Interpretation of stem CO\textsubscript{2} efflux measurements

TEEMU HÖLTTÄ\textsuperscript{1,2} and PASI KOLARI\textsuperscript{1}

\textsuperscript{1} Department of Forest Ecology, University of Helsinki, P.O. Box 24, FIN-00014, Finland
\textsuperscript{2} Corresponding author (teemu.holtta@helsinki.fi)

Received May 25, 2009; accepted August 1, 2009; published online 22 September 2009

Summary It is known that stem CO\textsubscript{2} efflux differs somewhat both temporally and spatially from actual stem respiration, but relations between these two are not fully understood. A physical model of CO\textsubscript{2} diffusion and advection by xylem sap flow is developed to interpret the CO\textsubscript{2} flux signal from the stem. Model predictions are compared against measured CO\textsubscript{2} efflux data from a field-grown 16-m \textit{Pinus sylvestris} L. tree. The ratio of CO\textsubscript{2} efflux to CO\textsubscript{2} production is predicted to be much larger in the upper part of the tree than in the lower part as the xylem sap carries the respired CO\textsubscript{2} upwards. The model also predicts the temperature dependency of real respiration to be higher than that of the CO\textsubscript{2} efflux due to the slowness of diffusion. The relation between stem respiration and CO\textsubscript{2} efflux depends strongly on the sap flow rate, radial diffusion resistance and stem geometry and size. The model may be used to scale individual CO\textsubscript{2} efflux measurements to evaluate the respiration rate of whole trees and forests.

\textit{Keywords}: advection, cuvette, diffusion, sap flow, stem respiration.

Introduction

Typically, the magnitude and the temporal pattern of stem respiration have been quantified by measuring the efflux of CO\textsubscript{2} from the stem although it has been known for a long time that these two do not strictly equal each other (e.g., Teskey and McGuire 2002, Teskey et al. 2008). CO\textsubscript{2} produced by respiration inside the stem diffuses radially out through the bark where its efflux can be measured, but it is also simultaneously transported upwards in the xylem by the transpiration stream. The dependence of stem CO\textsubscript{2} efflux on xylem sap flow is well recognized, but still the quantification of actual stem respiration rates from stem CO\textsubscript{2} efflux and sap flow measurements has remained ambiguous. For example in some studies, the proportion of CO\textsubscript{2} diffusing radially to the atmosphere has been found to decrease with increasing sap flow rate (e.g., Teskey and McGuire 2002, Bowman et al. 2005, Gansert and Burgdorf 2005), whereas other studies have found the opposite (Levy et al. 1999) or no trend (Maier and Clinton 2006) between sap flow rate and stem CO\textsubscript{2} efflux. Another interesting question, which has been under discussion (e.g., Hari et al. 1991, Levy et al. 1999), is the proportion of the CO\textsubscript{2} released by stem respiration that will be ‘recycled’, i.e., carried to the leaves where it could potentially be used for photosynthesis.

McGuire and Teskey (2004) have calculated quantitatively the proportions of CO\textsubscript{2} produced by respiration diffusing out, transported upwards or stored temporarily within the stem. For the three species under examination, CO\textsubscript{2} advection with the xylem sap was of key importance. The study of McGuire and Teskey (2004) demonstrated how the proportions of CO\textsubscript{2} diffusion and advection can be calculated at a local level from sap flow, CO\textsubscript{2} efflux and axial CO\textsubscript{2} concentration gradient measurements. Therefore, the ratio of stem respiration to CO\textsubscript{2} efflux from the stem can be estimated locally from in situ measurements of internal stem CO\textsubscript{2} concentration, sap flow and stem CO\textsubscript{2} efflux measurements. However, no theoretical framework exists to predict the relationship between stem respiration and CO\textsubscript{2} efflux, and how this relationship depends, e.g., on the spatial position in the tree, sap flow rate, internal resistance to CO\textsubscript{2} diffusion, and tree size and geometry. Internal CO\textsubscript{2} transport and its efflux from the stem are, in principle, straightforward to model and predict, as CO\textsubscript{2} diffusion and advection are basic physical processes. Diffusion is dependent on the CO\textsubscript{2} concentration gradient and on the diffusion resistance, which can vary at least according to temperature, tissue type, and the air and water content of the stem. Advection with the xylem sap is dependent on the dissolution of CO\textsubscript{2} in the sap, which in turn depends on the CO\textsubscript{2} concentration in contact with the gaseous phase, temperature and pH according to Henry’s law. However, the difficulty of the task lies in the description of the complex stem and branch geometry and the parametrization of the model. Difficult parameters to estimate include the diffusion coefficient of CO\textsubscript{2} in the living stem, which is a combination of pathways in air, water and cell wall in different types of tissues and the distribution of respiration within the stem. The respiring living

