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Variation in sugar maple root respiration with root diameter and soil depth

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Summary Root respiration may account for as much as 60% of total soil respiration. Therefore, factors that regulate the metabolic activity of roots and associated microbes are an important component of terrestrial carbon budgets. Root systems are often sampled by diameter and depth classes to enable researchers to process samples in a systematic and timely fashion. We recently discovered that small, lateral roots at the distal end of the root system have much greater tissue N concentrations than larger roots, and this led to the hypothesis that the smallest roots have significantly higher rates of respiration than larger roots. This study was designed to determine if root respiration is related to root diameter or the location of roots in the soil profile. We examined relationships among root respiration rates and N concentration in four diameter classes from three soil depths in two sugar maple (*Acer saccharum* Marsh.) forests in Michigan. Root respiration declined as root diameter increased and was lower at deeper soil depths than at the soil surface. Surface roots (0–10 cm depth) respired at rates up to 40% greater than deeper roots, and respiration rates for roots < 0.5 mm in diameter were 2.4 to 3.4 times higher than those for roots in larger diameter classes. Root N concentration explained 70% of the observed variation in respiration across sites and size and depth classes. Differences in respiration among root diameter classes and soil depths appeared to be consistent with hypothesized effects of variation in root function on metabolic activity. Among roots, very fine roots in zones of high nutrient availability had the highest respiration rates. Large roots and roots from depths of low nutrient availability had low respiration rates consistent with structural and transport functions rather than with active nutrient uptake and assimilation. These results suggest that broadly defined root classes, e.g., fine roots are equivalent to all roots < 2.0 mm in diameter, do not accurately reflect the functional categories typically associated with fine roots. Tissue N concentration or N content (mass × concentration N) may be a better indicator of root function than root diameter.

Keywords: Acer saccharum, modeling, root function, root respiration, root nitrogen.

Introduction

Root production and respiration can consume large portions of net primary productivity in forest ecosystems (Grier et al. 1981, Keyes and Grier 1981, Vogt et al. 1986, Bowden et al. 1993, Hendrick and Pregitzer 1993, Schimel et al. 1994). Consequently, much research has focused on understanding the factors that control C allocation to belowground processes. Many of these studies have focused on fine roots, which often comprise a majority of the C allocated belowground, and fine roots have high rates of respiration and turnover compared to larger roots. The definition of a fine root, however, varies among studies. Joslin and Henderson (1987) considered all roots < 5 mm to be fine roots. In other studies, the upper diameter for a fine root has typically been set at 2 mm (Hendrick and Pregitzer 1992, 1993, Hendricks et al. 1993) or 1 mm (Fahey and Hughes 1994, Burton et al. 1996, Zogg et al. 1996). It is known that many root branch orders and developmental states can occur within such diameter classes (Goldfarb et al. 1990, Hendrick and Pregitzer 1992, Pregitzer et al. 1997). Furthermore, roots of different sizes or orders within broadly defined classes probably perform different functions (e.g., nutrient uptake, water uptake or transport to other tissues), which should result in different rates of metabolic activity. Similarly, roots of a given size might differ in function or degree of metabolic activity in deeper, nutrient-poor mineral soil horizons compared with those in organic-rich surface horizons.

Diameter and depth classes are used rather than root orders or functional classes because they allow researchers to process samples systematically in a timely fashion. From a practical standpoint, it is difficult to imagine avoiding the use of such sampling schemes. Dividing root systems by branch order is extremely time consuming, and the use of functional classes causes the sample processing to rely heavily on subjective classifications or extensive previous knowledge. Still, it is desirable to know how accurately the root diameter and depth classes typically used for research purposes represent functional categories of the root system, and how combining roots of a variety of sizes and depths might impact estimates of

ecosystem-level processes such as root respiration.

We recently reported that the smallest lateral tree roots had much higher concentrations of N than slightly larger "fine" roots (Pregitzer et al. 1997). It seems logical that the smallest roots should have the highest rates of respiration because respiration rate is related to plant N concentration (Ryan 1991, Ryan et al. 1996). Thus, any variable that influences N availability in the soil, for example, soil depth or N deposition (Magill et al. 1997), should also influence root N concentration and respiration rate. We have attempted to confirm this supposition by examining respiration rates and N concentrations in roots of four diameter classes (< 0.5, 0.5–1.0, 1.0–2.0, and 2.0–10.0 mm) from three soil depths (0–10, 20–30, and 40–50 cm) in northern hardwood forests in Michigan. Objectives were: (1) to assess differences in root respiration among different diameter classes and soil depths; (2) to determine if N concentration could be used to predict root respiration across the root classes; and (3) to assess the extent to which different root functions are reflected by root diameter and depth classes.

