Movement of respiratory CO₂ in stems of loblolly pine (Pinus taeda L.) seedlings

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Summary

Temperature-independent fluctuations in stem CO₂ efflux were measured in Pinus taeda L. seedlings. Stem CO₂ efflux was measured during high and low transpiration rates, high and low net photosynthesis rates, and normal and interrupted substrate supply conditions. Stem CO₂ efflux rates were an average of 6.7% lower during periods of high transpiration compared to periods of low transpiration. This difference in stem CO₂ efflux rates was not due to water stress. The most likely cause was movement of respiratory CO₂ in the transpiration stream.

Interruption of substrate supply to the stem by phloem girdling reduced stem CO₂ efflux rates. Increasing net photosynthesis rates from low to high had no effect on stem CO₂ efflux, but decreasing net photosynthesis from high to low caused relatively small reductions in stem CO₂ efflux. These results indicate that diurnal changes in net photosynthesis rate may play a small role in temperature-independent afternoon depressions of stem CO₂ efflux.

The transport of respiratory CO₂ by the transpiration stream compromises measurements of woody tissue respiration obtained by commonly accepted gas exchange techniques. This phenomenon could also affect measurement of leaf net photosynthesis and branch woody tissue respiration.

Keywords: net photosynthesis, respiration, stem carbon dioxide efflux, transpiration.

Introduction

Tree physiologists frequently estimate tissue respiration rates by means of an exponential temperature function such as Equation 1:

\[ R_{t2} = R_{t1} Q_{10}^{(t2 - t1)/10}, \]

where \( R_{t2} \) is the predicted respiration rate at temperature \( t2 \), \( R_{t1} \) is the respiration rate measured at temperature \( t1 \), and \( Q_{10} \) is the experimentally derived temperature coefficient of respiration, usually between 2.0 and 2.3 (Sprugel and Benecke 1991). This equation is based on the assumption that both growth and maintenance processes are at least partially temperature-mediated in plants (Penning de Vries et al. 1974, Ryle 1984, Johnson and Thomley 1985).

In some cases, temperature-based predictions of woody tissue respiration appear
to mirror actual measurements closely (Figure 1). Temperature functions have been used to predict respiration rates under conditions where they cannot be measured, such as in photosynthesizing tissue during the day. Paembonan et al. (1991) used an equation similar to Equation 1 to estimate daytime respiration rates of the above-ground portion of a *Chamaecyparis obtusa* (Sieb et Zucc.) Endl. tree based on daytime air temperatures and night measurements of respiration. Temperature functions can also be used to normalize respiration measurements obtained over a range of temperatures. Ryan (1990) and Sprugel (1990) used $Q_{10}$ functions to standardize respiration rates measured at different temperatures to standard temperatures. Temperature-predicted respiration rates have also been used to study carbon balance (Kinerson et al. 1977, Dick et al. 1990) and seasonal changes in respiration rate (Butler and Landsberg 1981).

There are problems with this model, however, when it is used to predict woody tissue respiration of trees growing in the field. Respiration of tree stems and branches is usually quantified by measuring the radial CO$_2$ efflux from the intact organ (Sprugel and Benecke 1991). Negisi (1972, 1975, 1981, 1982) found that stem CO$_2$ evolution rates in several tree species were often lower than temperature-predicted rates by up to 50% on warm, sunny afternoons. Kakubari (1988) observed abrupt depressions in stem CO$_2$ efflux from *Fagus sylvatica* L. stems around 1800 h on clear days, when the temperature exceeded 20 °C. Edwards and McLaughlin (1978) measured diel cycles of CO$_2$ evolution in *Liriodendron tulipifera* L. and *Quercus alba* L. that were completely reversed from the temperature-based predictions. Although Matyssek and Schulze (1988) did not discuss it in their report, stem CO$_2$ efflux from *Larix decidua × leptolepis* stems appeared to depart from temperature-predicted respiration by 8 to 32% during the afternoon on three of the four days for which data were presented. This phenomenon has also been observed in stems of *Pinus taeda* L. seedlings (see Figure 2) and trees (Art Wiselogel, personal communication).

