

Biomass partitioning in red pine (*Pinus resinosa*) along a chronosequence in the Upper Peninsula of Michigan

J.S. King, C.P. Giardina, K.S. Pregitzer, and A.L. Friend

Abstract: Carbon (C) allocation to the perennial coarse-root system of trees contributes to ecosystem C sequestration through formation of long-lived live wood biomass and, following senescence, by providing a large source of nutrient-poor detrital C. Our understanding of the controls on C allocation to coarse-root growth is rudimentary, but it has important implications for projecting belowground net primary production responses to global change. Age-related changes in C allocation to coarse roots represent a critical uncertainty for modeling landscape-scale C storage and cycling. We used a 55 year chronosequence approach with complete above- and below-ground harvests to assess the effects of stand development on biomass partitioning in red pine (*Pinus resinosa* Ait.), a commercially important pine species. Averaged within site, individual-tree root/shoot ratios were dynamic across stand development, changing from 0.17 at 2-, 3-, and 5-year-old sites, to 0.80 at the 8-year-old site, to 0.29 at the 55-year-old site. The results of our study suggest that a current research challenge is to determine the generality of patterns of root–shoot biomass partitioning through stand development for both coniferous and hardwood forest types, and to document how these patterns change as a function of stand age, tree size, environment, and management.

Résumé : L'allocation du carbone (C) aux grosses racines pérennes des arbres contribue au piégeage du C des écosystèmes en produisant une biomasse vivante de bois d'une grande longévité et en créant, après la sénescence, une importante source de C dans des débris à faible teneur en nutriments. Cependant, notre compréhension des facteurs qui contrôlent l'allocation du C à la croissance des grosses racines est rudimentaire, ce qui entraîne d'importantes répercussions pour la prédiction de la production primaire nette des racines en réaction aux changements climatiques. Les changements dans l'allocation du C aux grosses racines en fonction de l'âge représentent une incertitude cruciale pour modéliser l'entreposage et le recyclage du C à l'échelle du paysage. Nous avons eu recours à une chronoséquence d'une durée de 55 ans, qui incluait la récolte complète des tissus aériens et racinaires, pour évaluer les effets du développement du peuplement sur l'allocation de la biomasse chez le pin rouge (*Pinus resinosa* Ait.), une espèce de pin importante du point de vue commercial. Le rapport moyen par peuplement entre la biomasse des racines et celle de la partie aérienne des arbres variait en fonction du stade de développement du peuplement, passant de 0,17 pour les peuplements âgés de 2, 3 et 5 ans à 0,80 pour le peuplement de 8 ans et à 0,29 pour le peuplement de 55 ans. Les résultats de notre étude indiquent qu'un des défis actuels de la recherche consiste à déterminer la portée générale du comportement du rapport entre la biomasse des racines et celle de la partie aérienne des arbres en fonction du stade de développement des peuplements, tant pour les peuplements feuillus que résineux. Un autre défi consiste à obtenir de l'information sur la façon dont le comportement de ce rapport peut changer en fonction de l'âge du peuplement, de la taille des arbres, de l'environnement et des pratiques d'aménagement.

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Introduction

Given the importance of accounting for the world's terrestrial carbon (C) (Dixon et al. 1994; Schimel 1995; Birdsey and Heath 2001; Houghton 2001; Heath et al. 2003), broad-scale forest-inventory efforts would benefit greatly from

comprehensive assessments of C storage in roots in major world forest ecosystems (Cairns et al. 1997). Summaries of the available data on root–shoot biomass partitioning for both coniferous and deciduous forests (Cannell 1985; Cannell and Dewar 1994; Gower et al. 1994; Cairns et al. 1997; Li et al. 2003) have been used to estimate

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belowground C stocks (Cannell and Dewar 1994; Gower et al. 1994; Jenkins et al. 2003; Li et al. 2003). For example, Gower et al. (1994) summarized data from pine forests of the world and concluded that the root/shoot ratio increased with latitude, from 0.16 in the tropics to 0.40 in the boreal zone. The average root/shoot ratio for all forests (from studies that reported above- and below-ground data) in this data set was 0.27. Li et al. (2003) modeled total root biomass for parts of the Canadian forest sector as $0.222AB$ (above-ground biomass) for conifers and $1.576AB^{0.615}$ for hardwoods. However, we know that above- to below-ground biomass partitioning is sensitive to endogenous factors such as tree age (Gerhardt and Fredriksson 1995; King et al. 1999) or life form (angiosperm vs. gymnosperm (Cuevas et al. 1991)), and exogenous factors such as nutrient and water availability (Axelsson and Axelsson 1986; Proe and Millard 1994; Gebauer et al. 1996), as well as climate/latitude (Gower et al. 1994). Variation in above- to below-ground biomass partitioning could be a source of error when fixed allocation constants are used to estimate belowground biomass (Giardina et al. 2005).

