Coarse and fine root respiration in aspen (Populus tremuloides)

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received June 7, 2001; accepted November 13, 2001; published online June 3, 2002

Summary Coarse and fine root respiration rates of aspen (Populus tremuloides Michx.) were measured at 5, 15 and 25 °C. Coarse roots ranged from 0.65 to 4.45 cm in diameter, whereas fine roots were less than 5 mm in diameter. To discriminate between maintenance and growth respiration, root respiration rates were measured during aboveground growing periods and dormant periods. An additional measurement of coarse root respiration was made during spring leaf flush, to evaluate the effect of mobilization of resources for leaf expansion on root respiration. Fine roots respired at much higher rates than coarse roots, with a mean rate at 15 °C of 1290 µmol CO₂ m⁻³ s⁻¹ during the growing period, and 660 µmol CO₂ m⁻³ s⁻¹ during the dormant period. The temperature response of fine root respiration rate was nonlinear: mean Q₁₀ was 3.90 for measurements made at 5–15 °C and 2.19 for measurements made at 15–25 °C. Coarse root respiration rates measured at 15 °C in late fall (dormant season) were higher (370 µmol CO₂ m⁻³ s⁻¹) than rates from roots collected at leaf flush and early summer (200 µmol CO₂ m⁻³ s⁻¹). The higher respiration rates in late fall, which were accompanied by decreased total non-structural carbohydrate (TNC) concentrations, suggest that respiration rates in late fall included growth expenditures, reflecting recent radial growth. Neither bud flush nor shoot growth of the trees caused an increase in coarse root respiration or a decrease in TNC concentrations, suggesting a limited role of coarse roots as reserve storage organs for spring shoot growth, and a lack of synchronization between above- and belowground growth. Pooling the data from the coarse and fine roots showed a positive correlation between nitrogen concentration and respiration rate.

Keywords: carbon, CO₂, maintenance respiration, non-structural carbohydrates, Q₁₀, temperature response.

Introduction Aspen (Populus tremuloides Michx.) is the most widely distributed tree species in North America, and forms extensive stands in the boreal forests (Perala 1990). Understanding aspen root respiration is important for several reasons. First, root carbon economy in aspen is critical for the production and subsequent growth of root suckers (Schier and Johnston 1971, Peterson and Peterson 1992). Second, root respiration, especially that of the large communal root system of aspen (DesRochers and Lieffers 2001), can consume large proportions of net primary production (Ericsson et al. 1996) and can therefore affect the maintenance and survival of aspen stands (Hogg 1999). Finally, ecosystem models of carbon dynamics depend on accurate estimation of root respiration (Fernandez et al. 1993, Hogg 1999).

Maintenance respiration, which is the component of respiration that is required to keep existing root cells and tissues alive, requires considerable amounts of carbohydrates (Kozlowski and Pallardy 1997) and is highly temperature-dependent (Sprugel and Benecke 1991). Root respiration also varies with season, because during the growing season, it comprises both maintenance respiration and growth respiration (Lambers et al. 1983). To isolate the maintenance component of respiration, respiration rates are commonly measured at the end of the growing season, when it is assumed that growth activity has ceased (Ryan 1990, Sprugel 1990, Ryan et al. 1995, 1996), although root growth can occur well into the fall (Lyr and Hoffman 1967). Root respiration rates are also affected by the proportion of metabolically active meristematic to non-meristematic tissues, leading to higher respiration rates in fine roots than in coarse roots (Pregitzer et al. 1998). Other endogenous factors, such as total nonstructural carbohydrate (TNC) and nitrogen concentrations in tissues, are also known to affect root respiration rates (Kramer and Kozlowski 1979) where the repair and replacement of proteins is the principal cause for maintenance respiration (Lexander et al. 1970). Finally, respiration rates may vary depending on the concentration of CO₂ at which they are measured (Burton et al. 1997, Clinton and Vose 1999).

The objectives of this study were to determine seasonal respiration rates of coarse and fine roots in aspen at three soil temperatures, and at the CO₂ concentration of soils of aspen stands. Because root growth is not observed in aspen at soil temperatures below 5 °C (Landhäusser and Lieffers 1998, Wan et al. 1999), we hypothesized that respiration rates measured on roots collected in late fall, when soil temperatures are below 5 °C, will be lowest and represent maintenance res-
piration. Respiration rates measured in the spring during leaf flush, when soil temperatures are still below 5 °C (no root growth), should reflect the additional energy required for the mobilization and translocation of reserve carbohydrates for developing leaves (Sprugel 1990). In early summer, when trees are actively growing and soil temperatures are above 5 °C, respiration rates should be highest and represent total respiration (maintenance + growth respiration).

