In vivo and in situ rhizosphere respiration in *Acer saccharum* and *Betula alleghaniensis* seedlings grown in contrasting light regimes

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**Summary** A perfusive method combined with an open-system carbon dioxide measurement system was used to assess rhizosphere respiration of *Acer saccharum* Marsh. (sugar maple) and *Betula alleghaniensis* Britton (yellow birch) seedlings grown in 8-L pots filled with coarse sand. We compared in vivo and in situ rhizosphere respiration between species, among light regimes (40, 17 and 6% of full daylight) and at different times during the day. To compute specific rhizosphere respiration, temperature corrections were made with either species-specific coefficients ($Q_{10}$) based on the observed change in respiration rate between 15 and 21 °C or an arbitrarily assigned $Q_{10}$ of 2. Estimated, species-specific $Q_{10}$ values were 3.0 and 3.4 for *A. saccharum* and *B. alleghaniensis*, respectively, and did not vary with light regime. Using either method of temperature correction, specific rhizosphere respiration did not differ between *A. saccharum* and *B. alleghaniensis*, or among light regimes except in *A. saccharum* at 6% of full daylight. At this irradiance, seedlings were smaller than in the other light treatments, with a larger fine root fraction of total root dry mass, resulting in higher respiration rates. Specific rhizosphere respiration was significantly higher during the afternoon than at other times of day when temperature-corrected on the basis of an arbitrary $Q_{10}$ of 2, suggesting the possibility of diurnal variation in a temperature-independent component of rhizosphere respiration.

**Keywords:** circadian variations, fine roots, open gas chamber, $Q_{10}$, root, sugar maple, temperature, yellow birch.

**Introduction**

When studying ecosystem carbon cycles or modeling tree growth or productivity, it is critical to describe both respiration and photosynthesis (Amthor 1984, Waring et al. 1998). Several studies have shown that, over a 1-year period, whole-plant respiration may consume over 50% of photosynthetically assimilated carbon (Mogensen 1977, Waring et al. 1998) through respiration (i.e., new tissue production; $R_g$) and maintenance respiration (i.e., existing tissue repair and functioning; $R_m$) (cf. McCree 1970, Thornley 1970). Roots represent both a large and a metabolically active fraction of total tree biomass (Amthor 1986, Larcher 1995, Lambers et al. 2000). Because of fine root turnover, root exudation and carbon allocation to mycorrhizae, root respiration may consume between 30 and 60% of the net carbon assimilation of trees (Ryan et al. 1996, Bouma et al. 1997). In a young Scots pine (*Pinus sylvestris* L.) carbon budget study, 63% of the photosynthetic production was allocated belowground (Ågren et al. 1980) and it has been estimated that in boreal forest stands 75% of the carbon allocated to roots is respired, with only 25% being added to belowground biomass (Högberg et al. 2001).

Despite the recognized importance of tree roots in mechanical support, carbohydrate storage and water and ion uptake, root processes are often neglected or oversimplified in modeling exercises (cf. LeRoux et al. 2001). Such treatment likely reflects a lack of reliable information on many aspects of root activity and highlights the need for new approaches to the study of root activity.

Several studies have reported seasonal variations in root contribution to total soil carbon dioxide (CO$_2$) efflux (e.g., Epron et al. 1999, 2001, Widén and Majdi 2001) and the higher contribution during summer compared with winter has been attributed mainly to higher soil temperatures and root growth. Numerous studies have shown a heavy dependence of root respiration on soil temperature (e.g., Burton et al. 1998, Pregitzer et al. 1998, Atkin et al. 2000), notwithstanding the concurrent influence of other factors such as soil water content, root volume, soil depth and nitrogen concentration in
roots (e.g., Zogg et al. 1996, Bouma et al. 1997, Davidson et al. 1998, Pregitzer et al. 1998, Burton et al. 2002). Soil CO₂ has also been thought to affect root respiration (Qi et al. 1994), although recent studies have concluded otherwise (Bouma et al. 1997, Burton and Pregitzer 2002).

Root respiration is believed to vary with aboveground activity (Högberg et al. 2001, Cardon et al. 2002, Singh et al. 2003). Amthor (1986) hypothesized that root respiration was higher during daytime than at night because shoot demand for mineral nutrients was higher and perhaps also because of diurnal changes in the translocation of carbohydrates from the shoot to the root. However, there is little direct evidence of diurnal variation in root respiration and there is no experimental evidence that the light environment affects root respiration, as would be expected if root respiration is affected by shoot activity.

