Tansley review

Origin, fate and significance of CO_2 in tree stems

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Summary

Although some CO_2 released by respiring cells in tree stems diffuses directly to the atmosphere, on a daily basis 15–55% can remain within the tree. High concentrations of CO_2 build up in stems because of barriers to diffusion in the inner bark and xylem. In contrast with atmospheric [CO_2] of *c.* 0.04%, the [CO_2] in tree stems is often between 3 and 10%, and sometimes exceeds 20%. The [CO_2] in stems varies diurnally and seasonally. Some respired CO_2 remaining in the stem dissolves in xylem sap and is transported toward the leaves. A portion can be fixed by photosynthetic cells in woody tissues, and a portion diffuses out of the stem into the atmosphere remote from the site of origin. It is now evident that measurements of CO_2 efflux to the atmosphere, which have been commonly used to estimate the rate of woody tissue respiration, do not adequately account for the internal fluxes of CO_2. New approaches to quantify both internal and external fluxes of CO_2 have been developed to estimate the rate of woody tissue respiration. A more complete assessment of internal fluxes of CO_2 in stems will improve our understanding of the carbon balance of trees.

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I. Introduction

It is usually assumed that CO_2 produced by respiration in woody tissues escapes almost immediately into the atmosphere. Recent measurements indicate that this assumption is often wrong and a large quantity of respired CO_2 remains inside the tree. An emerging understanding of the processes involved also indicates that a substantial portion of this CO_2 dissolves in xylem sap and is transported away from the site of origin. The amount transported is diurnally and seasonally variable and depends on a complex of factors, including sap velocity, temperature, and pH as well as anatomical barriers to diffusion. We now know that a portion of this CO_2 can diffuse to the atmosphere during transport and that another portion can be fixed by photosynthetic cells in woody tissues or leaves. A new approach for estimating woody tissue respiration, involving measurement of both internal and external CO_2 fluxes, indicates that the rate of CO_2 efflux to the atmosphere is often very poorly correlated to the actual rate of respiration. Quantification of internal CO_2 transport, as well as recognition of the factors contributing to its complexity, may help us understand why the apparent rate of stem respiration, as determined by CO_2 efflux measurements, has been so variable and difficult to predict for woody tissues within the same tree, among trees of the same species, among different species, and across seasons.

II. Quantity of CO_2 in tree stems

A tree can contain a substantial amount of gas. Gas can be found in the intercellular spaces, the pore spaces within cell walls, and the lumens of cells (Gartner *et al.*, 2004). Sachs (1887) calculated that the gas in fir trees (unidentified species) made up 17% of the xylem volume. According to MacDougal *et al.* (1929), trunks of *Quercus* sp. and *Salix* sp. contained approximately 25% gas by volume. Gartner *et al.* (2004) concluded that the sapwood of temperate softwoods and hardwoods contains 18 and 26% gas by volume, and the heartwood of temperate softwoods and hardwoods contains 50 and 26% gas, respectively.

The composition of gases inside tree stems differs greatly from that in ambient air. The first analysis of gas extracted from a tree stem was made in the early part of the 20th century by Bushong (1907). He withdrew gas from a hole drilled in a *Populus deltoides* stem and found it consisted of 7% CO_2, 1% O_2, 61% CH_4 and 31% N_2. Since then, published reports of stem CO_2 concentrations ($[CO_2]$) have been sporadic (Table 1). Measurements of stem $[CO_2]$ have ranged from < 1% to over 26%, that is *c.* 30–750 times higher than ambient atmospheric $[CO_2]$, indicating substantial barriers to diffusion of CO_2 from the stem into the atmosphere.

In addition to CO_2 in the gas phase, a large quantity of CO_2 in stems is dissolved in xylem sap. The gaseous phase in the xylem is in contact with the liquid phase (Hari *et al.*, 1991) and an equilibrium exists between the CO_2 concentration of the gaseous phase and the total amount of all forms of dissolved CO_2 in the liquid phase in the xylem.

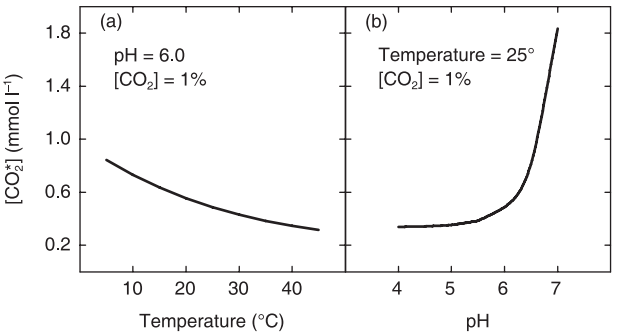

Fig. 1 (a) Modeled effect of temperature on the total concentration of dissolved inorganic carbon ($[CO_2^*]$) in xylem sap at constant gaseous CO_2 concentration (1%) and pH (6.0); (b) modeled effect of pH on the total concentration of dissolved inorganic carbon in xylem sap at constant gaseous CO_2 concentration (1%) and temperature (25°C).

According to Henry's law, the partial pressure of a gas over a solution is proportional to the concentration of that gas in the solution (Stumm & Morgan, 1996):

$$[CO_2^*] = \left(1 + \frac{K_1}{10^{-pH}} + \frac{K_1 K_2}{(10^{-pH})^2}\right) K_H \, pCO_2 \qquad \text{Eqn 1}$$

($[CO_2^*]$, total dissolved inorganic carbon in the solution, which is the sum of $[CO_2]_{aq}$, $[H_2CO_3]$, $[HCO_3^-]$ and $[CO_3^{2-}]$; K_1 and K_2, the first and second acidity constants, respectively; K_H, Henry's constant; pCO_2, partial pressure of CO_2 over the solution). Using Henry's law, it is possible to convert measured CO_2 concentrations in the gaseous phase ($[CO_2]$) to total dissolved CO_2 in the liquid phase ($[CO_2^*]$, mol l^{-1}). Details of these calculations can be found in McGuire & Teskey (2002). Therefore, it is possible to determine the amount of CO_2 dissolved in xylem sap by measuring the $[CO_2]$ of gas in holes drilled into the stem and this technique has been commonly used. In this review, CO_2 concentrations in the gaseous phase will be indicated as $[CO_2]$ (%) and the total amount of all forms of dissolved CO_2 in the liquid phase as $[CO_2^*]$ (mol l^{-1}).

The total amount of dissolved CO_2 in xylem sap depends on temperature, pH and the $[CO_2]$ of the gaseous phase in contact with the sap (Fig. 1). The constants K_1, K_2 and K_H in Eqn 1 are temperature-dependent. The solubility of CO_2 decreases with increasing temperature, so 1% $[CO_2]$ is equivalent to 0.73 mmol l^{-1} $[CO_2^*]$ at 10°C but only 0.35 mmol l^{-1} $[CO_2^*]$ at 40°C (Fig. 1a). pH has a more substantial effect on the quantity of CO_2 in solution (Fig. 1b). The primary form of dissolved CO_2 is carbonic acid (H_2CO_3) and the quantity of CO_2 in that form is independent of pH. However, at

Table 1 Carbon dioxide concentrations ($[CO_2]$) measured *in situ* in stems or branches of trees