A body of evidence suggests that the afternoon depression of stem respiration is

![Figure 1. Temperature response of respiration rates of woody tissue of 1-cm diameter branches excised from *Pinus taeda* trees. Filled circles are the average of measurements on five branches (three branches at 35 °C); error bars show ± 1 standard error of the mean. Hollow circles indicate respiration predicted with Equation 1, with $R_{01} = 0.48 \mu$mol m$^{-2}$ s$^{-1}$, $t_1 = 5$ °C, and $Q_{10} = 1.90$.](image-url)
related to high rates of transpiration. When Negisi (1975) reduced transpiration in stems of *Pinus densiflora* Sieb. et Zucc., by shading of the crown or partial defoliation, the depression effect was removed or obscured. Zabuga et al. (1983) found that stem CO$_2$ efflux rates in *Pinus sylvestris* L. were positively correlated with relative humidity, a relationship indicating reduced respiration during dry, sunny afternoons when high rates of transpiration occur. Lavigne (1987) interpreted his *Abies balsamea* (L.) Mill. data to show that thinned stands experienced more midday depressions of stem respiration than did unthinned stands. This would be consistent with increased individual tree transpiration in the warmer and higher light microclimate of a thinned stand (Whitehead et al. 1984). Negisi (1979) measured respiration rates of detached stem segments of *Pinus densiflora* under a range of artificially induced sap-flow rates, and found that increased sap flow resulted in lower rates of respiration (up to 70% reduction in CO$_2$ evolution at a sap flow rate of 55 cm h$^{-1}$).

There are two main theories to explain how transpiration can affect stem CO$_2$ efflux. The first is that increased rates of transpiration on sunny, hot afternoons lead to water deficits and stress in stem tissue, resulting in lower respiration rates (Lavigne 1987, Kakubari 1988). The second is that a portion of the CO$_2$ evolved by respiration becomes dissolved in the transpiration stream and is carried away from the site of measurement, resulting in stem CO$_2$ evolution lower than would be expected based on temperature (Negisi 1972, Ryan 1990, Sprugel 1990).

A third theory attributes temperature-independent variation in CO$_2$ efflux to variation in substrate supply in the stem. Diurnal changes in rates of carbohydrate export from photosynthesizing tissue could result in varying concentrations of respirable substrate in the tree stem. Because substrate supply can affect respiration rate (Osman 1971, Ludwig et al. 1975, Hansen 1977, Azcón-Bieto and Osmond 1983, Azcón-Bieto et al. 1983), CO$_2$ efflux rate could rise and fall with changes in the substrate concentration in the stem. Edwards and McLaughlin (1978) measured
reducing sugar concentrations of stem tissue of *Quercus alba* and *Liriodendron tulipifera* in parallel with measurements of CO₂ evolution. They found that respiration rates roughly paralleled reducing sugar concentrations throughout the day. However, when respiration was measured below a phloem girdle on a tree stem, the diel pattern continued, although at a reduced magnitude. This experiment discounted the effects of substrate transport from the crown on diurnal respiration fluctuation in the stem, although it confirmed the effect of substrate on long-term respiration rates.

The present study was designed to isolate the cause of temperature-independent midday depressions of stem CO₂ efflux. Experiments were performed to determine the effect of changing transpiration rates, net photosynthesis rates and substrate export on stem CO₂ efflux rates.

**Materials and methods**

**Plant material and growth conditions**

Half-sib *Pinus taeda* seedlings from a North Carolina seed source were germinated and grown in a greenhouse. The seedlings were well-watered with acidified water (pH 5.5–5.7), and fertilized weekly with a liquid nutrient solution containing N, P, K and micronutrients. Iron diethylene triamine penta-acetate chelate was applied monthly. Measurements were carried out on seedlings five to 12 months after germination. All-sided leaf area of seedlings was from 0.06 to 0.22 m², with stem diameters at the point of respiration measurement ranging from 0.58 to 0.96 cm.

**Carbon and water exchange measurements**

During each experiment, the crown of the seedling being measured was sealed in a 23-liter polycarbonate (Lexan) cuvette. Absolute humidity deficit (AHD), temperature, carbon dioxide concentration, and light were varied independently within the chamber.

Chamber temperature was controlled by pumping polyethylene glycol from a temperature-controlled water bath (Neslab Endocal RTE-9) through an aluminum heat exchanger installed in the cuvette. A shielded, 24 gauge chromel-alumel thermocouple measured chamber temperature. The air within the chamber was well stirred by two 12-cm diameter fans attached to the heat exchanger.