To investigate how rhizosphere respiration varies diurnally and in response to environmental factors, field data must be normalized to a standard temperature. Models based on the coefficient by which the rate of a process increases for each 10 °C increase in temperature ($Q_{10}$) are widely used to model temperature dependence of biological processes (Kirschbaum 1995, Ryan et al. 1996, Chen et al. 2000). Although often assumed to be essentially constant and close to a value of 2, wide variation in the $Q_{10}$ of rhizosphere or root respiration has been reported (e.g., Kirschbaum 1995, Ryan et al. 1996, Burton et al. 1998, Davidson et al. 1998, Buchmann 2000, DesRochers et al. 2002). Moreover, $Q_{10}$ estimates differ not only among species (Burton et al. 2002), but among tree organs (Ryan et al. 1996).

The $Q_{10}$ of root respiration may also vary seasonally because of changes in the rate of root turnover and in root uptake and growth activities. Moreover, seasonal variation in the relative magnitude of $R_t$ versus $R_m$ may cause the temperature response of total root respiration to vary seasonally. However, there are few reports of seasonal variability in temperature dependence of root respiration (Burton and Pregitzer 2003). Moreover, the $Q_{10}$ of root respiration may be itself temperature dependent, as has already been shown for soil respiration, N mineralization and dead root decomposition (Kirschbaum 1995, Winkler et al. 1996, Davidson et al. 1998, Chen et al. 2000). Although absolute respiration rates increase with temperature, the relative increase in rate is higher at lower temperatures. This may be because, at low temperatures, respiration is limited by enzymatic activities (processes highly dependent on temperature), whereas at high temperatures respiration is mainly limited by substrate availability (less dependent on temperature). Consequently, the range of temperatures used for $Q_{10}$ derivation and the range of temperature over which $Q_{10}$ correction is applied must be comparable (see Kirschbaum 1995).

The aim of this study was to test the hypothesis that the temperature dependence of rhizosphere respiration has a constant $Q_{10}$ of 2, which is unaffected by diurnal variation or light regime (cf. Epron and Badot 1997, Huc 2000). We used a perfusive method (Bouma et al. 1997) combined with an open-system gas exchange measurement system (Boone et al. 1998) to assess rhizosphere respiration of intact roots of potted seedlings of Acer saccharum Marsh. (sugar maple) and Betula alleghaniensis Britton. (yellow birch).

**Material and methods**

**Plant material and growth conditions**

*Acer saccharum* and *B. alleghaniensis* are co-existing species in eastern North American temperate deciduous forests. *Acer saccharum* is a shade-tolerant tree species, whereas *B. alleghaniensis* is an intermediate shade-tolerant species (Baker 1949, Forcier 1975). Seeds of both species were provided by the Natural Resources Ministry of Quebec from the Duchesnay forest station (46°55′ N, 71°40′ W). During spring 2002, the seeds were germinated in a greenhouse at Champenoux (48°44′ N, 60°14′ E) near Nancy, France. Seedlings were planted into 8-l pots filled with coarse sand. The substrate was topped with a layer of expanded clay balls to reduce evaporative water loss. Twenty potted seedlings per species were assigned to one of three light regimes (40, 17 and 6% of full daylight) in a nursery. Shading was with neutral density aluminized nets. Seedlings were fertilized at the beginning of May and in August with 40 g (4 g l⁻¹ of soil mixture) of a slow-release fertilizer (13,13,13 N,P,K with micro-elements). Pots were watered twice daily.

**Belowground respiration measurements**

Soil CO₂ flux was measured by a perfusive method (Bouma et al. 1997). In each pot, a perforated plastic tube was placed in...
the substrate before seedling establishment to allow air injection during measurements (Figure 1). To monitor rhizosphere respiration, the pots containing the seedlings were placed in closed PVC chambers. The chamber was sealed with Terostat mastic (Teroson, Glastech Oy, Vaasa, Finland) at the tube and stem insertion points and around the chamber cover. Outdoor air was passed through soda lime and over a desiccant to remove CO2 and water vapor. A controlled quantity of CO2 was injected into the CO2-free air to give a concentration of 320 ppm. The air flow was then divided, with one stream entering the reference cuvette of a differential CO2 gas analyzer (Infra-Red Gas Analyzer, Analytical Development Company Limited, Hoddesdon, U.K.) and the other stream passing through the perforated tube embedded in the course sand medium in the tree container (Figure 1), and exiting the tree chamber through a column of desiccant, before passing through the sample cuvette of the differential gas analyzer. Although the CO2 concentration used was lower than typical of forest soils (Larcher 1995, Widén and Majdi 2001), Burton and Pregitzer (2002) found that soil CO2 concentration does not affect root respiration in nine tree species studied including A. saccharum. Air flow was set at 1 liter min−1 to ensure that air present in soil pores and around the root system was replaced in less than 10 min.

