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 either 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). Sev-

eral 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 growth 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 CO_2 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_g 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 pot-

ted 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 CO_2 flux was measured by a perfusive method (Bouma et al. 1997). In each pot, a perforated plastic tube was placed in
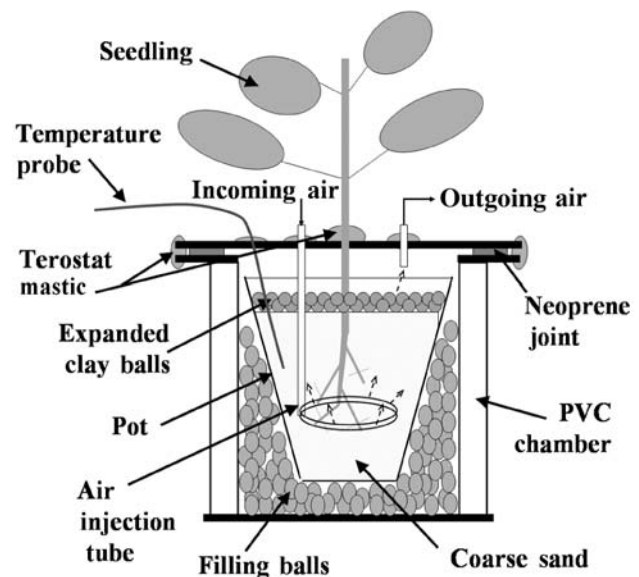

Figure 1. Diagram of the open-system chamber used to measure rhizosphere respiration of potted seedlings. Incoming air is injected into the substrate and flows to the outlet at the top of the chamber to allow continuous measurements without soil perturbation. A temperature probe (thermocouple) and a humidity sensor inserted in the substrate continuously measure soil temperature and humidity. An additional access tube (not shown) provided irrigation to the plant without opening the chamber.

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 though soda lime and over a desiccant to remove CO_2 and water vapor. A controlled quantity of CO_2 was injected into the CO_2-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 CO_2 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 CO_2 concentration used was lower than typical of forest soils (Larcher 1995, Widén and Majdi 2001), Burton and Pregistzer (2002) found that soil CO_2 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 CO_2 produced by rhizosphere respiration was calculated as:

$$R = F \left([CO_2]_{out} - [CO_2]_{in}\right) \tag{1}$$

where R is respiration, F is air flow and $[CO_2]_{in}$ and $[CO_2]_{out}$ are the CO_2 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 CO_2 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 ($R_{Substrate}$) which was always close to zero. Rhizosphere respiration ($R_{Rhizosphere}$), which was considered to be the respiration of the root system plus any associated microbial respiration, was calculated by subtracting $R_{Substrate}$ from respiration measured before seedling harvest ($R_{Rhizosphere + Substrate}$). The use of coarse sand, the confined environment and the removal of pot respiration after seedling harvest assured that measured $R_{Rhizosphere}$ 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:

$$\ln\left(R_{Rhizosphere}\right) = a\,T_{mes} + b \tag{2}$$

$$Q_{10} = e^{10a} \tag{3}$$

where $R_{Rhizosphere}$ is the specific rhizosphere respiration (nmol CO_2 g^{-1} of total roots s^{-1}) at the corresponding soil temperature T_{mes}.

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

$$R_{Rhizosphere\,ref} = \frac{R_{Rhizosphere}}{Q_{10}^{\left(\frac{T_{mes} - T_{ref}}{10}\right)}} \tag{4}$$

We set T_{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 $R_{Rhizosphere\,ref}$ 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_2 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_2 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; cm^2 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,
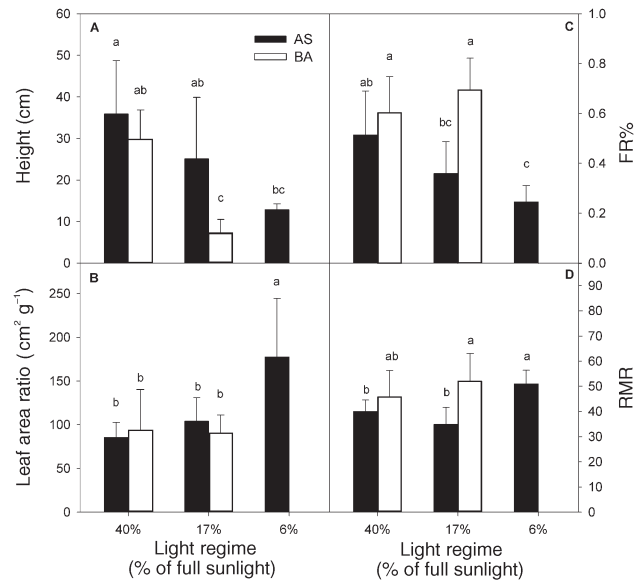