© The Author 2009. Published by Oxford University Press. All rights reserved.
For Permissions, please email: journals.permissions@oxfordjournals.org
cells are mainly located in the phloem and the cambium, but there are living cells in the parenchyma of the sapwood whereas the heartwood contains no living cells. This study presents a model where the transport of CO₂ inside the stem is modelled, and the connection between stem respiration and CO₂ efflux from the stem is established from physical grounds. This model can then also be used for scaling whole tree respiration from stem and branch CO₂ efflux measurements.

Materials and methods

Model description

The model tree was divided radially into the functional components of outer bark, phloem, cambium, sapwood and heartwood (Figure 1). CO₂ diffuses from its site of production following its concentration gradient. In cylindrical coordinates, the coordinate system best suited to describe the tree stem, the diffusion equation is as follows (e.g., Bird et al. 1960):

\[
\frac{\partial C_{\text{diff}}}{\partial t} = D \left[ \frac{\partial^2 C}{\partial r^2} + \frac{1}{r} \frac{\partial C}{\partial r} \right],
\]

where \( C \) is the CO₂ concentration in the stem (water phase) (mol m\(^{-3}\)), \( r \) is the radial distance from the pith (m) and \( D \) is the radial diffusion coefficient of CO₂ in the stem (m\(^2\) s\(^{-1}\)). CO₂ diffusion is found to occur in the water phase. The model is assumed to be symmetrical in the tangential direction, so there is no net movement of CO₂ tangentially. The diffusion of CO₂ in the axial direction is neglected. Although diffusion in the axial direction is 1–2 orders of magnitude higher than in the radial direction (Sorz and Hietz 2006), it is still insignificant in relation to axial advection by the xylem sap with the typical sap flow velocities. Equation for advection of CO₂ in the axial direction along with the xylem sap is as follows:

\[
\frac{\partial C_{\text{adv}}}{\partial y} = \nu \frac{\partial C}{\partial y} + \frac{\partial v}{\partial y} C,
\]

where \( y \) is the axial coordinate (m) and \( \nu \) is the sap flow velocity (m s\(^{-1}\)).

![Figure 1](https://example.com/figure1.png)

Figure 1. Schematic drawing of the functional components in the model stem (A) and an axial profile of their thicknesses in the model stem (B).
The second term in the right-hand side of Eq. (2) is assumed to be zero, as we assume that the cross-sectional area of the sapwood is preserved at each height and at each branching, which leads to the sap flow velocity being constant at each height. This is in accordance with the pipe-model theory (Tyree and Zimmermann 2002). The total change in CO₂ concentration was obtained from the sum of (1) and (2).

In some simulations, we calculated the transient CO₂ efflux with diurnally varying ambient temperature and sap flux values. Respiration rate was here estimated to be dependent on temperature, but in reality respiration could also be dependent on, e.g., water status (Saveyn et al. 2008), substrate availability (Pruyn et al. 2002) and oxygen concentration (Spicer and Holbrook 2007). Stem respiration \( R \) (mol s⁻¹) at each functional component (sapwood, cambium and phloem) was assumed to be a function of local stem temperature using an exponential relationship between temperature and respiration (e.g., Lavigne 1987)

\[
R = R_{10}Q_{10}^{(T-10)/10},
\]

where \( R_{10} \) is respiration at a temperature of 10 °C and \( Q_{10} \) is the factor by which respiration changes when temperature doubles. The radial temperature profile was also calculated inside the stem (e.g., Bird et al. 1960)

\[
\frac{\partial T}{\partial r} = \kappa \left( \frac{\partial^2 T}{\partial r^2} + \frac{1}{r} \frac{\partial T}{\partial r} \right),
\]

where \( T \) is the temperature and \( \kappa \) is the thermal diffusivity.