The quantity of CO2 produced by rhizosphere respiration was calculated as:

\[ R = F \left( [CO_2]_{\text{out}} - [CO_2]_{\text{in}} \right) \]

where \( R \) is respiration, \( F \) is air flow and \([CO_2]_{\text{in}}\) and \([CO_2]_{\text{out}}\) are the CO2 mole fractions in the incoming and outgoing air, respectively. Ten chambers (three per treatment plus an empty control) were placed in parallel and measured consecutively during 60-min cycles. For each chamber, the 6-min measurement period was divided into 3 min of gas replacement and system stabilization, followed by three 1-min periods during which CO2 concentration and soil temperature measurements (measured with a copper-constantine thermocouple) were averaged and stored in a Campbell 21X data logger (Campbell Scientific).

After three days of measurement, each plant was removed from the pot with minimal soil disturbance and root loss. The pot was then returned to the chamber for another three days to determine respiration of the substrate (\( R_{\text{Substrate}} \)) which was always close to zero. Rhizosphere respiration (\( R_{\text{Rhizosphere}} \)), which was considered to be the respiration of the root system plus any associated microbial respiration, was calculated by subtracting \( R_{\text{Substrate}} \) from respiration measured before seedling harvest (\( R_{\text{Rhizosphere} + \text{Substrate}} \)). The use of coarse sand, the confined environment and the removal of pot respiration after seedling harvest assured that measured \( R_{\text{Rhizosphere}} \) closely approximated root respiration.

For both species (\( n = 13 \) for A. saccharum and \( n = 6 \) for B. alleghaniensis), respiration measurements were performed during three consecutive weeks beginning at the end of July, 2002. Whenever possible, at least one individual of each species was represented in each treatment during each week.

Temperature correction of rhizosphere respiration
To compare specific rhizosphere respiration (respiration per unit root mass) between species and light regimes, a temperature correction was applied based on \( Q_{10} \). For each individual, \( Q_{10} \) was computed from measurements of the 3-day period and Equations 2 and 3:

\[ \ln \left( \frac{R_{\text{Rhizosphere}}}{R_{\text{Rhizosphere ref}}} \right) = a T_{\text{max}} + b \]

\[ Q_{10} = e^{10a} \]

where \( R_{\text{Rhizosphere}} \) is the specific rhizosphere respiration (nmol CO2 g−1 of total roots s−1) at the corresponding soil temperature \( T_{\text{max}} \).

We computed \( R_{\text{Rhizosphere ref}} \), the respiration normalized at the reference temperature \( T_{\text{ref}} \), as:

\[ R_{\text{Rhizosphere ref}} = \frac{R_{\text{Rhizosphere}}}{Q_{10}} \left( \frac{T_{\text{ref}}}{T_{\text{max}}} \right) \]

We set \( T_{\text{ref}} \) at 15 °C because this value was within the range of temperatures (15 ± 1.5 to 21 ± 1.4 °C) encountered when the measurements were performed and is within the range of summer values for a temperate deciduous forest soil (Larcher 1995). The \( Q_{10} \) value used for temperature correction was either derived from the measured temperature response or fixed at a value of 2 (Epron and Badot 1997, Huc 2000). Specific normalized rhizosphere respiration was then computed from \( R_{\text{Rhizosphere ref}} \) divided by the dry mass of tissue contained in the chamber during measurement. Mean daily values of temperature-corrected (normalized) rhizosphere respiration were then computed as the mean of the value recorded during a 24-h period. In the tables and figures, specific rhizosphere respiration normalized to 15 °C is denoted as either \( RR \) or \( RR_{R} \); depending on whether we used the species-specific \( Q_{10} \) calculated with Equation 2 or an arbitrarily fixed \( Q_{10} \) of 2, respectively. To test for circadian variation in rhizosphere respiration, each day was divided into three 8-h periods and \( RR \) and \( RR_{R} \) were computed as the mean respiration for each of these 8-h periods. The 8-h periods were defined as: morning (from 0600 to 1400 h), afternoon (from 1440 to 2200 h) and night (from 2200 to 0600 h). Over the measurement period, the 0600 and 2200-h times closely corresponded to sunrise and sunset, respectively.

