Oecologia (1997) 111:302–308

Kurt S. Pregitzer · Mark E. Kubiske
Chui Kwan Yu · Ronald L. Hendrick

Relationships among root branch order, carbon, and nitrogen in four temperate species

Received: 25 November 1996 / Accepted: 27 March 1997

Abstract The objective of this study was to examine how root length, diameter, specific root length, and root carbon and nitrogen concentrations were related to root branching patterns. The branching root systems of two temperate tree species, *Acer saccharum* Marsh. and *Fraxinus americana* L., and two perennial herbs from horizontal rhizomes, *Hydrophyllum canadense* L. and *Viola pubescens* Ait., were quantified by dissecting entire root systems collected from the understory of an *A. saccharum-Fagus grandifolia* Ehrh. forest. The root systems of each species grew according to a simple branching process, with laterals emerging from the main roots some distance behind the tip. Root systems normally consisted of only 4–6 branches (orders). Root diameter, length, and number of branches declined with increasing order and there were significant differences among species. Specific root length increased with order in all species. Nitrogen concentration increased with order in the trees, but remained constant in the perennial herbs. More than 75% of the cumulative root length of tree seedling root systems was accounted for by short (2–10 mm) lateral roots almost always < 0.3 mm in diameter. Simple assumptions suggest that many tree roots normally considered part of the dynamic fine-root pool (e.g., all roots < 2.0 mm in diameter) are too large to exhibit rapid rates of production and mortality. The smallest tree roots may be the least expensive to construct but the most expensive to maintain based on an increase in N concentration with order.

Key words Fine roots · Architecture · Nitrogen · Turnover

K.S. Pregitzer (✉)
School of Forestry and Wood Products,
Michigan Technological University, 1400 Townsend Ave.,
Houghton, MI 49931, USA

M.E. Kubiske
Department of Forestry, Box 9681,
Mississippi State University,
Mississippi State, MS 39762-9681, USA

C.K. Yu
Tall Timbers Research Station, Route 1, Box 678,
Tallahassee, FL 32312, USA

R.L. Hendrick
School of Forest Resources, University of Georgia,
Athens, GA 30602, USA

Introduction

It is widely appreciated that a better understanding of the factors that regulate carbon (C) allocation to roots and root turnover are important research objectives (Vogt et al. 1986; Gower et al. 1992; Nadelhoffer and Raich 1992; Hendricks et al. 1993; Fahey and Hughes 1994; Schoettle and Fahey 1994). Understanding C allocation to roots entails accurate measurements of the C costs for root construction and maintenance, root longevity, sloughing and exudation, allocation to mycorrhizal fungi, herbivory, and pathogenic losses. All of these potential fates of C are important to ecosystem function, and none are easily measured. Root production, death, and decay are only parts of the complex below-ground C cycle.

As a plant grows and develops, multiple orders of lateral roots arise from the primary axis. Most of the larger roots, like the branches of a tree, primarily serve support, transport, and storage functions, and they have relatively long average life expectancies. The small-diameter "fine roots" are located at the distal end of the branching root system. Sometimes these roots are adventitious. The overall length of the fine-root system is most important in determining the rate of water and nutrient uptake (Molz 1981; Nye and Tinker 1977).

We understand the importance of shoot system modularity, and how ontogeny and environment influence leaf age and C gain (Field 1983; Field and Mooney 1983; Reich et al. 1992). Like leaves, fine roots and mycorrhizae are modular in nature, and it is clear that the production and mortality of these roots can be

very dynamic (Eissenstat and Caldwell 1988; Hendrick and Pregitzer 1992; Hooker et al. 1995; Pregitzer et al. 1995; Fitter 1996). However, we do not understand which fine roots die and decay. Populations of fine roots are often studied by observing the change in the proportions of live or dead roots of a certain size class. In forests, roots less than 1 or 2 mm in diameter are commonly considered to be those exhibiting relatively rapid changes in demography. Categorizing roots by size ignores the functional significance of root architecture or the position of the root in the root system. Because it is very difficult to study intact root systems, the rationale for studying roots of a maximum size is understandable. However, studies with *Acer saccharum* Marsh. have clearly demonstrated that many of the roots sometimes considered a part of the dynamic fine-root pool in forests are too large in diameter to exhibit rapid rates of growth and mortality. Hendrick and Pregitzer (1993b) report that about 80% of the length of the fine-root system in forests dominated by *A. saccharum* was accounted for by roots less than 0.5 mm in diameter.