C is allocated below ground to support the growth and metabolism of the dynamic fine-root fraction and perennial coarse roots, and both contribute to ecosystem C sequestration by contributing detritus to soil organic C. Fine roots are produced and senesce on short time scales (often subannual), and more or less continuously contribute small amounts of C to soil organic C through microbial transformation of some fraction of the biomass to recalcitrant C (King et al. 2002, 2005; Pregitzer 2002; Loya et al. 2003). Coarse roots accumulate C for the life of the stand or ecosystem and, at time scales of decades to centuries, add large pulses of C to soil as stands are harvested or trees die from disease, fire, or other causes of mortality. Owing to their relatively large mass and physical configuration, dead coarse-root systems require decades to decompose (Chen et al. 2001; Ludovici et al. 2002), so when they are combined with the living portion of their life cycle they represent soil C pools that typically last decades to centuries. Quantification of both forms of root C inputs to soil has been hampered by methodological difficulties, so our understanding of how they are affected by endogenous and exogenous factors is still rudimentary (King et al. 1999, 2002; Nadelhoffer 2000; Pregitzer 2002).

The goal of the current study was to quantify C storage in above- and below-ground tree biomass of the commercially important red pine (*Pinus resinosa* Ait.), and observe patterns of biomass partitioning as a function of stand development. We used a chronosequence approach with complete above- and below-ground harvests to estimate standing stocks of C, including that in the soil volume down to 3 m deep. Red pine occurs on almost 2 million km², from the US Upper Midwest to northeastern Canada. It is important for pulp and sawtimber across its range, and so is the most widely planted species in the northern USA and in Canada (Rudolf 1990). Red pine is shade-intolerant, requiring stand-replacing disturbance, usually fire, to regenerate naturally. Its growth is moderately fast on mostly coarse-textured soils, and it has longevity of approximately 300 years. The species has limited genetic variability (Fowler and Morris 1977; Mosseler et al. 1991 1992), yet there is substantial variation in growth because of differences in environmental conditions

across its range. Several authors noted that the root/shoot ratio in Scots pine, *Pinus sylvestris* L., calculated from chronosequence data of Ovington (1957), reached a maximum at about age 7, after which it declined asymptotically until age 55 (King et al. 1999; Pregitzer 2003; Giardina et al. 2005). Accordingly, we hypothesized that the root/shoot ratio for red pine stands would reach a maximum early in stand development and decline asymptotically over time. We reasoned that such a temporal trend could have important implications for belowground C accumulation that should be accounted for when inventorying standing C stocks in red pine stands that vary in age.

Materials and methods

The chronosequence

The red pine chronosequence consisted of nine stands located in the western Upper Peninsula of Michigan and ranging in age from 2 to 55 years (Table 1). Soils at all sites are sand to sandy loams on glacial-outwash landforms that were deposited at the end of the last glacial retreat (Wisconsinin), 8000 – 10 000 years ago (Dorr and Eschman 1970). There is modest variation in mean annual temperature among the sites, from 3.8 to 5.4 °C. Similarly, there is modest variation in mean annual precipitation among the sites, from 771 to 867 mm (Table 1). Much of the site-to-site variation in temperature and precipitation occurs during the dormant season (Albert 1995), hence we expect that it had little effect on growth and biomass partitioning in the current study. The stands were all located on commercial forest land, and only one stand had been thinned because the dominant management objective at the time of this study was pulp production. The average density at most sites was 1750 trees·ha⁻¹; however, the 8- and 33-year-old sites had more than 2400 trees·ha⁻¹ (Table 1). The site that had been thinned for sawtimber production was the 55-year-old stand, which had 622 trees·ha⁻¹. The three sites with non-uniform density were retained in the study, however, because of the limited number of stands fulfilling the requirements regarding age, soils, and ownership of the chronosequence in the study area. Mean diameter at breast height (DBH) across sites ranged from less than 4.6 to 25.2 cm. Mean tree height across all sites ranged from less than 1.4 to 18.4 m. DBH and height were not measured at the two youngest sites, owing to the small size of the trees and logistical constraints. Basal area ranged from less than 3.1 to 59.3 m²·ha⁻¹; the higher value was for the 33-year-old stand and is unusually high for red pine (Rudolf 1990); as previously mentioned, the site was retained in the study because of the paucity of stands in this age class.

Field harvests

Complete above- and below-ground harvests were conducted during the summers of 2001, 2002, and 2003. Measurements were collected in a single 15 m × 15 m plot at each site for stand ages 5 and 12–55 years, in a single 10 m × 15 m plot for the 8-year-old stand, and in a single 10 m × 10 m plot for the 2- and 3-year-old stands. Generally, soil over the entire plot surface was excavated to 1 m deep, followed by excavation of one quarter of the plot area to 2 m deep, then excavation of one sixteenth of the plot area to 3 m deep (Fig. 1).

Table 1. Physical characteristics of the sites used in the study of biomass partitioning of red pine along a chronosequence in the western Upper Peninsula of Michigan.