CO₂ concentration at the outer edge of the stem \( (R) \) was equal to ambient CO₂ concentration \( (C_{\text{amb}}) \) at all times

\[
C(R, t) = C_{\text{amb}}.
\]

As in the case of CO₂ diffusion, the temperature at the outer edge of the stem \( (S_r) \) was equal to ambient temperature \( (T_{\text{amb}}) \):

\[
T(S_r, t) = T_{\text{amb}}(t).
\]

For the dynamic model, the sapwood was also divided into components of water, air and cell wall. In the simulation, CO₂ was released into the gas phase, and the concentration of total dissolved carbon in the xylem, in the form of \( \text{CO}_2 \) and \( \text{HCO}_3^- \), in the water phase was equilibrated with the gas phase according to Henry’s law (McGuire and Teskey 2002)

\[
C = K_H \left( 1 + \frac{K_1}{10^{pH}} \right) p_{\text{CO}_2},
\]

where \( p_{\text{CO}_2} \) [atm] is the partial pressure of CO₂ in the gas phase, \( K_H \) [mol atm⁻¹ l⁻¹] is Henry’s law’s coefficient for CO₂ in water and \( K_1 \) is the first acidity constant. Henry’s law coefficient of 0.036 mol atm⁻¹ l⁻¹ was used, which corresponds to a temperature of 25 °C. A pH value of 6, a typical pH value for xylem sap across many species (McGuire and Teskey 2002, Teskey et al. 2008), was assumed. These choices yield an ‘effective’ Henry’s law constant, i.e., the proportion between the water phase CO₂ concentration and the partial pressure of CO₂ of 0.053 mol atm⁻¹ l⁻¹.

For the numerical solution, the model tree was divided into \( N \) elements \((n = 25)\) radially and \( M \) elements axially \((m = 25)\), and the equations for diffusion of CO₂ in the radial direction and advection with the xylem sap flux were solved using explicit Euler finite difference scheme using Fortran 90 programming language. The numerical solution is described in detail in the Supplementary Material.

**Measurement description**

Measurements were taken at SMEAR II station (Hari and Kulmala 2005) located in southern Finland at Hyytiälä Forestry Field Station of the University of Helsinki. CO₂ efflux from the stems was measured twice an hour using an automated chamber system (Kolari et al. 2009). Two acrylic plastic chambers (height 20 cm and width 3.5 cm) were attached on the bark of one tree. The height of the tree was 16.5 m and the crown base was at 10.5 m. The chambers were located in the lower part of the living crown at heights of 12 and 13.7 m. There was a continuous flow of 11 min⁻¹ through the chamber, the efflux of CO₂ was determined from the difference of CO₂ concentration between the air drawn from the chamber and the replacement air led into the chamber.

Transpiration rate was measured with two chambers (Altimir et al. 2002) located at the top of the tree. The shoots were installed inside the chamber into a horizontal position, and the needles gently bent to form a plane. The chambers remained open most of the time but were closed intermittently for one minute, about 80 times per day. The measured \( \text{H}_2\text{O} \) fluxes were corrected for the damping of signal due to adsorption of water onto the chamber walls by multiplying the measured transpiration by an empirical factor \( c \) (Kolari et al. 2004):

\[
c = \text{MAX} \left( 1.55, 1.3 + 0.7 \times \left( \frac{\text{RH}}{100} \right) \right).
\]

Sap flow rate is taken to be the same as transpiration rate and the sap flow velocity is calculated from sap flow rate by dividing with sap wood cross-sectional area. Sap flow velocity trails the transpiration rate slightly, but the difference between these two is not very large for Scots pine at the measurement site (Perämäki et al. 2001).

