The vertical and horizontal distribution of roots in northern hardwood stands of varying age

Ruth D. Yanai, Byung B. Park, and Steven P. Hamburg

Abstract: Coring methods cannot reveal the distribution of roots with depth in rocky soil, and fine roots are typically sampled without regard to the location of trees. We used quantitative soil pits to describe rooting patterns with soil depth and distance to trees in northern hardwood stands. We sited three 0.5 m^2 quantitative soil pits in each of three young (19–27 years) and three older (56–69 years) stands developed after clear-cutting. Live roots were divided into diameter classes delimited at 0.5, 1, 2, 5, 10, 20, and 100 mm; dead roots were not distinguished by size. Mean total live-root biomass was 2900 ± 500 $g \cdot m^{-2}$ in older stands and 1500 ± 400 $g \cdot m^{-2}$ in young stands. The root mass in the 2–20 mm class was 2.7 times greater in the older stands ($p = 0.03$); fine-root (<2 mm) biomass was 1.5 times greater ($p = 0.12$), suggesting that fine-root biomass continues to increase past the age of canopy closure in this forest type. Root biomass density declined with soil depth, with the finest roots (<0.5 mm) declining most steeply; roots were found at low densities well into the C horizon. We analyzed root biomass density as a function of the influence of nearby trees (represented as the sum of basal area divided by the distance from the pit) and found that fine as well as coarse roots reflected this influence. In systems where this is the case, root measurements should be made with attention to patterns of tree distribution.

Résumé : Les méthodes de carottage ne permettent pas d'observer la distribution des racines en fonction de la profondeur dans les sols rocheux et les racines fines sont typiquement échantillonnées sans tenir compte de l'emplacement des arbres. Les auteurs ont utilisé des fosses d'observation quantitative pour décrire les patrons d'enracinement de forêts de feuillus nordiques. Ils ont placé trois fosses d'observation quantitative de 0,5 m^2 par peuplement dans trois jeunes peuplements (19–27 ans) et dans trois peuplements plus âgés (56–69 ans) issus d'une coupe totale. Les racines vivantes ont été divisées par classes de diamètre dont les limites étaient fixées à 0,5, 1, 2, 5, 10, 20 et 100 mm; les racines mortes n'ont pas été classées selon leur taille. La biomasse totale moyenne des racines vivantes était de 2900 ± 500 $g \cdot m^{-2}$ dans les peuplements plus âgés et de 1500 ± 400 $g \cdot m^{-2}$ dans les peuplements plus jeunes. La masse racinaire dans la classe de 2 à 20 mm de diamètre était 2,7 fois plus grande dans les peuplements plus âgés ($p = 0,03$); la biomasse de racines fines (<2 mm) était 1,5 fois plus grande ($p = 0,12$), ce qui indique que la biomasse de racines fines continue d'augmenter une fois passé l'âge de fermeture de la canopée dans ce type de forêt. La densité de la biomasse racinaire diminuait avec la profondeur du sol et celle des racines les plus fines (<0,5 mm) diminuait le plus rapidement; des racines ont été observées profondément dans l'horizon C mais leur densité était faible. Ils ont analysé la densité de la biomasse racinaire en fonction de l'influence des arbres avoisinants (représentée par la somme de la surface terrière divisé par la distance de la fosse) et ils ont découvert que les racines fines aussi bien que les grosses racines subissaient cette influence. Dans les systèmes semblables, la mesure des racines devrait être effectuée en portant attention aux patrons de distribution des arbres.

[Traduit par la Rédaction]

Introduction

It is relatively easy to determine when in stand development canopy closure occurs and to monitor the development of woody biomass aboveground. Roots, of course, are more difficult to measure, and many questions remain imperfectly resolved. One such question is the timing of "root closure" in forests. At the stand level, it seems reasonable to believe that fine-root biomass, like leaf area, should achieve a point where additional biomass allocation to resource acquisition would fail to pay off. Studies in a few different forest types have suggested that fine-root biomass peaks within 5 or 10 years of stand initiation (John et al. 2002; Claus and George 2005), which is similar to the timing of the peak in leaf area in northern hardwoods (Covington and Aber 1980). In Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) stands, fine-root biomass peaks at the time of canopy closure (Vogt et al. 1983). In contrast, coarse-root biomass presumably increases along with bole biomass (Fahey et al. 2006) for 80–100 years in northern hardwoods regenerated by clear-cutting. The development of fine- and coarse-root biomass as a function of stand age has yet to be described for the northern hardwood forest type.

The vertical distribution of roots is also difficult to measure. Soil cores are the easiest way to collect fine roots, but since they cannot sample below obstructions, the depth dis-

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Table 1. Sites used in this study.

Site	Stand age (years)	Lat., long.	Elevation (m a.s.l.)	Treatment	Dominant species
H6	19	44°08′N, 71°17′W	370	Clear-cut in 1983–1984, mechanical	*Betula papyrifera*, *Prunus pensylvanica*, *Betula alleghaniensis*
M6	24	43°59′N, 71°25′W	520	Clear-cut in 1979–1980, mechanical	*Prunus pensylvanica*, *Tsuga canadensis*, *Betula papyrifera*, *Acer saccharum*
M5	27	44°08′N, 71°14′W	460	Clear-cut in 1976–1977 followed by timber stand improvement thinning	*Betula papyrifera*, *Acer saccharum*, *Prunus pensylvanica*
T30	56	44°03′N, 71°14′W	550	Cut in 1948, intensity unknown	*Acer saccharum*, *Fagus grandifolia*, *Fraxinus americana*, *Betula papyrifera*
H1	65	44°08′N, 71°16′W	340	Clear-cut in 1939 after 1938 hurricane removing all stems >5 cm in diameter	*Acer rubrum*, *Betula papyrifera*, *Acer saccharum*
H4	69	44°08′N, 71°17′W	370	Commercial clear-cut in 1933–1935	*Betula papyrifera*, *Populus grandidentata*

Note: Stand ages are given for 2003, the year in which roots were sampled. Sites designated with "H" are located in the Bartlett Experimental Forest; the rest are in the White Mountain National Forest. Species listed are those that comprise at least 10% of basal area. Stem density and basal area by species in the areas around the pits are available in Figs. 3 and 4.

tribution of roots is best measured by excavation, at least in rocky soils (Lyford and Wilson 1964; Lyford 1980). Root biomass declines with depth in stands of all ages, but it is important to know how this depth distribution varies during the course of stand development. Young forests, because of their more rapid biomass accumulation, are also accumulating nutrients more rapidly than their older counterparts (Yanai 1998). We speculated that one reason young stands are better able to mobilize nutrients such as calcium from the mineral soil (Hamburg et al. 2003) could be a greater relative investment in deep roots. In older forests, where recycling of nutrients by decomposition is proportionally more important, we might expect relatively more roots to be found near the surface, where most mineralization occurs. This generalization is supported by an analysis of 19 published studies, which found that early successional species have proportionately more roots at greater depth (Gale and Grigal 1987).