Figure 2. Means and standard deviations of height at harvest (A); leaf area ratio (B); root mass ratio (RMR; C); and fine root fraction of total root dry mass (FR%; D) in *Acer saccharum* (AS; filled bars) and *Betula alleghaniensis* (BA; open bars) seedlings grown in a nursery in 40, 17 or 6% of external 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 Q_{10} 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 r^2 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 Q_{10} 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 Q_{10} 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 Q_{10} (RR) or a fixed Q_{10} of 2 (RR_2) 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 CO_2 g^{-1} s^{-1} for RR and RR_2, respectively, except in *A. saccharum* in the 6% light regime where RR and RR_2 significantly increased to 11.8 and 13.0 nmol CO_2 g^{-1} s^{-1}, respectively (Table 1; Figure 5).

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 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 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.

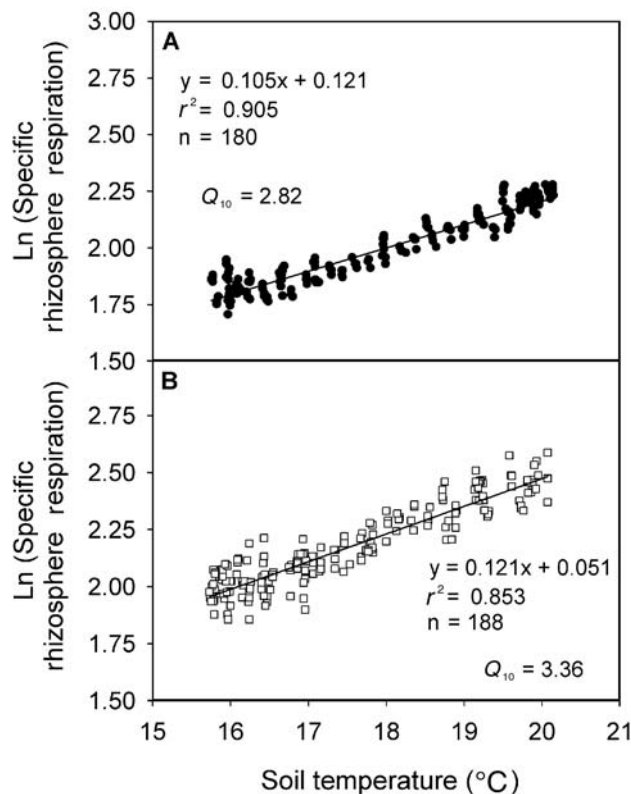| Source of variation	Species		LR		Sp. × LR	
	F	*P*	*F*	*P*	*F*	*P*
Height	5.001	0.042	6.123	0.012	1.084	0.315
LAR	0.017	0.897	5.316	0.019	0.293	0.069
RMR	18.191	0.001	0.126	0.728	3.260	0.597
FR%	6.795	0.021	2.966	0.084	1.520	0.238
RR 15 °C						
Species-specific Q_{10}	0.254	0.622	4.589	0.029	0.178	0.679
*RR*₂ 15 °C						
Fixed Q_{10} of 2	0.080	0.782	4.075	0.040	0.197	0.664

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.

In both species, there was a strong linear relationship between *RR* or RR_2 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

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 $\alpha = 0.05$.

