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ORIGINAL PAPER

Stem radial CO_2 conductance affects stem respiratory CO_2 fluxes in ash and birch trees

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Abstract The CO_2 released from respiring cells in woody tissues of trees can contribute to one of three fluxes: efflux to the atmosphere (E_A), internal xylem sap transport flux (F_T), and storage flux (ΔS). Adding those fluxes together provides an estimate of actual stem respiration (R_S).We know that the relative proportion of CO_2 in those fluxes varies greatly among tree species, but we do not yet have a clear understanding of the causes for this variation. One possible explanation is that species differ in stem radial CO_2 conductance (g_c). A high g_c would favor the E_A pathway and a low g_c would favor the F_T pathway. However, g_c has only been measured once in situ and only in a single tree species. We measured g_c using two methods in stems of *Fraxinus mandshurica* Rupr. (ash) and *Betula platyphylla* Suk. (birch) trees in situ, along with R_S, E_A, F_T and ΔS. Stem radial CO_2 conductance was substantially greater in ash trees than in birch trees. Corresponding to that finding, in ash trees over 24 h, E_A constituted the entire flux of respired CO_2, and F_T was negative, indicating that additional CO_2, probably transported from the root system via the xylem, was also diffusing into the atmosphere. In ash trees, F_T was negative over the entire 24 h, and this study represents the first time that has been reported. The addition of xylem-transported CO_2 to E_A caused E_A to be 9% higher than the actual R_S over the diel measurement period. Birch trees, which had lower g_c, also had a more commonly seen pattern, with E_A accounting for about 80% of the CO_2 released from local cell respiration and F_T accounting for the remainder. The inorganic carbon concentration in xylem sap was also lower in ash trees than in birch trees: 2.7 versus 5.3 mmol L^{-1}, respectively. Our results indicate that stem CO_2 conductance could be a very useful measurement to help explain differences among species in the proportion of respired CO_2that remains in the xylem or diffuses into the atmosphere.

Keywords Stem CO_2 conductance · Stem respiration · Stem CO_2 efflux · Transport flux · Stem temperature · Sap flow · Sap flux density

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Introduction

The CO_2 released by respiring cells in woody tissues can diffuse to the atmosphere through bark (CO_2 efflux, E_A), be transported in xylem sap (transport flux, F_T) or remain in the stem (storage flux, ΔS) (McGuire and Teskey 2004). Thus, the rate of stem respiration (R_S) can be calculated as $R_S = E_A + F_T + \Delta S$. The relative distribution of R_S to E_A, F_T and ΔS differ widely among tree species. In recent studies, over 24 h, the lowest distribution of R_S to E_A was 0.45 in *Platanus occidentalis* (McGuire and Teskey 2004),

and the highest was 1.00 in *Quercus pyrenaica* (Salomón et al. 2016). The lowest distribution of R_S to F_T was − 0.4 in *Q. pyrenaica* (Salomón et al. 2016), and the highest was 0.55 in *Populus deltoides* (McGuire and Teskey 2004).The calculated ΔS flux was small in all studies, usually less than 1–3% of E_A and F_T combined.

Many more studies have measured E_A than R_S. As for R_S, these studies have also shown that E_A differs greatly among tree species. For example, mean annual E_A in *Larix gmelinii* was 44% greater than that of *Pinus koraiensis* growing in adjacent stands under very similar air temperatures (Yang et al. 2012a).In another study, mean stem CO_2 efflux, standardized to 10 °C, in *Quercus acutissima*, *Pinus massoniana* and *Pinus taeda* growing at the same site was 1.87, 1.12 and 0.90 μmol m^{-2} s^{-1}, respectively (Yang et al. 2012b), a twofold difference between species that was not related to temperature. Species differences in E_A may reflect actual differences in rates of respiration among trees. However, we speculate that differences in E_A could also reflect species differences in anatomical and morphological characteristics that affect stem radial CO_2 conductance (g_c). Little is known about species variation in g_c because it has only been measured on one species in one study (Steppe et al. 2007). No measurements have compared g_c between species.

