Plant and Soil **225:** 129–139, 2000.

Contrasting fine-root production, survival and soil CO_2 efflux in pine and poplar plantations

M. D. Coleman[1,2], R. E. Dickson and J. G. Isebrands
USDA Forest Service, North Central Research Station, Forestry Sciences Laboratory, Rhinelander, WI 54501, USA. [1]*Current address: USDA Forest Service, Savannah River Institute, New Ellenton, SC 29809, USA.* [2]*Corresponding author**

Received 19 November 1999. Accepted in revised form 20 June 2000

Key words: fine-root turnover, hybrid poplar, minirhizotron, red pine, soil respiration

Abstract

Tree root activity, including fine-root production, turnover and metabolic activity are significant components of forest productivity and nutrient cycling. Differences in root activity among forest types are not well known. A 3-year study was undertaken in red pine (*Pinus resinosa Ait.*) and hybrid poplar (*Populus tristis* X *P. balsamifera* cv 'Tristis no. 1') plantations to compare belowground root dynamics. We measured fine-root production, mortality and standing crop, as well as soil CO_2 efflux. Pine fine-root production was only 2.9% of that of poplar during three years; 85 pine roots were observed in minirhizotron tubes compared with 4088 poplar roots. Live-root density oscillated seasonally for both species with late winter minimum and autumn maximum. Poplar reached constant maximum live-root length within the first growing season, but pine continued to increase observed fine-root length for three growing seasons. Within the first 100 days following initial appearance, 22% of the pine roots disappeared and 38% of the poplar roots disappeared. Median fine-root longevity of pine was 291 days compared with 149 days for poplar roots. Fine-root longevity increased with depth in the soil, and was greater for roots with initial diameter >0.5 mm. The probability of poplar root death from late February to May was more than three times that in any other season, regardless of root age. Despite the greater poplar root production and live-root length, fine-root biomass and soil CO_2 efflux was greater in pine. Greater metabolic activity in the pine stand may be due to greater fine-root biomass or greater heterotrophic respiration.

Introduction

Understanding differences in root activity among tree species is critical to evaluating differences in productivity among forest ecosystems and the impacts of disturbance on ecosystem processes. Total forest productivity is dependent upon acquisition of resources above and belowground. Although the importance of leaf production and duration to carbon acquisition is well understood (Landsberg and Gower, 1997), parallel root information is limited. The few studies that are available indicate that root absorptive surface is equal to or greater than leaf surface (Jackson et al., 1997). Although forest productivity is dependent upon production of live-root surface for acquisition of water and essential nutrients, most information about root biomass and surface area is based on static standing-crop measures. Temporal and spatial dynamics information indicates annual fine-root production and turnover is several times greater than standing crop (Vogt et al., 1996).

Species comparisons and compiled study results have not found distinct differences in root dynamics for different forest types such as evergreen conifers and deciduous hardwoods (Fogel, 1985; Harris et al., 1977; Jackson et al., 1997; McClaugherty et al., 1982; Nadelhoffer and Raich, 1992; Ruess et al., 1996; Steele et al., 1997; Vogt, 1991). However, these studies have generally used destructive coring

* FAX No: 8037251807. E-mail: mcoleman@ifx.net

Table 1. Structural characteristics and growth of red pine and hybrid poplar stands used for minirhizotron observations

	Stocking	Mean diameter 1996	Basal area	Diameter growth 1994 to 1996
	(trees ha^{-1})	(cm)	(m^2 ha^{-1})	(cm yr^{-1})
Pine	2418	18.5	65.0	0.12
Poplar	1619	13.0	21.5	0.54

or indirect methods for determining root production. Direct observations from greenhouse studies indicate important differences in root longevity among species – evergreen conifers are longer lived than deciduous hardwoods (Black et al., 1998) – but field data are lacking. Greater understanding of fine-root production and turnover in the field is possible by combining coring techniques for dry weight with nondestructive observation techniques for production and turnover (Majdi, 1996).

We compared fine-root dynamics of an evergreen conifer with those of a deciduous hardwood for three growing seasons to evaluate temporal and spatial variation in fine-root production, mortality and soil CO_2 efflux. We expected that the conifer would have less active root systems, than the hardwood, in both growth and metabolism.