Light regime (%)	Sp	*n*	Mean Q_{10} (SE)
40	AS	5	2.99 (0.18) a
	BA	3	3.47 (0.09) a
17	AS	5	3.06 (0.21) a
	BA	3	3.29 (0.04) a
6	AS	3	2.98 (0.42) a
	BA	–	–

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_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).
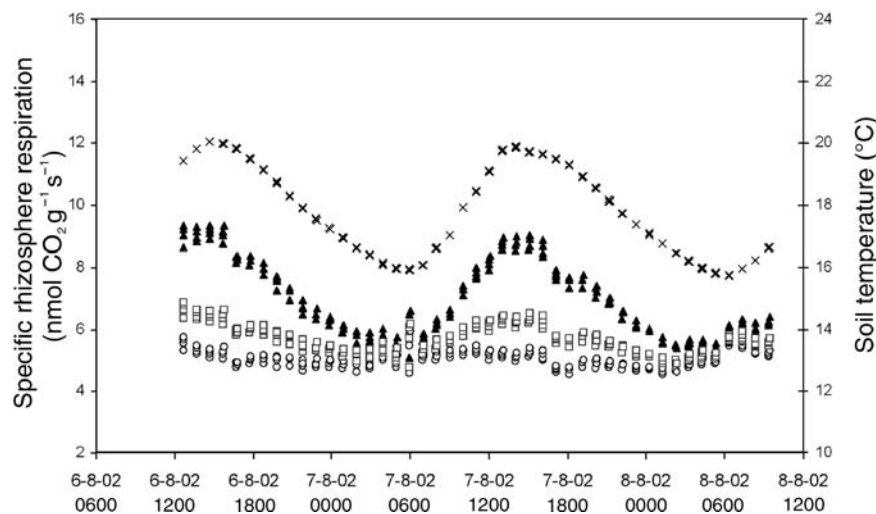

Figure 4. Specific rhizosphere respiration at soil temperature (▲), specific rhizosphere respiration normalized at 15 °C using species-specific estimated Q_{10} values (○), specific rhizosphere respiration normalized at 15 °C using a fixed Q_{10} of 2 (□) and soil temperature (×) of a potted *Acer saccharum* seedling grown in the 17% light regime in a nursery over a 48-h period during August 2002.
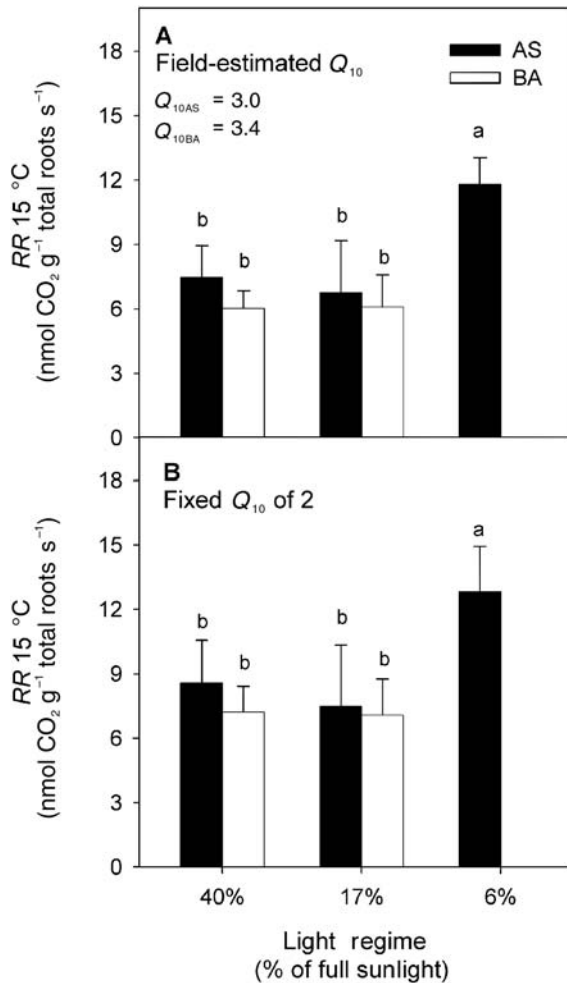
Figure 5. Means and standard deviations of rhizosphere respiration (*RR*) per gram of total root dry mass: (A) *RR* computed using species-specific Q_{10} values; and (B) RR_2 computed using a fixed Q_{10} of 2, measured in vivo and in situ in *Acer saccharum* (AS; filled bars) and *Betula alleghaniensis* (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.

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 Q_{10} values; and (B) RR_2 computed using a fixed Q_{10} 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.

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 CO_2 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 CO_2 g^{-1} s^{-1} rate recorded for roots of excavated whole seedlings (Walters et al. 1993*a*, 1993*b*, 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.