In all measurements thus far, the CO_2 concentration [CO_2] in stems has been much higher than the [CO_2] in the atmosphere. Across multiple studies, the [CO_2] measured in tree stems of different species ranged from 1.6 to 26%, substantially higher than the atmospheric [CO_2] of 0.04% (Teskey et al. 2008). The causes of high variability in stem [CO_2] among species have not been identified. This variation may reflect large differences among species in rates of CO_2 evolution from respiring cells or differences in the number, activity, or location of respiring cells in the stem. It may also reflect species differences in diffusional resistance. The high stem [CO_2] observed in all species relative to atmospheric [CO_2] indicates that CO_2 released from respiring cells in woody tissues cannot readily move from the stem into the atmosphere. The locations of the barriers to diffusion have not yet been clearly identified. However, the cuticle or barkon the surface of stems was shown to strongly reduce the exchange of CO_2 and O_2 (Lendzian 2006), and the xylem itself can also be a barrier to gaseous diffusion (Sorz and Hietz 2006). These factors are likely to vary among species and could affect g_c, which in turn would affect the quantity of CO_2 remaining within the stem or diffusing into the atmosphere. We already know that sap pH, temperature and sap flux density affect the concentration of CO_2 in the stem, which in turn affects the diffusional gradient for CO_2 to the atmosphere; however, we have not yet evaluated the role of g_c in the balance between E_A, F_T and ΔS fluxes.

In this study, we calculated stem radial CO_2 conductance as well as R_S, E_A, F_T and ΔS in *Fraxinus mandshurica* Rupr. (ash) and *Betula platyphylla* Suk. (birch) trees. Xylem anatomy is ring-porous in *Fraxinus* and diffuse-porous in *Betula*. We hypothesized that there would be differences in stem radial CO_2 conductance between the two species and that those differences would affect stem [CO_2] and the relative proportions of respired CO_2 distributed to E_A and F_T.

Materials and methods

Three ash trees and three birch trees growing outdoors in the Northeast Forestry University Arboretum (E126°38′, N45°43′) were used in this study. Measurements were made on ash trees with diameters between 13.1 and 16.1 cm and birch trees with diameters between 11.5 and 13.5 cm (Table 1).

Stem temperature and sap flow

Holes 5 mm in diameter were drilled to a depth of 1 cm on the north and south sides of the stem at 1.3 m above the ground. Thermostats (TR-1106, T&D Corp., Japan) were installed in the holes and sealed with rubber cement. Stem temperature was measured and recorded every 10 min with a datalogger (Tr-71U, T&D Corp. Japan).

Sap flow velocity (cm s^{-1}) was measured with pre-calibrated thermal dissipation sensors (TDP-30, DynaMax, Houston, TX, USA) installed at 1.3 m aboveground on the north and south sides of the stem on each tree. Sensors were protected from solar heating by wrapping stems with reflective insulation. Sap flow velocity was measured and recorded every 10 min with a datalogger (CR10X, Campbell Scientific, Logan, UT, USA). After all other stem measurements were complete; a radial core was taken from each tree with an increment borer (10-100-1007, Haglöf, Sweden) and used to calculate sapwood area. Sapwood area was used to convert measurements of sap flow velocity to sap flux density (J, g cm^{-2} h^{-1}) and sap flow (f_S, L h^{-1}) according to the equations of Granier (1985).

CO_2/H_2O gas exchange

The efflux of CO_2 and H_2O from the stem surface was measured in situ using a chamber that surrounded a portion of the stem. Chamber construction followed that described in McGuire and Teskey (2004). Chambers were constructed around each stem at a height of 0.5 m. First, to form the support rings at the top and bottom of the chamber, the stem was tightly wrapped with two elastic rubber tubes (20 mm diameter), which were placed 0.5 m

Table 1 Characteristics of stem segments of ash and birch trees used for in situ estimates of stem respiration: mean stem diameter, sapwood radial depth, area and volume enclosed in the efflux chamber

Species	Tree	Diameter (cm)	Sapwood depth (cm)	Sapwood volume (m^3)	Sapwood area (m^2)	pH
Ash	1	13.06	4.53	6.097×10^{-3}	12.128×10^{-3}	5.2
	2	16.08	5.54	9.272×10^{-3}	18.342×10^{-3}	5.3
	3	15.61	5.30	9.073×10^{-3}	17.154×10^{-3}	5.5
Birch	1	13.54	5.27	7.357×10^{-3}	13.674×10^{-3}	5.5
	2	11.46	5.23	5.265×10^{-3}	10.240×10^{-3}	5.6
	3	10.83	4.91	4.699×10^{-3}	9.125×10^{-3}	5.5

