominance. Therefore, it is likely that deviations from the expected rate of CO<sub>2</sub> efflux are likely to be greater in larger trees because of their increased water content and greater capacity for dissolved CO<sub>2</sub> storage (Barbour et al., 2003; Bowman et al., 2005). The sap flux density will, of its own accord, change with different sapwood depths and indirectly affect the measured value of CO<sub>2</sub> efflux. To investigate the relationship between tree form features and stem CO<sub>2</sub> efflux, the size and radius of the hysteresis loop of  $E_a$  in response to stem temperature ( $T_s$ ) could be used to indicate the effect of

tree form features on CO<sub>2</sub> efflux. It will help to reveal if the sap flow rate is the controlling factor responsible for the variation of CO<sub>2</sub> efflux across different tree individuals.

## 5 Conclusions

Recently, there has been renewed interest in investigating the origin and fate of CO<sub>2</sub> in the xylem sap and determining what effect this carbon flux may have on the measurement of stem respiration. This does help in understanding the new role of transpiration as a driving force for the radial diffusion of CO<sub>2</sub> in a tree stem. A correct understanding of the respiration rate of the tree stem is important for many reasons, including quantifying the carbon cycle of forests, estimating the net ecosystem productivity, evaluating the patterns of carbon allocation, and examining the causes for variation in growth rates or growth efficiencies among trees and stands. A detailed knowledge of the stem respiration and accurate measurement of the stem respiration are undoubtedly very meaningful in investigating the internal and external CO<sub>2</sub> of a tree stem and will contribute to our understanding of forest carbon budgets. Clearly clarifying the interaction of CO<sub>2</sub> concentration in the xylem, CO<sub>2</sub> efflux from the stem and the sap flow rate, as well as the effect imposed on them by environmental factors, would provide intensive insight into the dynamics of stem respiration and the fluxes of CO<sub>2</sub> inside a tree stem. It is expected that with newly invented

and more precise instruments, an accurate analysis and estimate of the internal and external respired CO<sub>2</sub> fluxes of the stem will be possible.