Methods

Root samples were collected from two sugar maple forests in Michigan: Site A is located in the northwestern portion of Michigan's Upper Peninsula (46°56′ N, 88°53′ W), and Site B is located in northern lower Michigan (45°33′ N, 84°51′ W). Both sites are occupied by second-growth northern hardwood forests, approximately 85 years in age, occurring on sandy, well-drained spodosols (Burton et al. 1991, MacDonald et al. 1991). Sugar maple is the dominant species at both sites, comprising more than 85% of stand basal area. Six 30 × 30 m study plots are located at each site. Three of these plots are control plots that have existed since 1987. The others are fertilized plots that were established in 1994 and have received annual fertilizer applications of 30 kg NO_3-N ha^{-1} since that time (Zogg et al. 1996). To date, the NO_3 additions have not altered root respiration or fine root N concentration on the fertilized plots (Zogg et al. 1996), so they are not separated from the control plots in this report.

In late August 1996, a small but characteristic portion of the root system of an adult sugar maple tree was collected from the upper 10 cm of soil at Site A in order to describe the typical architecture of the sugar maple roots being used to measure root respiration. We made every effort to extract the roots without disrupting any of the small lateral branches. The roots were immediately placed in a cooler and returned to the laboratory where soil was teased from the roots with deionized water and tweezers. Roots were kept in deionized water at 1 °C to prevent desiccation.

The branching root system was then dissected by order following the methods of Pregitzer et al. (1997), except that we labeled the smallest laterals as first-order roots following the approach of Fitter (1982, 1987). Root diameters and lengths were measured with a microscope (25×) fitted with an ocular micrometer. A scaled drawing of the branching root system was also constructed and digitized.

Samples for the measurement of root respiration were collected from Sites A and B in mid-July, 1996. Respiration rates were determined for excised roots in the < 0.5, 0.5–1.0, 1.0–2.0, and 2.0–10.0 mm diameter classes at three different soil depths: 0–10, 20–30, and 40–50 cm. Four soil cores (5 cm in diameter) from each soil depth were taken from a 10-m wide buffer surrounding each of the six plots at both sites. For the 0–10 cm depth, cores were taken beneath the loose litter layer (O_i) and were comprised of O_e and O_a material and mineral soil (A + E horizons) to a total depth of 10 cm. Beneath these cores, holes were dug to a depth of 20 cm and the 20–30 cm cores were collected. Holes were then deepened to 40 cm and the 40–50 cm cores were taken. The same locations were used for all soil depths to minimize disturbance to the study sites. To ensure the roots were fresh, no more than two plots were sampled at a time and soil cores were processed in laboratories located less than 30-min travel time from the sites. Sample processing and respiration measurements were completed within 3 h of sample collection.

Roots were sorted by diameter class then rinsed free of soil and organic material with deionized water. Samples were blotted with tissue paper to remove excess water, and 0.5-g subsamples (fresh weight) were wrapped in moistened tissue paper for use in respiration measurements. Root respiration (O_2 consumption at 24 °C) was measured with temperature-controlled O_2 electrodes (Model LD 2/2, Hansatech Instruments Ltd., Norfolk, England) connected to constant temperature circulating water baths (Burton et al. 1996, Zogg et al. 1996, Burton et al. 1997). Roots of different size classes were assigned randomly to four complete systems that were operated simultaneously, allowing respiration of all four diameter classes in a sample to be measured within 3 h of core collection. Following respiration measurements, roots were frozen until they could be returned to Michigan Technological University. At the MTU laboratory, root samples were oven-dried (65 °C, 24 h) for determination of dry weights, ground, and analyzed for N with a Carlo Erba NA 1500 Series II elemental analyzer (C.E. Elautech, Lakewood, NJ).

The relationship between root N concentration and respiration rate was examined by linear regression (Neter et al. 1989). Both the respiration and N data were further analyzed as a three-factor (site, root diameter, soil depth) analysis of variance (Montgomery 1984). All dry weights were corrected for ash content, which was always < 5%.

Results

The root system of sugar maple is finely divided with at least seven branch orders (Figure 1). More than 80% of the individual roots and total root length depicted in Figure 1 can be accounted for by roots < 0.5 mm in diameter (data not shown).