Absolute humidity deficit was controlled by varying the amount of chamber air diverted through an external desiccant loop. This drying loop removed air from the chamber, passed the air through a column of silica gel, then returned the dried air to the chamber. Air flow through the desiccant loop could be varied from 0 to over 9 liters per minute. Humidification of incoming air was unnecessary because of the large amount of transpiring leaf area in the crown cuvette; high humidity was easily obtained by reducing the flow rate of chamber air through the desiccant loop.

Air of a known carbon dioxide concentration was supplied to the cuvette from a compressed air cylinder. Carbon dioxide concentration of the air was varied by a gas diluter (Analytical Development Company GD 600) in the air line. By changing the
concentration of CO₂ in the crown chamber while AHD, temperature and light remained constant, net photosynthesis rates could be varied.

Irradiance was provided by two 300 W cool beam PAR lamps (General Electric 300PAR56/2WFL). Light intensity in the cuvette exceeded 1500 μmol m⁻² s⁻¹, which is near the maximum PPFD received in the Pinus taeda range and near net photosynthesis saturation intensity for Pinus taeda (Teskey et al. 1986).

The CO₂ concentration of air leaving the chamber was measured with an infrared gas analyzer (ADC 225 Mk3) set in the absolute measurement mode. The CO₂ differential created by net photosynthesis was determined by subtracting the CO₂ concentration of air leaving the cuvette from the concentration of CO₂ entering the chamber. Air flow rate through the chamber was measured by a variable-area flowmeter (Aalborg Instruments FMO 92). Net photosynthesis rate (corrected for dilution of CO₂ concentration due to transpired water vapor) was calculated as (Long and Hallgren 1985):

\[ P_{\text{net}} = \frac{f}{a} \left( C_e - C_l \right) \left( \frac{1 - X_l}{1 - X_e} \right) \]

where \( P_{\text{net}} \) is the net photosynthesis rate (μmol m⁻² s⁻¹), \( f \) is the molar flow rate of air into the cuvette (mol s⁻¹), \( a \) is all-sided leaf area (m²), \( C_e \) and \( C_l \) are the CO₂ concentrations (μmol mol⁻¹) of air entering and leaving the cuvette, respectively, and \( X_e \) and \( X_l \) are the mole fractions (mol H₂O mol⁻¹ air) of water vapor entering and leaving the cuvette, respectively.

The vapor pressure of air entering and leaving the chamber was measured with two capacitive relative humidity sensors (Vaisala HMP 31 UT). Transpiration was calculated with a formula from Long and Hallgren (1985):

\[ E = \frac{f}{a} \left( \frac{X_l - X_e}{1 - X_l} \right) \]

where \( E \) is transpiration rate in mol m⁻² s⁻¹ and \( a, X_l \) and \( X_e \) are defined as before.

To measure stem CO₂ efflux, approximately 25 cm² of stem area immediately below the crown was sealed in a cuvette made of a 2.5 x 7.5 cm section of PVC pipe. The needles attached to the lower part of the stem were removed at least 24 h before measurements. A 24 gauge, chromel-alumel thermocouple inserted into the xylem measured stem temperature. To minimize temperature fluctuations, the outside of the cuvette was wrapped with 1-cm diameter PVC (Tygon) tubing through which temperature controlled polyethylene glycol was circulated, then the entire stem apparatus was enclosed in 1-cm-thick, closed-cell, pipe insulation. All of the stem below the crown cuvette was shaded with aluminum foil to prevent corticular CO₂ refixation (Linder 1981, Sprugel and Benecke 1991).

Air was supplied to the stem cuvette from cylinders containing air with a known CO₂ concentration (350 μmol mol⁻¹). Air flow rate through the cuvette was measured with a variable-area flowmeter (Aalborg Instruments FMO 92). An infrared
gas analyzer (ADC 225 Mk3) set in the differential mode measured CO₂ evolution from the stem. Stem respiration was calculated by a modified photosynthesis equation from Long and Hallgren (1985):

\[ R = f / a (C_1 - C_e) , \]

where \( R \) is stem respiration in \( \mu \text{mol m}^{-2} \text{s}^{-1} \), \( f \) is the molar flow of air (mol s\(^{-1}\)), \( a \) is the surface area of the enclosed stem (m\(^2\)), and \( C_1 \) and \( C_e \) are the CO₂ concentrations (\( \mu \text{mol mol}^{-1} \)) of air leaving and entering the stem chamber, respectively.