Materials and methods

Fine-root production and mortality were studied in red pine (*Pinus resinosa Ait.*) and hybrid poplar (*Populus tristis* X *P. balsamifera* cv 'Tristis no. 1'). Plantations were located 0.9 km apart on the Harshaw Forestry Research Farm near Rhinelander, WI, USA (45° 38′ N lat., 89° 25′ E long.). The soil for both species is a well-drained Padus sandy-loam (Alfic Haplorthods) underlain by glacial outwash of stratified sand and gravel (1993, Oneida County Soil Survey, USDA Soil Conservation Service). Soil analyses of the top 30 cm were quite similar for pine (pH 5.1, 68% sand, 10% clay, 0.08% total N and 3.0% organic matter) and poplar (pH 5.7, 62% sand, 10% clay, 0.08% total N and 2.3% organic matter). Both stands were fully stocked with complete canopy closure and no understory vegetation (Table 1). The 900 m^2 pine stand was established in 1960 on a hay field. The poplar plantation was established as part of a genetics trial in 1984.

Four observation plots were designated in each plantation. Each square observation plot consisted of four trees. Located at the center of each four-tree plot was an acrylic minirhizotron and a soil CO_2 efflux measurement location. The pine observation plots were at least 5 m apart. The poplar observation plots were divided between two 64-tree blocks (400 m^2 each) with centers located 58 m apart. In each block, two measurement plots were located within the central 16 trees and separated by 5 m. Therefore, each plantation type was represented by four replicate observations.

Measurements

Fine-root growth was determined using 5 cm diameter acrylic minirhizotrons installed (20 May, 1994) at a 45° angle, 85 cm deep. Monthly observations occurred between May 1994 and September 1996 using a Bartz Technology[1] (Santa Barbara, CA, USA) video camera equipped with indexing handle to revisit identical tube locations at each observation time. Ninety frames per tube were imaged in an 18-mm-wide viewing transect along the top surface, totaling 210 cm^2 per minirhizotron. No observations were taken between December 1994 and February 1995 or between October 1995 and April 1996 due to snow pack and temperatures below equipment operating limits. Taped video images were quantified using ROOTS (Enslin et al., 1994). The length and width of new roots appearing on the outside of the acrylic tube were recorded, and the fate of roots was monitored until complete disappearance. Because the stands were free from understory vegetation, all observed roots were assumed to be from plantation trees. Roots were categorized as new, previously observed or missing. No attempt was made to classify previously observed roots as suberized, woody or dead, thus simplifying quantification and eliminating subjective cutoffs. Individual root survival time, or lifespan, was measured from the date of observed appearance to the date of complete disappearance.

Soil cores (4.7 cm diameter, 75 cm depth) were collected (25 June, 1996) to estimate fine-root biomass and specific root length from each of the observation plots. Roots were elutriated from soil mineral (Gilson, Benzonia, MI, USA), stored in 20% methanol and manually separated from litter and duff. Live fine (<0.5 mm) and coarse roots (>0.5 mm) were separated using calipers and their length was deter-

[1] Mention of trade names does not constitute endorsement by the U.S. Department of Agriculture.

mined from digital images of sub-samples (Optimus, Edmonds, WA, USA). Flaccid roots having a cortex that easily pulled away from the stele were considered dead. Each of the imaged samples were dried (70 °C), weighed and ashed (525 °C) so not to include any soil remaining after washing. Specific root length (mm g^{-1}) and root length per unit surface (mm m^{-2}) were calculated for each core.

Soil CO_2 efflux was measured using a transient gas exchange system (LI-6200, LICOR, Lincoln, NE, USA) equipped with a soil CO_2 flux chamber. Measurements were collected from permanently located 10-cm-diameter, 5-cm-long PVC plastic rings inserted 2 cm into the mineral soil. Monthly measurements were taken from each plot, except when rings were snow covered. Readings for both plantations were collected within 2 hours of solar noon on the same day. Soil temperature (15 cm depth) was recorded for each measurement using the temperature probe attached to the LICOR chamber. Chamber CO_2 concentration was drawn down using the scrub circuit of the LICOR. During each measurement, six flux rate estimates (5 mmol mol^{-1} intervals) were collected as the CO_2 concentration in the chamber rose from below and passed above ambient surface concentration. The first interval was discarded to avoid instability, and the five remaining intervals were averaged.