Species	$[CO_2]$	Method	Reference
Tracheid anatomy			
Pinus radiata	1.2–13.5	CA	MacDougal & Working (1933)
Sequoia sempervirens	0.8–10.4	CA	MacDougal & Working (1933)
Pinus strobus	1.1–12.3	CA	Chase (1934)
Picea abies	2–10	GC-MS	Eklund (1990)
Pinus sp.	0.3–2.0	IRGA	Hari *et al*. (1991)
Pinus strobus	0.1–0.2	GC	Cernusak & Marshall (2000)
Pinus taeda	1.0–8.0	Microelectrode	Maier & Clinton (2006)
Ring porous anatomy			
Quercus agrifolia	1.2–15.1	CA	MacDougal (1927)
Parkinsonia microphylla	0.0–15.9	CA	MacDougal & Working (1933)
Quercus agrifolia	1.2–26.3	CA	MacDougal & Working (1933)
Quercus borealis	0.4–5.5	CA	Chase (1934)
Quercus macrocarpa	0.4–3.0	CA	Chase (1934)
Ulmus americana	0.8–16.3	CA	Chase (1934)
Quercus rubra	13.5–16.5	CA	Jensen (1967)
Quercus robur	3.0–9.0	GC-MS	Eklund (1993)
Quercus alba	3.8–5.1	Microelectrode	McGuire & Teskey (2002)
Quercus alba	1.6–15.1	Microelectrode	Teskey & McGuire (2002)
Quercus robur	0.3–3.4*	Microelectrode	Saveyn *et al*. (2007b)
Diffuse porous anatomy			
Populus deltoides	7.2	CA	Bushong (1907)
Populus macdouglii	1.4–18.2	CA	MacDougal (1927)
Salix lasiolepis	5.0–13.1	CA	MacDougal (1927)
Juglans major	5.0–22.0	CA	MacDougal & Working (1933)
Populus macdougalii	0.0–18.5	CA	MacDougal & Working (1933)
Populus tremuloides	5.4	CA	MacDougal & Working (1933)
Salix lasiolepis	6.2–13.3	CA	MacDougal & Working (1933)
Populus deltoides	0.3–25.2	CA	Chase (1934)
Acer platanoides	2–4	GC-MS	Eklund (1993)
Betula pendula	3.0	IRGA	Levy *et al*. (1999)
Distemonanthus benthamianus	3.2	IRGA	Levy *et al*. (1999)
Musanga cecropioides	8.5	IRGA	Levy *et al*. (1999)
Liriodendron tulipifera	2.9–8.9	Microelectrode	McGuire & Teskey (2002)
Liriodendron tulipifera	1.9–15.9	Microelectrode	Teskey & McGuire (2002)
Fagus grandifolia	2.0–4.5*	Microelectrode	McGuire & Teskey (2004)
Liquidambar styraciflua	1.5–2.8*	Microelectrode	McGuire & Teskey (2004)
Platanus occidentalis	1.7–3.5*	Microelectrode	McGuire & Teskey (2004)
Fagus sylvatica	2.5–2.5	Microelectrode	Saveyn *et al*. (2006)
Populus deltoides	9.5–12.7	Microelectrode	Steppe *et al*. (2007)
Platanus occidentalis	6.9–12.1	NDIR	Teskey & McGuire (2007)
Populus deltoides	3.9–17.6	NDIR	Saveyn *et al*. (2007c)

Measurements were made using microelectrodes or nondispersive infrared (NDIR) sensors, or in extracted gas samples using chemical absorption (CA), gas chromatography (GC), mass spectrometry (MS), or infrared gas analysis (IRGA). All measurements were made in the gas phase and are expressed as a percentage, except where noted *, in which case they are expressed as mmol l^{-1} (liquid phase).

pH values of 5.6 or greater, significant quantities of CO_2 can also dissolve as HCO_3^-. At yet higher pH, >8.5, formation of a third species (CO_3^{2-}) allows even more CO_2 to dissolve, but tree xylem sap pH has not been reported that high. At 1% CO_2, the total quantity of CO_2 dissolved in xylem sap at pH 5 and 25°C is 0.35 mmol l^{-1}, but at pH 7 the quantity increases fivefold, to 1.83 mmol l^{-1}. Sap pH in stems has been reported in the range of 4.5–7.4 among different species and can vary seasonally by as much as 2.3 pH units (Table 2).

1. Temporal variation in stem $[CO_2]$

Early methods, which required extraction of gas samples, limited the frequency of sampling. However, when seasonal variation was reported, $[CO_2]$ increased during the growing season and decreased during the dormant season (MacDougal, 1927; MacDougal & Working, 1933; Chase, 1934; Eklund, 1990, 1993), giving support to the idea that the source of the CO_2 inside the stems was respiration of living cells. For

Table 2 pH values of xylem sap of trees

Species	pH	Reference
Pinus taeda	5.6	Carter & Larsen (1965)
Fagus sylvatica	4.5–6.8	Glavac *et al*. (1990a,b)
Populus deltoides	6.3	Stringer & Kimmerer (1993)
Acer platanoides	6.1–7.4	Schill *et al*. (1996)
Betula pendula	6.4	Levy *et al*. (1999)
Musanga cecropioides	6.8	Levy *et al*. (1999)
Distemonanthus benthamianus	5.2	Levy *et al*. (1999)
Liriodendron tulipifera, *Quercus alba*	5.4–6.8	McGuire & Teskey (2002)
Fagus grandifolia	6.5	McGuire & Teskey (2004)
Platanus occidentalis	6.0	McGuire & Teskey (2004)
Liquidambar styraciflua	5.6	McGuire & Teskey (2004)
Platanus occidentalis	5.6–6.0	Teskey & McGuire (2007)
Populus deltoides	6.8	Saveyn *et al*. (2007c)

In the first seven studies, pH was measured on sap expressed from excised twigs using a pressure chamber. In the last six studies, stems were cored with an increment borer and sap was expressed with a vise. All species have diffuse porous anatomy except *P. taeda* (tracheid anatomy).

example, MacDougal (1927), who was the first to study seasonal variations, reported that $[CO_2]$ in *Quercus agrifolia* stems increased from 1.4% in January to 15.1% in August. MacDougal & Working (1933) observed high $[CO_2]$ in the stems of several tree species during periods of rapid growth. Chase (1934) found similar seasonal variation in $[CO_2]$, which followed the annual pattern of mean air temperature. More recently, Eklund (1993) reported that $[CO_2]$ in stems of *Quercus robur* increased in early June to almost 6%, decreased in early July to 3%, and rose to a second peak of almost 9% in late August, while in *Acer platanoides*, $[CO_2]$ consistently remained *c*. 3–4% throughout the growing season, except for a drop to below 2% in late June.

The first measurement of the diurnal course of xylem sap $[CO_2]$ was made by Stringer & Kimmerer (1993). They found that the $[CO_2^*]$ in sap expressed from excised *Populus deltoides* twigs was highest at night and lowest at midday, ranging from 0.5 mmol l^{-1} at 14:00 h to 0.9 mmol l^{-1} at 22:00 h. Recent technological advances now allow continuous real-time measurement of $[CO_2]$ *in situ* using small electrodes and nondispersive infrared (NDIR) sensors (McGuire & Teskey, 2002; Teskey & McGuire, 2007). Often, $[CO_2]$ in stems is lowest during the day and highest during the night (McGuire & Teskey, 2002, 2004; Teskey & McGuire, 2002; Maier & Clinton, 2006; Saveyn *et al*., 2006, 2007b,c), but other patterns have been observed (McGuire & Teskey, 2004; Saveyn *et al*., 2007b). Kaipiainen *et al*. (1998) found that xylem $[CO_2]$ increased during the daytime in 6- to 8-yr-old branches of *Pinus sylvestris* trees, but the reverse was observed in 2- to 5-yr-old branches. Rain can alter the diurnal pattern, resulting in substantial, and reversible, increases in internal $[CO_2]$ (McGuire & Teskey, 2002; Saveyn *et al*., 2007c) regardless of the time of day. In many instances, the diurnal pattern of $[CO_2]$ does not correspond with diurnal patterns of temperature, suggesting that other factors in addition to cellular respiration can affect $[CO_2]$ in stems.