A datalogger (Campbell 21X) collected and processed all sensor signals. Pertinent variables were monitored in real time by means of a personal computer (IBM PC) and graphical data display software (Labtech Notebook).

**Experiment 1: Effect of transpiration on stem CO₂ efflux**

Transpiration was varied by changing the AHD within the cuvette, while maintaining all other environmental variables at a constant rate. High and low transpiration rates averaged 1.18 and 0.52 mmol m\(^{-2}\) s\(^{-1}\), respectively. Temperature in the crown cuvette was held at 28 ± 1 °C, light at saturating intensity (>1500 µmol m\(^{-2}\) s\(^{-1}\)), and CO₂ at a concentration such that whole crown net photosynthesis remained between 3.5 and 4.5 µmol m\(^{-2}\) s\(^{-1}\). Stem temperature was held at 24 ± 0.5 °C.

The order of treatments was determined randomly for each seedling. After establishing a transpiration treatment, all variables such as stem temperature, photosynthesis, and respiration were allowed to reach a steady state. Steady state was defined as less than 5% variation in each variable over approximately 1 h. The transpiration treatment was then changed, and stem CO₂ efflux was again allowed to reach a steady-state rate. Mean stem CO₂ efflux rate was calculated by averaging the last 20 1-min observations of stem CO₂ efflux at steady state for each treatment. Mean respiration rates were compared across treatments by repeated measures analysis of variance (Winer 1962). Twenty-five seedlings were measured in Experiment 1.

Water status of the stem during each transpiration treatment was quantified on a subset of five seedlings. This quantification was based on measurements of xylem pressure potential of five fascicles of needles removed during the last 10 min of each treatment. The needles were located on a branch within 5 cm of the stem cuvette. The branch had been sealed in a plastic bag and shaded for the duration of the experiment.

**Experiment 2: Effect of interrupted substrate supply on stem CO₂ efflux**

The measurement apparatus for this investigation was identical to that used in Experiment 1. In this experiment, stem respiration was allowed to come to a steady-state condition while transpiration was low (< 0.5 mmol H₂O m\(^{-2}\) s\(^{-1}\)) and net photosynthesis was high (≥ 4.0 µmol m\(^{-2}\) s\(^{-1}\)). A band of phloem 1-cm wide and approximately 5 cm above the stem cuvette was then removed. Carbon dioxide efflux rates were observed for 5 h or more following the girdling. Four seedlings were measured in this experiment.
Experiment 3: Effect of net photosynthesis rates on stem CO$_2$ efflux

Net photosynthesis was varied by changing the ambient concentration of CO$_2$ in the crown cuvette. High and low rates of net photosynthesis averaged 5.8 and 0.4 µmol m$^{-2}$ s$^{-1}$, respectively. The range between high and low net photosynthesis rates were similar to the range of rates found during diurnal cycles of Pinus taeda trees in the field (Fites and Teskey 1988). Other than CO$_2$ concentration in the crown cuvette, environmental conditions in the stem and crown cuvettes were identical to those in Experiment 2. Stem CO$_2$ efflux was monitored for at least 3 h after a treatment change. Stem CO$_2$ efflux was measured and analyzed in the same manner as in Experiment 1. Fourteen seedlings were measured.

Diurnal stem CO$_2$ efflux measurements

Diurnal stem CO$_2$ efflux measurements were performed on several seedlings in an open greenhouse. The stem temperature and stem CO$_2$ efflux measurement apparatus was the same as in Experiments 1–3, except that there was no temperature control; stem temperatures were allowed to fluctuate with ambient air temperatures. The seedlings were watered periodically during the diurnal measurements.

Woody tissue respiration versus temperature response

Woody tissue respiration versus temperature response curves were measured on 1-cm diameter branches from five Pinus taeda trees. Branches were cut in the field and transported immediately to the laboratory, where they were recut to a 30-cm length. A thermocouple was inserted approximately 0.5 cm into the branch. The cut ends of the branches were coated with silicone, then the branches were completely enclosed in cuvettes made of 3-cm diameter plastic pipe capped at both ends. A small electric fan stirred the air within the chamber. The entire chamber was then placed in a temperature controlled water bath (Neslab Endocal RTE-9) and branch temperature was allowed to equilibrate at each temperature. Compressed air cylinders with a known CO$_2$ concentration (350 µmol mol$^{-1}$) supplied air to the cuvette, and the CO$_2$ differential caused by respiration was measured with an infrared gas analyzer (ADC LCA-2) set in the differential mode.