Root respiration rates were lower at Site A than at Site B (Table 1 and Figure 2A). Root respiration rates were much higher in surface soils (0–10 cm depth) than in deeper soils, and they were greater for roots < 0.5 mm than for larger diameter roots (Figure 2A). Surface roots < 0.5 mm in diameter respired at rates 40% greater than similar sized roots deeper in the soil, and respiration rates of roots < 0.5 mm in diameter were 2.4 to 3.4 times those of roots in larger diameter classes. Mean respiration rates did not differ between the 20–30 and

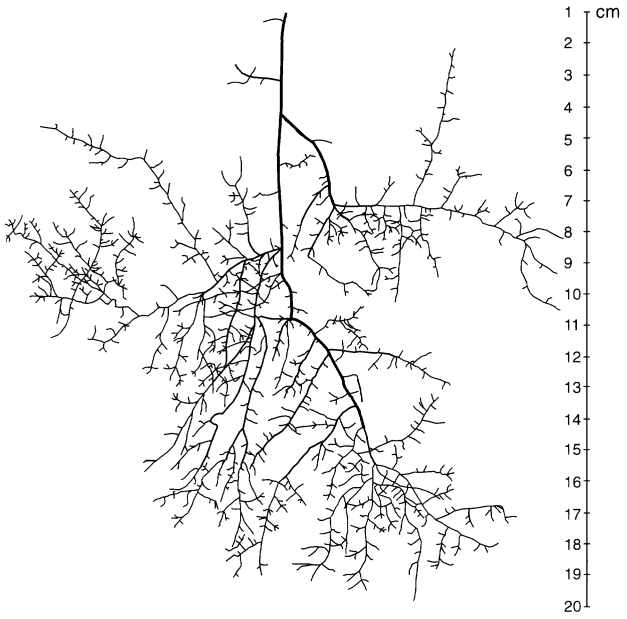

Figure 1. Sugar maple roots from the upper 10 cm of soil collected from Site A (46°56′ N, 88°53′ W). Root lengths are drawn to scale, whereas diameters are approximate.

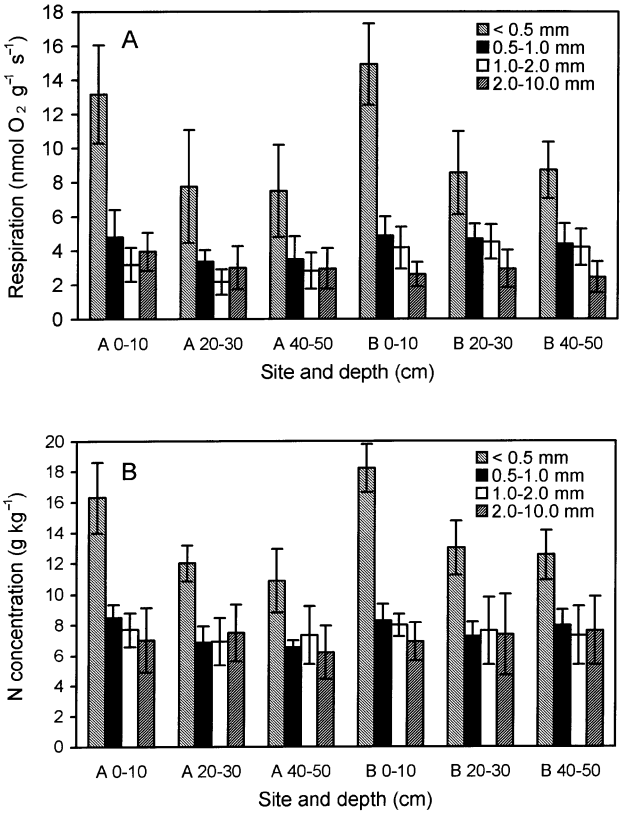

Figure 2. A. Root respiration (24 °C) by diameter class and soil depth at two Michigan northern hardwood forests. Error bars indicate one standard deviation of the mean (n = 6). B. Root N concentration by diameter class and soil depth at two Michigan northern hardwood forests. Error bars indicate one standard deviation of the mean (n = 6).

40–50 cm soil depths or between the 1.0–2.0 and 2.0–10.0 mm diameter classes. The much greater difference in respiration rates among root diameter classes in surface soils compared with deeper soils (Figure 2A) resulted in a highly significant diameter by depth interaction (Table 1).

Because the pattern in root N concentration among sites, root diameters and soil depths was similar to that observed for root respiration rate (Table 1 and Figure 2B), there was a highly significant linear relationship between fine root N concentration and rate of respiration. Root N concentration explained 70% of the observed variation in respiration rate across all samples and diameter classes (Figure 3).