The height of the center of the chamber was approximately 1 m above the ground. Sap pH values are means of measurements made on sap expressed from three twigs excised from each tree

apart vertically. Rubber cement was used to bond the rubber tube to the bark to form a gas-tight seal, and the cut ends of each tube were sealed together with waterproof silicone glue. Then, double-sided adhesive tape was applied to cover the entire surface of each the support ring, and polyethylene film was wrapped around the tree over the support rings and attached to the adhesive tape. The junction of the two vertical edges of the film was also sealed with tape. The chamber was connected to an infrared CO_2/H_2O analyzer (IRGA) (Model 7000; Li-Cor, Lincoln, NE, USA) via plastic tubing inserted through the support rings. Air was supplied to the chamber with a pump (model 6400-907; Li-Cor). The IRGA was operated in a differential configuration, i.e., it measured $[CO_2]$ and $[H_2O]$ of the air flowing both into the chamber (reference) and out of the chamber (sample). The CR10X datalogger was used to control three solenoid valves (E2-1-HC-1200VDC, Versa Products, Paramus, NJ, USA) to switch the gas flow to three chambers to measure three trees in sequence. The gas flow rate was measured with a mass flow meter (AWM5000, Honeywell, St. Morris, NJ, USA). Ash trees were measured on September 3, 2008, and birch trees were measured on September 13, 2008. The two species could not be measured simultaneously because the trees of the two species were not adjacent to each other, and we did not have duplicate equipment, so the trees were measured on two dates, 10 days apart, that had similar environmental conditions; warm and sunny with few clouds and no precipitation. Over 24 h, mean stem temperature was 20.8 °C in ash trees and 17.6 °C in birch trees, and soil volumetric water content at 20 cm depth was 18.47% in ash and 18.79% in birch on the measuring day. Each set of three trees was measured every 30 min over 24 h. Data were logged every minute and averaged and recorded with the datalogger at the end of each measurement (last 6 of 10 min averaged for each tree in each 30-min cycle).

Stem respiration and its component fluxes

Total stem respiration (R_S) was calculated following McGuire and Teskey (2004) as $R_S = E_A + F_T + \Delta S$. Stem CO_2 efflux (E_A) was calculated as

$$E_A = f_A \Delta[CO_2]/v, \quad (1)$$

where f_A is the mass air flow rate through the chamber, v is the sapwood volume of the stem surrounded by the chamber, and $\Delta[CO_2]$ is the difference in the CO_2 concentration of air entering and exiting the chamber.

To determine changes in the quantity of CO_2 stored in the xylem (ΔS) and the quantity of CO_2 transported in xylem sap (F_T), stem internal CO_2 concentration $[CO_2]$ was measured. To measure $[CO_2]$, holes with a diameter of 20 mm and depth of 50 mm were drilled above and below the efflux chamber. Non-dispersive infrared (NDIR) CO_2 sensors (GMM221, Vaisala, Finland) were placed in the holes to measure gaseous $[CO_2]$ in the xylem. The sensors were sealed to the tree with flexible putty adhesive (Blu-Tack, Bostik, Victoria, Australia) to prevent direct gas exchange between the xylem and the atmosphere. The sensors were connected to the data logger and measurements were made every minute and averaged and recorded at 10-min intervals.

The total dissolved inorganic carbon in the stem ($[CO_2^*]$, i.e., gaseous and dissolved CO_2, μmol L^{-1}), was calculated from measurements of $[CO_2]$, stem temperature, and sap pH using Henry's Law (Butler 1991; McGuire and Teskey 2002). To obtain sap pH, we used a pressure chamber (SKPM1400-50, Skye Instruments, Llandrindod Wells, UK) to express sap from several detached twigs of each tree during the measurement period. The pH of expressed sap was measured immediately with a pH microelectrode (Model PHS-3C, Shanghai INESA Scientific Instrument, Shanghai, PRC) and averaged for each tree (Table 1). Aubrey et al. (2011) observed that pH was similar when measured in sap expressed from stems andtwigs, and it remained relatively constant through a diel period.

The change in xylem $[CO_2^*]$ over time (storage flux, ΔS) was calculated as

$$\Delta S = \left([CO_2^*]_{st1} - [CO_2^*]_{st0} \right) L / \Delta t, \quad (2)$$

where $[CO_2^*]_{st0}$ and $[CO_2^*]_{st1}$ are the average CO_2 concentration for the stem segment (mean of measurements above and below the efflux chamber) at time t_0 and t_1, $\Delta t = t_1 - t_0$ (s) and L is the amount of water in the stem segment.

An estimate of the water content of the sapwood was needed to determine ΔS. In a test of the sensitivity of ΔS to volumetric water content, changing the value of from 300 to 700 L m^{-3} caused relatively small changes in the estimate of ΔS, the smallest component of R_S (McGuire and Teskey 2004). For this study, we assumed sapwood water content was 50% of sapwood volume, i.e., 500 L m^{-3}, based on the average specific gravity for hardwoods (Panshin and de Zeeuw 1980).

The upward transport of CO_2 in the sap (transport flux, F_T) was calculated as

$$F_T = f_S * \Delta [CO_2^*] / v, \quad (3)$$

where f_S is sap flow (L s^{-1}), $\Delta[CO_2^*]$ is the difference in the CO_2 concentration above and below the efflux chamber (above–below), and v is the volume of sapwood surrounded by the efflux chamber.