Site/age (years)	Location*	Geographic coordinates	Soil series and texture	MAT (°C)	MAP (mm)	Density (trees-ha ⁻¹)	Mean DBH (cm)	Mean height (m)	Basal area (m ² -ha ⁻¹)
2	South Range	47°05'N, 88°39'W	Kalkaska; sand	4.1	867	1791	nd	nd	nd
3	Champion	46°30'N, 87°54'W	Pence; sandy loam	3.8	844	1733	nd	nd	nd
5	Champion	45°31'N, 87°52'W	Pence; sandy loam	3.8	844	1733	4.6	1.4	3.1
8	Champion	46°30'N, 87°54'W	Pence; sandy loam	3.8	844	2533	5.6	3.5	6.7
12	Republic	46°15'N, 88°57'W	Rousseau; sand	5.4	771	1866	9.5	4.9	13.9
17	Atlantic Mine	47°06'N, 88°41'W	Kalkaska; sand	4.1	867	1955	14.1	7.8	32.1
22	Republic	46°15'N, 88°57'W	Mancelona; loamy sand	5.4	771	1422	17.9	11.1	38.1
33	Republic	46°18'N, 87°56'W	Rubicon; sand	5.4	771	2488	16.6	14.4	59.3
55	Atlantic Mine	47°06'N, 88°41'W	Kalkaska; sand	4.1	867	622	25.2	18.4	31.6

Note: All tree metrics were determined from the single 15 m × 15 m plot at each site. Soil and meteorological data were adapted from the respective Natural Resources Conservation Service county soil surveys (MAT, mean annual temperature; MAP, mean annual precipitation); nd, not determined.

*Town nearest the field site.

Trees at the 2- and 3-year-old sites were very small and were harvested by carefully "lifting" all trees in the plot out of the soil by hand. Visual inspection indicated little loss of coarse-root mass because of the coarse texture of the soil and shallow rooting of the young trees. Biomass was separated into total root and total shoot components and dried to constant mass at 65 °C. Subsamples of each tissue type were ground, homogenized, and analyzed for ash content by combustion in a muffle furnace at 450 °C for 8 h. Three to five dried subsamples of each tissue type were analyzed for C and nitrogen (N) concentration using a Carlo Erba 1500NA elemental analyzer (Carlo Erba, Beverly, Mass.) run with National Institute of Standards and Technology pine needle and peach leaf standards.

At the 5-year-old site, height and DBH were measured on all trees in the plot. All trees were harvested for above-ground biomass by cutting the stem with a chain saw 30 cm above the ground line. Shoots were separated into foliage, branch, and bole components. Total plot-level root biomass was quantified by excavating the plot to 1 m deep with an excavator and front-end loader. The entire volume of excavated soil was sieved with a mechanized soil screen that we developed specifically for this study (Fig. 1). A glacially deposited layer of cobbles prevented excavation (and rooting) deeper than 1 m. The openings of the soil-screen mesh were diamond-shaped and measured approximately 1.5 cm × 4 cm. This relatively large mesh allowed for rapid soil sieving, but without significant loss of coarse-root material, as indicated by repeated visual inspection and resieving of the soil that had passed through the screen. The majority of roots remained connected to the taproots, but the soil screen insured that we recovered any roots that were severed during the excavation. Because of the large plot size, we assumed that roots that were exiting the plot and severed at the plot edge were "replaced" by a similar amount of roots growing into the plot from the surrounding plantation. Loose roots recovered during sieving were added to individual tree root biomass in proportion to a tree's contribution to the total intact plot root biomass. Root systems were not divided into root size classes, and no attempts were made to accurately measure fine roots (<1 mm diameter). In forest stands, fine roots typically make up a small percentage of the total root biomass (Giardina and Ryan 2002; King et al. 2005), so we do not expect detectable errors due to loss of fine roots. All plant material was dried to constant mass and three to five subsamples of each tissue type were taken to determine ash content and C and N concentrations as described above.

All plots from 8 to 55 years of age were harvested using the following procedure. An average of five trees were felled in each plot for development of allometric regressions to estimate aboveground biomass across the chronosequence. These five trees were cut 30 cm above the ground line. Total height and DBH were measured and the trees were separated into foliage, live branches, dead branches, and boles. Foliage contained all green needles and small-diameter twigs associated with needle flushes. Boles were cut into bolts roughly 3 m in length to facilitate weighing. All tree components were fresh-weighed using a calibrated spring scale suspended from the front-end loader. Five subsamples of each tissue type were taken for determination of fresh mass to dry mass conversion factors, ash content, and C and N concen-

Fig. 1. (A) The "Quake" soil screen developed at the USDA Forest Service North Central Research Station (RWU 4159) specifically for this project to sieve the large volumes of excavated soil. It is constructed of widely available square tubular metal stock and powered by a 5 h.p. gasoline engine, allowing use and repair in remote locations. (B) Soil pit at the 33-year-old site, showing the volume of soil excavated in 1 m deep layers and sieved to recover total belowground biomass in the 15 m × 15 m plot.



trations as described above. All remaining trees on the plot were measured for DBH, felled, and then measured for total height. All stumps were labeled so that stump/taproot biomass could be related to aboveground biomass for each tree in the plot. All aboveground biomass was removed from the plot. The entire soil volume of the plot was excavated and sieved as described above to recover total root biomass (Fig. 1). Each stump/taproot was brushed clean of soil and weighed individually with the calibrated spring scale. Coarse roots severed during the excavation were recovered by sieving the soil. Five to 10 subsamples of coarse roots and stump/taproot wood were collected from each soil depth for fresh mass to dry mass conversion factors, ash content, and

C and N concentrations as described above. All excavations were backfilled and the soil was leveled upon completion of the harvests.