Results

Experiment 1: Effect of transpiration on stem CO$_2$ efflux

Stem CO$_2$ efflux rates were significantly ($P = 0.0001$) lower during periods of high transpiration than during periods of low transpiration (Table 1). Stem CO$_2$ efflux rates generally started changing within 15–20 min after a change in transpiration rate, and stabilized at the new rate within 45–60 min (Figure 3). There was no difference in xylem pressure potential between high and low transpiration treatments (Table 1).
Table 1. The effects of transpiration rate on stem CO$_2$ efflux rate and stem xylem pressure potential in *Pinus taeda* seedlings. Values in parentheses are average rates of transpiration in mmol m$^{-2}$ s$^{-1}$. Values in the same column followed by different letters are significantly different (P-value for stem CO$_2$ efflux rate is 0.0001).

<table>
<thead>
<tr>
<th>Transpiration treatment</th>
<th>Average stem CO$_2$ efflux rate ($\mu$mol m$^{-2}$ s$^{-1}$) ($n = 25$)</th>
<th>Average xylem pressure potential (MPa) ($n = 5$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>High (1.18)</td>
<td>2.50a</td>
<td>-0.17</td>
</tr>
<tr>
<td>Low (0.52)</td>
<td>2.68b</td>
<td>-0.17</td>
</tr>
</tbody>
</table>

Figure 3. The effect of transpiration on stem CO$_2$ efflux of two *Pinus taeda* seedlings. Times marked with crosshatching indicate periods of high transpiration, times marked with vertical hatching indicate periods of low transpiration. Average values for high and low rates of transpiration, respectively, were 9.20 (0.65) and 5.83 ml h$^{-1}$ (0.41 mmol m$^{-2}$ s$^{-1}$) for A and 3.3 (0.55) and 1.25 ml h$^{-1}$ (0.21 mmol m$^{-2}$ s$^{-1}$) for B. Differing magnitudes of high and low rates of transpiration were due to different seedling sizes. Seedlings A and B had stem diameters of 0.92 and 0.58 cm, respectively.

**Experiment 2: Effect of interrupted substrate supply on stem CO$_2$ efflux**

This experiment was designed to test whether stem CO$_2$ efflux rate was affected by changes in substrate export from the crown of the seedling. In all seedlings measured, stem CO$_2$ efflux rate remained steady or increased slightly for 1 to 2 h after the stem was girdled, then began decreasing. Carbon dioxide efflux rate continued to decrease as long as measurements were taken (Figure 4). The rate of decrease was very slow, from 0.01 to 0.08 $\mu$mol m$^{-2}$ s$^{-1}$ per hour.

**Experiment 3: Effect of net photosynthesis rates on stem CO$_2$ efflux**

This experiment was designed to test whether fluctuations in crown net photosynthesis, of the magnitude that would occur during a diurnal cycle, would cause changes in stem CO$_2$ efflux. When data from all experiments were analyzed together, changes in rates of photosynthesis had no effect ($P = 0.5669$) on stem CO$_2$ efflux rates during the experimental period (3–5 h). However, when the experimental data were broken into subsets based on the order of application of photosynthesis treatments, there was a significant ($P = 0.0052$) treatment effect in one of the subsets (Table 2). Stem CO$_2$
**MOVEMENT OF RESPIRATORY CO₂ IN STEM**

**Figure 4.** The effect of girdling on stem CO₂ efflux of *Pinus taeda* seedlings. Pre-girdling stem CO₂ efflux rates (in µmol m⁻² s⁻¹) were 2.26 for tree 1 (○), 0.99 for tree 2 (□), 1.61 for tree 3 (▽) and 3.25 for tree 4 (○).

**Table 2.** The effect of net photosynthesis rate on stem CO₂ efflux rate in *Pinus taeda* seedlings. Values in parentheses are average rates of net photosynthesis in µmol m⁻² s⁻¹. Efflux rates in the same column followed by different letters are significantly different (*P*-values for the high-first and low-first experiments are 0.0052 and 0.2605, respectively).