Stem radial conductance to CO_2

The radial conductance of CO_2 through the stems was calculated in two ways:

1. Stem CO_2 conductance was calculated based on H_2O conductance (g_{c-H_2O}, molCO_2 $m^{-2}s^{-1}$) following Wittmann et al. (2006) as

   $$g_{c-H_2O} = g_{tw} / 1.56, \quad (4)$$

   where g_{tw} was periderm conductance of water vapor and 1.56 is the ratio of the diffusivity of water vapor to the diffusivity of CO_2 in air (Campbell and Norman 1998).

   Periderm conductance to water vapor was calculated as

   $$g_{tw} = E_{H_2O} / (W_i - W_a), \quad (5)$$

   where E_{H_2O} was stem H_2O efflux W_i and W_a were the molar concentrations of water vapor in the stem and the air, respectively. (W_i was assumed to be at saturation.)

   Stem H_2O efflux (E_{H_2O}, mmol m^{-2} s^{-1}) was calculated as

   $$E_{H_2O} = f_A * \Delta[H_2O] / a, \quad (6)$$

   where f_A was the air flow rate through the stem chamber (mol s^{-1}), a was the surface area of the stem surrounded by the chamber (m^{-2}), and $\Delta[H_2O]$ was the difference in H_2O concentration of the air entering and exiting the chamber (mmol mol^{-1}).
2. Stem CO_2 conductance was also calculated based on the difference in CO_2 concentration between the xylem and the atmosphere (g_{c-CO_2}, m s^{-1}) following Steppe et al. (2007):

   $$g_{c-CO_2} = E_{A-S} / [CO_2]_D, \quad (7)$$

   where $E_{A\text{-}S}$ was stem CO_2 efflux on a stem surface area basis (μmol m^{-2} s^{-1}) and $[CO_2]_D$ was the difference in CO_2 concentration between air in the xylem and the atmosphere (μmol mol^{-1}) calculated as

   $$[CO_2]_D = \left([CO_2]_{xylem} - [CO_2]_{air} \right) / 22.4 \times 1000, \quad (8)$$

   where $[CO_2]_{xylem}$ is the mean $[CO_2]$ in the xylem measured with the NDIR sensors (μmol mol^{-1}), $[CO_2]_{air}$ was the $[CO_2]$ of the air entering the efflux chamber measured with the IRGA (μmol mol^{-1}), 22.4 is the molar volume of gas (L mol^{-1}), and 1000 converted values of $[CO_2]_D$ to units of μmol m^{-3}.

Statistical analyses

A multiple linear regression model was used to relate E_A with stem temperature (T_S) and sap flux density (J):

$$E_A = \beta_0 + \beta_1 T_s + \beta_2 f_s + \beta_3 T_s * J + \varepsilon, \quad (9)$$

where β_0, β_1, β_2 and β_3 are regression coefficients, T_S is stem temperature, J is sap flux density and ε is the random error term which followed a normal distribution N (μ, σ^2). The relative weight of each parameter was calculated using the R package RELAIMPO (Gromping 2006). A one-way ANOVA was used to detect differences in g_{c-H_2O} and g_{c-CO_2} between ash and birch trees (n = 3).

Results

Stem radial conductance to CO_2

Over 24 h, mean stem CO_2 conductance calculated from stem H_2O efflux (g_{c-H_2O}) was greater in ash trees than in birch trees ($p < 0.01$). It was 0.87 mol m^{-2} s^{-1} in ash trees and 0.06 mol m^{-2} s^{-1} in birch trees. Diel variation in g_{c-H_2O} was also much larger in ash trees than in birch trees (Fig. 1). It ranged from 0.56 to 1.35 mmol m^{-2} s^{-1} in ash trees. In comparison, g_{c-H_2O} varied from only 0.05 to 0.09 mmol m^{-2} s^{-1} in birch trees. Corresponding with this finding, diel variation in stem H_2O efflux was also much