The objective of this study was to examine how root length, diameter, specific root length (SRL), and root nitrogen (N) concentration were related to root order, i.e., position on the root system. A better understanding of how the root system is constructed would enable a deeper appreciation of the costs (sensu Eissenstat 1992) of building, maintaining, and shedding different portions of this branching network. We measured N as well as C because of the direct link between rates of fine root respiration and N content (Ryan 1991), and the lack of data on how N concentration is related to root order.

Materials and methods

Study site description and root system collection

The root systems of four species growing in the forest seedling-ground cover layer were collected from a sugar maple-beech-dominated woodlot (Lott Woodlot) on the Michigan State University Campus in East Lansing, Section 6, Town 3 North, Range 1 West, Ingham County, Mich. The species studied were two perennial herbs from horizontal rhizomes, *Viola pubescens* Ait. (downy yellow violet) and *Hydrophyllum canadense* L. (broad-leaved waterleaf), and seedlings of two trees, *A. saccharum* Marsh. (sugar maple), and *Fraxinus americana* L. (white ash). We chose *A. saccharum* for this study because we have worked with it before (Hendrick and Pregitzer, 1992, 1993a, b, 1996) and *F. americana* because it is a common associate of *A. saccharum* in natural forests. The two perennial herbaceous species were chosen for a contrast among life-forms. All species were collected from a single 15-m-radius plot.

Stems of the trees were between 0.5–1.0 cm in diameter at ground line and the trees were all less than 1.5 m tall. The entire root systems of three specimens of each species were very carefully excavated in mid-July 1993. The soil (Marlette fine sandy loam, Glossoboric Hapludalf, fine-loamy, mixed, mesic) was moist and friable with a mull humus layer. This aided the recovery of intact root systems. Some roots were undoubtedly lost in the excavation process, but we attempted to recover entire root systems without damaging them. Once excavated, the specimens were severed at the root collar and gently washed with deionized water to remove soil particles. Five primary laterals were then cut from the main axis of each specimen. These whole segments of the root system were sealed in plastic bags and frozen.

Root system dissection

Roots were kept in deionized water to prevent desiccation. They were classified by order beginning with the primary (first-order) root and increasing sequentially with each branch from the proximal to distal portions of the root system. This is the classic "developmental" approach to describing root architecture (Fitter 1982). Even though there are other very useful ways to study the form and function of root architecture (Fitter 1987, 1996), we chose to use the developmental approach because it corresponds with the ontogeny of the root system.

A fine paintbrush was used to remove remaining soil particles from the moist roots under a microscope. Care was taken to avoid desiccation. Length, diameter at the midpoint, and internodal distance were measured for every individual root on five of the second-order roots (primary laterals) collected from each of the 12 plants. Thus, 60 primary laterals (termed "second-order" roots in the Results) were completely dissected (4 species × 3 specimens per species × 5 primary laterals per specimen). These measurements also enabled calculation of the number of branches subtending any individual root of a given order. Diameters, lengths, and internodal distances were determined with a microscope (×25) fitted with an ocular micrometer.

Each of the 60 primary laterals was dissected by order and all individual roots of a given order were homogonized by plant (three plants per species), oven dried (70°C for 48 h), weighed, and finely ground. Root subsamples were placed in a muffle furnace (450°C for 4 h) to determine ash content; dry weights were corrected for ash content. Ground samples of roots from each order were combined on an individual-plant basis to assure a sufficient sample for C and N analysis. Samples of each order were analyzed for C and N concentration with a Carlo Erba elemental analyzer (model NA 1500, Series 2). SRL (m g^{-1}) was determined for each root order from the cumulative fresh lengths and ash-corrected mass.

Data analysis

Mean values were tabulated for root length, diameter, branches per root, proportion of roots with any branches, internodal distance, C and N concentration, C/N ratio, and SRL. Pooled means were used as observations in a two-way ANOVA with species and root order as experimental factors. These pooled means were log-transformed for root length, diameter, branches per root, and internodal distance, whereas means were arcsine square root transformed for root C, N, C/N, and SRL to satisfy model assumptions. For every parameter, the interaction term was significant ($P < 0.05$) and Fisher's protected LSD test was applied to paired comparisons among root orders within each species, and among species within each order. The level of significance for pairwise comparisons was $P < 0.05$. For root orders that were outside of the full-factorial 4×4 or 4×5 species × order matrix (i.e., orders >4 or 5 depending upon the parameter being tested), a *t*-test was used for the appropriate comparisons.

Schematic diagrams representing the statistical variation in root architecture were constructed for the two tree species. These diagrams represent the mean branching pattern plus or minus one standard deviation. Because of difficulty in condensing three-dimensional structures into two-dimensional figures, some actual values were compromised in favor of others according to the following rules: (1) lengths were always to scale, (2) proportion of roots with branches was always accurate, (3) root complexity decreased from proximal to distal, (4) accuracy in root numbers had priority over accuracy in internodal distance, (5) accuracy in root length had priority over accuracy in root numbers, (6) branch angle and phyllotaxy were arbitrary but consistent among species and root orders.