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Average stem CO₂ efflux rate (µmol m⁻² s⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>High photosynthesis treatment first (n = 8)</strong></td>
<td></td>
</tr>
<tr>
<td>High (5.44)</td>
<td>2.67a</td>
</tr>
<tr>
<td>Low (0.31)</td>
<td>2.60b</td>
</tr>
<tr>
<td><strong>Low photosynthesis treatment first (n = 6)</strong></td>
<td></td>
</tr>
<tr>
<td>High (6.28)</td>
<td>3.32a</td>
</tr>
<tr>
<td>Low (0.42)</td>
<td>3.38a</td>
</tr>
</tbody>
</table>

Efflux dropped significantly within 3–5 h after net photosynthesis rate was decreased from high to low. There was no significant change (*P* = 0.2605) in stem CO₂ efflux rate when photosynthesis rates were increased from low to high.

**Discussion**

*Transpiration and stem CO₂ efflux*

Experiment 1 showed that increased rates of transpiration in *Pinus taeda* seedlings were accompanied by decreased rates of stem CO₂ efflux. This is in agreement with several studies that described decreased CO₂ evolution from tree stems under conditions when a high rate of transpiration was likely (Negisi 1972, 1975, Edwards and McLaughlin 1978, Negisi 1981, 1982, Kakubari 1988, Matyssek and Schulze 1988). Our experiment provided evidence that the cause of the reduction in stem CO₂ efflux associated with increased transpiration was not water stress, as suggested by Lavigne (1987) and Kakubari (1988), because there was no difference in stem water status between transpiration treatments (Table 1).
The simplest explanation for this response is that respiratory CO$_2$ becomes dissolved in the xylem sap and is transported upward within the tracheids, away from the site of CO$_2$ evolution, rather than diffusing outward at that point. This does not imply that high rates of transpiration lower the actual rate of respiration of the stem tissue, only that lateral CO$_2$ efflux is not an accurate measure of stem respiration during high rates of transpiration.

Theoretical calculations confirmed that the water passing through the stem in the transpiration stream was capable of removing enough CO$_2$ to cause the observed reductions in stem CO$_2$ efflux. The amount of CO$_2$ dissolved in water can be described by the following equation from Stumm and Morgan (1981):

$$[\text{CO}_2] = \left(1 + \frac{K_1}{[\text{H}^+] + \frac{K_1 K_2}{[\text{H}^+]^2}}\right) K_H p\text{CO}_2,$$  \hspace{1cm} (5)

where $[\text{CO}_2]$ is the total dilution of all forms of dissolved CO$_2$ in water, $K_1$ and $K_2$ are the first and second acidity constants, respectively, $K_H$ is Henry’s constant, and $p\text{CO}_2$ is the partial pressure of CO$_2$ (atmospheres) in the air in equilibrium with the water. The values of the constants $K_1$, $K_2$ and $K_H$ are dependent on temperature and the medium (seawater, pure water, etc.).

Assuming xylem sap to be pure water, a saturated $[\text{CO}_2]$ of $7.98 \times 10^{-7}$ mol CO$_2$ ml$^{-1}$ H$_2$O can be calculated from Equation 3 for a stem temperature of 25°C, a xylem sap pH of 5.6 (Carter and Larsen 1965) and a $p\text{CO}_2$ of 0.02 atmospheres (Hari et al. 1991). If the transpiration rate of the tree is known, the maximum amount of CO$_2$ that can be carried through the stem in 1 h can be calculated and compared with the observed reduction in CO$_2$ evolution in the woody tissue at that transpiration rate.

As an example, stem CO$_2$ efflux from a seedling measured on September 4, 1991 was reduced by 614.16 μmol CO$_2$ m$^{-2}$ h$^{-1}$ when the transpiration rate was increased from 3 ml H$_2$O h$^{-1}$ (0.74 mmol m$^{-2}$ s$^{-1}$) to 6 ml H$_2$O h$^{-1}$ (1.47 mmol m$^{-2}$ s$^{-1}$). For a surface area of the sampled stem section of 0.0019 m$^2$, it can be calculated that 1.17 μmol CO$_2$ h$^{-1}$ was lost from that section during the period of high transpiration. It was calculated previously that 1 ml of water can transport $7.98 \times 10^{-7}$ mol CO$_2$, so an increase in transpiration of 3 ml h$^{-1}$ could carry 2.39 μmol CO$_2$ h$^{-1}$, which is almost twice the measured decrease in stem CO$_2$ efflux from the sampled section. Solving Equation 5 for the other 24 seedlings measured in Experiment 1 yielded similar results. These calculations confirm that the transpiration stream is capable of carrying CO$_2$ in sufficient quantities to cause the observed reductions in stem CO$_2$ efflux.