Growth and tree morphological measurements
Seedlings were harvested immediately after root respiration measurements. Seedling stem height and total leaf area (measured with a planimeter, Delta T, Hoddesdon, U.K.) were recorded. Tree biomass was divided into leaf, branches, stem, coarse roots (> 2 mm) and fine roots (< 2 mm), dried at 60 °C for 48 h and weighed. Leaf area ratio (LAR; cm² g⁻¹), root mass ratio (RMR) and fine root fraction of total root dry mass (FR%) were then calculated.
Statistical analyses

All statistical analyses were performed with SYSTAT v.10.0 (SPSS, Inc.). In the factorial design (2 species × 3 light regimes) one class was empty because all B. alleghaniensis seedlings died in the 6% light regime. Consequently, the analysis of variance (ANOVA) model used in the GLM procedure to assess the effects of all factors (i.e., species, light regimes and interaction) on growth traits and rhizosphere respiration of both species had to account for the unbalanced sets of data. Statistical analysis of the variation in rhizosphere respiration with fine roots fraction of total roots dry mass (FR%) was performed by analysis of covariance (ANCOVA) where the species was the factor and FR% was the covariate. Diurnal variation in species rhizosphere respiration was tested with a GLM procedure with light regimes and period of the day as factors. In this last analysis, species were separated to simplify the model because a previous exploratory analysis showed no differences between species, alone or in interactions with light regimes and time of the day.

Results

Seedling growth

For both species, survival and initial growth were low, especially in the low light regimes. None of the seedlings of the intermediate shade-tolerant species B. alleghaniensis survived in the 6% light regime. Height and total biomass (data not shown) at harvest decreased with decreasing light availability and B. alleghaniensis seedlings were significantly smaller than A. saccharum seedlings, especially in the 17% light regime (Table 1; Figure 2A). In both species, LAR significantly increased in the lowest light regime (Table 1; Figure 2B). In A. saccharum, low light reduced RMR, whereas B. alleghaniensis had a rather constant RMR across species.

Table 1. Summary of ANOVA for height, leaf area ratio (LAR), root mass ratio (RMR), fine root fraction of total root dry mass (FR%) and specific rhizosphere respiration normalized at 15 °C using species-specific Q10 values (RR 15 °C) and a fixed Q10 of 2 (RR2 15 °C). The F- ratio and P-values are presented for relationships between parameters and species (Sp: Acer saccharum and Betula alleghaniensis), light regime (LR: 40, 17 and 6% of external irradiance) and interactions using an a posteriori hypothesis test to account for the unbalanced set of data.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>Species</th>
<th>LR</th>
<th>Sp. × LR</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>F</td>
<td>P</td>
<td>F</td>
</tr>
<tr>
<td>Height</td>
<td>5.001</td>
<td>0.042</td>
<td>6.123</td>
</tr>
<tr>
<td>LAR</td>
<td>0.017</td>
<td>0.897</td>
<td>5.316</td>
</tr>
<tr>
<td>RMR</td>
<td>18.191</td>
<td>0.001</td>
<td>0.126</td>
</tr>
<tr>
<td>FR%</td>
<td>6.795</td>
<td>0.021</td>
<td>2.966</td>
</tr>
<tr>
<td>RR 15 °C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species-specific Q10</td>
<td>0.254</td>
<td>0.622</td>
<td>4.589</td>
</tr>
<tr>
<td>RRs 15 °C</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fixed Q10 of 2</td>
<td>0.080</td>
<td>0.782</td>
<td>4.075</td>
</tr>
</tbody>
</table>

Figure 2. Means and standard deviations of height at harvest (A); leaf area ratio (B); root mass ratio (RMR; C); and fine root fraction of total root dry mass (FR%; D) in Acer saccharum (AS; filled bars) and Betula alleghaniensis (BA; open bars) seedlings grown in a nursery in 40, 17 or 6% of external irradiance. Means followed by a different letter differ significantly at α = 0.05.

which was higher than in A. saccharum (Table 1; Figure 2C). Betula alleghaniensis had a significantly higher fine root fraction relative to total root mass (FR%) than A. saccharum (Table 1; Figure 2D). Light regimes had little effect on FR% in either species, except in A. saccharum where it increased in response to the 6% light treatment (Figure 2D).