The horizontal distribution of root biomass has not been well studied in closed forests. Coarse-root biomass is found close to the stems and has been shown to increase in size as the stem develops (Millikin and Bledsoe 1999). Fine roots, however, can extend long distances away from the stem (>15 m; Lyford and Wilson 1964; Lyford 1980), and their distribution in forests may reflect the distribution of nutrients in soils rather than the arrangement of tree stems (Mou et al. 1995). Many studies have asserted that fine roots are not sensitive to distance from trees (Millikin and Bledsoe 1999; Leuschner et al. 2001; Eamus et al. 2002). This assumption is implicit in the design of most root sampling studies in that samples are randomly or systematically located without reference to tree density. A homogeneous distribution of fine roots is consistent with the concept of root closure: if roots occupy the soil the way leaves occupy the canopy, then their density is not limited by the proximity of stems but by the available resources, which tend to be equalized by the proliferation of roots (Gross et al. 1993).

We measured coarse- and fine-root biomass in three young and three older northern hardwood stands that originated after logging. We hypothesized that coarse-root biomass would be greater in the older stands but that fine-root biomass would be similar between stands. We were also interested in the depth distribution of roots by diameter class, hypothesizing that young stands would have proportionately more fine roots, if not coarse roots, deployed at depth. Finally, we tested the relationship of root density to the proximity of trees. We hypothesized that fine roots would be more deeply distributed in the young stands than in the older stands and that the horizontal distribution of fine roots would be insensitive to the position of trees in the stand, while coarse roots would be found close to trees.

Materials and methods

Study sites

We studied three young (aged 19–27 years) and three older (aged 56–69 years) northern hardwood stands (Table 1) that were previously studied as part of a 13-stand chronosequence (Federer 1984; Yanai et al. 2000). The sites in the chronosequence were selected to be similar in elevation, landscape position, and soil type but to differ in the length

of time since they were regenerated by logging. To pinpoint the age of root closure, we would have liked to excavate pits in all 13 stands, but the expense was prohibitive. We elected to use multiple young and older sites as replicates of two widely separated age-classes.

Forest composition was measured in 2003, the same year that we collected roots from quantitative soil pits. White birch (*Betula papyrifera* Marsh.) and pin cherry (*Prunus pensylvanica* L.f.) were common dominant species in the young northern hardwoods regenerated after logging; sugar maple (*Acer saccharum* Marsh.) and red maple (*Acer rubrum* L.) were more important in older stands (Table 1).

Excavation of roots from soil pits

Three 0.5 m^2 square quantitative soil pits were excavated in each of the stands. The measurement area in each stand (generally 50 m × 50 m) was divided into nine cells, and three cells were randomly selected such that no two were in the same row or column. Pit locations were rejected if they had more than 50% rocks at the surface or if a tree with diameter at breast height (DBH) >10 cm was within 50 cm of the pit. We recorded the species, size, and distance to all trees with DBH >2 cm within 3 m of the center of the pit and all trees with DBH >10 cm within 6 m of the center of the pit.

The soil pits were excavated using a secured frame as a reference plane for calculating the volume of excavated soil (Hamburg 1984). The forest floor was collected in two layers, the Oie (L + F) and Oa (H). The thickness of the Oie was not measured because it depends on the method of measurement and the antecedent weather conditions. The mineral soil was collected in four depth intervals (0–10, 10–20, 20–30, and >30 cm to the C horizon). The C horizon was identified by a lighter, olive color and platy structure (commonly a fragipan). In one of the three pits in each stand, we excavated additional strata 0–25 and 25–50 cm into the C horizon except for two sites (those aged 27 and 69 years) in which bedrock or large erratics were encountered above that depth.

Most of the soil samples were sieved in the field, with the exception of the Oie, which is difficult to sieve when moist. The Oa horizon soils were sieved to 6 mm and all the other strata were sieved to 12 mm; we collected and weighed the roots that did not pass through the sieve. The soil passing through the sieve was repeatedly subsampled with a trowel for later root picking. The size of this subsample ranged from 72 to 433 g, which was, on average, one-seventieth of the mass of the soil layer. The Oie material was air dried and then sieved to 6 mm. We analyzed the roots that did not pass through the sieve, and we picked roots from a subsample of the sieved material. Vertical roots were cut to correspond to the multiple depth increments from which they were excavated.

Root processing

All roots and soil samples for root picking were stored in a cooler in the field and then refrigerated until they could be processed, which was generally within 2 months of sample collection. Live roots were divided into size classes; dead roots were separated from live roots but were not sorted by size. Dead roots were recognized because they were more brittle and darker in color than live roots. Dead roots were not identified in the Oie because this layer was dried before subsampling.

Root size classes were delimited at diameters of 0.5, 1, 2, 5, 10, 20, and 100 mm. Picking roots and sorting them into size classes is extremely time consuming, especially for the finest roots. We used subsampling to estimate the finer root classes to make this process more efficient. We picked out all roots >2 mm from the roots collected on the screens and the subsamples of sieved soil. The remaining roots and sieved soil were weighed and further subsampled prior to picking and sorting the finer roots. These subsamples were one-eighth or one-quarter of the remaining mass of roots. All root masses were scaled up and expressed on a 1 m^2 basis.

Roots were dried at 65 °C for at least 1 week before determining masses.

Data analysis

We calculated (*i*) the mass of roots per unit area, (*ii*) the mass per unit area per increment of soil depth, which is a measure of mass per unit volume, including rock volume, and (*iii*) the mass per unit volume of soil excluding the rock volume. Variance is reported as the standard error of the mean.

We used repeated-measures analysis of variance to test for differences in root biomass between young and older stands, with depth as the repeated measure. We also analyzed the distribution of roots with depth using the fraction of roots in each depth stratum to control for differences in total biomass among pits. The experimental unit was the stand, with three pits in each stand. There were three stands for each age-class, young and older. We also compared total root biomass (summed over depth) by size class between young and older stands using analysis of variance.