2. Spatial variation in stem $[CO_2]$

Most measurements of xylem $[CO_2]$ have been confined to the lower part of the stem, so little is known about within-tree variation. Chase (1934) made measurements at six heights up to 10 m in a *Populus deltoides* stem and found the highest $[CO_2]$ in the central part of the trunk, the lowest $[CO_2]$ in the lower trunk, and intermediate $[CO_2]$ in the upper trunk during the summer months. Overall, stem $[CO_2]$ declined substantially through the autumn and winter months, but the central part of the trunk continued to have higher $[CO_2]$ than the upper and lower trunk. When $[CO_2]$ began to increase in March and April, this pattern changed; the highest $[CO_2]$ was found in the lower trunk and the lowest $[CO_2]$ was found in the upper trunk. Chase (1934) also measured $[CO_2]$ at different depths in the stem of a *Populus deltoides* tree. He found that $[CO_2]$ in the sapwood was always lower than in the heartwood. Teskey & McGuire (2007) found that mean $[CO_2^*]$ of *Platanus occidentalis* stems was greater at 3 m height than at 0.1 m during the summer. Over small stem height intervals (< 1 m), stem $[CO_2]$ was often observed to increase in *Fagus grandifolia*, *Liquidambar styraciflua* (McGuire & Teskey, 2004), *Platanus occidentalis* (McGuire & Teskey, 2004; Teskey & McGuire, 2007) and *Populus deltoides* (Saveyn *et al*., 2007c).

III. Sources of CO_2 found in stems

1. Respiration of stem and roots

Most CO_2 within the stem originated from respiring cells in the stems and roots. In the stem, live cells are found in the

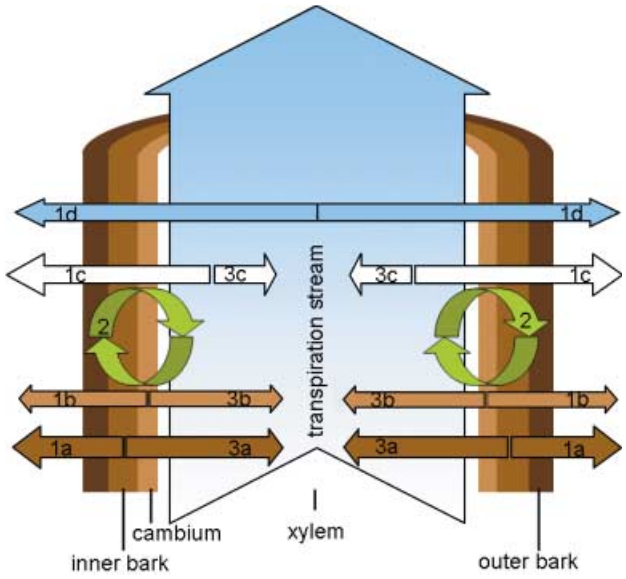

Fig. 2 Schematic of important sources and sinks of CO_2 inside a stem segment of a tree. 1, diffusion of CO_2 out of the stem from inner bark, brown arrow (a); cambium, light brown arrow (b); xylem ray cells, white arrow (c); or imported in xylem sap, blue arrow (d). 2, fixation of CO_2 by corticular photosynthesis (green arrows), which can utilize CO_2 from all four sources (a, b, c, d) above. 3, CO_2 diffusing into the transpiration stream. Sources of this CO_2 can be inner bark, brown arrow (a); cambium light brown arrow (b); or xylem ray cells, white arrow (c).

inner bark, vascular cambium, and xylem (Fig. 2). The outer bark, or rhytidome, does not contain living cells, but the inner bark, consisting of an outer layer of peridermal cells and phloem, has a substantial number of living cells, as does the thin layer of cells in the vascular cambium between the phloem and xylem. For simplicity, in this review, 'inner bark' refers to cells from the periderm through the vascular cambium. In the xylem, only ray cells in the sapwood are living, and these are the most likely local source of the CO_2 found within the stem. The volume of ray cells in the xylem of conifers ranges from 5 to 9%. Hardwoods generally have more ray volume, ranging from 5 to 34%, and in many of these species rays constitute 15–25% of the xylem volume (Panshin & de Zeeuw, 1980). The proportion of live cells in the xylem may change with tree size. In *Fagus sylvatica* trees, xylem ray volume decreased from approx. 25% to 20% as stem diameter increased from 6 to 16 cm, and from 48% in 1 mm branches to 21% in 8 mm diameter branches (Ceschia *et al.*, 2002). The proportion of live cells decreases rapidly with depth from the cambium in some species (Stockfors & Linder, 1998), but remains constant with depth in other species (Ryan, 1990; Ceschia *et al.*, 2002).

It is not known if the inner bark in woody tissues contributes to the high [CO_2] within the stem, but CO_2 may move inward from this region under some circumstances. Live cell volume in the inner bark has been reported to range from 56% in *Fagus sylvatica* (Ceschia, 2001) to 7% in *Pinus contorta* (Ryan, 1990). Growth rate may also affect live cell volume. In *Picea abies*, live cell volume increased from 21 to 30% when trees were fertilized with nitrogen (Stockfors & Linder, 1998).

The relative distribution of live cells between the inner bark and xylem in stems depends on species and tree size. In *Pinus contorta* and *Picea engelmanii* trees with diameters ranging from 4 to 40 cm, the xylem contained > 80% of the total live cell volume in stems (Ryan, 1990). Similarly, in *Fagus sylvatica* stems with diameters up to 16 cm, the live cell volume of the xylem and the live cell volume of the entire stem were very similar, indicating that the quantity of living cells in the inner bark was negligible compared with the xylem (Ceschia *et al.*, 2002). By contrast, in 7–10 cm *Picea abies* trees, only 20–25% of the live cell volume of the stems was found in the xylem (Stockfors & Linder, 1998).

The rate of cellular respiration may differ substantially with radial depth in the stem. Measurements of respiratory capacity have not yet been made *in situ*, and knowledge at this time is limited to the rate at which various excised tissue samples can evolve CO_2 or consume O_2 under controlled environmental conditions. In some instances, the rate of CO_2 efflux of inner bark tissues has been shown to be substantially higher than that of sapwood (Pruyn *et al.*, 2002a,b, 2003). In other studies, the rates of CO_2 efflux of inner bark and outer sapwood were similar (Zabuga & Zabuga, 1990; Bowman *et al.*, 2005). In the few studies that examined within-sapwood variation, the rate of CO_2 efflux of the outer sapwood was almost always higher than that of inner sapwood (Pruyn *et al.*, 2002a,b, 2003; Bowman *et al.*, 2005), but Zabuga & Zabuga (1990) found no change in the rate of CO_2 efflux with sapwood depth in *Pinus sylvestris* stems. Higher respiratory activity of inner bark and outer sapwood may be related to availability of carbohydrates or nitrogen concentrations (Pruyn *et al.*, 2002b, 2005). The nitrogen concentration of *Dacrydium cupressinum* stems was highest in the inner bark and declined with increasing depth into the stem (Bowman *et al.*, 2005). Total nitrogen content and total nonstructural carbohydrate content serve as a proxy for enzyme quantity and metabolic substrate availability, respectively. Variation in oxygen and CO_2 concentrations in the stem may be an additional source of spatial and temporal variation in respiration. Averaged across five tree species, the mean rate of oxygen consumption of excised sapwood tissue was reduced by as much as 27% when [O_2] was reduced from 10 to 5%, and by 14% when [CO_2] was increased from 0 to 10%, but the response to various combinations of gas concentrations was complex, and the effect of [O_2] on tissue oxygen consumption depended on the [CO_2] and vice versa (Spicer & Holbrook, 2007).

Pruyn *et al.* (2003) measured CO_2 efflux from stem cores of 10 tree species in the central Cascade Mountain range in Oregon and found that efflux at 25°C varied three-fold

among species. CO_2 efflux was inversely correlated to the live bole volumetric fraction (LBVF) (inner bark plus sapwood divided by whole bole volume). Tissues from tree species with < 20% LBVF had 1.3 to three times greater CO_2 efflux than did species with > 40% LBVF, suggesting that species that maintain large sapwood volumes also have less metabolically active stem tissues.