**Model parametrization**

Simulations were first carried out for a simple model tree structure where the tree was described as a non-tapering cylinder divided into heartwood, sapwood, cambium,
phloem and outer bark (Figure 1), and their proportions remained invariable with height. However, it was noticed that the results, especially in the upper parts of the stem, were very sensitive to the changes in proportion of the different functional compartments of the stem (heartwood, sapwood, phloem and outer bark) and that the results obtained from this simple geometry were not realistic for a real tree. Therefore, the stem was made to taper in diameter according to the detailed empirical measurements for Finnish Scots pine trees (Laasasenaho 1982). In addition, sapwood area was assumed to be constant below the crown, and no heartwood was assumed to occupy the tree above the crown. The thickness of the phloem and the outer bark was also a function of distance. These functions were also taken from the detailed empirical measurements for Finnish Scots pine (Hakkila 1967). The width of the heartwood, sapwood, cambium, phloem and bark as a function of tree height, which are fed as input to the model, is shown in Figure 1.

The model parametrization is shown in Table 1. Respiration was assumed to be proportional to the fraction of living cells in each tissue. The sap wood is assumed to have 5% of living cells, the phloem and cambium 50%, whereas the outer bark and heartwood are assumed to contain no living cells (Siau 1984). The absolute value of stem respiration at crown height was chosen iteratively, so that the total amount of modelled CO2 flux from the stem is of the same magnitude as in the measurements. This is a typical value observed in our measurements and also in another study for Scots pine in Finland (Zha et al. 2004). Root respiration is not modelled explicitly, but its effects on stem CO2 balance are simulated by varying the CO2 concentration of xylem sap entering the stem, which is considered to be the same as the soil water CO2 concentration. The relative amount of water, air and cell wall is used in the calculations done with the dynamic part of the model, i.e., in calculations shown from Figure 3 onwards. In these calculations, respired CO2 enters the air phase and then equilibrates with the water phase. The proportion of water and air in the stem are assumed to be constant. In reality, the water and air content of the stem may vary both diurnally and seasonally (e.g., Pausch et al. 2000). The value of $Q_{10}$ was chosen to be 2.5 as this reflects the temperature dependency generally observed in studies, although there is a large variation between studies (e.g., Ceschia et al. 2002, Damesin et al. 2002). Diffusion coefficient inside the stem is the most difficult of the parameters in the model to estimate. The diffusion coefficient of CO2 in the stem has been found to have a large variation between species (Steppe et al. 2007) and depends on the gas content of the specimen (Sorz and Hietz 2006). The diffusion coefficient may also be variable in space (e.g., Levy and Jarvis 1998, Pruyn et al. 2002) and time (e.g., Stockfors and Linder 1998, Steppe et al. 2007). One of the very few studies is that of Sorz and Hietz (2006) where the diffusion coefficient of gas in the stem has been measured explicitly. They measured several species and found that the diffusion coefficient for oxygen in water-saturated xylem was typically lower than the diffusion coefficient in water alone, illustrating that the xylem cell walls present a major barrier to gas diffusion, and that the diffusion coefficient increased above that of water with decreasing water content, as diffusion in the gas phase is many