To analyze the effect of nearby trees on root biomass, we calculated an index of tree influence near the pit, similar to a competition index used to describe tree neighbors (Biging and Dobbertin 1995). The tree influence index was the sum, for all trees up to a specified distance from the pit, of the square of tree DBH divided by the distance from the center of the pit

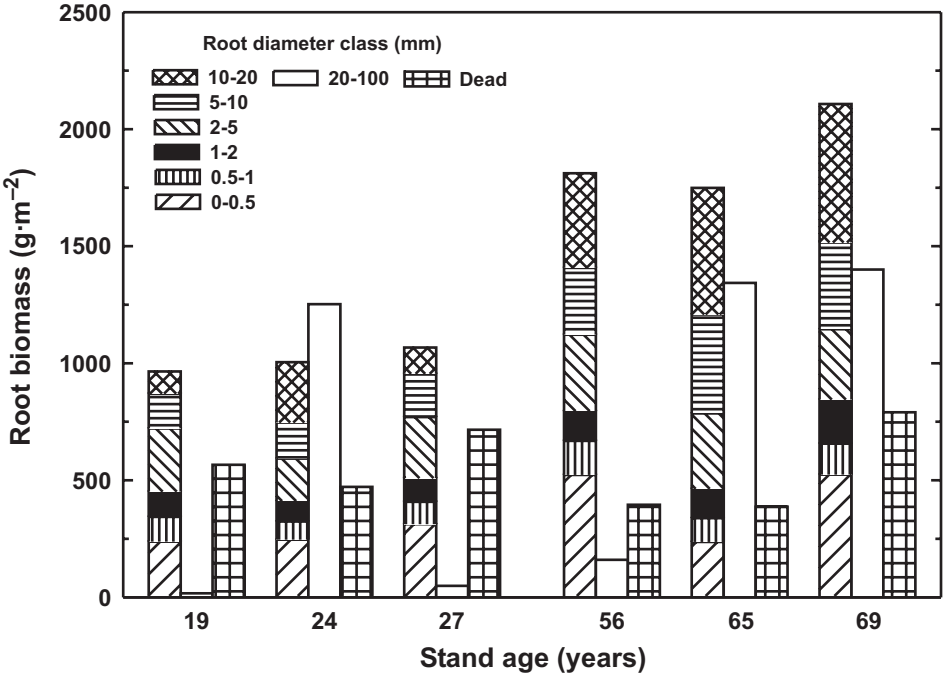
$$\sum_{i=1}^{t} \frac{\mathrm{DBH}_i^2}{d_i}$$

where t is the number of trees within the specified distance of the pit, DBH_i is the diameter of tree i, and d_i is the distance of tree i from the center of the pit. We analyzed the correlation between root biomass (total or by diameter class) in each pit and this tree influence index for varying distances from the center of the pit. For this analysis, the experimental unit was the pit. To increase our sample size, we included 18 additional pits from a similar study conducted in 2004 in the Bartlett Experimental Forest (Park et al., in press).

To analyze the effect of soil depth or volume on root biomass, we used the mineral soil from the base of the forest floor to the top of the C horizon. Correlation analysis was used to test the relationship between root biomass and soil depth or soil volume.

We used coefficients of variation to describe variation among plots within stands or stands within a forest age-class. We

Fig. 1. Live-root biomass showing the contribution of each root diameter class and total dead-root biomass in each of six stands. There were no significant differences in dead-root biomass between these classes.



used an inverse *t* test to calculate the number of observations required to detect a significant difference using an $\alpha = 0.05$ (Yanai 1998). For this test, we used the variance of all pits within an age-class, since the variation across pits was greater than the variation across stands.

Results

Root biomass as a function of stand age

The three older stands had about twice as much live-root biomass (1800 ± 120 g·m^{-2}, <20 mm diameter) as did the three young stands (950 ± 51 g·m^{-2}) ($p = 0.01$) (Fig. 1). This difference was due primarily to the greater mass of roots in the larger size classes; root biomass in the 5–20 mm diameter class was 2.7 times as great in the older stands than in the young stands ($p = 0.03$). Fine-root (<2 mm) biomass was 1.5 times greater in older than in young stands, but this difference was not statistically significant ($p = 0.12$). Similarly, biomass of 2–5 mm roots was 1.3 times greater but not statistically distinguishable between young and older stands ($p = 0.15$).

Coarse roots (>20 mm) potentially make up a considerable fraction of total root biomass but are spatially highly variable. One pit in a young stand (age 27) contained a small tree; the other pits in young stands had little coarse-root biomass (Fig. 1). In the older stands, biomass of roots >20 mm averaged 970 g·m^{-2}. Larger trees were not encountered in pits because we rejected locations close to trees with DBH >10 cm. Fine roots (<2 mm) accounted for 32% of the total root biomass (average of individual pit proportions) and 41% of roots <20 mm in diameter.

The mass of dead roots was similar across all stands, averaging 540 ± 53 g·m^{-2} for all six stands (Fig. 1). Given the greater live-root biomass in the older stands, this difference in dead-root biomass meant that a greater fraction of the root mass was dead in the young stands ($p = 0.02$). This difference could reflect shorter root life spans in the young stands or a longer residence time of dead roots; we have no information on either root longevity or decomposition rates.