The contribution of root respiration to the $[CO_2]$ in the stem is uncertain. A recent observation on *Plantanus occidentalis* trees showed that the $[CO_2]$ at the base of the stem was almost as high as the $[CO_2]$ at 3 m height, leading to speculation that much of the CO_2 in the stem may have originated below ground (Teskey & McGuire, 2007). However, the $[CO_2]$ at the base of the stem was too high to be attributed solely, or even mostly, to absorption of CO_2 from the rhizosphere. It is known that roots, especially of species resistant to waterlogged or flooded conditions, can tolerate high $[CO_2]$ in the root zone, but there is no information on root $[CO_2]$ (Greenway *et al.*, 2006). Effective anatomical and morphological features in roots create barriers for radial O_2 loss to the soil (Colmer, 2003). In tree roots, suberin formation on the root exodermis has been shown to reduce the efflux of O_2 (De Simone *et al.*, 2003) and may serve a similar function for efflux of CO_2. Diffusion of O_2 from the base of the stem into the root system through aerenchyma is common in many flood-tolerant plants (Colmer, 2003; Armstrong & Armstrong, 2005), and could also be a pathway for CO_2 movement upward from the roots to the stem, but aerenchyma tissue is poorly developed or nonexistent in upland tree species.

2. CO_2 from the rhizosphere

CO_2 in the rhizosphere, originating from microbial or root respiration, dissolves in soil water and can be absorbed by roots and transported into the stem in flowing sap. Forest soil $[CO_2]$ generally ranges from < 0.1 to 2% (Yavitt *et al.*, 1995; Hamada & Tanaka, 2001; Pumpanen *et al.*, 2003; Jassal & Black, 2006), and is rarely higher (4–5%) (see review by Amundson & Davidson, 1990). Soil $[CO_2]$ is often low near the soil surface and increases with soil depth through the rooting zone (Pumpanen *et al.*, 2003; Jassal *et al.*, 2005). The net flux of CO_2 from root respiration is outward into the soil, yet some inorganic C dissolved in soil solution is taken up by plants (cf. review by Enoch & Olesen, 1993). However, the $[CO_2]$ in stems is usually considerably greater than in soil (Table 1), suggesting that a large fraction must originate within the tree itself.

Salix aquatica was capable of absorbing ^{14}C-labeled dissolved inorganic carbon (DIC) from a nutrient solution and transporting it throughout the plant (Vapaavuori & Pelkonen, 1985; Vuorinen *et al.*, 1989). Ford *et al.* (2007) demonstrated that $^{13}CO_2$ dissolved in soil water can be absorbed and fixed in *Pinus taeda* seedlings. More than 50% of the $^{13}CO_2$ was recovered above ground, with about two-thirds fixed in stem tissues and one-third fixed in leaf tissues. However, the DIC supplied from the soil contributed < 1% to total seedling C gain. Similarly, Hibberd & Quick (2002) supplied inorganic carbon to roots and stems of *Nicotiana tabacum* plants as $[^{14}C]NaHCO_3$ and found that ^{14}C accumulated in organic compounds in cells of stems and petioles.

IV. Fate of CO_2 released by respiring cells in stems: loss, transport and fixation

1. Loss to the atmosphere

CO_2 produced by the living cells of xylem, cambium and inner bark (Fig. 2, arrows 1c, 1b and 1a, respectively) or CO_2 imported in the transpiration stream (arrow 1d) can diffuse radially from the stem to the atmosphere. The diffusion coefficient of CO_2 in air is 1.6×10^{-5} m^2 s^{-1}, whereas it is only 1.6×10^{-9} m^2 s^{-1} in water at 20°C and 101.3 kPa (Nobel, 1999), so radial diffusion of CO_2 in the gas phase will predominate. The flux of CO_2 diffusing out of the stem into the atmosphere can be characterized by a modified version of Fick's law of diffusion (Pfanz & Aschan, 2001):

$$E_A = \frac{\Delta[CO_2]}{R} \qquad \text{Eqn 2}$$

(E_A, flux of CO_2 out of the stem (μmol m^{-2} s^{-1}); $\Delta[CO_2]$, difference in CO_2 concentration between the gas spaces of the stem and the atmosphere; R, sum of a series of diffusion resistances). The sum of resistances depends on whether the CO_2 is located in the inner bark (Fig. 2 (arrow 1a)) or in the xylem (Fig. 2 (arrows 1c and 1d)).

From the inner bark to the atmosphere, diffusion resistances are mainly determined by the composition of the cortex, phloem, peridermal layers (phelloderm, phellem and phellogen) and rhytidome (i.e. the outer bark) (Ziegler, 1957). These tissues protect the tree against water loss, insects, and pathogens, but also limit the exchange of CO_2 and O_2 with the atmosphere. Resistance depends mainly on the amount of lignins, suberins, lipids, and waxes and on thickness (Schonherr, 1982; Lendzian, 2006) and appears to differ substantially with species and tissue age. Mean CO_2 conductance of the bark of small branches of *Pinus monticola* was 0.68 mmol m^{-2} s^{-1} (Cernusak & Marshall, 2000) and of the bark of 6-yr-old *Betula pendula* trees was 0.50 mmol m^{-2} s^{-1} (Wittmann *et al.*, 2006). However, CO_2 conductance of bark of *Syringa vulgaris* stems was substantially higher and proportional to age and bark thickness, ranging from 33, 18 and 10 mmol m^{-2} s^{-1} for current-year (thinnest bark), 1-yr-old and 3-yr-old (thickest bark) stems, respectively (Pilarski, 1994).

In most tree species, the cambium located between the xylem and inner bark significantly inhibits lateral gas movement (Kramer & Kozlowski, 1979). This may explain the

large difference in [CO_2] between xylem and bark tissues: xylem [CO_2] has been reported to be as high as 26% (Table 1), whereas published values of [CO_2] in bark tissues range between 0.06 and 0.17% (Cernusak & Marshall, 2000; Wittmann *et al.*, 2006). In some tree species adapted to waterlogged soil, the cambium may contain small intercellular spaces permitting radial CO_2 diffusion (Hook & Brown, 1972; Buchel & Grosse, 1990). The permeability of the cambial zone may change seasonally. In *Pseudotsuga menziesii*, actively dividing cambium cells and newly generated xylem and phloem cells, which have thin cell walls, appear to be able to exchange CO_2 and O_2 more efficiently in spring than in December, when cells have thicker cell walls and increased protoplasmic viscosity (Joseph & Kelsey, 2004).

Presumably, CO_2 diffusion through inner and outer bark is also facilitated by lenticels, cracks and wounds (Grosse, 1997; Langenfeld-Heyser, 1997). Groh *et al.* (2002) found that lenticels from *Betula potaninii* and *Sambucus nigra* were significantly more permeable to O_2 than phellem without lenticels. Groh *et al.* (2002) also demonstrated that the O_2 permeability of lenticels changed seasonally, and was higher during the growing season and lower in autumn and winter. However, data on CO_2 permeability are lacking, but we do know that removing some of the diffusional barriers in the bark by wounding dramatically increases the rate of CO_2 efflux (Teskey & McGuire, 2005).

The xylem may be an even greater barrier to free gas exchange than the cambium. Sorz & Hietz (2006) found that minimum diffusion coefficients for O_2 in water-saturated xylem were always lower than the diffusion coefficients in water alone, indicating that the cell walls presented a major barrier to gas diffusion.

Since diffusion occurs much faster in air than in water, diurnal and seasonal variation in the ratio of gas to water content in the xylem, cambium, and bark can also have an important influence on diffusion rates. During periods of diurnal stem shrinkage resulting from changes in water content, liquid water films are lost from gas spaces and the stem tissue may become more permeable to gas exchange (Hook *et al.*, 1972). The volumetric water content of the sapwood also changes seasonally. For example, it ranged from nearly 50% during winter and early spring, to 20% during the growing season in *Acer saccharum* trees (Pausch *et al.*, 2000). Sorz & Hietz (2006) measured radial diffusion of O_2 in wood at different water and gas contents and found that the diffusion coefficient increased five- to 13-fold in *Picea abies*, *Taxus baccata* and *Quercus robur*, 36-fold in *Fraxinus excelsior* and *c.* 1000-fold in *Carpinus betulus* and *Fagus sylvatica* at 40% gas volume compared to the diffusion coefficient at 15% gas volume.