Table 1 Pairwise comparisons of root characteristics. Means(±SD) among root orders within each species, and among species within each order, followed by the same letter are not significantly different ($P > 0.05$). For values with *asterisks*, $n = 1$

Order	*Acer saccharum*	*Fraxinus americana*	*Viola pubescens*	*Hydrophyllum canadense*
Root length (mm)				
1	140.0 ± 43.6 a	240.0 ± 60.3 b	56.0 ± 11.4 f	100.0 ± 15.3 a
2	45.7 ± 22.9 b	72.9 ± 13.7 h	94.0 ± 42.0 ah	125.8 ± 22.8 a
3	7.5 ± 0.5 c	10.8 ± 0.5 c	9.7 ± 0.4 c	10.7 ± 0.6 c
4	3.3 ± 0.1 d	5.9 ± 0.2 g	4.3 ± 0.1 dg	4.9 ± 0.2 g
5	2.1 ± 0.1 e	3.9 ± 0.3 h	2.5 ± 0.2 e	3.0 ± 0.2 ef
6	2.0 ± 0.2 e	3.6 ± 0.7 h		
7	2.0*			
Root diameter (mm)				
1	3.27 ± 0.65 a	4.83 ± 1.15 b	5.10 ± 0.60 b	12.73 ± 2.68 e
2	0.45 ± 0.04 be	0.67 ± 0.05 d	0.64 ± 0.05 de	0.87 ± 0.12 d
3	0.24 ± 0.01 cf	0.28 ± 0.01 c	0.19 ± 0.01 fh	0.15 ± 0.04 h
4	0.22 ± 0.01 c	0.21 ± 0.01 c	0.11 ± 0.01 a	0.11 ± 0.01 ah
5	0.21 ± 0.01 c	0.16 ± 0.01 ce	0.11 ± 0.01 a	0.10 ± 0.00 a
6	0.20 ± 0.01 c	0.10 ± 0.00 e		
7	0.23*			
Number of branches per root (all roots)				
1	32.67 ± 1.20 a	35.00 ± 11.4 a	55.00 ± 6.43 d	26.00 ± 5.03 a
2	19.40 ± 2.07 e	31.20 ± 4.80 ag	36.93 ± 4.81 g	24.21 ± 3.62 ae
3	2.89 ± 0.24 bc	1.54 ± 0.20 b	2.16 ± 0.15 b	1.64 ± 0.19 b
4	0.95 ± 0.08 c	0.33 ± 0.05 cf	0.24 ± 0.03 f	0.31 ± 0.06 cf
5	0.07 ± 0.02 d	0.03 ± 0.02 d		
6	0.00 ± 0.00			
7	0.00*			
Proportion of roots with any branches (%)				
1	100 ± 0 a	100 ± 0 a	100 ± 0 a	100 ± 0 a
2	100 ± 0 a	100 ± 0 a	100 ± 0 a	100 ± 0 a
3	57 ± 18 c	27 ± 6 b	48 ± 10 bc	33 ± 6 bc
4	24 ± 4 d	10 ± 4 e	8 ± 6 e	6 ± 5 e
5	3 ± 2 e	1 ± 1 d	0 ± 0 f	0 ± 0 f
6	0 ± 0 f	0*		
7	0*			
Internodal distance (mm)				
1	4.4 ± 0.7 c	7.1 ± 1.0 a	1.0 ± 0.1 f	3.7 ± 0.5 bc
2	2.5 ± 0.2 bd	2.5 ± 0.1 b	2.4 ± 0.1 b	5.2 ± 0.3 c
3	2.2 ± 0.1 d	3.5 ± 0.1 bc	3.0 ± 0.1 bd	3.8 ± 0.2 bc
4	1.7 ± 0.1 d	4.1 ± 0.3 c	3.3 ± 0.2 bc	2.9 ± 0.2 b
5	1.9 ± 0.2 d	6.3 ± 1.7 d		3.9 ± 0.7 bc
6	1.7 ± 0.2 d			
Root C (mg/g)				
1	475.3 ± 0.7 a	459.3 ± 13.2 a	410.6 ± 2.3 cd	390.7 ± 4.7 d
2	502.4 ± 4.9 ab	487.4 ± 4.1 b	428.4 ± 3.6 c	409.0 ± 5.9 d
3	486.6 ± 5.7 a	483.1 ± 6.0 ab	434.3 ± 10.5 ce	433.9 ± 7.6 e
4	491.5 ± 3.6 a	470.9 ± 8.2 ab	432.1 ± 15.2 ce	435.8 ± 16.2 e
5	479.0 ± 11.5 a	466.0 ± 27.4 ab	471.2*	436.3*
6	497.5 ± 2.4 a			
Root N (mg/g)				
1	11.5 ± 0.5 a	17.2 ± 4.2 b	33.0 ± 1.3 e	27.6 ± 0.6 ce
2	13.0 ± 0.6 b	14.3 ± 0.6 b	28.3 ± 0.6 ce	25.6 ± 0.9 c
3	17.4 ± 0.7 c	21.4 ± 1.0 a	28.9 ± 1.2 e	28.0 ± 0.6 ce
4	23.1 ± 0.7 d	26.2 ± 0.5 df	29.2 ± 1.1 ef	30.7 ± 1.9 e
5	24.4 ± 1.4 d	28.1 ± 1.0 d	31.0*	34.1*
6	29.4 ± 1.2 e			
Root C/N				
1	41.6 ± 1.7 a	31.0 ± 6.0 d	12.5 ± 0.5 h	14.2 ± 0.4 h
2	39.1 ± 1.6 a	34.6 ± 1.4 e	15.2 ± 0.4 h	16.2 ± 0.9 h
3	28.1 ± 1.0 b	22.8 ± 1.1 f	15.1 ± 0.6 h	15.5 ± 0.3 h