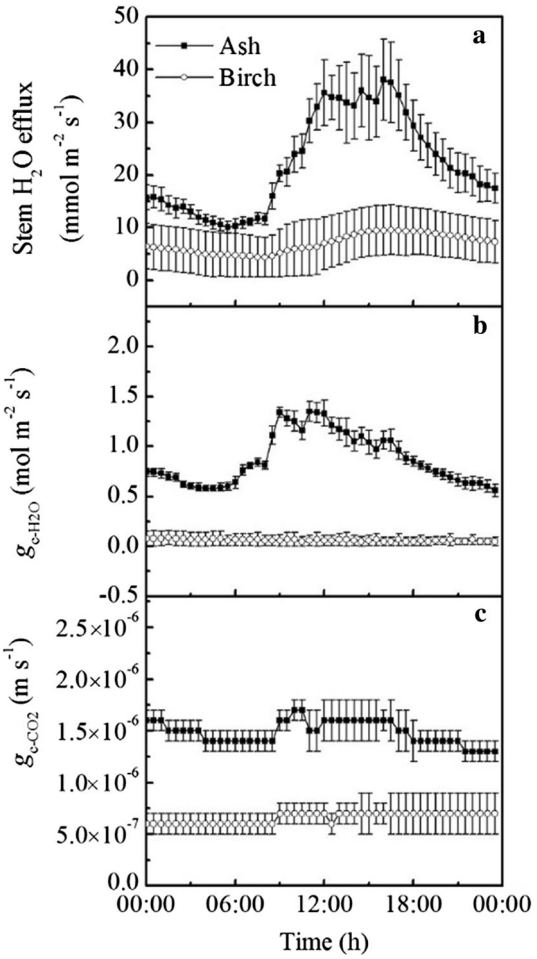

Fig. 1 The diel pattern of mean stem H_2O efflux (**a**), stem CO_2 conductance based on H_2O conductance (g_{c-H_2O}) (**b**), or CO_2 conductance (g_{c-CO_2}) (**c**) in ash trees and birch trees. Vertical bars indicate standard error

larger in ash trees than in birch trees. In ash trees, stem H_2O efflux ranged from 12 to 38 mmol m^{-2} s^{-1}. In birch trees, stem H_2O efflux varied between 4 and 10 mmol m^{-2} s^{-1}.

Mean stem CO_2 conductance calculated from the difference in $[CO_2]$ between stem and atmosphere (g_{c-CO_2}) was greater in ash trees than in birch trees: 1.48 e^{-06} versus 0.67 e^{-06} m s^{-1} ($p < 0.05$). Diel variation in g_{c-CO_2} was also greater in ash trees than in birch trees (Fig. 1). In ash trees, g_{c-CO_2} ranged between 1.30 e^{-06} and 1.71 e^{-06} m s^{-1} in ash trees and between 0.58 e^{-06} and 0.74 e^{-06} m s^{-1} in birch trees.

Between-species comparison of the component fluxes of stem respiration and sap $[CO_2]$

Stem CO_2 efflux was the main component of R_S over 24 h in both species (Fig. 2, Table 2). Mean 24-h E_A was 83.9 μmol m^{-3} s^{-1} in the ash trees and 67.0 μmol m^{-3} s^{-1} in the birch trees. In ash trees, which had higher stem CO_2 conductance, E_A exceeded R_S indicating that part of the CO_2 diffusing from the stem into the measurement cuvette was from xylem-transported CO_2. In birch trees, which had lower stem CO_2 conductance, E_A represented 80% of R_S with the remaining 20% accounted for by F_T. Over the 24-h measurement period, mean F_T was negative in ash trees (− 7.3 μmol m^{-3} s^{-1}) and positive in birch trees (21.5 μmol m^{-3} s^{-1}).Storage flux was a very small part of the total flux over 24 h, representing < 1% of R_S in both species.

Data were also examined in 6-h periods to determine whether there were diel differences between species in R_S and the component fluxes (Table 2). Stem respiration was substantially higher in birch trees than ash trees from 06:00 to 18:00 h, when most sap flow was occurring. However, E_A was lower in birch trees than in ash trees during that time. A substantial difference between the two species was that in ash trees F_T was negative at all times during the diel period, while it was positive in birch trees. From 06:00 to 18:00 h, in birch trees F_T accounted for − 37% of the CO_2 released from respiring cells and E_A accounted for − 63% of the CO_2. In contrast, for ash trees in the same time period, F_T was negative, caused by the diffusion outward of a combination of locally respired CO_2 and transported CO_2, which resulted in depletion of CO_2 in the xylem sap and inflated E_A estimates. In trees of both species, diel variation was larger in F_T compared with the other fluxes because F_T was − 0 at night when sap was not flowing. Mean maximum F_T was approximately − 13 μmol m^{-3} s^{-1} in ash trees, and 43 mol m^{-3} s^{-1} in birch trees, with the peak occurring between 12:00 and 18:00 h in conjunction with maximum sap flux density, which was 6.5 g cm^{-2} h^{-1} in ash trees and 15.4 g cm^{-2} h^{-1} in birch trees.