Recent studies have established a relationship between the internal stem [CO_2] concentration and stem CO_2 efflux. By directly manipulating the [CO_2] in the xylem, it was possible to demonstrate that CO_2 efflux was linearly related to the xylem [CO_2] in large intact stems of *Quercus alba* and

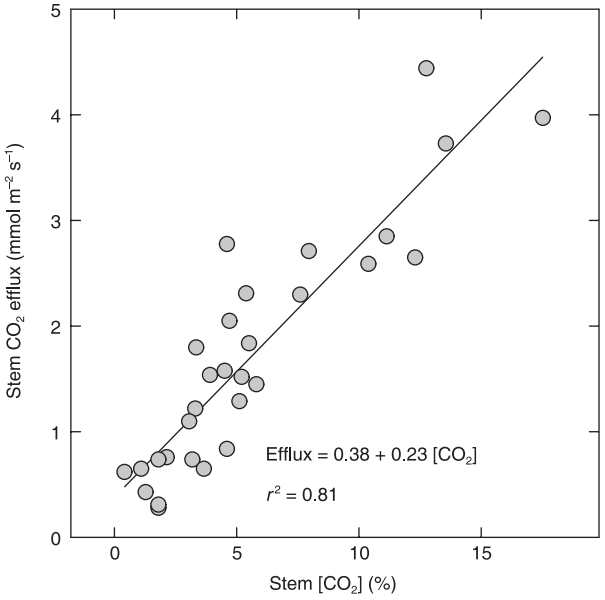

Fig. 3 Example of linear relationship between CO_2 efflux to the atmosphere and xylem CO_2 concentration [CO_2]. In this experiment, shoots of *Platanus occidentalis* and *Liquidambar styraciflua* were severed from their roots and placed in water with different [CO_2] which was taken up into the xylem as the plants transpired. In 10 replicates of the experiment (five replicates of each species), stem temperatures were similar and cannot explain the increase in CO_2 efflux (adapted from Fig. 2, Teskey & McGuire, 2005).

Liriodendron tuliperfera (Teskey & McGuire, 2002) and in excised shoots of *Liquidambar styraciflua* and *Platanus occidentalis* (Fig. 3) (Teskey & McGuire, 2005). These experiments indicated that although there are substantial barriers to diffusion in the stem, some dissolved CO_2 diffuses outward to the atmosphere as it is transported upward in the xylem. However, there is some evidence that this relationship may not exist under all conditions or in all species. In young *Pinus taeda* tree stems, when transpiration was reduced by removing foliage, xylem [CO_2] increased, but there was no apparent change in CO_2 efflux (Maier & Clinton, 2006). The authors suggested that during spring, the meristematic region might respire at a much higher rate than the xylem parenchyma and thus would be the major source of CO_2 efflux during periods of active growth (Fig. 2, arrows 1a,b, 3a,b). Saveyn *et al.* (2007b) measured xylem sap [CO_2] and stem CO_2 efflux in a young *Quercus robur* tree subjected to soil water depletion and found that [CO_2] was positively correlated with CO_2 efflux in the predrought period, but this correlation became less clear during early drought stress. Wittmann *et al.* (2006) concluded that the contribution of xylem CO_2 to efflux was negligible in small branches (< 2 cm diameter) of *Betula pendula* because small branches have a high surface area to volume ratio, so the proportion of live cells in the inner bark would be much larger than the proportion in the xylem. In stems of three individuals of a single *Populus deltoides*

clone, Steppe *et al.* (2007) found a strong linear relationship between xylem [CO_2] and efflux, but the slope varied among the stems, indicating substantial differences in the relationship between xylem [CO_2] and efflux, even within individual ramets of the same clone. This result suggests that barriers to diffusion of CO_2 may vary among stems and perhaps in different parts of the same tree.

The rate of diffusion of CO_2 from the stem to the atmosphere will depend on the concentration gradient, barriers to diffusion, and temperature, since the diffusion coefficient of a gas depends on temperature raised to the power 1.8 (Nobel, 1999). Stockfors & Linder (1998) calculated time lags between changes in stem temperature and stem CO_2 efflux in *Picea abies*. The shortest lag was observed in June and the lag increased in duration through the summer to a maximum in September. Perhaps these results were influenced by seasonal changes in tissue permeability or the effect of temperature on the rate of diffusion, or both.

2. Transport of dissolved CO_2 in xylem sap

Observations of midday depression in CO_2 efflux from stems has led to speculation that reduced carbohydrate availability (Azcon-Bieto *et al.*, 1983) or stress caused by water deficits (Lavigne, 1987; Kakubari, 1988; Wang *et al.*, 2003; Daudet *et al.*, 2005; Saveyn *et al.*, 2007a,b) lowered the rate of cellular respiration within stems and reduced the rate of CO_2 efflux. In some instances, corticular photosynthesis (Sprugel & Benecke, 1991) could also contribute to reduced efflux during daylight hours. An alternative explanation was that a portion of the CO_2 released by respiration of local cells dissolved in xylem sap and was transported away in the transpiration stream (Geurten, 1950; Negisi, 1975). Negisi (1979) provided evidence that CO_2 efflux from the stem was inversely correlated with sap velocity. In a manipulative experiment on excised stems of *Pinus densiflora* trees, he found that CO_2 efflux was inversely proportional to sap velocity, decreasing by 50% when sap velocity increased from 0 to 0.4 cm min^{-1}. Under field conditions, CO_2 efflux of mature stems of *Betula pendula* can be reduced by 40% at high rates of transpiration (Gansert & Burgdorf, 2005). A strong negative correlation between stem CO_2 efflux and sap flux density was found in *Dacrydium cupressinum* trees, but, interestingly, the slope of the relationship differed substantially from tree to tree, suggesting that diffusional gradients or stem [CO_2] varied among these individuals (Bowman *et al.*, 2005). A smaller reduction in CO_2 efflux (7%) was observed in *Pinus taeda* seedlings during periods of high transpiration compared with periods of low transpiration (Martin *et al.*, 1994). In these studies, as well as others in which midday depression in CO_2 efflux was observed (Edwards & McLaughlin, 1978; Kaipiainen *et al.*, 1998), it was not possible to separate the relative importance of the effect of CO_2 transport on CO_2 efflux vs factors that reduced the actual rate of respiration.

Recently, McGuire *et al.* (2007) demonstrated that under constant temperature conditions, and thus presumably a constant rate of respiration, changes in sap velocity caused large differences in CO_2 efflux in detached *Platanus occidentalis* branch segments (Fig. 3). At extremely high sap velocities (> 10 cm min^{-1}), CO_2 efflux accounted for < 10% of the total CO_2 released by respiring cells in the branch. At a more realistic maximum sap velocity (1 cm min^{-1}) (Wullschleger & King, 2000), efflux accounted for < 50% of the total CO_2. However, correlations between sap flow and CO_2 efflux are not always negative. In a field study, Levy *et al.* (1999) found a positive relationship between the rate of sap flow and CO_2 efflux, which they speculated was caused by water at high [CO_2] rising from the root system. In some instances, CO_2 efflux from stems was not affected by sap flow rates (Edwards & Wullschleger, 2000; Maier & Clinton, 2006). Under uncontrolled field conditions, diurnal changes in tissue temperature, water stress, carbohydrate availability and sap velocity vary in complex ways and can affect rates of both woody tissue respiration and CO_2 efflux, making it difficult to separate the importance of individual causal factors. Additionally, tissue size and time of year may affect the relative contributions of CO_2 diffusing from the xylem and CO_2 released by local respiring cells to CO_2 efflux from woody tissues.

The rate of sap flow can also have a substantial influence on xylem sap [CO_2]. A tight inverse coupling was observed between sap velocity and sap [CO_2] in the stem of a *Liriodendron tulipifera* tree (Fig. 4) (Teskey & McGuire, 2002). Xylem [CO_2] was high during the night, when sap velocity was zero, and decreased during the morning as sap velocity increased. During brief periods of cloud cover during the day, sap velocity decreased and xylem [CO_2] increased concurrently. As sap velocity decreased in late afternoon, xylem [CO_2] increased in proportion. Similarly, under controlled temperature conditions, xylem [CO_2] of *Platanus occidentalis* branches decreased rapidly as sap velocity increased from 0 to 1 cm min^{-1} and remained low at higher sap velocities (Fig. 5) (McGuire *et al.*, 2007). Xylem [CO_2] and sap flux in young *Pinus taeda* tree stems were also well coupled (Maier & Clinton, 2006). They found that removing most of the foliage caused a decrease of sap flux to near zero. Simultaneously, [CO_2] increased substantially. Similarly, during periods of rain, when sap flux is greatly reduced, xylem [CO_2] has been reported to double in stems of *Populus deltoides*, compared with xylem [CO_2] on sunny days (Saveyn *et al.*, 2007c).