Discussion

Most sugar maple roots are < 0.5 mm in diameter (Hendrick and Pregitzer 1993), and most of the absorbing root length is associated with short lateral roots < 0.5 mm in diameter (Pregitzer et al. 1997). Figure 1 is congruent with these earlier reports. The architecture of sugar maple root systems from mature trees is very similar to that of seedlings in terms of mean root length and diameter.

Root respiration can be sensitive to the [CO_2] at which measurements are made (Qi et al. 1994, Burton et al. 1997), and thus rates measured in the laboratory can differ from those that would occur at the actual soil [CO_2] in the field. For the two sites used in this research, we have found that root respi-

Table 1. Analysis of variance of respiration rate and N concentration of fine roots of sugar maple in two northern hardwood forests (n = 144).

		Respiration rate		Tissue N concentration	
Source	d.f.	MS	P	MS	P
Site	1	19.7	0.007	0.17	0.014
Diameter	3	392.8	< 0.001	3.76	< 0.001
Soil depth	2	56.0	< 0.001	0.47	< 0.001
Site × diameter	3	8.5	0.023	0.03	0.362
Site × soil depth	2	1.6	0.539	0.02	0.543
Diameter × soil depth	6	29.6	< 0.001	0.24	< 0.001
Site × diameter × soil depth	6	1.0	0.887	0.01	0.825
Error	120	2.6		0.03	

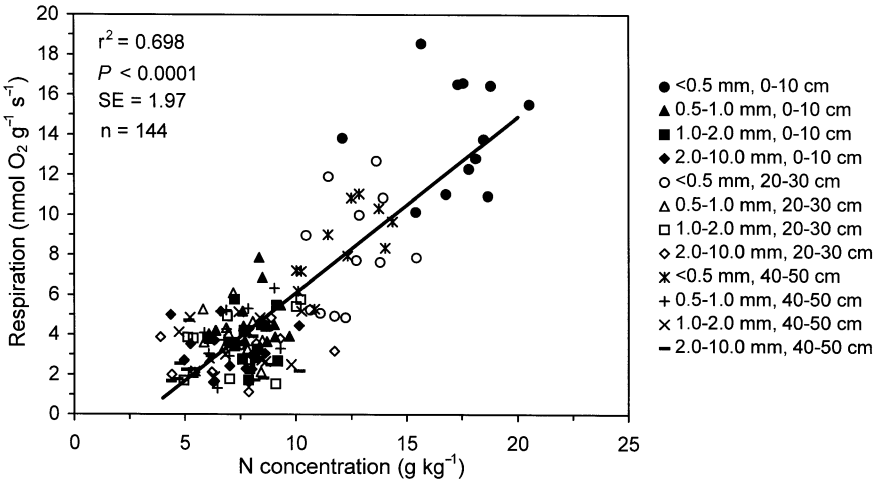

Figure 3. Root respiration versus N concentration for two Michigan northern hardwood forests. The plotted regression line displays the linear relationship of the data (n = 144).

ration declines as measurement [CO_2] increases from 350 to 3000 μl l^{-1}, with little additional change in respiration rate at measurement CO_2 concentrations above 3000 μl l^{-1} (Burton et al. 1997). The O_2 consumption rates reported in this paper were obtained at measurement CO_2 concentrations of 4000 to 14,000 μl l^{-1}. Actual respiration rates of surface roots in the field, where soil [CO_2] is 1200 μl l^{-1}, would be expected to be slightly higher (about 16%) than those reported here (Burton et al. 1997). In contrast, O_2 consumption rates for deeper roots in the field are probably less than 16% greater than those reported here, because soil [CO_2] at 20–30 and 40–50 cm depths in northern hardwoods is typically in the 1000–5000 μl l^{-1} range (Yavitt et al. 1995).

Differences in respiration rate among root diameter classes and soil depths at the sites were consistent with possible effects of variation in root function on metabolic activity. It is not surprising that the < 0.5 mm roots from the 0–10 cm soil depth exhibited the highest respiration rates, because the surface mineral soil and organic layers are zones of high nutrient availability and roots in this zone, especially very fine, high surface-area roots such as those < 0.5 mm in diameter, are active sites of nutrient uptake. Larger diameter surface roots, whose primary functions are support and transport of nutrients and water from the very fine roots to other portions of the tree, are not as active in nutrient uptake and would be expected to have lower respiration rates than the very fine roots, as was the case at both sites. Roots at deeper depths function more for water uptake and support than for nutrient uptake. These deeper roots have large amounts of structural and conductive tissue (Cox 1975) and low N concentration per unit mass (Figure 2B). The lower respiration rates observed for these deeper roots compared with surface roots are consistent with functions that require less metabolic activity per unit mass.