(Continued)

Order	*Acer saccharrum*	*Fraxinus americana*	*Viola pubescens*	*Hydrophyllum canadense*
4	21.4 ± 0.6 c	18.0 ± 0.4 g	14.8 ± 0.2 h	14.2 ± 0.4 h
5	19.9 ± 0.9 cd	16.6 ± 0.4 cg	15.2*	12.8*
6	17.0 ± 0.6 d			
Specific root length (mg^{-1})				
1	0.3 ± 0.0 af	0.2 ± 0.0 ae	0.5 ± 0.0 f	0.1 ± 0.0 e
2	11.5 ± 1.7 b	9.8 ± 3.1 b	13.0 ± 1.8 b	16.2 ± 9.4 b
3	39.5 ± 8.6 c	69.2 ± 8.7 c	204.0 ± 77.3 d	182.5 ± 67.2 d
4	70.5 ± 8.8 cd	108.2 ± 12.5 cd	697.2 ± 76.2 a	684.0 ± 210.0 a
5	83.1 ± 13.1 de	169.3 ± 20.9 d	1148.0 ± 569.0 a	715.8 ± 89.6 a
6	131.1 ± 48.1 e	170.9*		688.7*
7	80.2*			

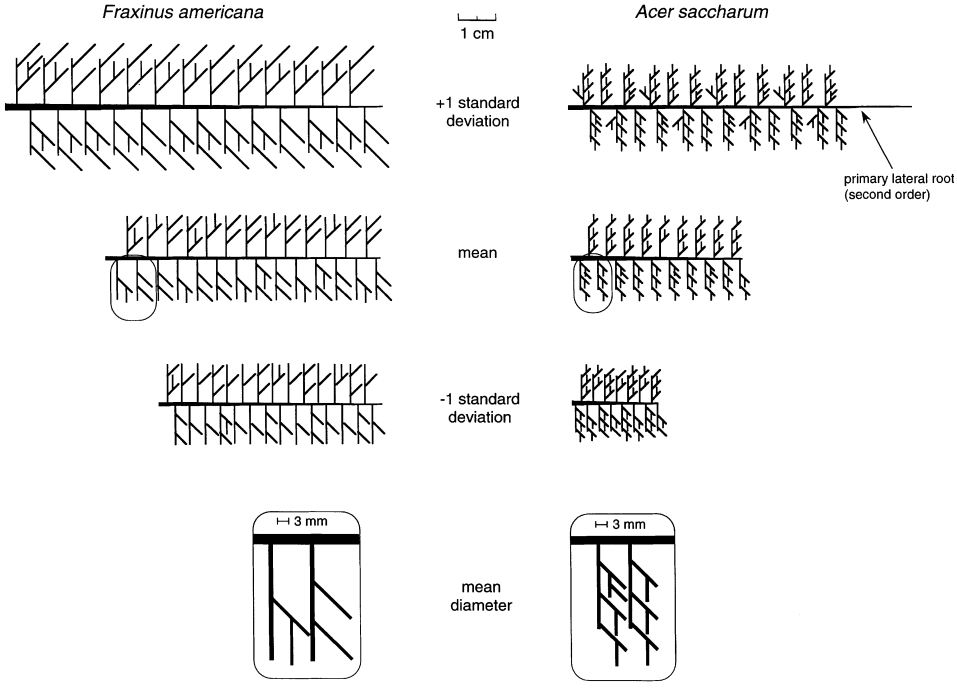

Fig. 1 Scaled schematic diagrams of tree roots based on measurements of three seedlings of each species. Three, second-order root systems are depicted representing mean and ±SD of root length, number of branches, and internodal distances. *Insets* show a threefold magnification of the *circled regions* of the mean root to illustrate scaled root diameters (see Materials and methods for a description of the rules used to assemble the schematics)