Root biomass distribution by soil depth

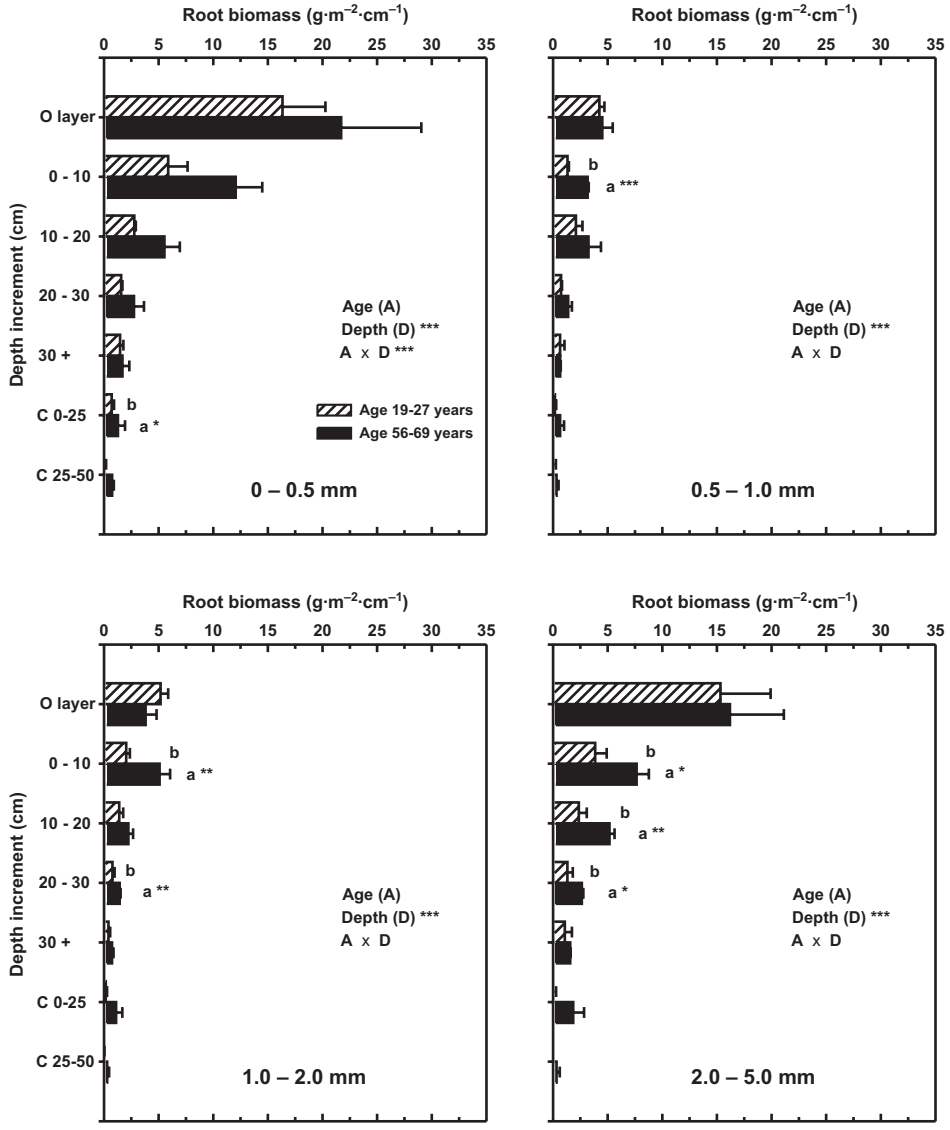
As expected, root biomass declined with depth in all diameter classes (Fig. 2). Across all stands, the forest floor (O horizon) contained 31% of total root biomass and 34% of fine-root (<2 mm) biomass, although it represented only 8% of soil depth, excluding the Oie. The Oa horizon contained 14 times more roots than the Oie on average. Although root biomass declined throughout the B horizon, roots extended into the C horizon. More roots had reached the C horizon in the older stands (180 g·m^{-2} to 50 cm depth in the C horizon) than in the young stands (25 g·m^{-2}).

Since many studies report root biomass collected from shallow soil cores, it is worth noting that, on average, across all six stands, 35% of fine-root biomass occurred below 10 cm depth, and 13% of fine-root biomass occurred below 30 cm depth.

The decline of root biomass with depth was not the same across all size classes or between young and old stands. The density (mass per unit soil volume) of roots finer than 5 mm in diameter was greatest in the forest floor and declined with depth in the mineral soil (Fig. 2). The coarser roots had a similar distribution to the fine roots in young stands, but in older stands, coarse roots were more common in the upper B horizon than in the forest floor (Fig. 2).

The pattern of greater root biomass in older than in young stands held true across all soil depths, but only some of these differences were statistically significant within a depth stratum (designated by different letters in Fig. 2). We had hypothesized that young stands would have proportionately greater root biomass allocated at depth after controlling for

Fig. 2. Live- and dead-root biomass by depth and size class in young and older northern hardwood stands. Standard error is based on $n = 3$ stands. Root biomass is reported per unit volume of each stratum because the strata differed in thickness. Dead roots were included with live roots in the Oie because this layer was dried before subsampling. Means within a soil depth stratum sharing the same letter are not significantly different between the two stand age-classes. Repeated-measures ANOVA identified the significance of age, depth, and the interaction of age with depth: *, $p < 0.10$; **, $p < 0.05$; ***, $p < 0.01$.



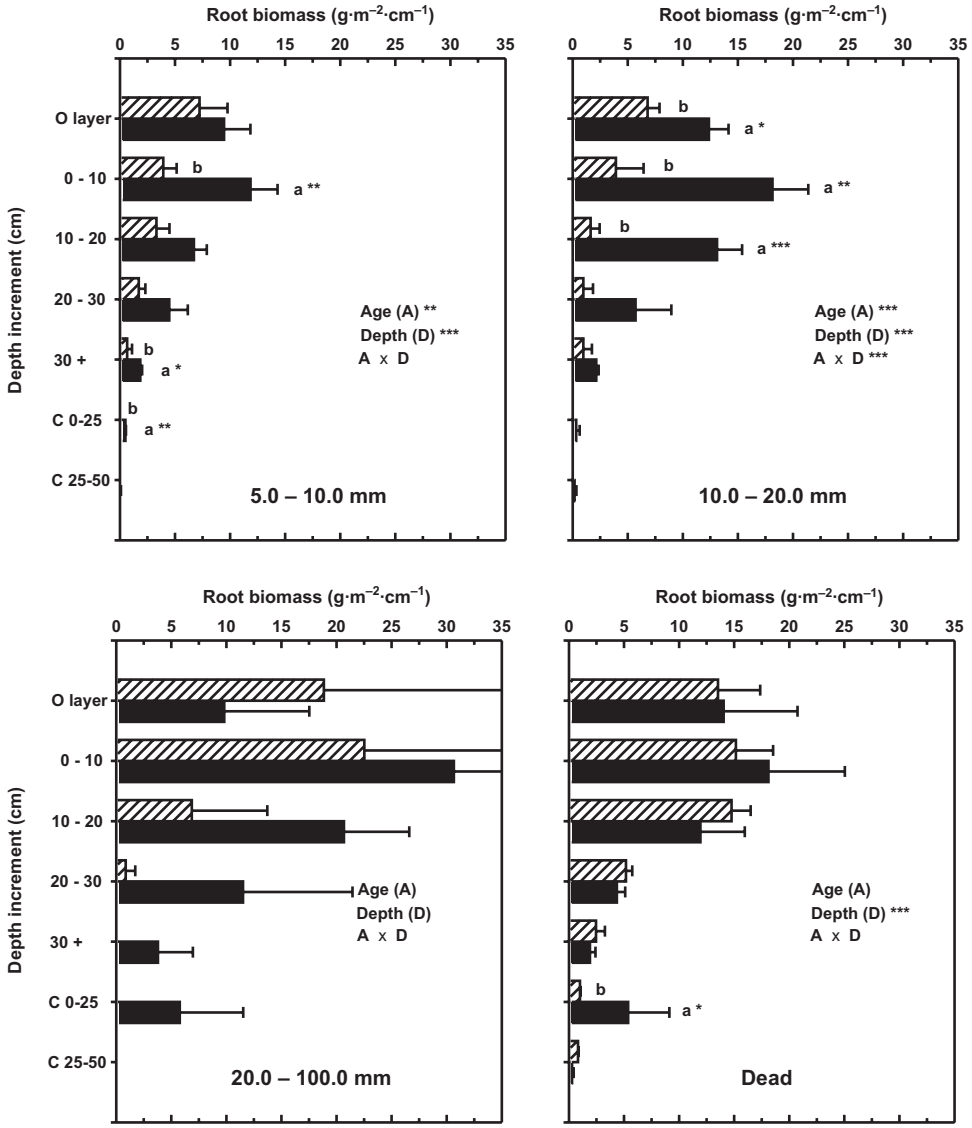
the difference in total root biomass, which was less in young stands. To test this hypothesis, we considered the fraction of total root biomass present in each size class in each stratum (data not shown). There were fewer significant differences in proportional allocation by depth when root distribution was described by root mass. In only one case did the young stands have a significantly greater proportion of roots at depth (at >30 cm for roots <0.5 mm, $p = 0.02$).