Analysis

Root depth distribution was analyzed for each species using a two-factor analysis of variance. The factors included two initial root diameter categories (<0.5 or >0.5 mm) and three depth categories (<30, 30 – 60, >60 cm). Further analyses for pine included only two depth categories (<30 or >30cm). Percentages were arcsin transformed to ensure uniform variance (Snedecor and Cochran, 1980).

Fine-root disappearance was analyzed with life-tables survival analysis techniques (Kalbfleisch and Prentice, 1980; Lee, 1992). Root survival time was defined as the period between first appearance and disappearance. Roots living past the last observation were considered right censored, meaning that survival time is at least as long as the time to final observation. Both survival and hazard functions were estimated. The survival function is the probability that an individual survives past a certain time. The hazard function is the probability of disappearance during a given time interval, assuming the root has survived to that interval. Tests between species and initial diameter (<0.5 mm and >0.5 mm), as well as among depth (<30 cm, 30 – 60 cm and >60 cm), and appearance month (January – March, April, May, June, July, August, Sepember, October, November – December) were determined using the log rank and Wilcoxon tests. The relative importance of these factors was also assessed by stepwise additions to the model. The SAS LIFETEST procedure (SAS Institute Inc., 1989) was used for all survival data analyses.

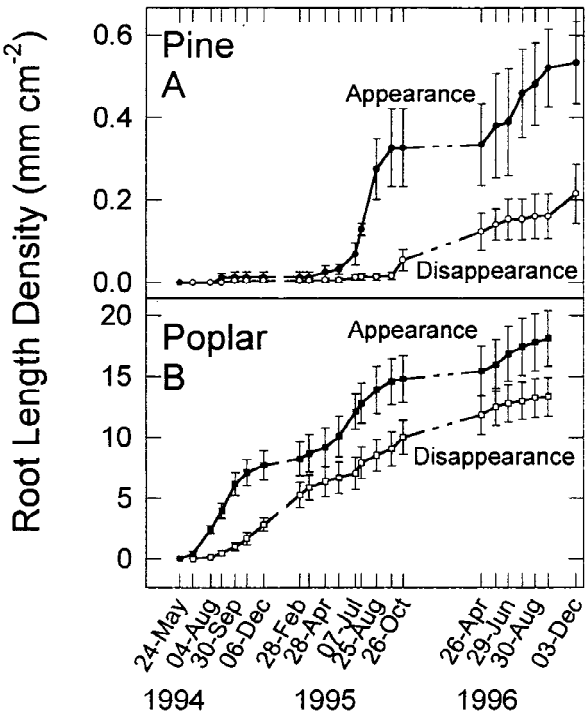

Figure 1. Cumulative root length density appearance and disappearance for pine (A) and poplar (B) over three growing seasons. Each point is the mean ± standard error (n=4).

Soil CO_2 efflux and temperature between stands were compared at each observation date using a paired Student's t-test. Species differences in log transformed soil CO_2 efflux as a function of temperature were compared with linear regression comparison techniques (Kleinbaum and Kupper, 1978).

Results

Fine-root production and disappearance

Fine-root production and disappearance were lower for pine than poplar. During three growing seasons, a total of 85 pine roots appeared on the minirhizotron surface compared with 4088 poplar roots. Pine