Plant allometry and estimation of biomass

Biomass at the 2-, 3-, and 5-year-old sites was determined by direct measurement (see above). For the remaining sites, aboveground biomass was determined by applying allometric regressions to height and DBH measurements of all trees in the plots of the chronosequence. In total, 69 trees were destructively harvested to develop allometric equations. Natural log-transformed estimates of ash-corrected tree-component biomass were regressed against log-transformed DBH, height, and age (Table 2). Models were selected on the basis of the best combination of predictor significance, improvement of fit (R^2), and analysis of residuals. Back-transformation bias was accounted for by applying Baskerville's (1972) correction when calculating absolute data from the log-log regressions. Ash-corrected root biomass was measured directly for all trees in the study, therefore allometry was not needed to estimate belowground biomass. To arrive at individual-tree total root biomass, ash-corrected loose coarse root biomass recovered from sieved soil was allocated to each tree in proportion to the ratio of its stump/taproot biomass to total plot stump/taproot biomass. C and N concentrations were applied to biomass component estimates for all trees in the plot, summed, and scaled to an area basis (e.g., $\text{kg}\cdot\text{ha}^{-1}$).

Results

Allometric relationships

A total of 304 trees were harvested across the chronosequence, 69 of which were separated into foliage, live branches, dead branches, and boles to develop allometric models for biomass estimation (Table 2). For all plant parts, linear models fit the data well, with DBH, height, and age accounting for most of the variation (R^2 values ranged from 0.781 to 0.987). The model for dead branches, which were present on 18 of the 69 allometry trees from sites ≥ 17 years old, yielded the lowest R^2 value. In terms of model additivity, the sum of the allometrically estimated live aboveground tree component biomass was highly correlated with the allometrically estimated live total shoot biomass ($R^2 = 0.981$), with a slope of 1.009 and a nonsignificant intercept. The sum of the allometrically estimated total shoot biomass was within 1.4% of the measured value for the 69 allometry trees.

As root biomass was measured for all 304 trees in this chronosequence study, allometric models were not used to estimate belowground biomass. However, because this allometry could be valuable for estimating coarse-root biomass at other red pine sites, the allometric model for total root biomass is provided (Table 2).

C and N accumulation

C concentrations averaged 40.8%–49.5% for all plant parts, with the lowest values in live and dead roots (Table 3). Variation in C concentration within plant parts across the chronosequence was low, with coefficients of variation (CV) ranging from 0.9% to 9.1%, and live and dead roots being

Table 2. Parameters of the allometric equations used to predict tree-component biomass of red pine along a chronosequence for trees 5–55 years of age in the western Upper Peninsula of Michigan.

Dependent variable	<i>a</i>	<i>k</i>	<i>t</i>	Mean square error	<i>R</i> ²	<i>n</i>
Total shoots	6.2731	1.4536 (<i>D</i>)	0.0306	0.0464	0.974	69
Foliage	6.4199	1.1496 (<i>D</i>)	ns	0.0697	0.899	69
Live branches	5.5616	0.8788 (<i>D</i>)	0.0306	0.1661	0.842	69
Dead branches	-10.1654	1.6193 (<i>D</i> ² <i>H</i>)	-0.0775	0.1651	0.781	18
Bole	0.3748	0.7735 (<i>D</i> ² <i>H</i>)	0.0221	0.0558	0.987	69
Total roots*	2.6858	0.5836 (<i>D</i> ² <i>H</i>)	0.0083	0.2553	0.863	260†

Note: Root biomass of all trees was measured, so allometry was not used to estimate it; however, the model is provided here for interest. Models had the form $\log(Y) = a + k \log(X) + t(Z)$, where *Y* is biomass (g), *X* is either diameter (*D*) (cm) or *D*² × height (*H*) (cm³), and is indicated in parentheses for each model. The independent variable *Z* is age (years). Regression predictors were considered significant at $p \leq 0.05$ (ns, not significant).

*Includes 30 cm stump, the height at which the trees were harvested.

†Height data were missing for 44 of the 304 trees.

the most variable. Strong trends in C concentration across the chronosequence were not apparent. Average plant-component N concentrations ranged from 0.20% to 0.89%, being lowest in the boles and highest in the foliage. Across the chronosequence, variation in concentration was much higher for N than for C, with CVs ranging from 4.5% to 47.9%. As with C concentration, no strong trends in N concentration for individual tissues across the chronosequence were apparent, a possible exception being that N concentrations in all plant parts were higher at the 5-year-old site than at the older sites. This would probably also have been the case at the 2- and 3-year-old sites, but individual-component biomass and C and N concentrations were not determined for these sites.

There was a strong trend for biomass of all plant parts to increase from ages 2 to 32 and then to decrease at age 55 because of thinning (Table 4). Total shoot biomass increased from 0.21 to 118.20 t C·ha⁻¹, decreasing to 87.94 t C·ha⁻¹ at the 55-year-old site. Total root biomass increased from 0.03 to 55.22 t C·ha⁻¹, decreasing to 26.35 t C·ha⁻¹ at the 55-year-old site. Between the 5- and 55-year-old sites, biomass as a proportion of total shoot mass decreased from 63% to 9% for foliage and from 22% to 9% for live branches and increased from 14% to 82% for boles. Biomass of dead branches ranged from 3.44 t C·ha⁻¹ at the 17-year-old site to 7.51 t C·ha⁻¹ at the 32-year-old site and decreased to 1.31 t C·ha⁻¹ at the 55-year-old site. Biomass of dead roots increased across the chronosequence, from 0.22 t C·ha⁻¹ at the 5-year-old site to 5.33 t C·ha⁻¹ at the 55-year-old site. There was a large increase in dead-root biomass between the 32- and 55-year-old sites, owing to root mortality associated with thinning the 55-year-old site. The effect of the thinning on temporal and spatial patterns of coarse-root death almost certainly differs from senescence patterns associated with stem exclusion. It should be noted that dead-root biomass was not quantified at the 2- and 3-year-old sites, and may have been comparable to or greater than that at the 55-year-old site, owing to harvest of the former stands.