Relation of root biomass to nearby trees

We tested whether the biomass of roots, by size class, depended on the size and proximity of nearby tree stems. We hypothesized that the finest roots would be distributed evenly rather than being predicted by the surrounding tree density. In contrast, we expected coarse roots to be found close to the base of large trees. Not surprisingly, the young stands were composed of small stems at high density and the older stands had much larger stems at lower density (Fig. 3). The most notable compositional features were the relatively high dominance of pin cherry and birches around the pits in the young stands and that of trembling aspen (*Populus tremuloides* Michx.) in the older stands (Fig. 4).

We related root biomass by size class to the influence of the surrounding trees (represented by the sum of each tree's basal area divided by the distance to that tree). We calculated this sum at varying distances from the soil pit and found that the relationship of basal area to root biomass with distance from the pit depends on the size class of roots (Table 2). For this analysis, we used the 18 pits reported in this paper plus 18 additional pits excavated in similar sites the following year (2004) (Park et al., in press). Stronger correlations might be found by including the smaller trees farther

Fig. 2 (*concluded*).



from the pit (we did not record trees with DBH <10 cm more than 3 m from the pit) and by extending the analysis beyond 6 m.

Surprisingly, even the finest roots (<0.5 mm in diameter) showed a significant influence of nearby trees, with the best prediction resulting from trees within 2 m of the center of the soil pit. Roots 0.5–1 mm reflected the influence of trees up to 3–5 m from the soil pit. In the pits excavated in 2004, 0–1 mm roots were analyzed as a single size class; this size class showed no relationship with the density of trees (data not shown).

All root classes from 1 to 20 mm showed a significant correlation between root biomass and the presence of trees within 4–6 m of the soil pit (Table 2). We did not record trees more than 6 m distant. It was not surprising that there was no significant correlation between tree influence index and root biomass in the 20–100 mm diameter class because this class was so variable (Fig. 1).

Dead-root biomass was correlated with trees within 3 m of the pit ($\rho = 0.5$, $p = 0.03$), which is intermediate between the distance that best predicted the finest roots (2 m) and the coarser roots (up to 6 m). Dead roots were not divided by size class and should reflect a weighted average of all size classes.

We repeated this analysis separately for young and older stands, combining the two finest root classes from the 2003 data set to correspond to the 0–1 mm diameter class collected in 2004. There were more significant correlations in young stands than in older stands between fine-root biomass and tree influence index, calculated at varying distances from the soil pit. Note that variation in the tree influence index in young stands mainly reflects differences in stem density, while in older stands, stems are few and the index mainly reflects the proximity of the pit to a large tree.

Relation of root biomass to soil volume

We expected that root biomass would reflect the available soil volume, being greater where soil was deeper or rock volume was less. Depth to the C horizon (from the base of the O horizon) varied from 20 to 92 cm (Table 3) (including

Fig. 3. Density of trees with DBH >2 cm within 3 m of the center of the pit and of trees with DBH >10 cm within 6 m of the center of the pit.