Temperature response

Species-specific Q10 values of rhizosphere respiration were calculated for individual seedlings (cf. two examples in Figure 3) over the temperature range from 15 ± 1.5 to 21 ± 1.4 °C. The r² of the linear relationships varied from 0.52 to 0.98 and from 0.72 to 0.85 for A. saccharum and B. alleghaniensis, respectively. Mean Q10 values in each light regime are shown in Table 2. Neither light treatment nor species had a significant effect (P = 0.073). When all light treatments were pooled, mean Q10 was 3.0 and 3.4 for A. saccharum and B. alleghaniensis, respectively.

Rhizosphere respiration

Figure 4 shows a representative example of a 3-day record of substrate temperature, rhizosphere respiration and rhizosphere respiration normalized to 15 °C based on either the species-specific Q10 (RR) or a fixed Q10 of 2 (RR2) for one A. saccharum seedling grown in the 17% light regime. In both species, the mean daily value of rhizosphere respiration normalized to 15 °C was 6.5 and 7.5 nmol CO2 g⁻¹ s⁻¹ for RR and RR2, respectively, except in A. saccharum in the 6% light regime where RR and RR2 significantly increased to 11.8 and 13.0 nmol CO2 g⁻¹ s⁻¹, respectively (Table 1; Figure 5).
In both species, there was a strong linear relationship between RR or R\textsubscript{R2} and FR\% (Figure 6). In Figure 6, light regimes were pooled to generate a regression line and equation for each species. A higher FR\% resulted in higher specific rhizosphere respiration and the slope of the relationship did not differ significantly between species (Figure 6). The use of a fixed \( Q_{10} \) of 2 to normalize specific rhizosphere respiration to a temperature of 15 °C resulted in a residual daily variation in rhizosphere respiration (Table 3). In both species, RR\textsubscript{2} was higher during the afternoon than at night or in the morning and similar patterns were observed in each light regime (Figure 7; Table 3).

**Discussion**

**Species-specific \( Q_{10} \) values**

We computed species-specific \( Q_{10} \) over a narrow range of temperatures (from 15 to 21 °C) from data gathered at different points during the temperature cycle. The mean species-specific \( Q_{10} \) values in all light regimes of 3.0 and 3.4 in *A. saccharum* and *B. alleghaniensis*, respectively, are within the range of values reported for total root respiration of a number of temperate zone tree species (cf. Table 4).

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**Table 2.** Means and standard errors (SE) for species-specific \( Q_{10} \) coefficients of *Acer saccharum* (AS) and *Betula alleghaniensis* (BA) seedlings grown in 40, 17 or 6% of external irradiance in a nursery. All *B. alleghaniensis* seedlings in the 6% light regimes died. Means followed by a different letter differ significantly at \( \alpha = 0.05 \).

<table>
<thead>
<tr>
<th>Light regime (%)</th>
<th>Sp</th>
<th>n</th>
<th>Mean ( Q_{10} ) (SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>40</td>
<td>AS</td>
<td>5</td>
<td>2.99 (0.18) a</td>
</tr>
<tr>
<td></td>
<td>BA</td>
<td>3</td>
<td>3.47 (0.09) a</td>
</tr>
<tr>
<td>17</td>
<td>AS</td>
<td>5</td>
<td>3.06 (0.21) a</td>
</tr>
<tr>
<td></td>
<td>BA</td>
<td>3</td>
<td>3.29 (0.04) a</td>
</tr>
<tr>
<td>6</td>
<td>AS</td>
<td>3</td>
<td>2.98 (0.42) a</td>
</tr>
<tr>
<td></td>
<td>BA</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

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**Figure 3.** Examples of the relationship between the natural logarithm of specific rhizosphere respiration and soil temperature for (A) an *Acer saccharum* seedling grown in 40% of external irradiance; and (B) a *Betula alleghaniensis* seedling grown in 17% of external irradiance. The \( Q_{10} \) coefficients were computed with Equations 2 and 3.