Results

The length of an individual root decreased from the proximal to the distal end of the root system (Table 1). Fourth-, fifth- and sixth-order roots of the tree species ranged from 2 to 6 mm in length. The roots of *F. americana* were significantly longer than those of *A. saccharum*. The number of branches per root and the proportion of individual roots with branches decreased with increasing order. Mean root diameter decreased progressively with increasing root order, and again, there were significant differences among species (Table 1). *A. saccharum* root systems usually branched five times, with occasional sixth- and seventh-order roots. *F. americana* tended to branch less and the individual roots were longer, thinner, and further apart than those of *A. saccharum* (Table 1, Fig. 1). The two perennial species, *V. pubescens* and *H. canadense*, had much simpler branching patterns and rarely branched more than four times (Table 1).

More than 80% of the total length of the *A. saccharum* and *F. americana* root systems were accounted for by roots <1.0 mm in diameter, roots of orders three–seven (Fig. 2). Therefore, the vast majority of tree root length was in short lateral "branches" with individual roots rarely >0.3 mm in diameter (Table 1).

As expected, the C concentration of roots within a species was relatively constant, although there were significant differences among species (Table 1). The contrast between the trees and herbaceous species was most notable, probably reflecting anatomical differences among the life-forms.

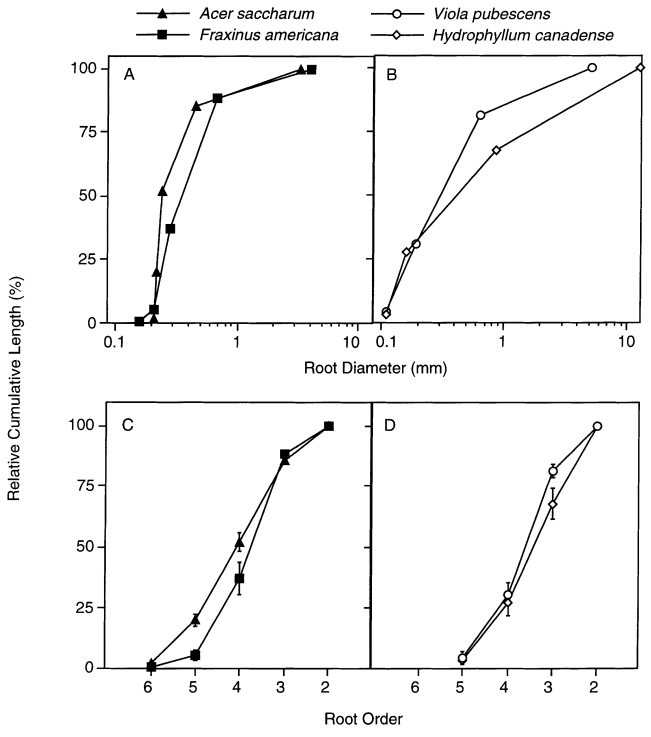

Fig. 2 Relative cumulative length of roots of four species according to the mean root diameter of a given order (**A**, **B**) and by root order (**C**, **D**). Note that the cumulative diameter distributions of the trees (**A**) begin with the sixth-order root and progress to the point where the primary lateral (second-order root) was severed from the main axis. The perennial herb cumulative diameter distributions (**B**) begin with the fifth-order root and progress to the point where the second-order roots were severed from the horizontal rhizomes

Interestingly, tree roots exhibited a progressive and significant increase in N concentration toward the distal portion of the root system (Table 1). For example, third-order *A. saccharum* roots had a mean N concentration of 17.4 mg g^{-1}, while sixth-order roots had 29.4 mg g^{-1}, a 68% increase. The increase in N concentration of the short, high-order lateral tree roots resulted in a decrease in their C/N ratio (Table 1). It is noteworthy that the C/N ratio of the higher-order roots of all species was relatively low, ranging from 14 to 20.

For all species, SRL increased progressively with root order and significant differences occurred among species. For example, the longer, thinner, higher-order branches of *F. americana* (Fig. 1) were less expensive to construct per unit length compared to those of *A. saccharum* (Table 1) . In all species, the last two–three branches (orders) were both significantly shorter and much less expensive to construct per unit length, i.e., they had a greater SRL (Table 1).