Table 1. Model parameters. The first set of parameters is used in all the calculations while the latter ones are used only in the case of a dynamic model, i.e., in the simulations leading to results presented in Figure 3 and onwards. Tree height, tree diameter, radial diffusion coefficient for CO2 and sap flow rate are included if the scaling parameter is $F$.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree height</td>
<td>16.5 m</td>
<td>Measured</td>
</tr>
<tr>
<td>Tree diameter at the bottom</td>
<td>19 cm</td>
<td>Measured</td>
</tr>
<tr>
<td>Radial diffusion coefficient for CO2</td>
<td>$1.25 \times 10^{-9} \text{ m}^2 \text{ s}^{-1}$</td>
<td>Estimated from the literature (Sorz and Hietz 2006, Spicer and Holbrook 2007)</td>
</tr>
<tr>
<td>Xylem sap flow velocity</td>
<td>$1 \times 10^{-4} \text{ m s}^{-1}$</td>
<td>Measured</td>
</tr>
<tr>
<td>Volume proportion of living cells in xylem sapwood</td>
<td>5%</td>
<td>Siau (1984)</td>
</tr>
<tr>
<td>Volume proportion of living cells in cambium and phloem</td>
<td>50%</td>
<td>Estimation</td>
</tr>
<tr>
<td>$R_{10}$ of cambium and phloem</td>
<td>$1.9 \times 10^{-4} \text{ mol m}^3 \text{ s}^{-1}$</td>
<td>Iterated to match measurements</td>
</tr>
<tr>
<td>$R_{10}$ of sapwood</td>
<td>$1.9 \times 10^{-5} \text{ mol m}^3 \text{ s}^{-1}$</td>
<td>Iterated to match measurements</td>
</tr>
<tr>
<td>Parameters (used only in the dynamic model)</td>
<td>$Q_{10}$</td>
<td>2.5</td>
</tr>
<tr>
<td>Stem thermal diffusivity of wood</td>
<td>$2.86 \times 10^{-7} \text{ m}^2 \text{ s}^{-1}$</td>
<td>Siau (1984)</td>
</tr>
<tr>
<td>Henry’s law coefficient</td>
<td>0.036 mol atm$^{-1}$</td>
<td>McGuire and Teskey (2002), temperature 25 ºC.</td>
</tr>
<tr>
<td>Proportion of wood</td>
<td>0.35</td>
<td>Estimation</td>
</tr>
<tr>
<td>Proportion of water</td>
<td>0.5</td>
<td>Estimation</td>
</tr>
<tr>
<td>Proportion of air</td>
<td>0.15</td>
<td>Estimation</td>
</tr>
</tbody>
</table>
orders of magnitude higher in air compared to water. The diffusion coefficient inside the stem was given a constant value equal to half of the diffusion coefficient for CO$_2$ in water. This choice represents a ‘bulk’ diffusion coefficient, based on empirical measurements, whereas in reality the diffusion process would be expected to be much more complicated occurring through air, water and cell wall and the diffusion coefficient would vary between tissue type.

Scaling parameter for $F$ for steady-state case

It turns out that the values of many of the individual parameters per se do not determine the ratio of CO$_2$ efflux to production in the tree in steady state. Several parameters can actually be clamped together into a scaling parameter that describes the ratio of CO$_2$ diffusion out of the stem to CO$_2$ advection with the xylem sap at any height of the tree. Radial diffusion of CO$_2$ is proportional to the diffusion coefficient divided by the diffusion distance (or stem radius $S_r$) squared:

$$\text{Diff} \propto DS_r^{-2}. \quad (9)$$

Axial advection of CO$_2$ is proportional to the sap flow velocity divided by advection distance (or tree length $L$):

$$\text{Adv} \propto vL^{-1}. \quad (10)$$

We define a scaling parameter $F$ to denote the relative (relative to a ‘base case’ scenario) ratio of the rapidity of diffusion to advection:

$$F = \frac{\text{Diff}}{\text{Adv}} \propto \frac{DS_r^{-2}}{vL^{-1}} = \frac{DL}{vS_r^2}. \quad (11)$$

This means that we can calculate how stem efflux (relative to CO$_2$ production or stem volume) changes if one or many of the parameters involved in the calculation of $F$ change, i.e., we do not have to consider the changes in the individual parameters per se to find out how the relation between stem CO$_2$ efflux is affected. For example, if the tree length would change by a factor of 4 while the stem diameter would simultaneously change by a factor of 2, $F$ and the stem CO$_2$ efflux at any height (in relation to CO$_2$ production or stem volume) would remain unchanged. In another example, $F$ changes in the same proportion as the diffusion coefficient ($D$) and in inverse proportion to sap flow velocity ($v$). Doubling of the diffusion coefficient doubles $F$ and doubling of the sap flow velocity decreases $F$ to half. $F$ is expressed in relation to the ‘base case’ values given in Table 1.