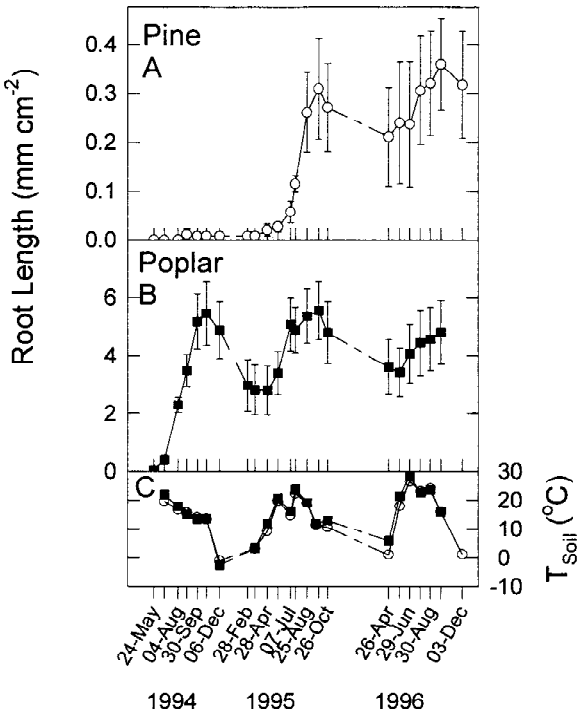

Figure 2. Standing live-root length density for pine (A) and poplar (B) over three growing seasons. Live-root length is calculated as the difference between cumulative appearance and cumulative disappearance (Figure 1). Soil temperature (T_{Soil}) measured at 15 cm depth at each sampling time is also presented (C). Each point is the mean ± standard error (n=4).

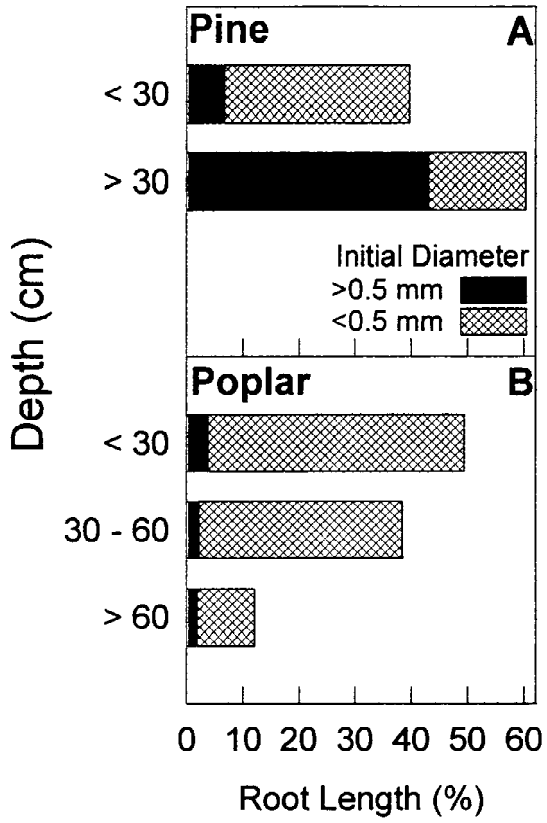

Figure 3. Percentage of total root length for pine (A) and poplar (B) in each different depth by initial root diameter category. Initial root diameters represent fine feeder roots (<0.5 mm) and pioneer roots (>0.5 mm). Percentages are based on root length in each depth by size category compared to total root length per minirhizotron. Values are the means of four replicate minirhizotrons. See Table 2 for statistical analysis.

fine-root length production was 2.9% of that of poplar (Figure 1). Pine fine-root length disappearance was 1.2% that of poplar. Pine live-root density was minimal during the first growing season and increased the following 2 years (Figure 2). In contrast, poplar live-root density reached a maximum the first season, which was equivalent to that of subsequent seasons. Because pine roots continued to increase on the minirhizotron surface, the difference in live-root density between pine and poplar decreased in each successive season. In 1994, pine live-root length averaged 0.2% that of poplar, in 1995, it was 2.7%, and in 1996 it was 6.7%. Consequently, even though pine root production and disappearance was less than 3% of poplar, the amount of live-root length maintained by both equalized during the observation period.

Seasonal patterns of cumulative root appearance and disappearance were similar for both species (Figure 1). Fine root growth, especially for poplar, began early in spring, increased exponentially until mid-growing season and decreased in fall and winter. Annual changes in root disappearance rate were not as large as those of root appearance. The small annual changes evident in the rate of cumulative disappearance were seasonally delayed compared to those for root appearance rate. The most rapid disappearance occurred during the dormant season, the least rapid occurred during the early growing season. Relative difference in annual changes and the offset in annual fine-root appearance and disappearance resulted in an oscillation in live fine-root length with a late growing season maximum and early spring minimum (Figure 2). The oscillation period was identical for both species due to seasonal climate, but the amplitude for pine was 11% of that for poplar. Root length oscillation maximum was later than that of soil temperature (Figure 2C).