Discussion

The root systems of each of these species grew by a simple branching process, with laterals emerging from the main roots some distance behind the root tip (Fig. 1). In all species, a single branch emerged at any point along the root. This is the normal pattern of growth and development for many plant species (Fitter 1996).

An important question is how the architecture of the root systems of seedlings differs from that of large, mature trees. We expect some differences to occur. For example, the length of large-diameter lateral roots in trees is proportional to tree height (Hansen 1981). Branching patterns may also vary with age, although the seven orders observed for *A. saccharum* in this study are the maximum reported for trees (Sutton and Tinus 1983). The cumulative length versus root diameter distribution shown in Fig. 2 is very similar to that reported by Hendrick and Pregitzer (1993) for two 80-year-old *A. saccharum*-dominated forests. Variability in root architecture can also be related to genotype and environment (Eissenstat 1991, 1992; Fitter and Stickland 1992; Lynch 1995; Fitter 1996). Further investigation is necessary to determine if the relationships we report here among roots that occur on different parts of the root system change significantly with plant size or age. We expect that the general relationships of decreasing length and diameter from the proximal to distal portions of the root system are common among temperate deciduous trees of any age or size.

We know that the small-diameter roots of *A. saccharum* (Hendrick and Pregitzer 1992, 1993a), like the roots of many species (Eissenstat and Caldwell 1988; Cheng et al. 1990; Pregitzer et al. 1993, 1995; Hooker et al. 1995; Fitter 1996), are produced and die rapidly. However, we do not know *which* roots die. This study did not resolve this problem, but provides some insight into the C costs of losing roots from different topological positions. For example, when *A. saccharum* or *F. americana* roots >0.5 mm in diameter die, the C cost to the plant is significant. In these tree seedlings, if a root >0.5 mm died it would take much of the remaining root system with it (Table 1, Fig. 1). In temperate deciduous forests, many of the roots 0.5–2.0 mm in diameter, often considered to be a part of the fine-root pool, probably live much longer than roots <0.5 mm in diameter. Almost all of the *A. saccharum* and *F. americana* roots that grow and die in response to seasonal growth rhythms and fluctuations in the soil environment are probably <0.5 mm in diameter (Hendrick and Pregitzer 1993b).

The consequences of ignoring the functional architecture of plant root systems at the ecosystem level remain mostly unexplored. We know that root mortality is important in below-ground C and N cycling (Vogt et al. 1986; Nadelhoffer and Raich 1992; Hendrick and Pregitzer 1993b). Obviously, it is necessary to learn which roots on the branching root system die, when they die, and what controls the probability of mortality. Do entire "branches" die, analogous to compound leaves or branchlets above ground? *F. americana* has a compound leaf. New leaves develop each spring. In the fall, the process of leaf senescence involves the dropping of individual leaflets and then the rachis. This all occurs in a

brief 2- to 3-week period. Does *F. americana* loose all third- to fifth-order roots (Fig. 1, 2) at once, or do fourth- to fifth-order roots have a higher probability of dying than third-order roots? Do some lateral roots located on different portions of the root system exhibit a greater probability of dying than others? Is it normal for just a portion of the small individual laterals to die? How is the probability of death related to position on the root system and to changing soil environments? During the growing season, leaf senescence in the lower canopy occurs when the C balance becomes negative; what is the economic threshold for fine-root mortality? We understand a great deal about how light and N control leaf C gain and leaf life span (Field 1983; Field and Mooney 1983; Reich et al. 1992). The branching root system has many analogies to the branching shoot system (Caldwell 1987; Fitter 1996), but little information exists on relationships among root architecture, root life span, and the acquisition of soil resources.

Most estimates of root decomposition have come from buried-bag studies. In these studies, roots are excised from the soil and sometimes washed, removing their associated microbial community. They are then placed back in the soil and their decomposition is monitored over time. In the past few years, several investigators conducting direct observational studies of roots have reported a rapid disappearance of small-diameter roots (Hendrick and Pregitzer 1992; Pregitzer et al. 1993; Fahey and Arthur 1994; Fahey and Hughes 1994; Dubach and Russelle 1995). These observations conflict with the slow decomposition rates reported in many buried-bag studies (McClaugherty et al. 1984; Whitford et al. 1988, Van Viuren et al. 1993). Figures 1 and 2 suggest that to realistically study the decomposition of *A. saccharum* or *F. americana* roots using the buried-bag technique, roots 2–10 mm in length and 0.1–0.3 mm in diameter must be teased from the soil and placed in very small mesh bags. The C/N ratio of these roots (assuming no retranslocation) is 15–20, a favorable substrate for relatively rapid microbial utilization (Paul and Clark 1989). Roots with such a low C/N ratio probably contain relatively high concentrations of protein and other labile organic compounds compared to the tissue of larger roots with higher proportions of structural compounds like cellulose or lignin. It is perhaps not surprising then, that the rapid disappearance of small-diameter roots does not match rates of decomposition of larger roots typically used in buried-bag studies. Tree roots 0.5–3.0 mm in diameter had C/N ratios double that of the small-diameter roots that account for most of the root length (Table 1).