Total dissolved inorganic carbon in xylem sap $[CO_2^*]$ was also lower in ash trees than in birch trees (Table 2). Over 24 h, mean $[CO_2^*]$ was 2.7 mmol L^{-1} in ash trees and 5.3 mmol L^{-1} in birch trees. Diel variation in $[CO_2^*]$ was also observed. In ash trees, the mean maximum $[CO_2^*]$ was 3.1 mmol L^{-1} and occurred between 18:00 and 24:00 h. In birch trees, the mean maximum $[CO_2^*]$ was 5.6 mmol L^{-1} and occurred later at night, between 00:00 and 06:00 h.

Correlating T_S and J with E_A

A regression analysis was done for the 06:00–18:00 time period, i.e., when sap was flowing, to compare the effect of T_S and J on E_A in the two species. During that time, T_S and J explained most of the variation in E_A for both species, with a combined r^2 of 0.90 for the ash trees and 0.87 for the birch trees (Table 3). In birch trees, T_S alone accounted for

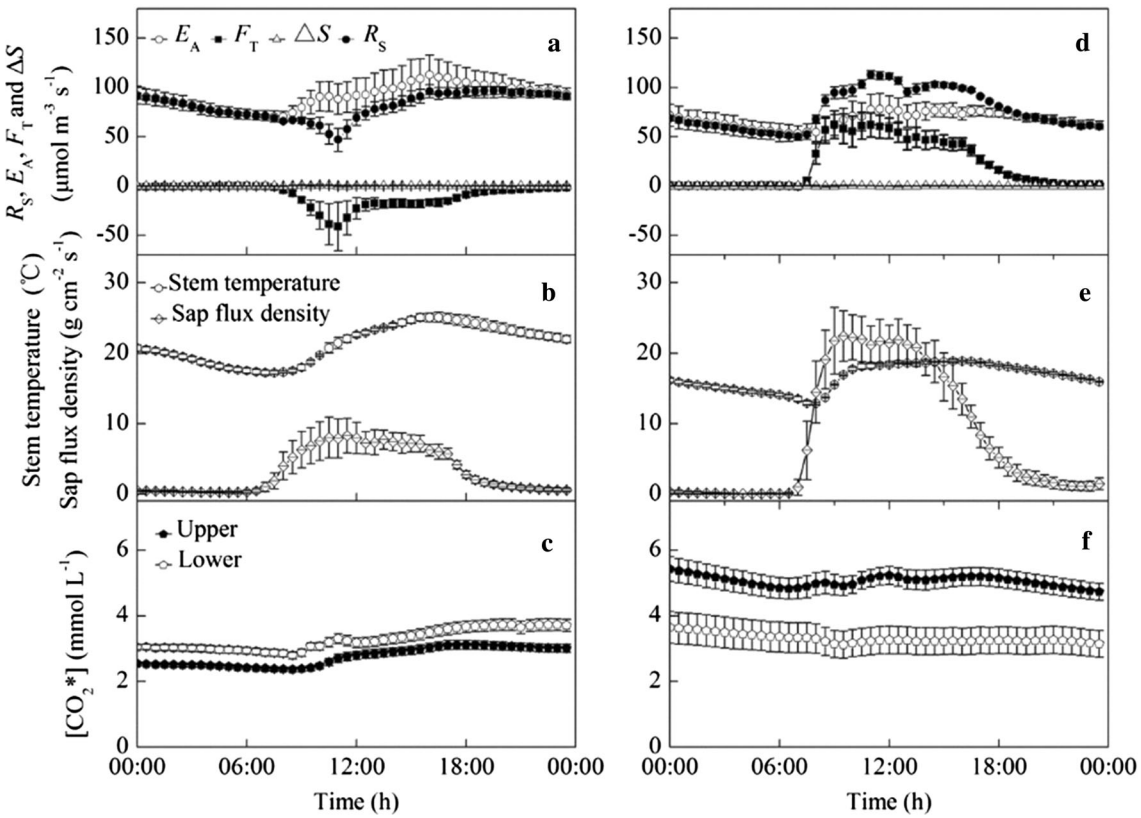

Fig. 2 Diel patterns of **a**, **d** mean stem respiration (R_S) and mean component fluxes: efflux to atmosphere (E_A), transport flux (F_T), and storage flux (ΔS) and **b**, **e** mean sap flux density and stem temperature of the stem segment enclosed in the chamber, and **c**, **f** mean xylem sap CO_2 concentration [CO_2^*] above (upper) and below (lower) the chamber. Left panels, ash; right panels, birch. Symbols represent mean of three trees per species. Error bars indicate standard error

88% of the variation in E_A, while J only accounted for 11%. In contrast, in birch trees T_S accounted for 43% of the variation in E_A, while J accounted for 57%.