Total root length production did not differ with depth for pine but declined with depth for poplar (Fig-

Table 2. Analysis of variance of root lengths for different depths and root diameters (see Figure 3). The categories included two depths for pine (<30 or >30 cm) or three depths for poplar (<30, 30 – 60, >60 cm) by two initial root diameter categories (<0.5 or >0.5 mm). Percentages were arcsin transformed. There were four replicate tubes per species

	Total length		Percentage in each category	
	pine	poplar	pine	poplar
Soil Depth	ns[a]	ns	ns	**
Root Diameter	ns	***	ns	***
Depth × Diameter	*	ns	*	ns

[a] Level of *F*-test significance: ***, $0.001 < P < 0.01$; **, $0.01 < P < 0.05$; *, $0.05 < P < 0.1$; ns, non-significant *F*-test, $P > 0.1$.

ure 3, Table 2). Pine roots with initial root diameters greater than 0.5 mm comprised a smaller percentage of total root length in the upper layers but were a greater percentage at depths greater than 30 cm (significant Depth × Diameter interaction in Table 2). This shift in pine diameter class with depth was associated with morphological differences. Many short bifurcate roots occured in surface soil layers, while long roots were more common at depth. The interaction between depth and initial diameter was evident in pine only if two depth categories were used instead of three because so few roots occurred at lower depth causing insufficient statistical testing power for three layers. For poplar, total root length declined with depth (Figure 3), but the percentage of roots greater than 0.5 mm was similar at each depth (no interaction, Table 2). The percentage of poplar roots greater than 0.5 mm averaged less than 3% of total root length compared with 7 and 43% in pine, indicating pine had larger diameter roots.

Survival analysis

Analysis of survival curves can be used to understand the effect of various plant and soil factors on fine-root longevity. Estimated survival functions (Figure 4) show pine median root longevity was 291 days compared with 149 days for poplar. The percentage of surviving pine roots was greater than that of poplar at each time point on the survival curves ($P < 0.0001$).

To test controls on longevity, survival functions were stratified by initial diameter, depth and appearance month. Larger diameter and deeper roots survived longer than thinner, shallower roots for both species (Figure 5). Similar results were found with both log rank and Wilcoxon tests. Of the three covariates considered in univariate tests, each was highly significant in poplar (*P*-value < 0.01). For pine, the

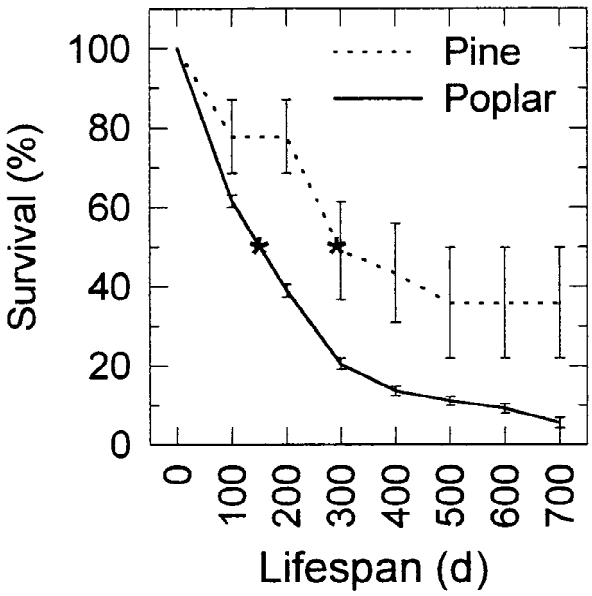

Figure 4. Fine-root survival curves for pine and poplar. Data are midpoints of life-table survival estimates for 60-day time intervals. The symbol (*) shows median root lifespan for each species. Species survival curves are significantly different (*P*-value < 0.0001) according to log rank and Wilcoxon test. Error bars are 95% confidence intervals of the estimate.

initial diameter (*P*-value < 0.05) and depth (*P*-value < 0.10) were significant, but appearance month was not. When introduced stepwise into a multivariate model, they ranked diameter>depth>month for pine and month>diameter>depth for poplar. Each factor significantly improved the poplar model (*P*-value < 0.008), but only diameter improved the pine model (*P*-value = 0.04).