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**Figure 4.** Specific rhizosphere respiration at soil temperature (\( \bigtriangleup \)), specific rhizosphere respiration normalized at 15 °C using species-specific estimated \( Q_{10} \) values (\( \bigcirc \)), specific rhizosphere respiration normalized at 15 °C using a fixed \( Q_{10} \) of 2 (\( \bigcirc \)) and soil temperature (\( \times \)) of a potted *Acer saccharum* seedling grown in the 17% light regime in a nursery over a 48-h period during August 2002.
Interspecific differences in rhizosphere respiration

Acer saccharum specific rhizosphere respiration (Figures 5A and 4B) was at the lower end of the range of rates (from 5 to 16 nmol CO₂ g⁻¹ s⁻¹) reported for excised fine root respiration of this species (Zogg et al. 1996, Burton et al. 1998, Burton and Pregitzer 2002, Burton et al. 2002, Comas et al. 2002). Specific rhizosphere respiration rates for both species were much lower than the 35 nmol CO₂ g⁻¹ s⁻¹ rate recorded for roots of excavated whole seedlings (Walters et al. 1993a, 1993b, Reich et al. 1998). Measuring excised fine roots or excavated seedlings may overestimate root respiration if mechanical injury stimulates respiration. However, we calculated specific respiration of the whole root system which must be lower than respiration of excised fine roots.

Comas et al. (2002) reported that slow growing species have lower root respiration rates than rapid growing species in three tree families supporting the hypothesis that rapid growth implies higher root activity in response to greater water and nutrient demands. In contrast, Burton and Pregitzer (2002) reported higher root respiration of A. saccharum compared with more shade-intolerant and fast growing species. In our study, no interspecific differences in root respiration rates were observed, although B. alleghaniensis is a faster growing species than A. saccharum. However, in our experiment, B. alleghaniensis made only minimal growth and suffered higher mortality than A. saccharum in all light regimes as a result, perhaps, of the low waterholding capacity of the substrate which tended to dry rapidly.

Rhizosphere respiration in contrasting light regimes

Light regimes did not affect rhizosphere respiration of either species, except in A. saccharum in 6% of full daylight, where respiration was higher (Figure 5). Reich et al. (1998) observed no apparent differences in seedling root respiration of nine tree species including B. alleghaniensis between 5 and 25% of full sunlight. In the 6% light treatment, A. saccharum seedlings were smaller and had a larger fraction of fine roots in total root mass (FR%) and specific rhizosphere respiration (RR) normalized at 15 °C: (A) RR computed using species-specific Q₁₀ values; and (B) RR computed using a fixed Q₁₀ of 2, in Acer saccharum (AS; circles) and Betula alleghaniensis (BA; squares) potted seedlings. Black, gray and white symbols represent the individuals grown in the 6, 17 and 40% light regimes, respectively. Solid and dotted lines represent the linear regressions (when light regimes are pooled) for A. saccharum and B. alleghaniensis, respectively.

Figure 6. Relationship between fine root fraction of total root dry mass (FR%) and specific rhizosphere respiration (RR) normalized at 15 °C: (A) RR computed using species-specific Q₁₀ values; and (B) RR computed using a fixed Q₁₀ of 2, in Acer saccharum (AS; circles) and Betula alleghaniensis (BA; squares) potted seedlings. Black, gray and white symbols represent the individuals grown in the 6, 17 and 40% light regimes, respectively. Solid and dotted lines represent the linear regressions (when light regimes are pooled) for A. saccharum and B. alleghaniensis, respectively.

Figure 5. Means and standard deviations of rhizosphere respiration (RR) per gram of total root dry mass: (A) RR computed using species-specific Q₁₀ values; and (B) RR computed using a fixed Q₁₀ of 2, measured in vivo and in situ in Acer saccharum (AS; filled bars) and Betula alleghaniensis (BA; open bars) seedlings grown in 40, 17 or 6% of external irradiance. Means followed by a different letter differ significantly at α = 0.05.
dry mass compared with *B. alleghaniensis* (Figure 3). Specific rhizosphere respiration of both species was correlated to the proportion of fine roots in total root dry mass (Figure 6), supporting the observation that fine root respiration rates largely exceed those of other root tissues (Gansert 1994, Ryan et al. 1996), which is likely because of their higher nitrogen content (Pregitzer et al. 1998). Numerous energy-dependent reactions linked with growth, soil exploration, microbial-associated and direct resource uptake occur in fine roots (Lambers et al. 2000), whereas the metabolism of larger roots is more limited. These findings indicate the importance of taking into account the proportion of fine roots when estimating the amount of carbon released through respiration by an entire root system or an entire tree.