Materials and methods

Coarse roots sampling

Coarse roots were collected from a 55-year-old pure aspen stand near Devon (53°23′ N, 113°45′ W), Alberta, Canada, within a 50 × 50 m area. The stand, categorized as an aspen-dominated low-bush cranberry ecotone (Beckingham and Archibald 1996), is on a moderately well-drained mesic site with a medium to rich nutrient supply. Mean elevation is 682 m, with undulating terrain and podzolic sandy loam soil (Bowser et al. 1962). Mean summer and winter air temperatures are 14.4 and –8.7 °C, respectively, and mean annual precipitation is 424 mm (Strong and Leggat 1992).

Roots were collected in late fall (early December 1998) and during leaf flush in spring (May 1999). Soil temperatures at 20-cm depth were below 5 °C at both collection times. Because fall 1998 was unusually warm, it can be expected that soil temperatures drop below 5 °C earlier in the season during more typical years. A third root collection was made 1 month after leaf flush, in early June 1999, when soils were warming (range 6–8 °C), to estimate total respiration. On each collection date, a large pit was excavation and 50-cm-long sections of roots ranging from 0.5 to 5 cm in diameter were carefully hand-excavated at soil depths ranging from 10 to 30 cm, mostly in the B soil horizon. Ninety roots were collected per sampling date. The roots were gently cleaned with diluted bleach solution (1 ml of 5% hypochlorate per liter of distilled water) and stored in moistened sphagnum moss at 2 °C for a week. Before the respiration measurements, the roots were gently washed free of sand by rinsing the root mass with distilled water. Excess water on the roots was blotted with a paper towel.

Respiration measurements

Because studies have shown that respiration may be artificially increased by low CO₂ concentrations (Qi et al. 1994, Burton et al. 1997, Clinton and Vose 1999), we measured soil CO₂ concentrations at a depth of 20 cm at 16 random locations in the aspen stand. Samples were collected by slowly drawing 20 ml of soil air with a syringe connected to an aluminum probe. The air was injected in Vacutainers™ (Fisher Scientific) tubes and the CO₂ concentrations measured by gas chromatography. Soil concentrations at 5 °C were 3233 ± 609 ppm. We therefore used a CO₂ concentration of 3000 ppm in the air circulated through the respiration chamber during measurements.

A clamp-on respiration chamber was constructed from ABS pipe to accommodate both the coarse and fine roots. It included a small fan for air circulation and a set of fine-gauge copper-constantan thermocouple wires inserted in the xylem (coarse roots) or root mass (fine roots) to monitor root temperature inside the respiration chamber. The respiration chamber was sealed from outside air with non-toxic, non-drying putty and placed inside a dark cooling chamber (Landhäusser et al. 1996) while respiration was measured at constant root temperatures of 5, 15 and 25 °C. Respiration was measured with an open-system infrared gas analyzer (IRGA, CIRAS I, PP Systems, Haverhill, MA). Bottled gas containing CO₂ at a concentration of 3000 ppm was supplied to a 9.6-l mixing chamber to maintain a stable CO₂ concentration in the supplied air. A slightly positive pressure was maintained inside the respiration chamber to avoid outside air leaking into the chamber. This positive pressure was monitored after each sample was installed inside the respiration chamber, and again before each measurement, with a water bubble system linked to the outflow pipe going to the IRGA. Inflow rate to the chamber was maintained at 200–350 ml min⁻¹. Because the respiration calculations were based on the flow rate into the chamber, and the IRGA sampled CO₂ concentrations in the chamber, assuming complete mixing, minor leaks should not have caused substantial errors. This system is similar to open systems used for measurements of photosynthesis.

Roots were allowed to acclimate to the measurement temperature and CO₂ concentration for 45 to 90 min, and respira-
tion rate was allowed to stabilize for about 20 min before it was recorded. Over the range of measurement temperatures, relative humidity was maintained at near saturation. For coarse root respiration, a range of root sizes was randomly assigned to a measurement temperature of 5, 15 or 25 °C. To avoid wound respiration caused by cutting the roots (Müller 1924), the respiration chamber was clamped around the mid-section (10-cm long) of the 50-cm-long coarse root segment, thereby excluding the cut parts of the root. Root volume enclosed in the respiration chamber was calculated assuming that roots were cylindrical.