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## References

- Amthor J S (1989). Respiration and crop productivity. New York: Springer-Verlag
- Barbour M M, Whitehead D (2003). A demonstration of the theoretical prediction that sap velocity is related to wood density in the conifer, *Dacrydium cupressinum* (rimu). *New Phytologist*, 158: 477–488
- Bowman W P, Barbour M M, Turnbull M H, Tissue D T, Whitehead D, Griffin K (2005). Sap flow rates and sapwood density are critical factors in within- and between-tree variation in CO<sub>2</sub> efflux from stems of mature *Dacrydium cupressinum* trees. *New Phytologist*, 167: 815–828
- Campbell G S, Norman J M (1998). An Introduction to Environmental Biophysics. New York: Springer-Verlag
- Cavaleri M A, Oberbauer S T, Ryan M G (2006). Wood CO<sub>2</sub> efflux in a primary tropical rain forest. *Global Change Biology*, 12: 2442–2458
- Chambers J Q, Tribuzy E S, Toledo L C, Crispim B F, Higuchi N, Santos J D, 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: S72–88
- Damesin C, Ceschia E, Le Goff N, Ottorini J M, Dufrière E (2002). Stem and branch respiration of beech: from tree measurements to estimation at the stand level. *New Phytologist*, 153: 159–172
- Eklund L (1990). Endogenous levels of oxygen, carbon dioxide and ethylene in stems of Norway spruce trees during one growing season. *Trees*, 4: 150–154
- Gansert D (2004). A new type of cuvette for the measurement of daily variation of CO<sub>2</sub> efflux from stems and branches in controlled temperature conditions. *Trees*, 18: 221–229
- Gansert D, Burgdorf M (2005). Effects of xylem sap flow on carbon dioxide efflux from stems of birch (*Betula pendula* Roth). *Flora*, 200: 444–455
- Hari P, Nygren P, Korpilahti E (1991). Internal circulation of carbon dioxide within a tree. *Canadian Journal of Forest Research*, 21: 514–515
- Janssens I A, Lankreijer H, Matteucci G, Kowalski A S, Buchmann N, Epron D, Pilegaard K, Kutsch W, Longdoz B, Grünwald T, Montagnani L, Dore S, Rebmann C, Moors E J, Grelle A, Rannik Ü, Morgenstern K, Oltchev S, Clement R, Guðmundsson J, Minerbi S, Berbigier P, Ibrom A, Moncrieff J, Aubinet M, Bernhofer C, Jensen N O, Vesala T, Granier A, Schulze E D, Lindroth A, Dolman A J, Jarvis P G, Ceulemans R, Valentini R (2001). Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, 7: 269–278
- Kakubari Y (1988). Diurnal and seasonal fluctuations in the bark respiration of standing *Fagus sylvatica* trees at Solling, West Germany. *Journal of Japanese Forest Society*, 70: 64–70
- Larcher W (2001). *Ökophysiologie der Pflanzen*. Stuttgart: Verlag Eugen Ulmer, 150–157
- Lavigne M B (1987). Differences in stem respiration responses to temperature between balsam fir trees in thinned and unthinned stands. *Tree Physiology*, 3: 225–233
- Lavigne M B, Franklin S E, Hunt E R Jr (1996). Estimating stem maintenance respiration rates for dissimilar balsam fir stands. *Tree Physiology*, 16: 687–695
- Levy P E, Jarvis P G (1998). Stem CO<sub>2</sub> fluxes in two Sahelian shrub species (*Guiera senegalensis* and *Combretum micranthum*). *Functional Ecology*, 1998, 12: 107–116
- Levy P E, Meir P, Allen S J, Jarvis P G (1999). The effect of aqueous transport of CO<sub>2</sub> in xylem sap on gas exchange in woody plants. *Tree Physiology*, 19: 53–58
- Maier C A, Clinton B D (2006). Relationship between stem CO<sub>2</sub> efflux, stem sap velocity and xylem CO<sub>2</sub> concentration in young loblolly pine trees. *Plant, Cell and Environment*, 29: 1471–1483
- Maier C A, Zarnoch S J, Dougherty P M (1998). Effects of temperature and tissue nitrogen on dormant seasonal stem and branch maintenance respiration in a young loblolly pine (*Pinus taeda*) plantation. *Tree Physiology*, 1998, 18: 11–20
- Martin T A, Teskey R O, Dougherty P M (1994). Movement of respiratory CO<sub>2</sub> in stems of loblolly pine (*Pinus taeda* L.) seedlings. *Tree Physiology*, 14: 481–495
- McGuire M A, Teskey R O (2004). Estimating stem respiration in trees by a mass balance approach that accounts for internal and external fluxes of CO<sub>2</sub>. *Tree Physiology*, 24: 571–578
- McGuire M A, Teskey R O, Cerasoli S (2007). CO<sub>2</sub> 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
- Meir P, Grace J (2002). Scaling relationships for woody tissue respiration in two tropical rain forests. *Plant, Cell and Environment*, 25: 963–973
- Pfanz H, Aschan G (2001). The existence of bark and stem photosynthesis in woody plants and its significance for the overall carbon gain. An eco-physiological and ecological approach. *Progress in Botany*, 62: 477–510
- Pruyn M L, Gartner B L, Harmon M E (2002). Within stem variation of respiration in Douglas fir trees. *New Phytologist*, 154: 359–372
- Pruyn M L, Harmon M E, Gartner B L (2003). Stem respiratory potential in six softwood and four hardwood tree species in the central cascades of Oregon. *Oecologia*, 137: 10–21
- Ryan M G, Gower S T, Hubbard R M, Waring R H, Gholz H L, Cropper W P, Running S W (1995). Woody tissue maintenance respiration of four conifers in contrasting climates. *Oecologia*, 101: 133–140
- Ryan M G, Hubbard R M, Clark D A, Sanford R L (1994). Woody-tissue respiration for *Simarouba amara* and *Minquartia guianensis*, two tropical wet forest trees with different growth habits. *Oecologia*, 100: 213–220
- Saveyn A, Steppe K, Lemeur R. Report on non-temperature related variations in CO<sub>2</sub> efflux rates from young tree stems in the dormant season (2008). *Trees*, 22(2): 165–174
- Stringer J W, Kimmerer T W (1993). Refixation of xylem sap CO<sub>2</sub> in *Populus deltoides*. *Physiol Plant*, 89: 243–251