The higher respiration of *A. saccharum* in the 6% light regime compared to *B. alleghaniensis* may be the consequence of fine roots comprising a larger fraction of total roots because of their smaller size rather than higher root activity in low light. This explanation agrees with the decreasing root respiration observed with ontogeny by Walters et al. (1993b) and the decrease in the proportion of fine roots in total roots or tree dry mass reported with increasing tree size (Delagrange et al. 2004). We were unable to corroborate the assumption that higher growth rates in response to higher light regimes require greater fine root activity per mass unit.

Diurnal variation in rhizosphere respiration

Specific root respiration normalized to 15 °C on the basis of an arbitrarily fixed $Q_{10}$ of 2 resulted in residual diurnal changes, whereas, as predicted, the correction based on the species-specific values of $Q_{10}$ did not result in any residual changes. This finding highlights the need for care in attributing all the observed variation in respiration to temperature dependence when calculating species-specific $Q_{10}$. Moreover, higher values were recorded during the afternoon when temperatures were maximal than at other times of the day. Although this finding suggests a higher root activity during the photosynthetically active period, we are unable to draw definitive conclusions because photosynthetic activity was not measured concurrently with rhizosphere respiration. Any photosynthetically induced stimulation of belowground activity may have been slightly delayed relative to the peak of photosynthetic activity, which would have been expected to occur before noon when tree water status was still high and stomata were wide open. This inability to disentangle the effects of temperature diurnal factors on root respiration indicates the need for continuous measurements with a controlled soil temperature to

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Table 3. Summary of ANOVA for specific rhizosphere respiration ($RR$) normalized at 15 °C using species-specific $Q_{10}$ values ($RR_{15}$ °C) and a fixed $Q_{10}$ of 2 ($RR_{2}$ 15 °C). The $F$-ratio and $P$-values are presented for relationships between parameters and light regime (LR: 40, 17 and 6% of external irradiance), period of day (P; morning, afternoon or night) and interactions. One analysis was performed for each species.

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>LR</th>
<th>P</th>
<th>LR × P</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$F$</td>
<td>$P$</td>
<td>$F$</td>
</tr>
<tr>
<td><em>Acer saccharum</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$RR_{15}$ °C Species-specific $Q_{10}$</td>
<td>17.213</td>
<td>&lt; 0.001</td>
<td>1.609</td>
</tr>
<tr>
<td>$RR_{2}$ 15 °C Fixed $Q_{10}$ of 2</td>
<td>14.342</td>
<td>&lt; 0.001</td>
<td>3.716</td>
</tr>
<tr>
<td><em>Betula alleghaniensis</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$RR_{15}$ °C Species-specific $Q_{10}$</td>
<td>0.181</td>
<td>0.678</td>
<td>0.995</td>
</tr>
<tr>
<td>$RR_{2}$ 15 °C Fixed $Q_{10}$ of 2</td>
<td>0.110</td>
<td>0.746</td>
<td>6.592</td>
</tr>
</tbody>
</table>

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**Figure 7.** Means and standard deviations of rhizosphere respiration ($RR$) rates per gram of total root dry mass normalized at 15 °C using a fixed $Q_{10}$ value of 2 ($RR_{2}$ 15 °C). The $RR_{2}$ was measured in vivo and in situ in *Acer saccharum* (A) and *Betula alleghaniensis* (B) seedlings grown in 40, 17 or 6% of external irradiance. Values are presented for the morning (diagonal lines), afternoon (open bars) and night (filled bars) periods.
demonstrate unequivocally diurnal variation in root respiration.

In conclusion, the use of either species-specific estimated $Q_{10}$ or a fixed $Q_{10}$ of 2 for temperature correction did not change the rhizosphere respiration responses of A. saccharum and B. alleghaniensis to light regime, but the use of a fixed $Q_{10}$ suggested a possible residual diurnal pattern in rhizosphere respiration. No statistical differences in rhizosphere respiration were observed between the two species, but B. alleghaniensis showed minimal growth on the neutral sandy substrate which probably affected its belowground activity. However, our results highlight a strong relationship between fine roots fraction of total root dry mass and rhizosphere respiration.

The open-system chamber used in this study allowed accurate in vivo and in situ measurements of seedling belowground respiration. Although changes are needed to improve nutrient and water supply to ensure better growth, especially for more shade-intolerant species, this continuous and nondestructive measurement system opens up numerous possibilities for obtaining a better understanding of the relationships between root activity and seasonal above- and belowground phenology.

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