N accumulation across the chronosequence showed a similar pattern to biomass C, with the N concentration increasing until age 32, then decreasing at the 55-year-old site because of thinning (Table 5). Total live shoot N ranged from 4.40 kg·ha⁻¹ at age 2 to 712.41 kg·ha⁻¹ at age 32, then decreased to 370.45 kg·ha⁻¹ at the 55-year-old site. Total live root N ranged from 0.42 to 304.60 kg·ha⁻¹ at the 32-year-old

site and decreased to 184.11 kg·ha⁻¹ at the 55-year-old site. Between the 5- and 55-year-old sites, the fraction of total shoot N decreased from 78% to 40% in foliage, remained constant at 12%–13% in live branches, and increased from 8% to 49% in boles. Dead branches accumulated up to 42.46 kg N·ha⁻¹ by age 32 and dead roots up to 28.78 kg N·ha⁻¹ by age 55. The large increase in dead-root N concentration between the 32- and 55-year-old sites was due to root mortality associated with thinning.

Root–shoot biomass partitioning

Individual-tree root/shoot ratios calculated from allometrically estimated total live shoot biomass and measured total live root biomass displayed significant within-site variation (Fig. 2A). The CVs of the within-site root/shoot ratio were 38%, 58%, 24%, 26%, 24%, 22%, 28%, 32%, and 30% for the 2-, 3-, 5-, 8-, 12-, 17-, 22-, 32-, and 55-year-old sites, respectively. Averaged within site, the individual-tree root/shoot ratio was about 0.17 for the 2-, 3-, and 5-year-old sites, increased to about 0.80 for the 8-year-old site, and decreased more or less asymptotically to 0.29 at the 55-year-old site (Fig. 2B). The exception to this overall trend was at the 32-year-old site, where the root/shoot ratio was 0.49. A similar pattern of root/shoot ratios occurred at the stand level as well. Root/shoot ratios calculated from stand-level estimates of total live root and shoot biomass (Table 4) increased from 0.14 at the 2-year-old site to 0.86 at the 8-year-old site, then decreased asymptotically to 0.30 at the 55-year-old site. The exception to this pattern of declining stand-level root/shoot ratio with age was the 32-year-old site, which had a ratio of 0.47 (Table 4).

Discussion

We hypothesized that above- to below-ground biomass partitioning in red pine, expressed as the root/shoot ratio, would peak early in stand development and then decline asymptotically through time. Results from this 55 year chronosequence study using complete above- and below-ground biomass harvests largely support this hypothesis. The findings of this study have important implications for our understanding of how forest ecosystems develop through time and store C.

Table 3. Carbon (C) and nitrogen (N) concentrations of all tissue types from a chronosequence of red pine in the western Upper Peninsula of Michigan.

Site/age (years)	Foliage	Live branch	Dead branch	Bole	Stump	Live root	Dead root
C concn. (%)							
2	51.3	51.3	na	51.3	45.3	45.3	na
3	50.6	50.6	na	50.6	47.5	47.5	na
5	48.9	48.6	na	49.2	40.8	40.8	43.2
8	49.7	47.8	na	48.6	46.9	43.7	42.9
12	49.6	49.4	na	48.5	46.6	41.0	42.2
17	50.6	49.6	49.9	49.0	46.5	37.8	44.3
22	49.5	49.6	49.6	49.8	46.6	39.4	40.8*
32	48.6	48.6	49.5	49.0	46.2	42.3	33.4
55	48.5	47.8	48.8	47.8	45.6	44.9	38.9
Mean	49.3	48.8	49.5	48.8	45.6	41.4	40.8
CV	1.5	1.6	0.9	1.3	4.7	5.9	9.1
N concn. (%)							
2	1.10	1.10	na	1.10	0.65	0.65	na
3	1.26	1.26	na	1.26	0.84	0.84	na
5	0.85	0.41	na	0.40	0.61	0.61	0.52
8	0.85	0.23	na	0.23	0.33	0.51	0.31
12	0.89	0.29	na	0.17	0.41	0.59	0.91
17	0.88	0.13	0.18	0.17	0.31	0.47	0.52
22	0.89	0.23	0.19	0.16	0.24	0.24	0.50*
32	0.97	0.35	0.28	0.14	0.23	0.34	0.52
55	0.90	0.26	0.30	0.12	0.28	0.38	0.21
Mean	0.89	0.27	0.24	0.20	0.34	0.45	0.50
CV	4.5	33.4	25.8	47.9	38.3	30.2	44.1

Note: Concentrations were determined on three to five ash-corrected samples using a Carlo Erba NA 1500 Series II elemental analyzer (Carlo Erba, Beverly, Mass.). Trees from the 2- and 3-year-old sites were not separated into component parts, so component the C and N concentrations shown here are actually aggregated root and shoot values. Means and coefficients of variation (CV) were calculated without the 2- and 3-year-old sites, since they did not have component C and N concentrations; "na" denotes "not applicable", as no dead branches or roots were found at these sites.