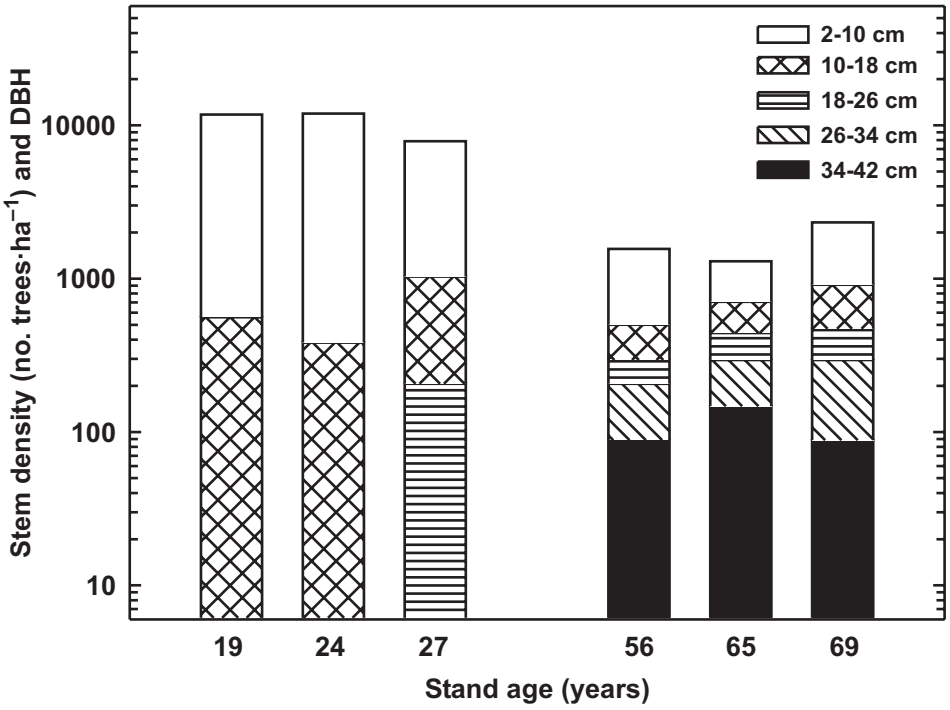
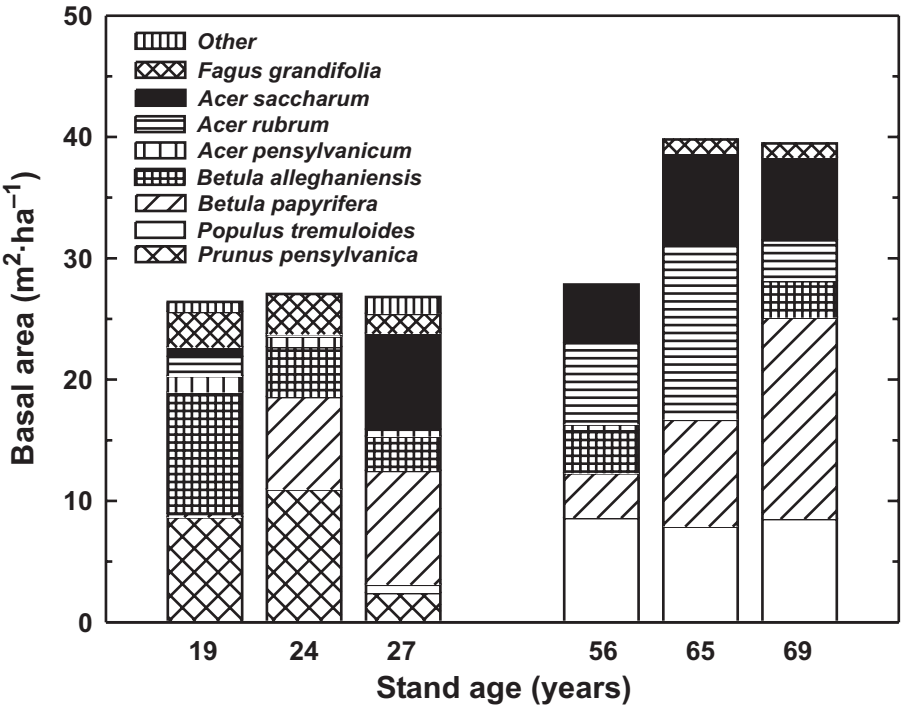


Fig. 4. Basal area by species of trees with DBH >2 cm within 3 m of the center of the pit and trees with DBH >10 cm within 6 m of the center of the pit.



the Oa horizon, soil depth ranged from 28 to 124 cm). Rock volume (defined as particles >2 mm) varied from 5% to 51% for the mineral soil. The volume of soil (<2 mm) varied almost sixfold across our 18 soil pits, from 0.14 to 0.82 $m^3 \cdot m^{-2}$, with no significant difference between the young and older stands. Similarly, soil mass ranged from 100 to 780 $kg \cdot m^{-2}$. To our surprise, there was only a weak correlation between total root mass and soil volume ($\rho = 0.36$, $p = 0.08$) or between root mass and soil mass ($\rho = 0.30$, $p = 0.15$). Most of the roots were in the forest floor and the upper mineral soil

Table 2. Pearson's correlation coefficient between root biomass in each diameter class and tree influence index summed over various distances from the center of the pit (see Methods for details about this index).

		Distance from the center of the pit (m)					
Root diameter (mm)		1	2	3	4	5	6
0–0.5	ρ	–0.21	**0.50**	0.46	0.22	0.24	0.26
	p	0.41	**0.04**	0.06	0.39	0.34	0.29
0.5–1	ρ	–0.13	0.20	**0.49**	**0.47**	**0.48**	0.45
	p	0.60	0.43	**0.04**	**0.05**	**0.04**	0.06
1–2	ρ	–0.09	0.15	0.18	0.25	**0.38**	0.32
	p	0.62	0.39	0.30	0.14	**0.02**	0.06
2–5	ρ	–0.07	0.19	0.31	**0.36**	**0.40**	**0.34**
	p	0.70	0.27	0.07	**0.03**	**0.02**	**0.05**
5–10	ρ	–0.15	–0.02	0.33	**0.58**	**0.62**	**0.53**
	p	0.39	0.93	0.06	**0.00**	**0.00**	**0.00**
10–20	ρ	0.04	0.19	0.18	**0.44**	**0.43**	**0.42**
	p	0.81	0.27	0.30	**0.01**	**0.01**	**0.01**
20–100	ρ	0.14	0.18	0.07	–0.04	0.14	0.20
	p	0.44	0.31	0.69	0.80	0.43	0.26
Dead	ρ	–0.07	–0.07	–0.05	–0.09	–0.04	–0.12
	p	0.68	0.70	0.76	0.61	0.81	0.49

Note: All trees with DBH >2 cm within 3 m of the center of the pit were measured; all trees with DBH >10 cm within 6 m of the center of the pit were measured. For the two smallest size classes, n = 18 pits; for the larger size classes, n = 36 pits because we included data collected in a related study in 2004. Statistics significant at $\alpha = 0.05$ are shown in bold.

Table 3. Characteristics of soil pits (mean and standard error) possibly important to root distributions.