Transport of respiratory CO$_2$ in the transpiration stream of trees could complicate several well established measurement techniques. By inspecting Equation 5, it can be seen that almost all of the CO$_2$ dissolved in the xylem sap would be released as a gas when the water reached the relatively low $p\text{CO}_2$ environment of the leaf mesophyll (0.01 to 0.04 kPa, Teskey et al. 1986). Carbon dioxide released in the leaf mesophyll could be fixed in the chloroplasts (Zelawski et al. 1970, Stringer et al. 1989); because this fixation would occur without CO$_2$ exchange through the leaf
stomata, it could not be measured by conventional gas-exchange techniques. This would result in an underestimate of the carbon fixed by photosynthesis.

Equation 5 can be used to estimate the impact of dissolved CO$_2$ being released as a gas in the leaf mesophyll. For the seedling measured on September 4, 1991, it can be shown that, at a transpiration rate of 6 ml H$_2$O h$^{-1}$, a maximum of 1.33 $\times$ 10$^{-9}$ mol CO$_2$ s$^{-1}$ would be transported in the transpiration stream. This seedling had a total crown leaf area of 0.063 m$^2$, so the maximum CO$_2$ released into the mesophyll on a leaf area basis would be 0.02 $\mu$mol CO$_2$ m$^{-2}$ s$^{-1}$, only about 0.6% of the average canopy net photosynthesis of this seedling (3.50 $\mu$mol m$^{-2}$ s$^{-1}$). Hari et al. (1991) also estimated that the error caused by refixation of CO$_2$ from the transpiration stream would be small, on the order of about 2% of net photosynthesis.

Transport of CO$_2$ in the transpiration stream could also affect CO$_2$ exchange measurements in branches. If the xylem sap became completely saturated with CO$_2$ during its passage through the stem, or if the $p$CO$_2$ in branches was lower than in the stem, gaseous CO$_2$ would be released in the branches. Branches have thinner bark than stems, perhaps making the outward diffusion of CO$_2$ easier, which could in turn cause $p$CO$_2$ to be lower in the branches. The release of gaseous CO$_2$ from the xylem sap into branch tissue would cause increased CO$_2$ efflux and erroneously high estimates of branch respiration. Sprugel (1990) cited this as one possible explanation for branch respiration rates in *Abies amabilis* that were high relative to stem respiration rates.

Another interesting implication of respiratory CO$_2$ movement in stems is related to the photosynthetic error discussed above. If respiratory CO$_2$ is released into the leaf mesophyll and refixed (cf. Zelazwski et al. 1970, Stringer et al. 1989), then a pathway for carbon recycling exists in trees that has not been seriously addressed. The implications of this recycling on calculation of carbon budgets may be rather small. In Experiment 1, an average of 6.7% of stem respiratory C was removed from the site of measurement during the high transpiration treatment (Table 1). If stem respiration consumes around 20% of gross primary production in temperate forests (Kinerson 1975, Tranquillini 1979, Linder and Troeng 1980, Sprugel 1989), the recycling or refixing of 6% of stem-respired C would produce carbon budget calculation errors on the order of 1%. Carbon transport in the xylem and subsequent refixation could be greater under field conditions, where transpiration rates can reach 5 mmol m$^{-2}$ s$^{-1}$ (Fites and Teskey 1988), four times the average high rate of transpiration imposed in this experiment. It should be noted that, for conifers with stomata sensitive to high AHD, increased afternoon temperatures (and AHD) could result in decreased transpiration rates, which would presumably reduce the afternoon depression of stem CO$_2$ efflux caused by transport of respiratory CO$_2$ in the transpiration stream.