For the fine roots, the whole seedling root system was enclosed in the respiration chamber, with the aboveground portions left intact but excluded from the chamber. For each seedling, respiration was measured at 5, 15 and 25 °C (repeated measures). Root volume was calculated by water displacement immediately after respiration was measured. Values of $Q_{10}$ (respiration rate at temperature $T$ over respiration rate at temperature $T-10$) were calculated for coarse and fine roots.

**Tissue analyses**

The age of each coarse root was determined by counting the number of annual growth rings in a cross section. A 2-cm section of root was soaked for 24 h in a solution of 1% triphenyltetrazolium chloride, to identify sapwood area (Ryan 1990). Another section was oven-dried at 68 °C to constant mass and ground in a Wiley mill to 40 mesh. For the seedlings, the entire fine root system was dried and ground. For total nitrogen analysis, ground samples were digested by the Kjeldhal method (Kalra and Maynard 1991), and total nitrogen was quantified with a Technicon AutoAnalyzer II (Tarrytown, NY). For TNC (sugars and starch), samples were digested for 1 h in 0.2 N H$_2$SO$_4$ at 115 °C, mixed with phenolsulfuric acid and quantified spectrophotometrically (Smith et al. 1964).

**Experimental design and statistical analyses**

Coarse root respiration rates were analyzed as a randomized 3×3 factorial design with three seasons (fall, spring and summer) and three temperatures (5, 15 and 25 °C) as fixed main effects. The fine root respiration data were analyzed as a univariate repeated measures design with two seasons (growing and dormant) and a repeated temperature factor (5, 15 and 25 °C). Respiration data were log-transformed for the coarse and fine roots, to correct for unequal variances. Relationships between respiration rate and total nitrogen and TNC were tested with linear regression, and as covariates in analyses of covariance. Least significant difference (LSD) procedure was used for comparison of treatment means. We used SAS statistical software (SAS Institute, Cary, NC) to perform the data analysis. A significance level of $P < 0.05$ was chosen.

**Results**

**Coarse roots**

Cross sections of coarse roots showed that radial growth was completed in roots collected in the fall and had not yet started in roots collected in spring and summer. Even in the largest coarse roots, no heartwood (central portion of xylem without live parenchyma cells) was observed. Occasionally, small dead areas were observed in the xylem; however, these areas constituted less than 5% of root volume. Mean coarse root diameter was 2.06 cm (range 0.65–4.45 cm), and mean root age was 30 years (range 4–56 years). Nitrogen concentrations did not vary with season ($P = 0.07$), averaging 0.4% of root dry mass (Figure 1a). Mean TNC concentration was 11.7, 15.4 and 17.1% of root dry mass for coarse roots collected in the fall, spring and summer, respectively (Figure 1b). Coarse roots collected in the fall had lower TNC concentrations than coarse roots collected in the spring and summer ($P < 0.05$), whereas there was no difference in TNC concentrations between roots collected in the spring and summer ($P > 0.05$, Figure 1b).

![Figure 1](https://academic.oup.com/treephys/article-abstract/22/10/727/1642725)
Coarse root respiration rate was significantly affected by season \((P = 0.002)\). Respiration rates were significantly higher in roots collected in the fall \((370 \mu\text{mol CO}_2 \text{m}^{-3} \text{s}^{-1})\) than in roots collected in spring and summer \((200 \mu\text{mol CO}_2 \text{m}^{-3} \text{s}^{-1})\) \((P < 0.05)\), whereas there was no difference between respiration rates of roots collected in spring and summer \((P > 0.05, \text{ Figure 1c})\). As expected, respiration rates increased exponentially with measurement temperature \((P < 0.001)\). The respiration response to changing temperature was similar in roots collected in fall, spring and summer, i.e., the slopes of the regression lines between respiration rates and temperature were not significantly different between seasons \((P > 0.05)\). Mean \(Q_{10}\) over all three seasons was 2.15; however, mean \(Q_{10}\) was 1.72 for the 5–15 °C temperature range and 2.57 for the 15–25 °C temperature range (statistically non-testable).