	Stand age (years)					
Soil layer (cm)	19	24	27	56	65	69
Actual layer thickness (cm)						
O	13.2 (2.7)	5.2 (1.7)	7.3 (1.3)	5.7 (2.2)	5.5 (2.5)	4.4 (0.8)
0–10	10.8 (0.2)	9.8 (0.1)	11.8 (1.1)	12.1 (1.7)	10.3 (0.6)	10.8 (0.6)
10–20	9.3 (0.2)	13.6 (2.1)	8.5 (1.5)	8.6 (1.5)	9.9 (0.7)	9.2 (0.7)
20–30	11.8 (0.9)	8.1 (1.2)	9.5 (0.7)	11.3 (0.1)	9.5 (0.8)	10.4 (0.3)
30+	50.1 (5.7)	34.4 (3.5)	18.1 (2.2)	29.2 (19.0)	38.5 (14.6)	42.5 (9.7)
C0–C25	23.5	24.7	na	24.2	29.6	10.5
C25–C50	28.7	31.3	na	23.0	19.9	na
Coarse fraction (% volume)						
0–10	30 (21)	32 (8)	43 (7)	25 (6)	11 (5)	11 (3)
10–20	18 (7)	27 (10)	36 (9)	16 (4)	12 (4)	16 (4)
20–30	20 (5)	43 (9)	35 (7)	19 (1)	14 (5)	25 (7)
30+	17 (8)	35 (11)	41 (7)	29 (9)	16 (5)	32 (8)
C0–C25	54	38	na	46	35	54
C25–C50	45	48	na	21	36	na
Soil mass ($kg \cdot m^{-2}$)						
0–10	61 (15)	47 (6)	46 (16)	63 (18)	65 (6)	61 (1)
10–20	79 (8)	68 (13)	35 (2)	64 (17)	78 (11)	66 (11)
20–30	98 (11)	36 (12)	77 (22)	69 (14)	91 (3)	76 (6)
30+	417 (22)	199 (58)	109 (37)	206 (127)	357 (139)	318 (86)
C0–C25	200	172	na	274	249	53
C25–C50	240	234	na	283	223	na

Note: The coarse fraction is the percentage of pit volume occupied by rock fragments >2 mm in diameter. Sample size was three pits except for C horizon samples, which were collected from one pit per site. na, not available.

(Fig. 2), while the variation in total soil volume among pits was due to differences in the depth to the C horizon and to differences in rock volume deeper in the soil profile.

Scale of spatial variation

Root biomass is spatially variable; we found as much or more variation in fine-root (<2 mm in diameter) biomass

among the pits within a single stand as we did among stands of similar age. Coefficients of variation averaged 35% within stands, while the coefficient of variation among stands was 11% for the young stands and 30% for the older stands (see Fig. 1). The coarser roots are even more variable, especially in young stands, where the average coefficient of variation within stands was 50% and among stands was 89% (see Fig. 1). In the older stands, the average coefficient of variation within stands was 49% and among stands was 13%.

Because of this variability, even large differences between stands or between sets of stands are difficult to detect with small sample size (we had three pits in each stand and three stands of each age). With this sampling intensity and the variance we observed, we would be unable to detect a significant difference ($\alpha = 0.05$) in fine-root biomass between young and older stands unless the magnitude of the difference were >280 $g \cdot m^{-2}$. To detect smaller differences would require greater sampling intensity. For example, it would take 60 pits to detect a 20% difference in fine-root biomass between stands, given the variance that we observed in the older stands. In the young stands, which were less variable for fine-root biomass, it would require about 12 pits per stand to distinguish a 20% difference between stands.

Discussion

We were unable to pinpoint the age of "root closure" in this forest type, defined as the age at which fine-root biomass reaches a dynamic steady state. Our three stands aged 56–69 years old had 53% more fine-root biomass than our three stands aged 19–27 years, suggesting that root biomass likely continues to increase beyond the first few decades of forest development ($p = 0.12$). Our older stands were similar in root biomass to a similar 70-year-old northern hardwood site in New Hampshire studied by the same method (Fahey et al. 1988).

In some other forest types, fine-root biomass has been reported to achieve steady state much earlier, between 5 and 10 years. In a study of pine forests in India, 6-, 15-, and 23-year-old stands had similar fine-root biomass but increasing coarse-root biomass (John et al. 2002). Norway spruce (*Picea abies* (L.) Karst.) in Germany had statistically indistinguishable fine-root biomass in stands aged 24, 42, and 97 years but more than at age 5 (Claus and George 2005). A European turkey oak (*Quercus cerris* L.) forest in Italy had similar fine-root biomass in stands aged 9 and 16 years, more than in a 3-year-old stand (Claus and George 2005). Our results suggest that in northern hardwoods, fine-root biomass increases for much longer than 5 or 10 years, although leaf biomass peaks in that time frame (Covington and Aber 1980). We also found a significant increase in coarse-root biomass with stand age, which is not surprising.

Some of the differences that we report between our young and older stands may be caused in part by differences in species composition rather than tree age. Species composition can change dramatically during forest succession in the northern hardwood type; for example, our young stands averaged 32% of basal area around the soil pits in pin cherry, which is short-lived and generally not found in older stands (Fig. 4). Other differences in species composition between stands may be due not to successional stage but to variation in site conditions or regeneration history. Our older stands had 11%–21% of basal area around the pits in trembling aspen, which were probably present in those stands when they were young, but were not present in our young stands. Our study design does not permit us to distinguish the effects of species composition from stand age in explaining variation in root distributions across our stands.

The question of whether fine roots are randomly or evenly distributed in forests is important to designing efficient sampling methods for root biomass as well as to understanding competition and biomass allocation. As seedlings grow into trees, their roots extend out from the stem (Thomas et al. 2000). But it is surprising to find that in stands 20–70 years old, fine-root biomass is still greatest close to tree stems (Table 2). This observation could be related to the possibility that fine-root biomass is still increasing in stands in this age range. Alternatively, the concentration of roots in proximity to trees could reflect the distribution of soil resources rather than the extension of roots from the parent tree over time.

It is puzzling that although roots <0.5 mm and 0.5–1 mm showed the effect of tree proximity in the 18 pits studied in 2003, in 18 additional pits studied in 2004, the roots in a combined 0–1 mm diameter class showed no such pattern. The difference is important because fine roots are more often studied than coarse roots, and a sampling method that ignores the position of trees would be satisfactory for a study of fine roots, were they randomly distributed. There were other differences between the 2003 and 2004 samples, which shed some light on uncertainty in root sampling using the pit method. The method of subsampling the sieved soil in the field for later root picking is very important because the subsample is necessarily a very small fraction of the total (one-seventieth, on average, in this case), and so minor errors are magnified in scaling up to the pit. We measured 72% more fine-root (<2 mm) biomass in 2004 than in 2003, which might be associated with an improvement in subsampling tools from trowels to tongs (Park et al., in press). Alternatively, there may be changes in root biomass of this magnitude between years owing to differences in environmental or biotic conditions affecting carbon gain and allocation to roots (Farrish 1991). Our study design does not allow us to distinguish differences in methods from differences associated with the year of the measurement, in this case.