*Determined by averaging all other dead-root values because some data were missing.

Table 4. Carbon content ($\text{t}\cdot\text{ha}^{-1}$) in all plant parts and root/shoot ratios along a chronosequence of red pine in the western Upper Peninsula of Michigan.

Age (years)	Foliage	Live branch	Bole	Stump/taproot	Loose root	Dead branch	Dead root	Live shoot	Live root	Root/shoot ratio*
2	nd	nd	nd	nd	nd	0	0	0.21	0.03	0.14
3	nd	nd	nd	nd	nd	0	0	0.53	0.06	0.12
5	2.97	1.06	0.68	0.74	0.13	0	0.22	4.71	0.87	0.18
8	5.83	0.88	3.18	7.64	0.88	0	1.27	9.89	8.52	0.86
12	8.19	2.90	7.52	9.36	2.29	0	0.51	18.61	11.65	0.63
17	14.33	4.90	22.66	7.55	3.49	3.44	0.02	41.89	11.04	0.26
22	11.94	4.90	36.56	12.82	1.51	7.00	0.19	53.39	14.33	0.27
32	19.23	10.54	88.42	45.50	9.71	7.51	1.07	118.20	55.22	0.47
55	7.86	8.04	72.03	16.75	9.60	1.31	5.33	87.94	26.35	0.30

Note: Values were determined by multiplying allometrically determined aboveground biomass and directly measured belowground biomass by their respective C concentrations ("nd" indicates that individual biomass components were not determined at these sites. "Loose root" refers to severed roots recovered by sieving; "live root" is the sum of stump/taproot and loose roots; "live shoot" is the sum of foliage, live branch, and bole.

*Calculated from live biomass only.

Harvest methodology

Few studies have provided as complete a description of above- and below-ground biomass for a commercially important tree species as the current work. The development of the mechanized soil screen and the use of tractors to excavate and sieve large volumes of soil enabled us to accurately quantify total root biomass down to a depth of 3 m in very large plots. Although each age in the chronosequence was

represented by only a single plot, the large size of the plots helped to ensure that sampled trees and soils were representative of the surrounding pine plantations. The unthinned plots contained 40–44 trees and the thinned 55-year-old site still had 14 trees in the plot. The large number of trees per plot provided an excellent basis for capturing the variation in tree dimensions in the respective plantations. Fresh mass to dry mass conversion factors, C and N concentrations, and

Table 5. Nitrogen content ($\text{kg}\cdot\text{ha}^{-1}$) in all plant parts along a chronosequence of red pine in the western Upper Peninsula of Michigan.

Age (years)	Foliage	Live branch	Bole	Stump/taproot	Loose root	Dead branch	Dead root	Live shoot	Live root
2	nd	nd	nd	nd	nd	0.00	0.00	4.40	0.42
3	nd	nd	nd	nd	nd	0.00	0.00	13.15	1.14
5	51.55	8.73	5.53	6.75	2.02	0.00	2.57	65.80	8.76
8	99.75	4.23	15.06	53.74	10.27	0.00	0.00	119.03	64.01
12	147.04	17.03	26.35	82.33	33.00	0.00	11.06	190.41	115.32
17	249.17	12.85	78.60	50.32	43.39	12.41	0.22	340.62	93.71
22	214.71	22.70	117.45	66.04	9.20	26.81	2.37	354.87	75.25
32	383.85	75.93	252.63	226.53	78.07	42.46	16.67	712.41	304.60
55	145.86	43.76	180.84	102.87	81.23	8.04	28.78	370.45	184.11

Note: Values were determined by multiplying allometrically determined aboveground biomass and directly measured belowground biomass by their respective N concentrations ("nd" indicates that individual biomass components were not determined at these sites. "Loose root" refers to severed roots recovered by sieving; "live root" is the sum of stump/taproot and loose roots; "live shoot" is the sum of foliage, live branch, and bole.

ash content were determined for all plant parts for each plot. Further, the plots were located on landforms and soils typical for the species in our region and the stands were managed using common industry practice, making our results highly relevant from a C-accounting perspective.

Although many studies since the International Biological Program era have included ecosystem-level assessments of C standing stocks (Ovington 1957; Kinerson et al. 1977; Cole and Rapp 1981; Grier et al. 1981; Gholz et al. 1982; Vogt 1991; Albaugh et al. 1998, 2004; Nadelhoffer et al. 1999; Mund et al. 2002), the current study is unique because of the thoroughness of the accounting of belowground C contained in coarse roots. Whereas in many studies, root biomass is estimated from regressions based on a relatively small number of trees (e.g., Haynes and Gower 1995; Albaugh et al. 1998), we excavated and directly measured the root systems of a total of 304 trees. The volumetric soil sampling allowed recovery of roots severed during the harvest and direct extrapolation of tree biomass on an area basis. Excavation to 3 m deep permitted a thoroughness of root-biomass recovery that is rarely reported in the literature.