Fitter (1996) reported that longer branches must transport materials farther from the point of acquisition to the shoot base. Individual root length, width, and resistance are all important in optimizing root architecture (Eissenstat 1992; Lynch 1995; Fitter 1996). The relationships between the C cost of constructing and maintaining roots and the benefits they provide to the plant in terms of the acquisition of essential growth-limiting resources have not been fully explored. The fact that most of the root length displayed by the trees is in the form of short laterals may be due to trade-offs between the optimization of transport and the minimization of C expended (Fitter 1996). Horsley and Wilson (1971) found that in order for a *B. papyrifera* Marsh. root to become a permanent member of the root system, it had to have a primary xylem diameter at least 25% that of the parent root. If we knew more about the physiological and anatomical constraints that controlled the life span of roots, we could much more accurately predict the C costs of constructing and maintaining root systems.

One of the most interesting findings of this study was that the N concentration increased with root order in trees, but remained relatively constant in perennial herbs. Leaf longevity is inversely related to N content in a wide range of species (Reich et al. 1992). In the two trees we studied, the least expensive roots to construct were those with the highest N concentrations. Yani et al. (1995) modeled the relationship between root diameter, rates of nutrient uptake, and root longevity. The model assumed that the C cost of constructing and maintaining a root was directly proportional to SRL. Under these constraints, the optimal root for nutrient absorption would be infinitely fine (Yani et al. 1995). Our results clearly demonstrate that the short, lateral, high-order roots contained more N per unit C invested. These roots are probably expensive to maintain because their higher N concentrations should be associated with high rates of respiration (Ryan 1991; Ryan et al.1996). We predict that these short laterals are the shortest-lived tree roots, and that they are cheap to build and expensive to maintain. It may be that models of optimal C allocation and root longevity will need to vary costs of ion uptake according to the root position on the root system. Root age may also influence metabolism and rates of ion uptake (Yani et al. 1995). Rates of nutrient absorption may also be limited by uptake kinetics (Caldwell et al. 1992; Yani et al. 1995). The higher N concentrations of the finest roots may be related to greater active uptake of nutrients, either from the soil and/or from mycorrhizal tissues commonly associated with the small, lateral roots. The first step in understanding the significance of higher N concentrations is to determine if rates of root respiration are associated with the position of roots on the root system. Our results suggest that simple, universal assumptions about the costs of constructing and maintaining roots may not be valid.

The two perennial herbs might lose all their roots except the rhizomes each autumn (Fitter 1996). Their constant N concentrations (Table 1), and a more uniform distribution of length across orders (Fig. 2), suggest a different functional architecture. These predictions need further study as does the entire area of functional root architecture.

Acknowledgements This research was funded by The National Science Foundation (DEB 92-21003, DBI 9413407, and an REU supplement).

References

Caldwell MM (1987) Plant architecture and resource competition. In: Schulze E-D, Zwolfer H (eds) Potentials and limitations of ecosystem analysis. Ecological Studies, vol 61. Springer, Berlin Heidelberg New York, pp 164–179

Caldwell MM, Dudley LM, Lilieholm B (1992) Soil solution phosphate, root uptake kinetics and nutrient acquisition: implications for a patchy soil environment. Oecologia 89:305–309

Cheng W, Coleman DC, Box JE (1990) Root dynamics, production and distribution in agroecosystems on the Georgia piedmont using minirhizotrons. J Appl Ecol 27:592–604

Dubach M, Russelle MP (1995) Reducing the cost of estimating root turnover with horizontally installed minirhizotrons. Agron J 87:258–263

Eissenstat DM (1991) On the relationship between specific root length and the rate of root proliferation: a field study using citrus rootstocks. New Phytol 118:63–68

Eissenstat DM (1992) Costs and benefits of constructing roots of small diameter. J Plant Nutr 15:763–782

Eissenstat DM, Caldwell MM (1988) Seasonal timing of root growth in favorable microsites. Ecology 69:870–873

Fahey TJ, Arthur MA (1994) Further studies of root decomposition following harvest of a northern hardwood forest. Forest Sci 40:618–629