The month of root appearance was significantly related to longevity of poplar roots, but not pine roots. The majority of roots (87% pine, 65% poplar) appeared in July, August and September. Only 11 pine roots appeared in the remaining 9 months of the year, so further analysis of seasonal patterns was not possible for this species. The impact of appearance month on poplar root longevity was analyzed with the help of hazard functions, also known as the age-specific failure rate (Lee, 1992). When poplar hazard functions were stratified by month of root appearance, distinct patterns emerged (Figure 6). The failure rate was typically high for all roots shortly after appearance, indicating early mortality, but then declined, only to peak once or twice more. The one or two post-appearance peaks in age-specific failure rates occurred between 26 February and 22 May (Figure 6), indicat-

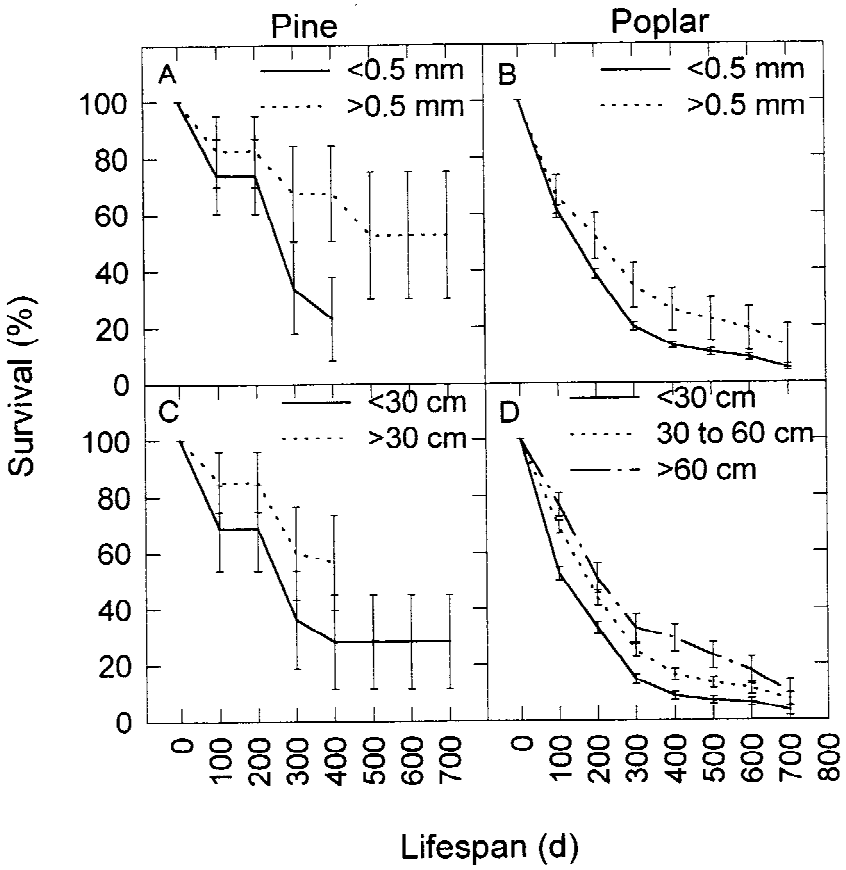

Figure 5. Fine-root survival curves for the association between initial diameter (A and B) and depth (C and D) of pine and poplar. Data are midpoints of life-table survival estimates for 60-day time intervals. Diameters less than 0.5 mm were compared to greater diameters. Poplar roots growing in 30-cm soil depth layers were compared. The limited pine data only allowed comparison of the first 30 cm depth with greater depths. Each frame represents a significant log rank and Wilcoxon test (P-value < 0.1 for pine; P-value < 0.01 for poplar). Error bars are 95% confidence intervals of the estimate.

Table 3. Pine and poplar root biomass and root length comparisons. Ash-free root weights and lengths (soil cores) expressed per unit soil surface, and root diameters (minirhizotron images). Coarse roots were greater than 0.5 mm diameter. Fine-root length is calculated as the product of specific root length and fine-root weight. Root diameter is the average initial diameter of all roots observed in minirhizotrons. Values in parentheses are standard deviation of the mean (n=4)

	Fine-root biomass ($g\ m^2$)	Coarse-root biomass ($g\ m^2$)	Specific root length ($m\ g^{-1}$)	Fine-root length ($m\ m^{-2}$)	Root diameter (mm)
Pine	620	357	16.32	10126	0.505
	(83)	(207)		(1348)	(0.214)
Poplar	356	412	56.61	20157	0.246
	(37)	(157)		(2099)	(0.192)