Red pine allometry

In the current study, the allometry of red pine was very consistent across the chronosequence, with linear models based on DBH, and sometimes height, providing an excellent fit to component-biomass data for trees ranging in age from 5 to 55 years. This is consistent with previous studies of red pine. Alban and Laidly (1982) developed generalized biomass equations for red pine aged 20–61 years across the northern Lakes States. They found that nonlinear models based on diameter and height provided a good fit to biomass for trees of all ages and a wide range of site index, especially for bole and total aboveground biomass. In a study examining the effects of fertilization on pine allometry, Gower et al. (1993) developed diameter-based linear biomass equations for 30-year-old red pine. The fit of the models was good for all aboveground biomass components, with high R^2 values and low standard errors of the estimate. Fertilization did not alter allometric relationships of wood, branch, and foliage biomass relative to diameter, but did alter the vertical distribution of foliage in the canopy. Reed et al. (1995) examined allometric relations in precompetitive (8 years old) red pine at three sites in northern Michigan. The authors

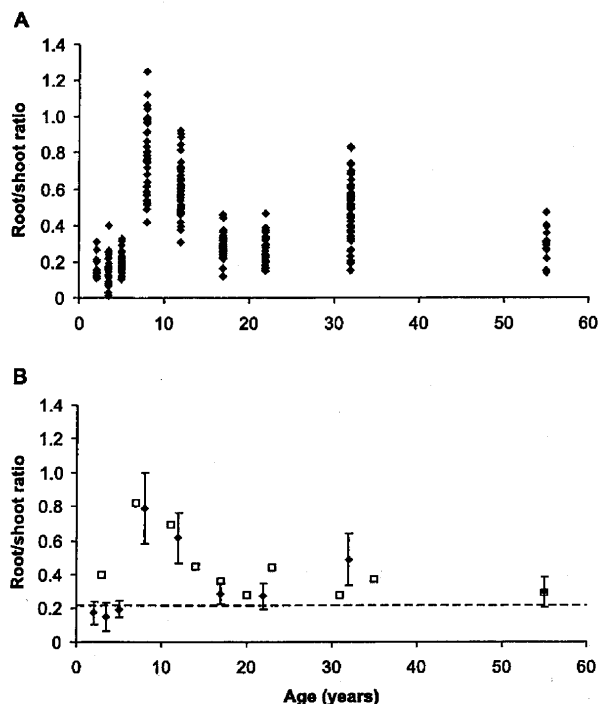
used logarithmic equations to relate above- and belowground biomass to basal diameter, and found no differences in these relationships across the range of tree biomass examined (from 3 to 6720 g) or among sites. The results of these studies, together with our results, suggest that the allometry of red pine is very stable across wide ranges of age, size, and site quality. Some authors have attributed this to the limited genetic diversity of the species (Alban and Laidly 1982), but whatever the cause, it allows for robust estimation of tree biomass with diameter-based biomass equations.

The stability of allometry we show here is consistent with the literature review and analysis by Enquist (2002), which suggests that allometric scaling relationships are strongly conserved, even universal, within and across tree species and ecosystems.

Biomass partitioning and accumulation through time

In the current study we determined the partitioning of biomass to live roots and shoots at the individual-tree and stand level in red pine ranging in age from 2 to 55 years. Aboveground biomass was modeled, except at the 2- to 5-year-old sites, where it was measured directly. In contrast to most studies of forest C accounting, we measured belowground biomass directly for all trees in the chronosequence. In support of our main hypothesis, the observed pattern of root-shoot biomass partitioning through stand development was very similar to that of Scots pine reported in the tree-based chronosequence study of Ovington (1957, Figs. 2 and 3): the root/shoot ratio was low (~ 0.15) in the youngest stands, increased to a maximum (~ 0.82) at age 8, and then declined (to ~ 0.30) asymptotically from 8 to 55 years of age. This finding was supported by the allometric analysis (Fig. 2), which showed that relative biomass partitioning to roots was greater in the 8- and 12-year-old stands than in the other age classes. However, within a site, individual-tree root/shoot ratios were quite variable, with CVs ranging from 22% to 58%. The within-site variation in root/shoot ratio could be related to the range of sizes of trees present in each plot as dominants, codominants, and suppressed individuals (Naidu et al. 1998). It has been shown that plant allometric relationships are often more sensitive to plant size than age, recognition of which is especially important when interpreting biomass-partitioning responses to changes in resource availability or environmental conditions (Gebauer et al. 1996;

Fig. 2. Root/shoot ratios for red pine along a chronosequence in the western Upper Peninsula of Michigan. (A) Root/shoot ratios for all individual trees in the study ($n = 299$), consisting of allometrically determined aboveground biomass and belowground biomass estimated by excavation of coarse roots (see Methods). (B) The mean ($\blacklozenge$) and 1 standard deviation root/shoot ratio for each site, showing a pattern of maximum root/shoot ratio at age 8, declining asymptotically thereafter. Root/shoot ratios for *Pinus sylvestris* ($\square$) were calculated from the chronosequence data of Ovington (1957). The broken line is the mean root biomass fraction of softwoods in the Canadian forest sector reported by Li et al. (2003).



Gedroc et al. 1996; King et al. 1996, 1999; Norby et al. 1999). Competition for light, which depends on relative position in the canopy, has also been shown to exert a strong influence on shoot biomass partitioning (Nilsson and Hällgren 1993). The high within-site variation in root/shoot ratio that we observed suggests that conclusions regarding biomass partitioning in forests should be based on a relatively large number of trees for each forest or site.