3. Fixation by photosynthesis

Some of the CO_2 within stems and branches may be fixed by corticular, wood or leaf photosynthesis. Zelawski *et al.* (1970) supplied $^{14}CO_2$-enriched water to the stem transpiration stream of *Pinus elliottii* seedlings and found that large amounts of ^{14}C were fixed in needles and stems. Stringer & Kimmerer (1993) examined the fixation of xylem sap CO_2 in

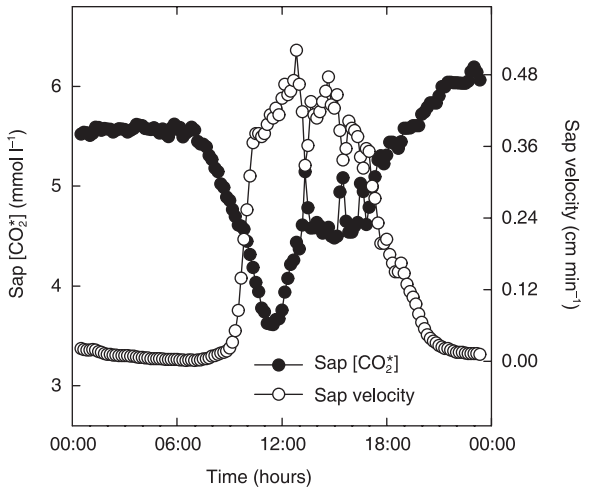

Fig. 4 Diurnal pattern of xylem sap $[CO_2^*]$ (closed symbols) and sap velocity (open symbols) in a 25-cm-diameter *Liriodendron tulipifera* tree stem measured *in situ*. Rapid fluctuations in sap $[CO_2^*]$ between 12:00 and 17:00 h correspond to fluctuations in sap velocity caused by passing clouds (adapted from Fig. 1, Teskey & McGuire, 2002).

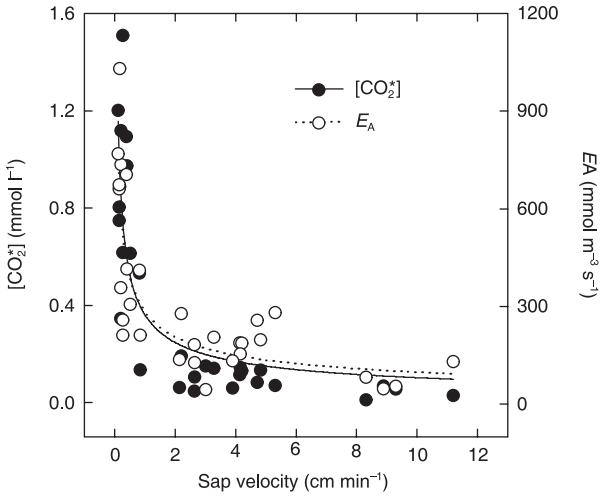

Fig. 5 Relationship of xylem sap $[CO_2^*]$ (closed symbols) and CO_2 efflux (E_A,open symbols) to sap velocity in detached branch segments of *Platanus occidentalis* perfused with water at controlled flow rates. Lines indicate regression relationships: $[CO_2^*] = 0.3617$ (sap velocity$^{-0.5452}$), $E_A = 283.38$ (sap velocity$^{-0.4588}$). Both sap $[CO_2^*]$ and CO_2 efflux are affected by sap velocity. *In situ*, in most instances, sap velocity will be in the range of 0–1 cm min^{-1}, which is the range where the most dramatic effect of sap velocity on $[CO_2^*]$ and CO_2 efflux occurs (adapted from Fig. 2, McGuire *et al*., 2007).

Populus deltoides leaves. Excised leaves were allowed to transpire a 1 mM [^{14}C]$NaHCO_3$ solution, and 99.6% of the label was fixed in the leaf veins under illumination. Teskey & McGuire (2002) reasoned that a large proportion of xylem-transported CO_2 was likely fixed by leaf photosynthesis; however, recent evidence indicated that most fixation occured in stem, branch and petiole tissues (M. A. McGuire *et al*., unpublished).

Chloroplast-containing tissues can be found in many different locations in stems, including adjacent to the cork cambium, within the phloem in the inner bark, in xylem rays, and in the pith (Fig. 6) (Pfanz & Aschan, 2001). The chlorophyll content of young twigs can be as much as 50–70% of the chlorophyll content of adjacent leaves (Kharouk *et al*., 1995; Solhaug *et al*., 1995; Schmidt *et al*., 2000; Pfanz *et al*., 2002). The bark of some *Populus tremuloides* and *P. tremula* trees contained 42% of the total tree chlorophyll (Kharouk *et al*., 1995).

The existence of bark and wood photosynthesis and its significance for overall carbon gain has recently been reviewed (Pfanz & Aschan, 2001; Aschan & Pfanz, 2003). Corticular photosynthesis has been reported in a wide variety of tree species (Table 3). These studies indicate that a substantial amount of internal CO_2 can be fixed by chloroplast-containing tissues.

Corticular and wood photosynthesis have two advantages over leaf photosynthesis: since no stomata are involved, corticular and wood photosynthesis have little associated water loss; and since $[CO_2]$ in woody tissues is high, photorespiration is low (Cernusak & Marshall, 2000). In contrast with leaf photosynthesis, CO_2 is not a limiting factor for corticular photosynthesis. However, high $[CO_2]$ can reduce the photochemical efficiency of photosystem II and may increase photoinhibition (Manetas, 2004). Corticular and wood photosynthesis may be critical for maintaining sufficient O_2 concentrations in stems to avoid anoxia (Pfanz *et al*., 2002). Corticular photosynthesis can fix up to 100% of the respiratory CO_2 emissions (Cernusak & Marshall, 2000) and may occasionally exceed CO_2 release; that is, stems may also take up CO_2 from the atmosphere (Damesin, 2003; Berveiller *et al*., 2007) (Table 3). Refixation of internal CO_2, especially in young trees, compensates for a portion of respiratory carbon loss.

An important limiting factor for corticular and wood photosynthesis is irradiance. For photosynthesis to occur, adequate photosynthetically active radiation must pass through the epidermal, peridermal, and/or rhytidomal layers to reach the light-harvesting complexes of the chloroplasts. A study of woody tissues of 21 species found that light was conducted axially as well as radially in vessels, fibers, tracheids and parenchyma cells, but light quality was modified and its intensity was attenuated proportional to the distance conducted (Sun *et al*., 2003). The amount of light transmitted in stems of young trees varies between < 10 and 50% of incident light, depending on species and age of the stem segment (Aschan & Pfanz, 2003). Light transmission and the capacity for fixation usually decrease as stems age and develop a thick layer of outer bark.

V. What do we know about woody tissue respiration?

Beginning in the early part of the 20th century, CO_2 efflux from tree stems was suggested as an estimate of stem respiration (Johansson, 1933). In a critique of Johansson's

Fig. 6 Segments of a young *Platanus occidentalis* stem. In the current-year growth (far right) chlorophyll is found throughout the stem. Less chlorophyll is evident in the xylem of 1-yr-old stem segments (second and third segments from right). With increasing size, age and bark thickness, chlorophyll is found mostly in the inner bark.