This study has other implications for the selection of root sampling methods. One advantage of the quantitative pit method is that the depth distribution of roots can be measured in rocky soils; sampling roots in the organic horizon and the top 10 cm of the mineral soil using soil cores would have missed one third of the fine roots in the stands that we studied. Soil pits also allow larger roots to be studied than do soil cores; we found the pit method to be appropriate for roots up to 2 cm in diameter. Larger roots are infrequently encountered and should be measured at a larger spatial scale or estimated allometrically relative to measurements of tree stems (Fahey et al. 1988; Park et al., in press).

Coring is a very efficient method for studying fine roots (<2 mm) in upper soil horizons, but it is not effective in estimating large roots or roots in rocky soil. We cored for fine roots in conjunction with pit sampling and found that cores overestimated fine-root biomass by 27% compared with pits

(Park et al., in press). Soil compaction caused a 10% overestimate of root biomass density inside the cores. The remaining 17% bias is presumably due to avoiding obstructions when coring. This effect could be much smaller in a less rocky soil.

Sampling effort should be allocated based on the sources of variation in the system studied. We found that root biomass within a stand was not very similar among pits; greater statistical power could be achieved by locating pits independently across the area to be studied. Multiple soil samples can be composited to reduce variation before picking roots, if the effort to collect samples is small relative to processing them, as for root cores. When collecting samples is a major effort, as for pits, samples should be sited as independently as possible.

Finally, if fine-root biomass depends on the location of the sample relative to tree stems, sampling locations should be selected with reference to tree density. Roots could be sampled at points having a tree basal area representative of the stand, or sampling locations could be stratified by tree density. Random sampling could result in higher variance.

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References

Biging, G.S., and Dobbertin, M. 1995. Evaluation of competition indices in individual tree growth models. For. Sci. **41**: 360–377.

Claus, A., and George, E. 2005. Effect of stand age on fine-root biomass and biomass distribution in three European forest chronosequences. Can. J. For. Res. **35**: 1617–1625.

Covington, W.W., and Aber, J.D. 1980. Leaf production during secondary succession in northern hardwoods. Ecology, **61**: 200–204.

Eamus, D., Chen, X., Kelley, G., and Hutley, L.B. 2002. Root biomass and root fractal analyses of an open *Eucalyptus* forest in a savanna of north Australia. Aust. J. Bot. **50**: 31–41.

Fahey, T.J., Hughes, J.W., Mou, P., and Arthur, M.A. 1988. Root decomposition and nutrient flux following whole-tree harvest of northern hardwood forest. For. Sci. **34**: 744–768.

Fahey, T.J., Siccama, T.G., Driscoll, C.T., Likens, G.E., Campbell, J., Johnson, C.E. et al. 2006. The biogeochemistry of carbon at Hubbard Brook. Biogeochemistry, **77**: 109–176.

Farrish, K.W. 1991. Spatial and temporal fine-root distribution in three Louisiana forest soils. Soil Sci. Soc. Am. J. **55**: 1752–1757.

Federer, C.A. 1984. Organic matter and nitrogen content of the forest floor in even-aged northern hardwoods. Can. J. For. Res. **14**: 763–767.

Gale, M.R., and Grigal, D.F. 1987. Vertical root distributions of northern tree species in relation to successional status. Can. J. For. Res. **17**: 829–834.

Gross, K.L., Peters, A., and Pregitzer, K.S. 1993. Fine root growth and demographic responses to nutrient patches in four old-field successional species. Oecologia, **95**: 61–64.

Hamburg, S.P. 1984. Effects of forest growth on soil nitrogen and organic matter pools following release from subsistence agriculture. *In* Forest soils and treatment impacts. *Edited by* E.L. Stone. University of Tennessee, Knoxville, Tenn. pp. 145–158.

Hamburg, S.P., Yanai, R.D., Arthur, M.A., Blum, J.D., and Siccama, T.G. 2003. Biotic control of calcium cycling in northern hardwood forests: acid rain and aging forests. Ecosystems, **6**: 399–406.

John, B., Pandey, H.N., and Tripathi, R.S. 2002. Decomposition of fine roots of *Pinus kesiya* and turnover of organic matter, N and P of coarse and fine pine roots and herbaceous roots and rhizomes in subtropical pine forest stands of different ages. Biol. Fertil. Soils, **35**: 238–246.

Leuschner, C., Hertel, D., Coner, H., and Buttner, V. 2001. Root competion between beech and oak: a hypothesis. Oecologia, **126**: 276–284.

Lyford, W.H. 1980. Development of the root system of the northern red oak (*Quercus rubra* L.). Harv. For. Pap. **21**: 1–30.

Lyford, W.H., and Wilson, B.F. 1964. Development of the root system of *Acer rubrum* L. Harv. For. Pap. **10**: 1–17.

Millikin, C.S., and Bledsoe, C.S. 1999. Biomass and distribution of fime and coarse roots from blue oak (*Quercus douglasii*) trees in the northern Sierra Nevada foothills of California. Plant Soil, **214**: 27–38.

Mou, P., Jones, R.H., Mitchell, R.J., and Zutter, B. 1995. Spatial distribution of roots in sweetgum and loblolly pine monocultures and relations with above-ground biomass and soil nutrients. Funct. Ecol. **9**: 689–699.

Park, B.B., Yanai, R.D., Vadeboncoeur, M.A., and Hamburg, S.P. 2006. How best to estimate root biomass: pits, cores, or allometric equations?. Soil Sci. Soc. Am. J. In press.

Thomas, S.M., Cook, F.J., Whitehead, D., and Adams, J.A. 2000. Seasonal soil-surface carbon fluxes from the root systems of young *Pinus radiata* trees growing at ambient and elevated CO_2 concentration. Global Change Biol. **6**: 393–406.

Vogt, K.A., Grier, C.C., Meier, C.E., and Keyes, M.R. 1983. Organic matter and nutrient dynamics in forest floors of young and mature *Abies amabilis* stands in western Washington, as affected by fine-root input. Ecol. Monogr. **53**: 139–157.

Yanai, R.D. 1998. The effect of whole-tree harvest on phosphorus cycling in a northern hardwood forest. For. Ecol. Manage. **104**: 281–295.

Yanai, R.D., Arthur, M.A., Siccama, T.G., and Federer, C.A. 2000. Challenges of measuring forest floor organic matter dynamics: repeated measures from a chronosequence. For. Ecol. Manage. **138**: 273–283.