Mean root respiration at Site B was 1.15 times that at Site A. This result agrees with previous results for roots < 1 mm at these sites, in which higher root respiration at Site B was associated with greater site N availability and higher root N concentrations (Burton et al. 1996, Zogg et al. 1996). We conclude that greater nutrient availability at Site B than at Site A has led to higher root metabolic activity associated with greater nutrient uptake, assimilation and transport per unit C.

We previously reported a positive, linear relationship between root N concentration and root respiration among four northern hardwood sites having different rates of N mineralization (Burton et al. 1996, Zogg et al. 1996). Within sites, however, these studies did not find linear relationships between root N and root respiration. This was attributed in part to variation within sites in root N concentrations that were small relative to between-site differences, and to the use of a single diameter-depth class (0–10 cm deep, < 1.0 mm in diameter, with most of the roots < 0.5 mm). Similarly, examination of Figure 3 indicates that, within a diameter-depth class, variation in N concentration and respiration rates is much less than occurs for the entire data set, and that much of the variation in root respiration rate within a diameter-depth class is due to factors other than root N concentration. It is only when root respiration rates are compared across diameter-depth classes that vary widely in root N concentration that the effects of N concentration on root respiration rate become evident (Figure 3).

At all soil depths and sites, the smallest roots had the highest respiration rates. The < 0.5 mm class contained all of the terminal root segments and often the next several higher root orders as well (Figure 1). This diameter class also contained all of the actively elongating root tips and the youngest, unsuberized portions of the root system (Goldfarb et al. 1990, M.J. Laskowski, personal observation).

Clearly, combining roots from multiple diameter classes or several depths can obscure root system activity. Estimates of root system activity similarly could be in error, especially in circumstances where the response to a factor is nonlinear. In some cases, the effect of a factor such as N may be the same or similar across a variety of root diameter or functional classes. This was generally the case for the roots that we studied (Figure 3). However, knowing that the effect of N on root respiration is the same for all root size and depth classes does not mean that roots of different functional classes can or should be sampled and analyzed together. In our case, although 70% of the variation in respiration is explained by root N concentration, much variability still exists. Results of an analysis of

covariance, with N as the covariate, indicated that this remaining variability is sufficiently structured to create significant differences among the diameter and depth classes that cannot be explained by N. These differences could be related to one or more of several factors, such as the availability of nutrients other than N, root age, use of roots for nutrient and C storage, secondary chemical defense, or degree of symbiotic association with mycorrhizal fungi. Although we cannot explain all of the differences observed among the diameter and depth classes, they are probably related to root function. Other aspects of root activity, such as root longevity, similarly might be controlled in part by root function.

Ideally, functional classes should be the basis on which root systems are sampled and modeled; however, this would be time consuming and, in many cases, impractical. Nonetheless, it is important that root sampling schemes be linked to root function whenever possible and that diameter classes, when used as a basis for root sampling, be matched as closely as possible to functional categories.

We have demonstrated that root respiration is much greater per unit C in the smallest sugar maple size class (roots < 0.5 mm in diameter) compared with larger "fine roots" (roots > 0.5 mm, but < 2.0 mm in diameter; Figure 2A). Pregitzer et al. (1997) reported that N concentrations of sugar maple and white ash (*Fraxinus americana* L.) increase toward the distal end of the branching root system until diameters decline to about 0.25 mm. Root respiration costs are not simply related to C content, rather they increase in a linear manner as N increases (Figure 3). Respiration rates per gram C can vary threefold within traditional fine root size classes, i.e., all sugar maple roots < 2 mm in diameter.

The relationship between root respiration and N concentration confirms the findings of Ryan et al. (1996). It seems likely that N concentration of fine roots is closely related to growth and other factors such as protein content, nutrient assimilation and maintenance of ionic gradients. Understanding how root N concentration varies according to root architecture may be a useful and practical surrogate for understanding how root enzyme activity and respiration rate vary within the complex and finely divided branching root system of temperate deciduous trees (Figure 1).

In conclusion, short lateral roots < 0.5 mm in diameter account for most of the length of the fine root system of sugar maple (Figure 1; Pregitzer et al. 1997). Within the root system, these roots have the highest concentrations of N and much higher rates of respiration (Figure 2). Across all size classes and soil depths, root respiration rate was linearly related to tissue N concentration (Figure 3). Factors that increase root N concentration (e.g., atmospheric N deposition; Magill et al. 1997), will increase rates of root respiration. Arbitrary root size classes are probably poorly related to the functional categories that have been typically assigned to them. Tissue N concentration or root N content (mass × N concentration) may be better indicators of root function than root diameter.

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