Although the implications of respiratory CO$_2$ movement for leaf net photosynthesis measurements, branch respiration measurements and carbon budget calculations are not clearly established, it is apparent that this phenomenon has important impacts on measurement of stem respiration. Even commonly accepted measurement protocols become complicated when consideration is given to CO$_2$ transport in transpiring
stems. For example, the temperature-response of stem respiration is often calculated by measuring CO$_2$ efflux from stems throughout a diurnal cycle during which temperature varies. Yet such measurements often result in linear or hysteretic temperature responses (data not shown), rather than the expected exponential response to temperature found in non-transpiring tissue (Figure 1). The linearity or hysteresis in temperature response curves generated from diurnal data presumably is a result of varying magnitudes of respiratory CO$_2$ transport under different evaporative environments, and is not necessarily a reflection of the true temperature response of stem respiration. Although temperature response curves generated from diurnal data may be useful for predicting net CO$_2$ exchange between the tree stem and the environment under similar evaporative conditions, their ability to predict actual stem respiration under varying environmental conditions is questionable. In short, when measuring stem CO$_2$ efflux, it is important to consider that not all of the respiratory CO$_2$ evolved within woody tissue cells necessarily diffuses laterally to the stem bark.

**Photosynthesis, substrate supply and stem CO$_2$ efflux**

To summarize the primary results from Experiments 2 and 3, when temperature and transpiration rate were held constant, the CO$_2$ efflux rate from the stem was dependent on substrate supply from the crown, and large fluctuations in net photosynthesis affected CO$_2$ evolution rate only when net photosynthesis rates were changed from high to low. Several conclusions regarding the relationships among photosynthesis, substrate supply and stem respiration can be drawn from these results.

First, when temperature and transpiration rate are constant, the rate of stem CO$_2$ evolution appears to be positively correlated with substrate supply. Disrupting carbohydrate supply to the stem by girdling or reducing net photosynthesis rates caused small, gradual reductions in stem CO$_2$ efflux. Other researchers have found that respiration of leaves (Osman 1971, Hansen 1977) and roots (Ludwig et al. 1975, Azcón-Bieto and Osmond 1983, Azcón-Bieto et al. 1983) is affected by substrate supply or photosynthesis rates. However, increasing net photosynthesis rate from low to high did not affect stem CO$_2$ efflux rate. This could be due to the dynamics of carbohydrate storage in the seedlings. Experimental runs were started in the morning, when the seedlings’ carbohydrate reserves were probably depleted. When an experiment began with low (only slightly positive) net photosynthesis rates, little excess photosynthate was available to replenish leaf starch reserves or to permit photosynthate export from the crown. When net photosynthesis rate was increased, most of the excess photosynthate was used to replenish leaf starch reserves, leaving little for export to the stem. On the other hand, when experiments began with high net photosynthesis, starch reserves would be replenished during the initial hour of the experiment, then substrate export from the crown would begin, raising stem respiration rate from its morning low. When net photosynthesis rates were then reduced, substrate export from the crown was reduced, which eventually lowered carbohydrate concentrations, and therefore respiration rates, in the stem. Additional investigation is needed to clarify the dynamics of carbohydrate storage and movement, and its relationship to stem respiration.
Although stem CO$_2$ evolution is affected by substrate supply, this does not appear to be the primary cause of short-term diurnal variations in stem CO$_2$ efflux. The stem CO$_2$ efflux response to a complete blockage of substrate export from the crown took 1–2 h to occur, and then the change was very gradual. The diurnal fluctuations observed in field measurements of stem CO$_2$ efflux usually occurred much more rapidly. Afternoon reductions in net photosynthesis rates could contribute to the midday depression in stem CO$_2$ efflux rates, but the effect is not large enough to explain totally the CO$_2$ efflux reductions observed in field studies.

Conclusions

Several investigators have observed departures of tree stem CO$_2$ efflux rates from temperature-predicted rates of respiration, especially on hot, sunny afternoons. Laboratory experiments suggest that this "midday depression" of stem CO$_2$ efflux can largely be attributed to transpiration stream transport of respiratory CO$_2$ away from the site of CO$_2$ efflux measurement. For this reason, stem CO$_2$ efflux should not be used as a measure of stem respiration rates when transpiration rates are high. It must also be considered that CO$_2$ released from the transpiration stream into branches or leaf mesophyll may affect measurements of branch respiration and leaf photosynthesis. Variations in substrate export from photosynthesizing tissue may be a secondary cause of midday depressions of stem CO$_2$ efflux.

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References