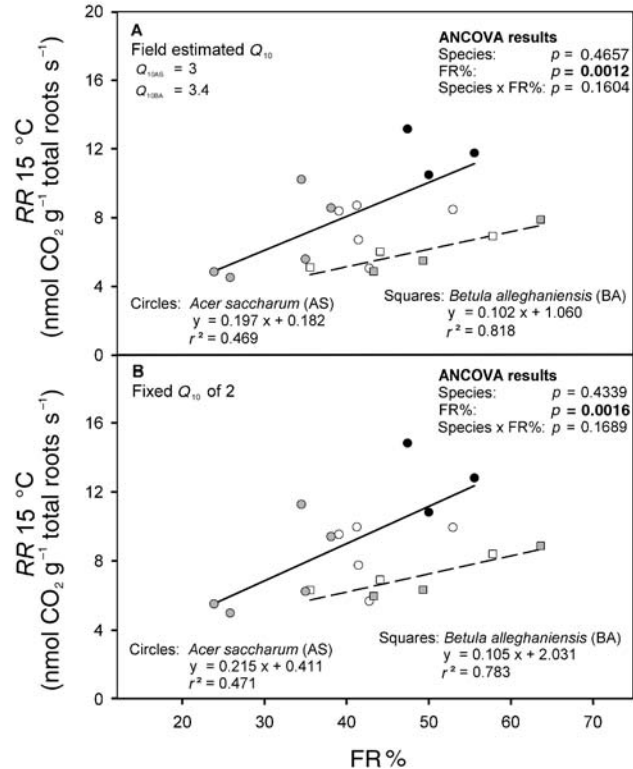Comas et al. (2002) reported that slow growing species have lower root respiration rates than rapid growing species in three tree families supporting the hypothesis that rapid growth implies higher root activity in response to greater water and nutrient demands. In contrast, Burton and Pregitzer (2002) 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 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

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.

Source of variation	LR		P		LR × P	
	F	P	F	P	F	P
Acer saccharum						
RR 15 °C Species-specific Q_{10}	17.213	< 0.001	1.609	0.217	0.067	0.991
RR_2 15 °C Fixed Q_{10} of 2	14.342	< 0.001	3.716	0.036	0.156	0.959
Betula alleghaniensis						
RR 15 °C Species-specific Q_{10}	0.181	0.678	0.995	0.398	0.270	0.767
RR_2 15 °C Fixed Q_{10} of 2	0.110	0.746	6.592	0.012	0.358	0.706

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

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). 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.

(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. (1993*b*) 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.
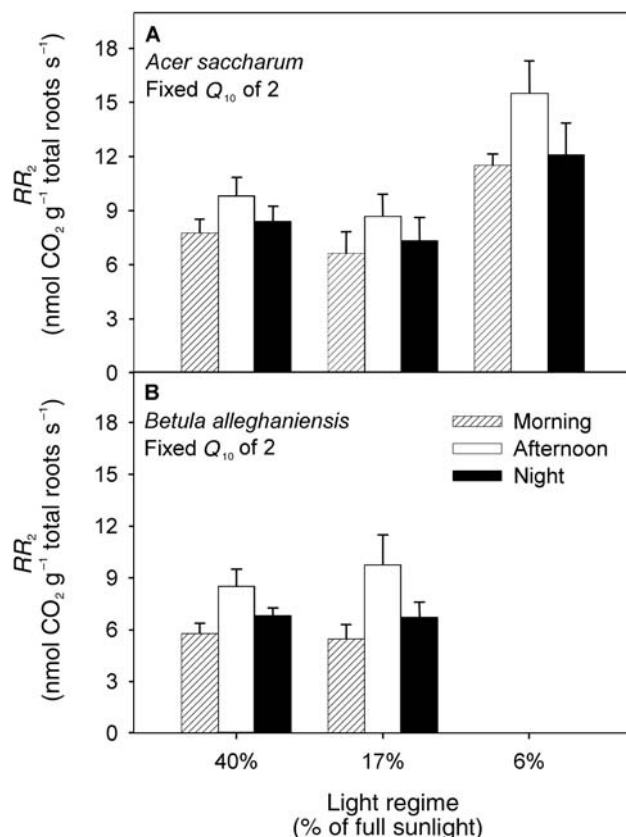
Diurnal variation in rhizosphere respiration

Specific root respiration normalized to 15 °C on the basis of an abitrarily 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

Table 4. Summary of a literature review of the temperature-dependence coefficients (Q_{10}) of soil respiration, rhizosphere respiration or root respiration in tree species. The table includes: author(s) of the study, Q_{10} coefficient, range of temperature within which Q_{10} was calculated and species or soil type for which Q_{10} was calculated. References (a non-exhaustive list) were ranked from highest to lowest Q_{10} values for soils and then tree species.