Results

CO$_2$ production in the stem exceeds its efflux through the bark at the base of the tree, as a major part of the CO$_2$ produced is carried upwards instead of diffusing outwards (Figure 2A). Moving upwards in the tree CO$_2$ efflux starts to increase in relation to CO$_2$ production as CO$_2$ accumulates in the xylem sap raising its CO$_2$ concentration, which promotes a faster outward diffusion along with the decreasing diffusion distance due to stem tapering. CO$_2$ efflux...
again decreases very close to the leaves as the CO₂ concentration of the xylem sap starts to decrease. The effects of changes in diffusion coefficient for CO₂, sap flow velocity, stem diameter and tree length are all included in the scaling parameter $F$. When radial diffusion slows down in relation to axial advection ($F < 1$), the proportion of CO₂ diffusing out in relation to CO₂ production decreases (Figure 2). The proportion of CO₂ produced in the tree entering the leaves was 5% for the ‘base case’, and 1, 2, 12 and 44% for $F = 0.1$, $F = 0.5$, $F = 2$ and $F = 10$, respectively (not shown). However, the scaling parameter $F$ does not incorporate all of the parameters affecting stem CO₂ efflux. At least stem form (tapering), spatial distribution of CO₂ production and the effect of CO₂ flux from the soil remain outside of its reach. The effect of CO₂ flux from the soil was marginal at typical soil CO₂ concentrations of 10 times the ambient, but was larger at 100 times the ambient concentrations (Figure 2B). Soil CO₂ concentration was assumed to be diurnally constant, which is likely not to differ too much from reality (Pumpanen et al. 2008). The radial position of CO₂ production was found to have large effects on the results. When respiration was divided evenly within the sapwood, phloem and cambium, the average diffusion distance was larger, advection had a larger role compared to base case and the ratio of CO₂ efflux to production differed more from unity both at the bottom and at the top of the tree. The opposite was true when the site of respiration was only in the phloem and the cambium (Figure 2B). Both axial position (tree base, 8 m and apex) and radial position (distance from pith) had a large effect on the predicted CO₂ concentration (Figure 2C). The peak value for CO₂ reaches values of about 80 times the ambient CO₂ concentration at the middle of the tree. CO₂ concentrations varied much in both axial and radial directions. The CO₂ concentrations are also affected by changes in other parameters (such as the absolute amount of respiration), but the CO₂ concentrations do not scale with $F$ in the same way as the ratio between CO₂ production and efflux does.

In a dynamic scenario, stem respiration rate was temperature dependent according to Eq. (3) and temperature was varied diurnally. Temperature inside the stem was found to follow ambient temperature quite rapidly, with a time lag of only seconds (at phloem near the needles) or tens of minutes (at inner sapwood at the base) (not shown). The time lag between stem efflux and change in ambient temperature was much longer, of the order half an hour (near the needles) or hours (at the base) (Figure 3A) as diffusion of CO₂ inside the stem is an order of magnitude slower than heat conduction. However, heat conduction could be delayed in relation to diffusion if the thermal and diffusive properties of the outer bark would be taken explicitly into account. In addition to resulting in a time lag between ambient temperature and stem efflux, slow CO₂ diffusion also caused a dampening in the diurnal variation of stem CO₂ efflux. This implicates that the actual temperature dependency of stem respiration is typically stronger, i.e., $Q_{10}$ is higher, from what is inferred from temperature dependency of stem CO₂ efflux measurements. In the lower part of the stem, the diurnal variation in the CO₂ efflux becomes almost unnoticeable, partly due to the slow radial diffusion and partly due to the assumed constant CO₂ concentration of the sap entering the tree from the soil.