An apparent departure from the above pattern of root-shoot partitioning across the chronosequence occurred at the 32-year-old site. This site had a root/shoot ratio of about 0.47, which is higher than the ratios of 0.27 and 0.30 for the 22- and 55-year-old sites, respectively. This is probably related to the high density of this stand. For a pine, red pine is known to have relatively high shade tolerance (Rudolf 1990) and therefore can maintain a high stem density and basal area. In the current study, density-dependent mortality had not occurred at the 32-year-old site; all the trees in the plot had a small DBH and small crowns, but appeared vigorous (and probably would respond to thinning). The high stem

density apparently caused greater relative allocation to roots in this stand. Although it might seem counterintuitive, this finding is consistent with that of Litton et al. (2003), who found a strong relationship between tree density and biomass partitioning to roots in young lodgepole pine (*Pinus contorta* Dougl.) forests 13 years after stand-replacing fire. Even with the relatively high root/shoot ratio at the 32-year-old site, the overall pattern of declining root-shoot biomass partitioning after age 8 was maintained. It should be noted that in the current study, the 8-year-old site also had high stem density, which may have contributed to the greater relative biomass partitioning at this site, but maintained a root/shoot ratio twice that at the 32-year-old stand.

Other patterns of root-shoot biomass partitioning than that shown here have been observed, although the number of studies examining biomass partitioning over such long time scales (55 years) are rare. Calculations from the data of Reed et al. (1995) show declining root/shoot ratios in red pine over the first 10 years of stand development (D.D. Reed, personal communication), whereas our study and that of Ovington (1957) show increasing root/shoot ratios until about age 8 and then a decline. Similarly, a decline in the root/shoot ratio was observed with increasing tree size in Litton et al.'s (2003) study, which is counter to the trend in the first 8 years of our study. It is possible that some fraction of total root biomass was missed in the 2- and 3-year-old stands in our study, owing to the lifting of the trees, but this cannot explain the observed pattern. The 5-year-old site was excavated in the same manner as the older stands, and Ovington (1957) harvested entire trees using a standard protocol. Interestingly, in our study the 8- and 32-year-old stands, which had a relatively high density, also had relatively high root/shoot ratios. Together, the results of these studies suggest that root-shoot biomass partitioning peaks early and then declines through stand development, and that it may vary according to environmental conditions, stand history, and management (especially density). Clearly, more work is needed to understand the controls on root-shoot biomass partitioning during stand development.

How patterns of root-shoot biomass partitioning change with stand development has important implications for the role of forests in the global C cycle and the potential of forests to sequester atmospheric C (King et al. 1999; Pregitzer 2003; Giardina et al. 2005). An important finding of the current work is that the pattern of root-shoot biomass partitioning observed for individual trees was conserved at the stand level. That is, the pattern of root-shoot partitioning observed on an individual-tree basis (Fig. 2) was maintained after scaling above- and below-ground biomass estimates to the stand level (Table 4). Therefore, use of constant allocation coefficients to estimate belowground biomass from above-ground biomass (e.g., Li et al. 2003) may not be appropriate in all cases and may underestimate the allocation of C below ground for some stands. In the present case, roots in 8-year-old plantations contained 8.5 t C ha^{-1} compared with 9.9 t C ha^{-1} in shoots, or 86% of shoot C. In the 55-year-old plantation (after thinning), roots contained 26.3 t C ha^{-1} compared with $87.94 \text{ t C ha}^{-1}$ in shoots, or 30% of shoot C. Clearly, constant allocation coefficients would not accurately describe belowground C stocks in the red pine plantations

we sampled on glacial-outwash landforms in the Upper Great Lakes region.

Conclusions

The results of our study suggest that a current research challenge is to determine the generality of patterns of root-shoot biomass partitioning through stand development for both soft- and hardwood forest types, and to document how these patterns change as a function of resource availability, environment, and management. Brute-force C-accounting studies such as this, though not easy or glamorous, are critical for the continuing effort to develop and validate inventory-based methods of accounting for terrestrial C storage in forest ecosystems, especially belowground C (Birdsey and Heath 1995, 2001; Heath et al. 2003). Based on USDA Forest Service Forest Inventory and Analysis data, Heath et al. (2003) estimated C density (above- and below-ground live biomass) for the white-red-jack pine forest type at 72.7 t-ha^{-1} , occurring on 4 795 000 ha in the eastern USA, for a total C stock of $348.6 \times 10^6 \text{ t}$ (or 348.6 Mt). This average estimate is for all age classes distributed across the landscape containing all species on managed timberland. Although it is difficult to make direct comparisons with such broad-scale estimates, in our study total live tree C density ranged from 0.24 to 114.30 t-ha^{-1} for the 2- to 55-year-old sites. Notably, C density increased to 173.41 t-ha^{-1} for the overstocked 32-year-old site. This suggests that stands of some moderately shade-tolerant species could be managed for greater C sequestration by maintaining higher stem density. However, the benefits to C sequestration would have to be weighed against the increased risk of higher fuel loading, suitability for end-product use (e.g., sawtimber, pulp, etc.), and consequences for other environmental services such as water cycling (Jackson et al. 2005).

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