Reference	Soil (with roots)	Soil (without roots)	Total roots	Coarse roots	Fine roots	Temperature range used for calculation (°C)	Species
Lessard et al. 1994[1]	4.5					5–15	Cultivated and forest soils
Epron et al. 2001[1]	3.9					2–18	Beech forest (*Fagus sylvatica* L.)
Davidson et al. 1998[1]	3.4–5.6					1–20	Mixed temperate forest
Boone et al. 1998[1]	3.5	2.5				3–22	Mixed temperate forest
Buchmann 2000[1]	2.39–4.11					2.5–17	*Picea abies* (L.) Karst. stands
Psarras et al. 2000[1]	2.3					–	Apple (*Malus sylvestris* Hill.)
Thierron and Laudelout 1995[1]	2.2					0, 13, 20 and 25	Oak–hornbeam forest
Widén and Majdi 2001[1,2]	2.1					6–15	Mixed Norway spruce and Scots pine forest
Winkler et al. 1996[2]	1.7–1.9					4, 15, 22 and 38	Mixed temperate forest
Kirschbaum 1995[1]		1–12.9	Data from 12 contrasting measured terrestrial biomes with and without roots and a literature review				
Boone et al. 1998[1]			4.6			3–22	Mixed temperate forest
DesRochers et al. 2002			3.9			5 and 15	Aspen (*Populus tremuloides* Michx.)
Psarras et al. 2000[1]			3.1			–	Apple (*Malus sylvestris*)
Burton et al. 2002[2]			2.4–3.1			6, 18 and 24	Eight spp.
			2.7			6, 18 and 24	Sugar maple (*Acer saccharum*)
Huc 2000[3]			2.4			15–22	Common oak (*Quercus robur* L.)
DesRochers et al. 2002			2.19			15 and 25	Aspen (*Populus tremuloides*)
Maïer and Kress 2000[2]			2[4]			–	Loblolly pine (*Pinus taeda* L.)
Huc 2000[3]			1.9			19–31	Common oak (*Quercus robur*)
Widén and Majdi 2001[1,2]				1.5[5]	5	9–17C	Mixed Norway spruce and Scots pine forest
Gansert 1994[1]					2.8–2.9	1–15	Beech forest (*Fagus sylvatica*)
					3.0	4.3–19.2	Red pine forest (*Pinus resinosa* Ait.)
					2.4	5.3–20.9	Sugar maple forest (*Acer saccharum*)
Burton and Pregitzer 2003[2]					3.0	6, 18 and 24	Red pine (*Pinus resinosa*)
					2.7	6, 18 and 24	Sugar maple (*Acer saccharum*)
Burton et al. 1998[2]					2.1–3	6 and 24	Sugar maple forest (*Acer saccharum*)
Epron and Badot 1997[2]					2.2	5, 10, 15 and 20	European beech (*Fagus sylvatica*)
Bouma et al. 1997[3]					2.1	22–31	Volkamer lemon (*Citrus volkameriana* V. Ten. & Pasq.)
Ryan et al. 1996[2]				1.5	2	5–25	Pine (*Pinus radiata* D. Don)
Zogg et al. 1996[2]					1.95	6–19	Four sugar maple stands (*Acer saccharum*)

[1] = Measurements made in situ, in field conditions.
[2] = Measurements made on excised roots.
[3] = Measurements made in situ, in controlled conditions.
[4] = Theoretical value.
[5] = Value from Ryan et al. (1996).

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.

References

Ågren, G.I., B. Axelsson, J.G.K. Flower-Ellis, S. Linder, H. Persson, H. Staaf and E. Troeng. 1980. Annual carbon budget for a young Scots pine. Ecol. Bull. 32:307–313.

Amthor, J.S. 1984. The role of maintenance respiration in plant growth. Plant Cell Environ. 7:561–569.

Amthor, J.S. 1986. Evolution and applicability of a whole plant respiration model. J. Theor. Biol. 122:473–490.

Atkin, O.K., E.J. Edwards and B.R. Loveys. 2000. Response of root respiration to changes in temperature and its relevance to global warming. New. Phytol. 147:141–154.