- Teskey R O, McGuire M A (2002). Carbon dioxide transport in xylem causes errors in estimation of rates of respiration in stems and branches of trees. *Plant, Cell and Environment*, 25, 1571–1577
- Teskey R O, McGuire M A (2005). CO<sub>2</sub> transported in xylem sap affects CO<sub>2</sub> efflux from *Liquidambar styraciflua* and *Platanus occidentalis* stems, and contributes to observed wound respiration phenomena. *Trees*, 19: 357–362
- Wang M, Liu Y Q, Hao Z Q, Wang Y S (2006). Respiration rate of broadleaved Korean pine forest ecosystem in Changbai Mountains. *Chinese Journal of Applied Ecology*, 17(10): 1789–1795 (in Chinese)
- Wang W J (2004). Methods for the determination of CO<sub>2</sub> flux from non-photosynthetic organs of trees and their influences on the results. *Acta Ecologica Sinica*, 24(9): 2056–2067
- Wang W J, Wang H M, Zu Y G, Li X Y, Takayoshi K (2005). Characteristics of root, stem, and soil respiration Q<sub>10</sub> temperature coefficients in forest ecosystems. *Acta Phytoecologica Sinica*, 29(4): 680–691 (in Chinese)
- Wang W J, Yang F J, Zu Y G, Wang H M, Kentaro T, Kaichiro S, Takayoshi K (2003). Stem Respiration of a Larch (*Larix gmelini*) Plantation in Northeast China. *Acta Botanica Sinica*, 45(12): 1387–1397
- Waring R H, Schlesinger W H (1985). *Forest ecosystems: concepts and management*. London: Academic Press
- Xiao F M, Wang S L, Du T Z, Chen L C, Yu X J (2005). Respiration of Chinese fir in plantations in Huitong, Hu'nan Province. *Acta Ecologica Sinica*, 25(10): 2514–2519 (in Chinese)
- Xu M, Debiase T A, Qi Y, Goldstein A, Liu Z (2001). Ecosystem respiration in a young ponderosa pine plantation in Sierra Nevada Mountains, California. *Tree Physiology*, 21: 309–318
- Yan Y P, Sha L Q, Cao M (2008). Diurnal Variation of Stem Respiration of Three Tropical Tree Species in Xishuangbanna, Southwest China. *Journal of Plant Ecology*, 32(1): 23–30 (in Chinese)
- Yoder B J, Ryan M G, Waring R H, Schoettle A W, Kaufmann M R (1994). Evidence of reduced photosynthetic rates in old trees. *Forest Science*, 40: 513–527
- Zeng X P, Peng S L, Zhao P (2000). Measurement of respiration amount in artificial *Acacia Mangium* forest in a low subtropical hill forest region of Guangdong. *Acta Phytoecologica Sinica*, 24(2): 420–424 (in Chinese)
- Zeng X P, Zhao P, Sun G C (2006). Effects of climate warming on terraneous plants. *Chinese Journal of Applied Ecology*, 17(12): 2445–2450 (in Chinese)
- Zeng Z P (2007). Productivity, structure and function of 3 types of man-made forest communities in Heshan, South China. Guangzhou: PhD Dissertation of Graduate School of Chinese Academy of Sciences (in Chinese)
- Zhao P, Lu P, Ma L, Sun G C, Rao X Q, Cai X A, Zeng X P (2005). Combining sap flow measurement-based canopy stomatal conductance and <sup>13</sup>C discrimination to estimate forest carbon assimilation. *Chinese Science Bulletin*, 50(18): 2021–2027
- Zhao P, Rao X Q, Ma L, Cai X A, Zeng X P (2006a). Sap flow-scaled stand transpiration and canopy stomatal conductance in an *Acacia mangium* forest. *Acta Phytoecologica Sinica*, 30(4): 655–665
- Zhao P, Rao X Q, Ma L, Cai X A, Zeng X P (2006b). The variations of sap flux density and whole-tree transpiration across individuals of *Acacia mangium*. *Acta Ecologica Sinica*, 26(12): 4050–4058
- Zhao X S, Guan D X, Wu J B, Zhang M, Jin C J, Han S J (2006c). The relationship between CO<sub>2</sub> flux and temperature of the mixed forest of broadleaved and Korean-Pine in Changbai Mountain. *Acta Ecologica Sinica*, 26(4): 1088–1095