(1933) technique, Boysen-Jensen (1933) raised the concern that CO_2 efflux from the stem may not be equivalent to the CO_2 released by respiration of woody tissues. Boysen-Jensen (1933) made the point that it was entirely uncertain that the CO_2 produced by respiration of a segment of the stem would flux outward through the overlaying bark of that segment. He gave two reasons for this uncertainty: (i) the bark of trees was very often impermeable to air, and (ii) transpiration could easily carry the CO_2 upward, where it could flux outward from parts of the tree other than where it was produced. Despite these criticisms, the approach of Johansson (1933) was adopted as the principal field method for estimating stem respiration, presumably because it was nondestructive, allowing measurements on intact trees. With the advent of the use of infrared gas analyzers, the Johansson (1933) technique was modified by providing a stream of air through the cuvette (Pisek & Winkler, 1958), allowing real-time continuous measurements. Since then, CO_2 efflux measurements have been reported as stem respiration in hundreds of papers. It is notable that although there is a long record of these measurements, finding consistent relationships between rates of woody tissue CO_2 efflux and tissue sizes and types, tree ages, species, and environmental conditions has been difficult (Lavigne *et al.*, 1996). Remarkable variation exists even among trees of the same age growing on the same site. For example, within trees, Sprugel (1990) found 10- to 40-fold differences between CO_2 efflux rates in 30-yr-old *Abies amabilis* trees in the same stand. Similarly, Cernusak & Marshall (2000) found a 20-fold difference in the CO_2 efflux among branches of *Pinus monticola* trees growing on the same site.

Since it is now well-established that a large amount of respired CO_2 remains within tree stems and that CO_2 is transported upward in the transpiration stream, we ask the question: how accurately do efflux measurements represent the rate of actual respiration of woody tissues?

To address this question, McGuire & Teskey (2004) developed a mass balance approach that accounts for all fluxes of CO_2 from and within a stem segment: efflux to the atmosphere through bark (E_A), dissolved CO_2 entering (I_T) and exiting (E_T) the stem segment in flowing sap, and the increase or decrease in xylem CO_2 concentration over time (ΔS). Therefore,

$$R_S = E_A + F_T + \Delta S \quad \text{Eqn 3}$$

where F_T (transport flux) = $E_T - I_T$; R_S is μmol m^{-3} sapwood s^{-1}) and

$$E_A = (f_A/v)\Delta[CO_2] \quad \text{Eqn 4}$$

$$F_T = (f_S/v)\Delta[CO_2^*] \quad \text{Eqn 5}$$

$$\Delta S = ([CO_2^*]_{T1} - [CO_2^*]_{T0})L/T \quad \text{Eqn 6}$$

and f_A is the rate of air flow through a cuvette surrounding the stem segment, v is the volume of the segment, $\Delta[CO_2]$ is the difference in $[CO_2]$ of air entering and exiting the cuvette, f_S is the flow rate of sap through the segment, $\Delta[CO_2^*]$ is the difference in $[CO_2^*]$ of the xylem at the top and bottom of the segment, $[CO_2^*]_{T1}$ and $[CO_2^*]_{T0}$ are mean $[CO_2^*]$ at T_1 and T_0, respectively, L is amount of water in the segment, and T is time interval. To calculate respiration from these equations, diurnal measurements of CO_2 efflux, sap flux, xylem $[CO_2^*]$ and xylem water content were made. Teskey & McGuire (2007) modified the E_A calculation to account for efflux of CO_2 transported into the stem segment from lower parts of the tree, as

$$E_{AR} = E_A - E_{A[CO_2]} \quad \text{Eqn 7}$$

where $E_{A[CO_2]}$ is calculated from a tissue-specific linear regression of efflux and $[CO_2^*]$ measured at the bottom of the stem segment.

Using this approach, stem respiration was measured on five *Platanus occidentalis* trees during summer (Teskey & McGuire, 2007). Transport flux (F_T) was the most important internal CO_2 flux, and it was a major component of stem respiration during the daytime hours when sap was flowing, accounting for as much as 70% of the CO_2 released from respiring cells

Table 3 Reported values of maximum stem CO_2 refixation rates

Species	Maximum re-fixation rate (%)	Tree organ	Age (year)	Reference
Tracheid anatomy				
Pinus monticola	76	Branch	3–4	Cernusak & Marshall (2000)
Ginkgo biloba	57 (winter) 67 (summer)	Stem	0–1	Berveiller *et al*. (2007)
Picea abies	50 (winter) 71 (summer)	Stem	0–1	Berveiller *et al*. (2007)
Pinus sylvestris	55 (winter) 69 (summer)	Stem	0–1	Berveiller *et al*. (2007)
Ring porous anatomy				
Quercus alba	19 (winter)	Branch	0–1	Coe & McLaughlin (1980)
Prunus persica	66	Stem	0–1	Alessio *et al*. (2005)
Quercus robur	72 (winter) 69 (summer)	Stem	0–1	Berveiller *et al*. (2007)
Fraxinus excelsior	126 (winter) 67 (summer)	Stem	0–1	Berveiller *et al*. (2007)
Diffuse porous anatomy				
Populus tremuloides	90 (winter) 92 (summer)	Stem	6–8	Foote & Schaedle (1976)
Acer rubrum	31 (winter)	Branch	0–1	Coe & McLaughlin (1980)
Cornus florida.	79 (winter)	Branch	0–1	Coe & McLaughlin (1980)
Liriodendron tulipifera	23 (winter)	Branch	0–1	Coe & McLaughlin (1980)
Fagus crenata	98		5	Han & Suzaki (1981)
19 species (desert shrubs)	83			Comstock *et al*. (1988)
Alnus glutinosa	45		10	Steinborn *et al*. (1997)
Guiera senegalensis	76	Stem		Levy & Jarvis (1998)
Populus tremuloides	80	Branch	0–1	Aschan *et al*. (2001)
Populus tremula, *Fagus sylvatica*	90	Branch	0–1	Wittmann *et al*. (2001)
Betula pendula	50	Stem	1.5	Matyssek *et al*. (2002)
Fagus sylvatica	110 (winter)	Branch	0–1	Damesin (2003)
Eucalyptus miniata	55	Branch	na	Cernusak *et al*. (2006)
Betula pendula	97	Branch	6	Wittmann *et al*. (2006)
Alnus glutinosa	122 (winter) 81 (summer)	Stem	0–1	Berveiller *et al*. (2007)
Betula pendula	123 (winter) 69 (summer)	Stem	0–1	Berveiller *et al*. (2007)
Fagus sylvatica	114 (winter) 74 (summer)	Stem	0–1	Berveiller *et al*. (2007)
Tilia cordata	75 (winter) 68 (summer)	Stem	0–1	Berveiller *et al*. (2007)

na, not available.
Refixation was estimated from CO_2 efflux in the dark (E_A(d)) and in the light (E_A(l)): % refixation = (E_A(d) – E_A(l))/E_A(d) × 100. Values higher than 100% indicate net CO_2 uptake.

at midday. At night, F_T was negligible because sap flow ceased. However, at night, CO_2 efflux to the atmosphere greatly overestimated stem respiration because it consisted of both CO_2 produced by local cells and CO_2 that had been transported upward in the transpiration stream from the roots and lower part of the stem.

Over a 24 h period, 55% of the CO_2 efflux to the atmosphere consisted of CO_2 that had been transported from lower in the tree. On average, over the 24 h period, when efflux was corrected for the flux of imported CO_2, it represented 66% of the total respiration of the living cells in the measured segment. Perhaps more importantly, mean hourly uncorrected efflux, which included transported and locally derived CO_2, was not related to stem respiration calculated by the mass balance approach (Fig. 7). Using a modified version of this technique, Bowman *et al.* (2005) also concluded that there was no significant relationship between CO_2 efflux and the respiratory activity of stems of *Dacrydium cupressinum* trees.