Baker, F.S. 1949. A revised tolerance table. J. For. 47:179–181.

Boone, R.D., K.J. Nadelhoffer, J.D. Canary and J.P. Kaye. 1998. Roots exert a strong influence on the temperature sensitivity of soil respiration. Nature 396:570–572.

Bouma, T.J., K.L. Nielsen, D.M. Eissenstat and J.P. Lynch. 1997. Estimating respiration of roots in soil: interaction with soil CO_2, soil temperature and soil water content. Plant Soil 195:221–232.

Buchmann, N. 2000. Biotic and abiotic factors controlling soil respiration rates in *Picea abies* stands. Soil Biol. Biochem. 32: 1625–1635.

Burton, A.J. and K.S. Pregitzer. 2002. Measurement carbon dioxide concentration does not affect root respiration of nine tree species in the field. Tree Physiol. 22:67–72.

Burton, A.J. and K.S. Pregitzer. 2003. Field measurements of root respiration indicate little to no seasonal temperature acclimation for sugar maple and red pine. Tree Physiol. 23:273–280.

Burton, A.J., K.S. Pregitzer, R.W. Ruess, R.L. Hendrick and M.F. Allen. 2002. Root respiration in North American forests: effect of nitrogen concentration and temperature across biomes. Oecologia 131:559–568.

Burton, A.J., K.S. Pregitzer, G.P. Zogg and D.R. Zak. 1998. Drought reduces root respiration in sugar maple forests. Ecol. Appl. 8: 771–778.

Cardon, Z.G., A.D. Czaja, J.L. Funk and P.L. Vitt. 2002. Periodic carbon flushing to roots of *Quercus rubra* saplings affects soil respiration and rhizosphere microbial biomass. Oecologia 133:214–223.

Chen, H., M.E. Harmon, R.P. Griffiths and W. Hicks. 2000. Effects of temperature and moisture on carbon respired from decomposing woody roots. Forest Ecol. Manage. 138:51–64.

Comas, L.H., T.J. Bouma and D.M. Eissenstat. 2002. Linking root traits to potential growth rate in six temperate tree species. Oecologia 132:34–43.

Davidson, E.A., E. Belk and R.D. Boone. 1998. Soil water content and temperature as independent or confounded factors controlling soil respiration in a temperate mixed hardwood forest. Global Change Biol. 4:217–227.

Delagrange, S., C. Messier, M.J. Lechowicz and P. Dizengremel. 2004. Physiological, morphological and allocational plasticity in understory deciduous trees: importance of individual size and light availability. Tree Physiol. 24:775–784.

Desrochers, A., S.M. Landhausser and V.J. Lieffers. 2002. Coarse and fine root respiration in aspen (*Populus tremuloides*). Tree Physiol. 22:725–732.

Epron, D. and P.-M. Badot. 1997. Fine root respiration in forest trees. *In* Plant Science. Eds. J.C. Puech, A. Latché and M. Bouzayen. Société Française de Physiologie Végétale, Paris, pp 199–200.

Epron, D., L. Farque, E. Lucot and P.-M. Badot. 1999. Soil CO_2 efflux in a beech forest: the contribution of root respiration. Ann. For. Sci. 56:289–295.

Epron, D., V. Le Dantec, E. Dufrene and A. Granier. 2001. Seasonal dynamics of soil carbon dioxide efflux and simulated rhizosphere respiration in a beech forest. Tree Physiol. 21:145–152.

Forcier, L.K. 1975. Reproductive strategies and the co-occurrence of climax tree species. Science 189:808–811.

Gansert, D. 1994. Root respiration and its importance for the carbon balance of beech saplings (*Fagus sylvatica* L.) in montane beech forest. Plant Soil 167:109–119.

Högberg, P., A. Nordgren, N. Buchmann, A.F.S. Taylor, A. Ekblad, M.N. Hogberg, G. Nyberg, M. Ottosson-Lofvenius and D.J. Read. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. Nature 411:789–792.

Huc, F. 2000. Respiration rhizosphérique et environnement lumineux. DEA Biologie Forestière. Université Henri Poincarré Nancy I, Ecole Doctorale RP2E, 33 p.

Kirschbaum, M.U.F. 1995. The temperature dependence of soil organic matter decomposition and the effect of global warming on soil organic C storage. Soil Biol. Biochem. 27:753–760.