Fahey TJ, Hughes JW (1994) Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. J Ecol 82:533–548

Field C (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control of the allocation program. Oecologia 56:348–355

Field C, Mooney HA (1983) Leaf age and seasonal effects of light, water, and nitrogen use efficiency in a California shrub. Oecologia 56:348–355

Fitter AH (1982) Morphometric analysis of root systems: application of the technique and influence of soil fertility on root system development in two herbaceous species. Plant Cell Environ 5:313–322

Fitter AH (1987) An architectural approach to the comparative ecology of plant root systems. New Phytol 106:61–77

Fitter AH (1996) Characteristics and functions of root systems. In: Waisel Y, Eshel E, Kafkafi U (eds) Plant roots, the hidden half, 2nd edn. Dekker, New York, pp 1–20

Fitter AH, Stickland TR (1992) Architectural analysis of plant root systems. III. Studies on plants under field conditions. New Phytol 121:243–248

Gower ST, Vogt KA, Grier CC (1992) Carbon dynamics of Rocky Mountain Douglas-fir: influence of water and nutrient availability. Ecol Monogr 62:43–65

Hansen EA (1981) Root length in young hybrid *Populus* plantations: its implication for border width of research plots. For Sci 27:808–814

Hendrick RL, Pregitzer KS (1992) The demography of fine roots in a northern hardwood forest. Ecology 73:1094–1104

Hendrick RL, Pregitzer KS (1993a) Patterns of fine root mortality in two sugar maple forests. Nature 361:59–61

Hendrick RL, Pregitzer KS (1993b) The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. Can J For Res 23:2507–2520

Hendrick RL, Pregitzer KS (1996) Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. J Ecol 84:167–176

Hendricks JJ, Nadelhoffer KJ, Aber JD (1993) Assessing the role of fine roots in carbon and nutrient cycling. Trees 8:174–178

Hooker JE, Black KE, Perry RL, Atkinson D (1995) Arbuscular mycorrhizal fungi induced alteration of root longevity of poplar. Plant Soil 172:327–329

Horsley SB, Wilson BF (1971) Development of the woody portion of the root system of *Betula papyrifera*. Am J Bot 58:141–147

Lynch J (1995) Root architecture and plant productivity. Plant Physiol 109:7–13

McClaugherty CA, Aber JD, Melillo JM (1984) Decomposition dynamics of fine roots in forested ecosystem. Oikos 42:378–386

Molz FJ (1981) Models of water transport in the soil-plant system: a review. Water Resour Res 17:1245–1260

Nadelhoffer KJ, Raich JW (1992) Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73:1139–1147

Nye PH, Tinker PB (1977) Solute movement in the soil-root system. Blackwell, Oxford

Paul EA, Clark FE (1989) Soil microbiology and biochemistry. Academic Press, New York, p 273

Pregitzer KS, Hendrick RL, Fogel R (1993) The demography of fine roots in response to patches of water and nitrogen. New Phytol 125:575–580

Pregitzer KS, Zak DR, Curtis PS, Kubiske ME, Teeri JA, Vogel CS (1995) Atmospheric CO_2, soil nitrogen and turnover of fine roots. New Phytol 129:579–585

Reich PB, Walters MB, Ellsworth DS (1992) Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecol Monogr 62:365–392

Ryan MG (1991) Effects of climate change on plant respiration. Ecol Appl 1:157–167

Ryan MG, Hubbard RM, Pongracic S, Raison RJ, McMurtrie RE (1996) Foliage, fine-root, woody-tissue and stand respiration in *Pinus radiata* in relation to nitrogen status. Tree Physiol 16:333–343

Schoettle AW, Fahey TJ (1994) Foliage and fine root longevity of pines. Ecol Bull 43:136–153

Sutton RF, Tinus RW (1983) Root and root system terminology. For Sci Monogr 24

Van Vuuren MMI, Berendse F, De Visser W (1993) Species and site differences in the decomposition of litters and roots from wet heathlands. Can J Bot 71:167–173

Vogt KA, Grier CC, Vogt DJ (1986) Production, turnover, and nutrient dynamics of above- and belowground detritus of world forests. Adv Ecol Res 15:303–377

Whitford WG, Stinnett K, Anderson J (1988) Decomposition of roots in a Chihuahuan Desert ecosystem. Oecologia 75:8–11

Yani RD, Fahey TJ, Miller SL (1995) Efficiency of nutrient acquisition by fine roots and mycorrhizae. In Smith WK, Hinkley TM (eds) Resource physiology of conifers: acquisition, allocation, and utilization. Academic Press, New York, pp 75–103