Discussion

This study has shown for the first time that the CO_2 conductance through the stem (g_c) substantially differed between two tree species, with lower g_c in birch trees than in ash trees. The bark of birch trees forms multiple layers of large contiguous thin sheets, which are single layers of phellem (Schonherr and Ziegler 1980). The low radial water and CO_2 transport measured in birch suggests that these heavily suberized cell layers were a barrier to the diffusion of both water vapor and CO_2. In contrast, the bark of ash does not form large sheets, but is thick and spongy with many longitudinal ridges and furrows (Zhang 2010).This anatomy may have been more conducive to the escape of water vapor and CO_2 and could be a reason why E_A was a much greater proportion of R_S in ash trees than in birch trees. In addition to bark anatomy, several other factors could affect g_c including wood anatomy, xylem water content, and stem temperature (Lendzian 2006; Sorz and Hietz 2006).

We observed diel variation in g_c using both methods of calculation, although it was much more pronounced in the calculation based on H_2O efflux and more pronounced in ash trees than in birch trees. The cause of that variation is unknown, but we suggest that it may have been related to changes stem or bark water content or water potential or to the diffusion gradient for water vapor and CO_2 from stem to atmosphere. The difference between the two approaches was probably a major cause of the differing lengths of the pathway for H_2O and CO_2. However, because the stem g_c measurement using CO_2 is the more direct measurement, which avoids the assumption that water and CO_2 move through the stem proportionally, and the greater diel consistency in the measurements suggest that g_{c-CO_2} is the better approach for comparing stem conductance among species. It is likely that g_c not only varies among species, but that it also varies in different parts of trees and in trees of different sizes. Stems and branches have very different bark and cambial thickness and morphology, live cell volume, radial path length for the movement of CO_2 from respiring cells in the xylem, and [CO_2] (Teskey et al.

Table 2 Mean (± SE) diel and 6-h fluxes and the relative contribution of fluxes to stem respiration (R_S) from three stem segments each of ash and birch in situ, calculated by mass balance

Species	Time (h)	Stem temperature (°C)	Sap flux density (g cm^{-2} h^{-1})	Xylem [CO_2^*] (mmol L^{-1})	Flux components (μmol m^{-3} s^{-1})						
					E_A	F_T	ΔS	R_S	E_A/R_S (%)	F_T/R_S (%)	$\Delta S/R_S$ (%)
Ash	00:00–06:00	19.16 ± 0.21	0.33 ± 0.23	2.54 ± 0.26	76.2 ± 17.7	− 0.3 ± 0.3	− 0.0 ± 0.0	75.9 ± 17.4	100.4	− 0.4	0.0
	06:00–12:00	18.48 ± 0.12	4.94 ± 2.77	2.50 ± 0.30	73.9 ± 13.6	− 11.9 ± 6.0	1.2 ± 1.1	63.2 ± 13.6	116.9	− 18.8	1.9
	12:00–18:00	23.40 ± 0.26	6.50 ± 2.17	2.86 ± 0.50	96.1 ± 17.8	− 13.3 ± 5.4	0.7 ± 0.1	83.5 ± 19.8	115.1	− 16.0	0.8
	18:00–24:00	22.30 ± 0.46	1.14 ± 0.62	3.09 ± 0.50	89.2 ± 17.6	− 3.6 ± 1.6	0.1 ± 0.1	85.7 ± 17.2	104.1	− 4.2	0.1
	24 h mean	20.84 ± 0.24	5.93 ± 1.35	2.74 ± 0.38	83.9 ± 11.9	− 7.3 ± 2.8	0.5 ± 0.3	77.1 ± 18.8	109.2	− 9.8	0.7
Birch	00:00–06:00	15.78 ± 0.65	0.10 ± 0.04	5.56 ± 1.29	62.9 ± 11.4	0.2 ± 0.2	− 0.0 ± 0.0	63.1 ± 11.4	99.7	0.3	0.0
	06:00–12:00	15.83 ± 0.35	11.68 ± 2.92	5.21 ± 1.15	62.8 ± 12.9	37.6 ± 31.5	0.1 ± 1.4	100.5 ± 35.4	62.5	37.4	0.1
	12:00–18:00	20.07 ± 1.33	15.40 ± 1.31	5.28 ± 1.04	75.2 ± 9.5	43.0 ± 26.4	− 0.4 ± 0.3	117.8 ± 29.2	63.8	36.5	− 0.3
	18:00–24:00	18.83 ± 1.65	1.95 ± 0.44	5.17 ± 1.01	67.3 ± 4.6	5.3 ± 4.2	− 0.3 ± 0.1	72.3 ± 3.1	93.0	7.4	− 0.4
	24 h mean	17.63 ± 1.01	7.28 ± 1.14	5.31 ± 1.12	67.0 ± 9.16	21.5 ± 15.57	− 0.2 ± 0.4	88.4 ± 18.1	79.8	20.4	− 0.2

The flux components are efflux to the atmosphere (E_A), transport flux (F_T), and storage flux (ΔS)

2008). High variation in E_A was observed in simultaneous measurements of branches and stems of *Abies amabilis* trees, which was attributed to differences in the permeability of bark layers to CO_2 (Sprugel 1990). Cavaleri et al. (2006) reported that E_A at 25 °C of branches of tropical trees decreased with decreasing branch diameter and increased with canopy height for the same branch diameter.