Lambers, H., F.S. Chapin III and T.L. Pons. 2000. Plant physiological ecology.1st Edn. Springer-Verlag, New York, 540 p.

Larcher, W. 1995. Physiological plant ecology: ecophysiology and stress physiology of functional groups. 3rd Edn. Springer-Verlag, Berlin, 506 p.

Le Roux, X., A. Lacointe, A. Escobar-Gutiérrez and S. Le Dizès. 2001. Carbon-based models of individual tree growth: a critical appraisal. Ann. For. Sci. 58:469–506.

Lessard, R., P. Rochette, E. Topp, E. Pattey, R.L. Desjardins and G. Beaumont. 1994. Methane and carbon dioxide fluxes from poorly drained adjacent cultivated and forest sites. Can. J. Soil Sci. 74:139–146.

Maïer, C.A. and L.W. Kress. 2000. Soil CO_2 evolution and root respiration in 11 year-old loblolly pine (*Pinus taeda*) plantations as affected by moisture and nutrient availability. Can. J. For. Res. 30:347–359.

McCree, K.J. 1970. An equation for the rate of respiration of white clover plants grown under controlled conditions. *In* Prediction and Measurement of Photosynthetic Productivity. Eds. PUDOC, Wageningen, pp 221–229.

Mogensen, V.O. 1977. Field measurements of dark respiration rates of roots and aerial parts in Italian ryegrass and barley. J. Appl. Ecol. 14:243–252.

Pregitzer, K.S., M.J. Laskowski, A.J. Burton, V.C. Lessard and D.R. Zak. 1998. Variation in sugar maple root respiration with root diameter and soil depth. Tree Physiol. 18:665–670.

Psarras, G., I.A. Merwin, A.N. Lakso and J.A. Ray. 2000. Root growth phenology, root longevity and rhizosphere respiration of field grown 'Mutsu' apple trees on 'Malling 9' rootstock. J. Am. Soc. Hortic. Sci. 125:596–602.

Qi, J., J.D. Marshall and K.G. Mattson. 1994. High soil carbon dioxide concentrations inhibit root respiration of Douglas fir. New Phytol. 128:435–442.

Reich, P.B., M.B. Walters, M.G. Tjoelker, D. Vanderklein and C. Buschena. 1998. Photosynthesis and respiration rates depend on leaf and root morphology and nitrogen concentration in nine boreal tree species differing in relative growth rate. Funct. Ecol. 12:395–405.

Ryan, M.G., R.M. Hubbard, S. Pongracic, R.J. Raison and R.E. McMurtrie. 1996. Foliage, fine root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. Tree Physiol. 16:333–343.

Singh, B., A. Nordgren, M. Ottosson Löfvenius, M.N. Högberg, P.-E. Mellander and P. Högberg. 2003. Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. Plant Cell Environ. 26:1287–1296.

Thierron, V. and H. Laudelout. 1995. Contribution of root respiration to total CO_2 efflux from the soil of a deciduous forest. Can. J. For. Res. 26:1142–1148.

Thornley, J.H.M. 1970. Respiration, growth and maintenance in plants. Nature 227:304–305.

Walters, M.B., E.L. Kruger and P.B. Reich. 1993*a*. Growth biomass distribution and CO_2 exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. Oecologia 94:7–16.

Walters, M.B., E.L. Kruger and P.B. Reich. 1993*b*. Relative growth rate in relation to physiological and morphological traits for northern hardwood tree seedlings: species, light environment and ontogenetic consideration. Oecologia 96:219–231.

Waring, R.H., J.J. Landsberg and M. Wiliams. 1998. Net primary production of forest: a constant fraction of gross primary production? Tree Physiol. 18:129–134.

Widén, B. and H. Majdi. 2001. Soil CO_2 efflux and root respiration at three sites in a mixed pine and spruce forest: seasonal and diurnal variation. Can. J. For. Res. 31:786–796.

Winkler, J.P., R.S. Cherry and W.H. Schlesinger. 1996. The Q_{10} relationship of microbial respiration in a temperate forest soil. Soil Biol. Biochem. 28:1067–1072.

Zogg, G.P., D.R. Zak, A.J. Burton and K.S. Pregitzer. 1996. Fine roots respiration in northern hardwood forest in relation to temperature and nitrogen availability. Tree Physiol. 16:719–725.