Storage of roots collected in fall and spring for more than 1 day increased respiration rates measured at 15 °C \((P = 0.01)\) (Table 1). However, storage time had no effect on respiration rates of roots collected in the summer or on respiration rates measured at 5 and 25 °C. Respiration rate was negatively correlated with root diameter \((r^2 = -0.28; P < 0.001)\) and weakly positively correlated with nitrogen concentration \((r^2 = 0.08; P < 0.001)\). Analysis of covariance showed that root diameter \((P < 0.001)\) and nitrogen \((P < 0.001)\) were significant covariates for coarse root respiration rates; however, season and measurement temperature still significantly affected root respiration rates after adjusting for root diameter, nitrogen concentration and days of storage. There was no relationship between TNC concentration and respiration rate across seasons and measurement temperature combinations \((P > 0.05)\), and TNC concentration did not contribute significantly to the model as a covariate \((P = 0.76)\). The TNC concentration was unrelated to root diameter \((P = 0.85)\).

Fine roots

Root systems of aspen seedlings consisted mostly of fine roots less than 2 mm in diameter, but a small portion of the fine roots were larger, ranging up to 5 mm in diameter (~5% of total root mass). Nitrogen concentration of fine roots did not vary between the growing and dormant seasons \((P = 0.36)\), with a mean of 1.6% of dry mass (Figure 2a). Fine roots had significantly higher mean TNC concentrations during the growing period than during the dormant period (13.2 versus 9.2% of root dry mass; \(P = 0.03\)) (Figure 2b). The decrease in TNC during the dormant period was accompanied by an increase in root dry mass \((P = 0.02, \text{ Table 2})\), whereas root volumes did not differ between the start and end of dormancy \((P = 0.56)\).

Fine root respiration rates were on average 49% higher during the growing season compared with the dormant season.

Table 1. Mean respiration rate at 15 °C of aspen coarse roots collected in the fall, spring and summer and stored at 2 °C for 1–4 days before measurement. Values followed by the same letter are not significantly different at \(P < 0.05\).

<table>
<thead>
<tr>
<th>Storage days</th>
<th>Respiration rate ((\mu\text{mol CO}_2 \text{m}^{-3} \text{s}^{-1}))</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Fall</td>
</tr>
<tr>
<td>1</td>
<td>190 a</td>
</tr>
<tr>
<td>(n = 5)</td>
<td>(n = 16)</td>
</tr>
<tr>
<td>2</td>
<td>400 b</td>
</tr>
<tr>
<td>(n = 10)</td>
<td>(n = 9)</td>
</tr>
<tr>
<td>3</td>
<td>430 b</td>
</tr>
<tr>
<td>(n = 7)</td>
<td>(n = 4)</td>
</tr>
<tr>
<td>4</td>
<td>330 b</td>
</tr>
<tr>
<td>(n = 7)</td>
<td>(n = 4)</td>
</tr>
</tbody>
</table>

Figure 2. Fine root (a) nitrogen concentration (N), (b) total nonstructural carbohydrate concentration (TNC) and (c) respiration rates (logarithm scale) measured at 5, 15 and 25 °C. Bars with the same letter are not significantly different at \(P < 0.05\).
Table 2. Mean volume and dry mass and relationship between volume (V) and dry mass (M) of fine roots of growing and dormant aspen seedlings. Standard deviations are given in parentheses. Values followed by the same letter are not significantly different at P < 0.05.

<table>
<thead>
<tr>
<th></th>
<th>Growing seedlings</th>
<th>Dormant seedlings</th>
</tr>
</thead>
<tbody>
<tr>
<td>Volume (cm³)</td>
<td>17.6 a (4.9)</td>
<td>19.9 a (10.9)</td>
</tr>
<tr>
<td>Dry mass (g)</td>
<td>2.60 b (0.77)</td>
<td>4.51 c (2.69)</td>
</tr>
<tr>
<td>Relationship</td>
<td>$M_2 = 0.14V + 0.41$ (R² = 0.41, P &lt; 0.001)</td>
<td>$M_2 = 0.23V$ (R² = 0.97, P &lt; 0.001)</td>
</tr>
</tbody>
</table>

($P = 0.001$, Table 3, Figure 2c). Mean respiration rate at 15 °C was 1290 µmol CO₂ m⁻³ s⁻¹ during the growing period compared with 660 µmol CO₂ m⁻³ s⁻¹ during the dormant period. Respiration rates increased exponentially with increasing temperature, with a mean $Q_{10}$ of 3.06 over the 5–25 °C temperature range. However, the increase in respiration rate was significantly higher between 5 and 15 °C ($Q_{10} = 3.90$) than between 15 and 25 °C ($Q_{10} = 2.19$) ($P = 0.001$). The temperature response of respiration rate did not differ between dormant and growing seedlings ($P = 0.31$).