To quantify exclusively the effect of variation in sap flow velocity on CO₂ efflux, sap flow velocity was varied diurnally while the stem respiration rate was kept constant. In the lower and middle parts of the stem, the CO₂ efflux decreases (with a time lag) when the sap flow velocity increases (Figure 3B) as CO₂ is then carried away faster by the transpiration stream. The situation is opposite in the upper parts of the tree: acceleration of sap flow carries more CO₂ from below and the CO₂ efflux from the stem increases. We also tried varying Henry’s law coefficient, but the effect on the magnitude and the diurnal pattern of the modelled stem CO₂ efflux was small with small changes in the coefficient (not shown).

Next, ambient temperature and sap flow velocity were fed as input to the model, and the resulting stem efflux of CO₂ was predicted (Figure 4). Stem respiration was assumed to
depend solely on stem temperature. The $Q_{10}$ value was chosen iteratively to be 3.5, so that the model gave a similar daily variation in CO$_2$ efflux to the measurements. To estimate the effect of sap flow velocity on the measured CO$_2$ effluxes, we also calculated ‘a temperature normalized CO$_2$ efflux rate’ by subtracting the measured CO$_2$ efflux from the CO$_2$ efflux predicted from the temperature alone according to Eq. (3). ‘Apparent $Q_{10}$’, i.e., the temperature dependency of the CO$_2$ efflux and not the true respiration, values of 2.5 and 3.2 were used at 12 and 13.7 m height, respectively, as these values gave the best fits for the temperature dependency of the CO$_2$ efflux measurements (Figure 5 insert). The ‘temperature normalized CO$_2$ efflux rate’ decreased with increasing sap flow velocity (Figure 5B and C) as is predicted by the model (see Figure 2) to occur at locations that are not very close to the needles.

**Discussion**

The proportion of CO$_2$ diffusing out of the stem to CO$_2$ production by respiration is predicted to vary much depending on the spatial position, on the tree structure and on the sap flow rate. In any case, the amount of CO$_2$ carried away by the xylem is of the same order of magnitude as that diffusing to the atmosphere through the bark in typical conditions for trees of any structure and size, and therefore it cannot be neglected. CO$_2$ efflux measurements done on the trunk likely underestimate stem respiration, whereas the CO$_2$ efflux measurements very close to the leaves most likely overestimate stem respiration. Several studies have measured higher CO$_2$ effluxes in the upper parts of the trunk or in the branches than in the stem in relation to surface area or mass (e.g., Ceschia et al. 2002, Bowman et al. 2005). However, this does not necessarily signify higher respiration rates in the upper crown. CO$_2$ will accumulate in the xylem sap on its way up, and diffusion through the bark is strongly accelerated when the stem and branches taper as diffusion rate is proportional to the inverse of the diffusion distance squared. This should be a general trend in all circumstances. Stem efflux of CO$_2$ should be larger than CO$_2$ production near the apex and smaller than CO$_2$ production at the base. This has important consequences for the estimation of whole tree respiration rates from stem CO$_2$ efflux measurements.
Our modelling results suggest that measuring CO₂ efflux quite close, but not too close, to the apex would result in unity between CO₂ efflux and production (Figure 2A), but that the position where CO₂ efflux and production should equal each other should also depend on different factors such as the sap flow rate, the tree size and the distribution of respiration. According to our model results, proportion of ‘recycled’ CO₂ could be noticeable (it was 8% in our ‘base case’ simulation and increased considerably with slower diffusion), but it is more difficult to predict than the relation between local CO₂ production and efflux since it is affected by small-scale branch (and possibly leaf) geometry near the apex. The time lag between ambient temperature and stem efflux rate resulted mainly from the slowness of the diffusion of CO₂ radially through the stem. Also sap flow rate, within-stem storage of CO₂ and heat propagation contributed slightly to the time lag. Predicted CO₂ concentration showed large variations both axially (stem base, 8 m, apex) and radially (distance from pith), and was found to reach values about 80 times the ambient. There is a wide range of measured CO₂ concentrations in the literature, and our value is well within the scope of values reported in the literature (Teskey et al. 2008). Moreover, it has been demonstrated that differences in CO₂ concentration between xylem and bark tissues are large: values for xylem CO₂ concentration have been reported to be as high as 26% (Wittman et al. 2006), whereas those for CO₂ concentrations in bark tissues are reported to be around 0.06–0.17% (Cernusak and Marshall 2000). The stem CO₂ efflux predicted by our model was naturally linearly related to CO₂ concentration in the outer bark. The linear relationship between stem CO₂ concentration and stem has also been found in various studies (e.g., Teskey and McGuire 2002, Steppe et al. 2007), which should not be surprising as this is true for any diffusive process, and the proportionality between these two is the effective diffusion coefficient of CO₂ in the stem.