Within-species variation in g_c has also been reported (Steppe et al. 2007). We found some variation in stem g_c among trees of the same species, but much less than the sixfold variation in g_{c-CO_2} found in three trees of *Populus deltiodes* of similar size growing on the same site reported by Steppe et al. (2007). They also found that the *Populus* trees with lower g_{c-CO_2} had lower E_A and higher stem [CO_2^*] compared to those with higher g_{c-CO_2}, which had higher E_A and lower stem [CO_2^*]. In our study, there was a similar relationship between stem g_c and stem [CO_2^*]. In ash trees, high E_A due to high g_c likely resulted in low stem [CO_2^*] and low F_T, while in birch, low E_A, high stem [CO_2^*] and high F_T corresponded with low g_c. These findings support our hypothesis that species differences in stem g_c affects the proportion of respired CO_2 distributed to E_A versus F_T.

Many studies have reported differences in E_A among species. For example, E_A normalized to 15 °C varied from 0.5 to 2.7 nmol C mol^{-1} C sapwood s^{-1} among *Pinus banksiana*, *Picea mariana* and *Populus tremuloides* trees (Lavigne and Ryan 1997). While there are many possible reasons for these differences, including the number of live cells in the xylem and inner bark, stem oxygen concentration, and the respiratory activity of those cells, our results suggest that g_c contributes to species differences in E_A.

Teskey and McGuire (2007) found that, on average, 45% of E_A in large *P. occidentalis* stems was from xylem-transported CO_2, i.e., was from the diffusion of CO_2 that originated below the site of measurement and was unrelated to the current rate of stem respiration. We observed that during the day in ash trees, E_A was greater than R_S, which indicated that high stem radial conductance allowed the CO_2 that had been transported from lower in the stem or roots to flux outward to the atmosphere. This conclusion is also supported by the observed decrease in stem [CO_2^*] with height in ash trees. Assuming that the g_c of the ash stems was similar from the 0.5 m measurement height to the base of the stem, it is likely that the source of the transported CO_2 was the root system. Aubrey and Teskey (2009) observed that − 67% of root-respired CO_2 was transported into the stem in flowing sap in *P. deltoides* trees, indicating that root-respired CO_2 could be a significant contributor to stem F_T. They speculated that a large quantity of CO_2 transported from roots into the stem would

Table 3 Fixed effects of linear mixed models describing the effects of stem temperature (T_S) and sap flux density (J) on stem CO_2 efflux in ash trees and birch trees

Species	Coefficient	Estimate	SE	p value	Proportion of variance explained by model (%)	Relative weight (%)	Adjr^2
Ash					89.95		0.90
	Intercept	0.0195	0.0365	0.594			
	T_S	0.8665	0.0366	< 0.001		88.33	
	J	0.1955	0.0375	< 0.001		11.08	
	$T_S * J$	− 0.0974	0.0473	0.043		0.59	
Birch					88.53		0.87
	Intercept	− 0.0116	0.0631	0.856			
	T_S	0.5313	0.0633	< 0.001		43.13	
	J	0.6466	0.0637	< 0.001		56.72	
	$T_S * J$	0.0430	0.0735	0.563		0.14	

confound measurements of stem respiration based on E_A alone and also those based on $E_A + F_T + \Delta S$. Our study has provided empirical results to support that contention. Dissolved CO_2 in the sap and F_T in birch was greater than in ash. The CO_2 transported in the xylem can be fixed, and the fixed CO_2 delivered in the sap accounts for 2–9% of the CO_2 produced via photosynthesis (Hari et al. 1991). It is possible that more CO_2 could be re-fixed into the leaves for reuse in birch than in ash.

The results of this study suggest that g_c can vary substantially among species, but it is important to note that the two species were measured 10 days apart. Even though the environmental conditions on the 2 days were similar, if environment has a large influence on g_c it might have affected the results. We also do not know how g_c changes with morphological development and whether species will have lesser or greater differences in g_c at different stages of development or different ages. The values of g_c may also change seasonally. Although there is still a great deal to learn about stem conductance, we conclude that measurements of g_c have great potential to provide a better understanding stem respiration and the flux of respired CO_2.

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