Analysis of covariance showed that nitrogen and TNC were not significant covariates for fine root respiration rate (nitrogen: $P = 0.06$; TNC: $P = 0.40$). However, TNC concentration was positively correlated with respiration rate measured at 15 °C ($r^2 = 0.49$; $P = 0.03$) and 25 °C ($r^2 = 0.61$; $P = 0.01$), whereas there was no correlation between TNC concentration and respiration rate measured at 5 °C ($r^2 = 0.27$; $P = 0.27$). There was no correlation between nitrogen concentration and respiration rate when respiration rates were examined individually at each measurement temperature ($P > 0.05$).

Discussion

Fine root respiration rates of growing seedlings were nearly double the rates measured in dormant seedlings. Fine root respiration of dormant seedlings was assumed to represent maintenance respiration alone (Figure 2c). However, although the seedlings did not grow new roots or increase in root diameter during the dormant period, root mass increased (Table 2), which could account for respiration expenditures unrelated to maintenance. Despite the possible overestimation of maintenance respiration, root respiration rates of dormant seedlings were 15–30% lower than other published estimates for aspen. On a dry mass basis, we found a respiration rate of 3.0 nmol CO₂ g⁻¹ s⁻¹ at 15 °C in dormant seedlings (Table 3), compared with rates of 4.4 nmol CO₂ g⁻¹ s⁻¹ at 15 °C (Lawrence and Oechel 1983) and 3.5–4.2 nmol CO₂ g⁻¹ s⁻¹ at 10 °C in field-excavated fine roots (Ryan et al. 1997). Assuming that the respiration chamber remained leak-proof during measurements, lower respiration rates in our study could be attributed to higher concentrations of CO₂ during measurement (3000 ppm compared with 500–1400 ppm in the study by Ryan et al. 1997). Low CO₂ concentrations artificially increase root respiration rates (Qi et al. 1994, Burton et al. 1997, Clinton and Vose 1999). For example, Coleman et al. (1996) reported a fine root respiration rate of 15.3 nmol CO₂ g⁻¹ s⁻¹ at 20 °C and 350 ppm of CO₂ for aspen, which is almost twice the respiration rates we measured, at 15 °C and 3000 ppm of CO₂ in growing seedlings (Table 3). However, it was recently found that even minor leaks in respiration chambers when making measurements at high CO₂ concentrations can result in underestimation of root respiration rates (Burton and Pregitzer 2002).

Our experimental design was based on the assumption that, in coarse roots collected in the fall, growth respiration had ceased because soil temperatures were below 5 °C and the annual growth ring was fully developed. However, we found that roots collected in the fall had 31% higher respiration rates (when measured at 15 and 25 °C) than roots collected in the spring and summer (Figure 1c). This suggests that respiration rates of roots collected in the fall included growth expenditures, in which case they did not solely represent maintenance respiration. Root growth can occur even if shoots are in deep dormancy (Lyr and Hoffmann 1967, Vogt et al. 1980). Lavigne (1988) also noted high respiration rates in balsam fir (Abies balsamea (L.) Mill.) stems for over a month after radial growth had stopped. It appears that roots collected in the fall...
retained high overall cell activity after a recent period of radial growth, possibly because of cell wall thickening. We found that fine roots increased in dry mass during the dormancy period, even though fine root volumes did not change. High respiration rates could also be a result of increased cell activity associated with the transformation of reserve starch into sugars at the onset of low temperatures (Marvin et al. 1971).

The spring and early summer growth flush was accompanied by an increase in coarse root respiration rates. Coarse roots collected in the spring and early summer had increased TNC concentrations compared with coarse roots collected in the fall (Figure 1b). This seasonal pattern of TNC concentrations contrasts with the generally acknowledged pattern for deciduous species, where root TNC concentrations are maximal in the fall and minimal at and just after bud flush (Siminovitch 1981, Larcher 1995). The low TNC concentrations that we observed in coarse roots collected in the fall suggests that root TNC reserves were depleted by fall root growth and high root respiration rates. Translocation of TNC to the coarse roots in the spring and summer resulted in high concentrations in preparations for summer radial root growth. A similar seasonal pattern of TNC accumulation in coarse roots has been observed in Sitka spruce (Picea sitchensis (Bong.) Carr.) (Deans and Ford 1986) and sugar maple (Acer saccharum Marsh.) (Wargo 1979), i.e., substantial carbohydrate storage in roots in spring preceding radial root growth. Although leaf and shoot growth of trees had started by the summer collection date, radial growth of coarse roots had not begun. These results suggest that the role of coarse roots as carbohydrate storage organs to sustain bud flush and early growth of mature trees may be limited. In mature aspen trees, aboveground biomass represents about 60–80% of total tree biomass (Peterson and Peterson 1992), hence carbohydrates stored in the branches, twigs and stem may play a more important role than coarse roots as TNC storage organs for bud flush and early growth. A potential role of branches and twigs as major TNC storage organs for spring growth flush has also been suggested for Pacific silver fir (Abies amabilis Dougl. (Forbes)) (Sprugel 1990).