Our model predicts that the temperature dependency of stem respiration, i.e., the real \( Q_{10} \), is distinct from the temperature dependency of the CO₂ efflux, the ‘apparent’ \( Q_{10} \) (see Figure 3A). The real \( Q_{10} \) is likely to be higher than the apparent one, as the latter is affected by the large diffusion resistance. An iterative estimation for the real temperature dependency of respiration in our measurements yielded 3.5 for \( Q_{10} \), while the ‘apparent’ \( Q_{10} \) was 2.5 and 3.2 at 12 and 13.7 m height, respectively. Other studies have typically reported \( Q_{10} \) values lower than our real \( Q_{10} \), but they have not brought about a distinction between the real and ‘apparent’ \( Q_{10} \). \( Q_{10} \) in other studies has been found to vary over a large range of at least 1 to well over 3 (Paembonan et al. 1991, Ceschia et al. 2002, Damesin et al. 2002), and even up to 6 (Kim et al. 2007). There could also be other reasons for the high real \( Q_{10} \) in this study. Warming of the stem by solar irradiation could cause the actual stem temperature to rise considerably above ambient temperature during the day (Stockfors 2000), thus giving an overestimate for \( Q_{10} \). It must be remembered that the model presented is a simplification as respiration and radial CO₂ diffusion are in reality more complicated processes than those indicated in the model description. Diffusion would in reality occur separately in the gas and liquid phase, whereas the model does not separate between these two. As the diffusion coefficient is of four orders of magnitude higher in air than in water, diffusion would be expected to speed up with increasing stem air content. The diffusion coefficient would also be expected to vary between tissue type with the xylem offering less resistance to diffusion compared to the outer layers. Differing relations between tissue type thicknesses on different species and individuals would then be expected to influence the model result significantly. It is likely that temperature and sap flow rate alone cannot explain stem respiration and stem CO₂ efflux, but there are also likely to be other influencing factors. Cambial activity during xylem development, which is not taken into account in the model, can be distinguished from stem CO₂ efflux measurements (Gruber et al. 2009). Growth and maintenance respiration processes are likely to occur in different proportions in the different parts of the stem. Growth respiration due to cambial activity should make the surface a larger source of CO₂ in proportion to the radially deeper layers. Photosynthetic re-fixation of CO₂ at the stem can also affect CO₂ effluxes from the stem (e.g., Cernusak and Marshall 2000, Wittmann and Pflanz 2007, Savery et al. 2008b, Cerasoli et al. 2009). Substrate availability (Pruyn et al. 2002), water status (Savery et al. 2008a) and oxygen concentration (Spicer and Holbrook 2007) have also been hypothesized to affect stem respiration. More detailed measurements for model parametrization are needed, especially on the spatial distribution and temporal variation of diffusion resistance and the radial distribution of CO₂ production within the tree stem.

Conclusions

A model was presented to interpret the relationship between CO₂ production by stem respiration and its efflux from the stem. This model predicts the ratio of CO₂ production to its efflux from the stem to increase from the tree bottom to the top as CO₂ accumulates in the transpiration stream on its way up. This model also predicts the temperature dependency of stem respiration to be larger than the temperature dependency of CO₂ efflux from the stem and provides a potential tool to scale respiration from local level to whole tree and stand level.
Funding

This research was supported by the Academy of Finland Centre of Excellence program, Project No. 1118615 and by the Academy of Finland Project No. 124531 (Ympäristölohusideen vaikutus puuaineen muodostumiseen).

Supplementary Data

Supplementary data for this article are available at Tree Physiology Online.

References