Undoubtedly, estimates of CO_2 efflux from stems to the atmosphere have contributed to our understanding of tree

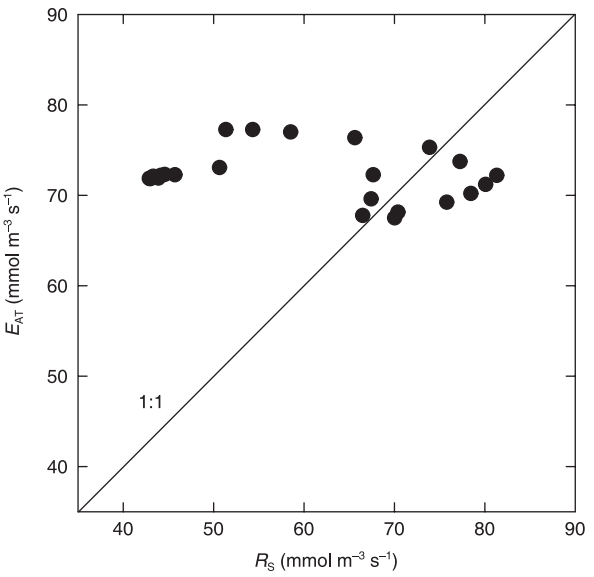

Fig. 7 Relationship between hourly mean total stem CO_2 efflux (E_{AT}, CO_2 from local cell respiration + CO_2 imported in flowing sap from lower in the stem) and mean stem respiration (R_S) measured *in situ* in five *Platanus occidentalis* stem segments. Respiration is calculated as $R_S = E_{AR} + F_T + \Delta S$, where E_{AR} is efflux of CO_2 respired by local cells, F_T is locally respired CO_2 transported out of the segments in flowing sap, and ΔS is the change in locally respired CO_2 stored within the stem segment (adapted from Fig. 5, Teskey & McGuire, 2007).

and ecosystem carbon budgets. However, we conclude that we have gained little specific knowledge about woody tissue respiration from these measurements. Some of the CO_2 released by respiring cells does diffuse into the atmosphere at the point of origin, but the amount is often obscured by the simultaneous diffusion of CO_2 that has been transported in the xylem from woody tissues lower in the tree or from the roots and rhizosphere. These processes cannot be separated easily because the concentration of CO_2 in the xylem varies substantially both diurnally and seasonally, and is influenced by many factors simultaneously, including temperature, sap pH, barriers to diffusion in the xylem and bark, rates of sap flow, and the number and rate of activity of live cells in various tissues along the pathway. For woody tissues, CO_2 efflux to the atmosphere is not equivalent to respiration.

VI. Why do trees have the capacity for internal capture of CO_2?

The entrapment of [CO_2] within tree stems may not have evolved as a carbon-conserving strategy, but rather may have its origins in the development of barriers designed to minimize water loss to the atmosphere. Regardless, a consequence of these barriers is that the CO_2 released from respiration of living cells is prevented from rapidly diffusing out of the stem. Trees take advantage of this source of CO_2 by fixing a portion of it in green woody tissues or leaves before it can diffuse to the atmosphere. Aschan & Pfanz (2003) concluded that internal recycling of CO_2 is an important function of stems.

Although the [CO_2] within tree stems is very high relative to that of the atmosphere, the overall quantity of CO_2 available to be fixed by stem photosynthesis is often small compared with that fixed from the atmosphere via leaf photosynthesis. For example, carbon gain from corticular photosynthesis in midsummer has been reported to be 10–15% of total carbon assimilation (see reviews by Schaedle & Foote, 1971; Pfanz & Aschan, 2001). In some instances, a more substantial fraction of total plant carbon gain has been contributed by woody tissue photosynthesis. In a group of woody desert species, twig photosynthesis contributed over 80% of the annual plant carbon gain due in part to the relatively small investment in leaves in these species (Comstock *et al.*, 1988). Similarly, Foote & Schaedle (1978) concluded that when leaves were absent on *Populus tremuloides*, corticular photosynthesis contributed substantially to the carbohydrate supply of the tree.

Trees are among the most productive plants on earth, yet they have the most massive support structures for their foliage of any plant form. Recycling of carbon released by the respiration of woody tissues reduces the carbon cost of these support structures. Stem photosynthesis can reduce the loss of CO_2 from woody tissues to the atmosphere by 50 to > 100% (Table 3), suggesting that on a 24 h basis, 20–40% recovery of respired carbon may be feasible, at least in canopy branches. Also, the overall carbon gained from refixation has likely been underestimated if CO_2 transported in xylem sap is also being refixed, since this carbon would not be accounted for by the current methods of calculating refixation; that is, by the difference in the rate of CO_2 diffusion to the atmosphere in light and dark. Evidence for fixation of transported CO_2 in the xylem was observed in an experiment in *Alnus glutinosa* in which supplementing the [CO_2] in the xylem produced an increase in O_2 output from the stem (Armstrong & Armstrong, 2005). Indirect evidence has also been seen in stem [CO_2] measurements made in *Fagus sylvatica* and *Populus deltoides* in the dormant season (Saveyn *et al.*, 2006; M. A. McGuire *et al.*, unpublished). In both instances stem [CO_2] decreased when the stem was illuminated, and increased when the stem was in the dark.

Recycling of respired CO_2 may be particularly important during periods of environmental stress. Similar to desert species with low leaf areas (Comstock *et al.*, 1988), corticular photosynthesis may become a substantial component of a tree's carbon gain during periods of severe water stress when daily leaf carbon gain may be negative, or when there has been substantial leaf abscission. The segmentation hypothesis of Zimmermann (1983) suggests that under water stress, the hydraulic architecture of trees allows them to excise extremities; first leaves, then twigs, then branches, etc., so that the main stem survives the longest. In a stress situation when a

tree has few or no leaves remaining, corticular photosynthesis may be a substantial aid to survival.

Internal carbon recycling may have been a more important contributor to overall carbon gain at times when atmospheric [CO_2] was lower. The [CO_2] in the atmosphere has been estimated as low as 185 μmol mol^{-1} during the last glacial maximum 21 000 yr ago (Otto-Bliesner *et al.*, 2006). Under those conditions, maximum rates of leaf net photosynthesis may have been only one-half of present values. Leaf transpiration rates would also have been higher as a result of either higher stomatal density or conductance (Ainsworth & Rogers, 2007), which would cause greater sap velocity and a higher proportion of CO_2 transport in xylem sap (McGuire *et al.*, 2007). Photosynthetic cells in the stem, surrounded by water at high [CO_2], are presumably CO_2-saturated, and may have contributed more to overall woody plant carbon gain under those circumstances. However, this hypothesis is speculative, as we are not aware of any studies that have examined it.

Corticular and wood photosynthesis may be more critical for maintaining sufficient O_2 concentrations in stems to avoid anoxia than for carbon gain *per se* (Pfanz *et al.*, 2002). The [O_2] in xylem is often half that of ambient air, or *c.* 10% (Gansert *et al.*, 2001; Spicer & Holbrook, 2005) and there are reports of it reaching concentrations of 5% or less (Jensen, 1969; Eklund, 2000). However, we are not aware of any comparisons between the quantity of oxygen released by stem photosynthesis and that supplied by either sap transport or diffusion through bark. Sap flux is considered the major source of O_2 in the xylem (Gansert, 2003; Spicer & Holbrook, 2005) but the importance of O_2 generated by stem photosynthesis may increase when sap flux is diminished. Gansert (2003) reported that when sap flow was reduced, the O_2 deficit in *Betula pubescens* stems increased dramatically; under these conditions any O_2 provided by stem photosynthesis would help in maintaining adequate rates of respiration.

VII. Conclusions

There is a high concentration of CO_2 in the xylem of tree stems that may be a consequence of anatomical and morphological adaptations to limit the loss of water from the xylem. Stem photosynthesis utilizes a portion of this CO_2, providing aeration to living cells in the xylem, and offsetting the carbohydrate cost of building and maintaining the massive woody structural system of trees. A consequence of the retention and transport of CO_2 in stems is that the respiration of woody tissues has not been accurately estimated by measurements of CO_2 efflux to the atmosphere. To determine the actual rate of stem respiration, internal CO_2 fluxes as well as CO_2 efflux to the atmosphere must be measured or accounted for in some other way. Although the picture is not yet complete, the mass balance approach may provide a more accurate estimate of stem respiration than other methods. However, whatever methods are used, it is clear that we must move beyond our current reliance on CO_2 efflux as a measure of woody tissue respiration.

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