The acid digestion method used for determination of TNC concentrations has been used previously for aspen roots (Sheperd and Smith 1993). However, in roots of grasses and legumes, it has been observed that this method is likely to overestimate TNC concentrations when little starch is present and to underestimate TNC concentrations when large amounts of starch are present (Grotelueschen and Smith 1967, Greub and Wedin 1969). If the same holds true for aspen coarse roots, the seasonal differences in TNC may be larger than reported, because starch concentrations are usually lower in the winter than in the summer (Kramer and Kozlowski 1979).

On a wet volume basis, fine root respiration rates at 15 °C were 2.5–3.5 times higher than coarse root respiration rates (Figures 1 and 2), probably reflecting the higher physiological activity and higher proportions of meristematic and phloem tissues in fine roots compared with coarse roots (Kramer and Kozlowski 1979). No heartwood was observed in the coarse roots; however, sapwood xylem contains proportionally fewer living cells than cambium and phloem tissues (Ryan 1990). Pregitzer et al. (1998) showed that root nitrogen concentration is a better indicator of root activity and respiration than root size. A large part of maintenance respiration supports repair and replacement of proteins (Amthor 1984), and because most of the nitrogen in plant tissue is associated with proteins (Lexander et al. 1970), nitrogen is usually a good indicator of root activity. There was no clear relationship between maintenance respiration and nitrogen concentration when coarse root or fine root data were analyzed independently, because there was little variation in nitrogen concentration in the samples of a treatment combination (Figures 1a and 2a). In addition, maintenance respiration may match poorly with nitrogen concentration in systems where nitrogen is in excess (Ryan 1995), which could explain why it was not a significant covariate for fine roots in our well-fertilized seedlings. However, after pooling the data obtained from both coarse and fine roots to increase the range in nitrogen concentrations, as suggested by Pregitzer et al. (1998) for sugar maple, a relationship was evident and explained 65% of the variation in respiration rates (Figure 3). Inferences from the data presented in Figure 3 must be made carefully, however, because the coarse and fine roots came from two different populations of roots. The absence of a significant relationship between nitrogen concentrations and respiration rates of coarse and fine roots may result from a failure to measure maintenance respiration independently of growth respiration.

In fine roots, the increasing positive correlation between TNC concentration and respiration rate with increasing measurement temperature suggests that TNC became more limiting as temperature increased. This was not observed in coarse roots, probably because they respire at much lower rates than fine roots, even at 25 °C (Table 3). The changing temperature dependency of fine root TNC may be a result of
the affinity between enzymes and their substrate, which usually declines with temperature and is modified by substrate concentration (Hunt and Loomis 1979). Limited access to TNC at high respiration rates could explain the lower Q10 observed between 15 and 25 °C than between 5 and 15 °C for fine roots (Wassink 1972, cited by Hunt and Loomis 1979). Lawrence and Oechel (1983) also found a lower Q10 for the 15–25 °C temperature range than for the 5–15 °C temperature range. Thus, Q10 values are affected by temperature (Thierron and Laudelout 1996), and should therefore be applied with care.

In summary, respiration rates and TNC concentrations of coarse roots indicated that roots collected in the fall still comprised growth expenditures, whereas roots collected in the spring and summer were still dormant even though the aboveground portions of the trees had started to grow. Similarly, in fine roots, the increase in dry mass and low TNC concentrations during the dormancy period suggest growth respiration expenditures in fine roots during the aboveground dormant season. We conclude that respiration rates measured on seemingly dormant seedlings or trees may not represent only the maintenance component of respiration.

Acknowledgments

We thank Ben Seaman, Goeff Eerkes, Sarah Lieffers, Alain Plante and Line Blackburn for field and laboratory assistance. The study was financially supported by Ainsworth lumber, Alberta-Pacific Forest Industries, Daishowa Marunouchi International, Millar Western Forest Products, Slave Lake Pulp Corporation, Weyerhaeuser Canada, the University of Alberta and the Natural Sciences and Engineering Research Council of Canada.

References