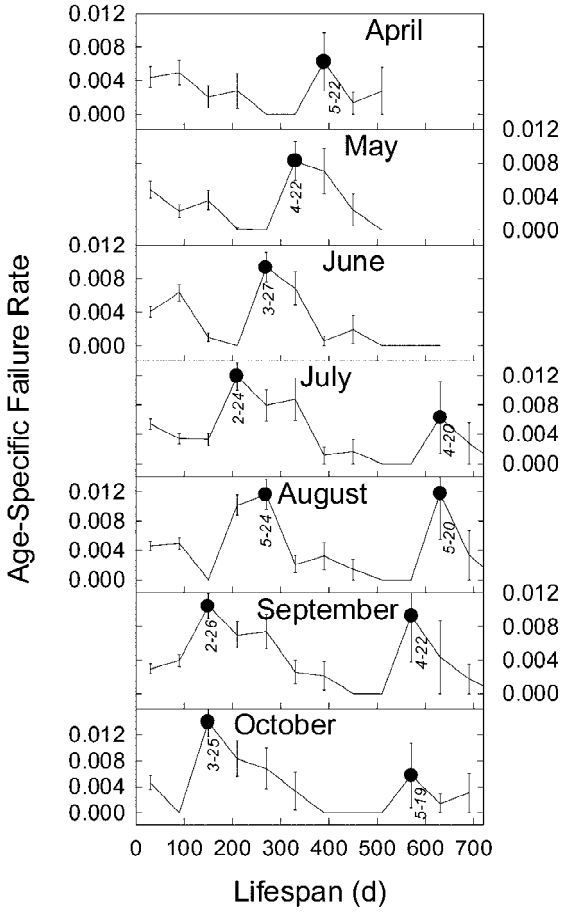

Figure 6. Estimated hazard functions versus lifespan for poplar roots stratified by month of appearance for the growing season. The hazard function is the probability that a root of a specific age will fail during the given time period (age-specific failure rate). All roots appearing during the specified month during the 1994 – 1996 observation period were included in the analysis. The appearance month is indicated with bold letters in each panel. Data are midpoints of the 60-day time interval. Symbols (•) mark peak hazard times for each appearance month. Numeric labels show peak hazard date. Error bars indicate the 95% confidence interval of the estimate.

ing relatively high root mortality during late winter to early spring.

Standing crop – minirhizotrons vs. coring

Pine had nearly twice the fine-root biomass as poplar and statistically similar coarse-root biomass in soil core samples (Table 3). Pine specific root length (length per unit root weight) was 30% that of poplar, resulting in pine having almost half the total root length per unit soil surface. This specific root length difference is consistent with finding that initial diameters of pine roots observed in minirhizotrons were twice that of poplar (Table 3).

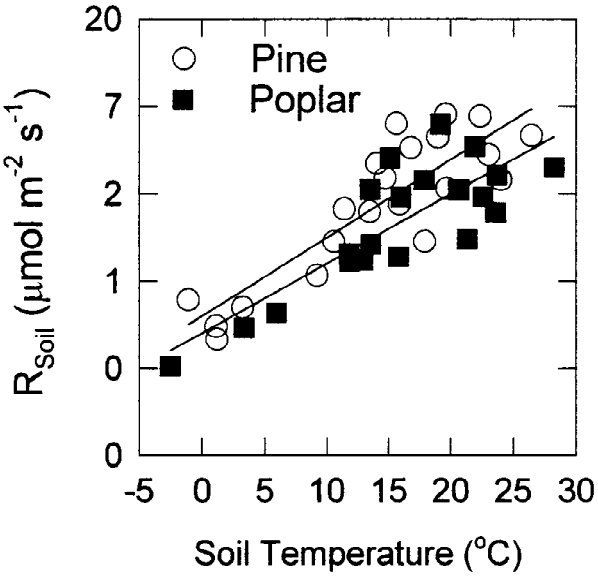

Figure 7. Soil CO_2 efflux (R_{Soil}) response to soil temperature (T_{Soil}). The linear model $\ln(R_{Soil}) = B_0+B_1T_{Soil}$ was fitted for pine (B_0 =−0.396; B_1 = 8.96×10^{-2}; R^2=0.752) and for poplar (B_0 = −0.589; B_1 = 7.90×10^{-2}; R^2=0.676). The regression lines tested parallel and the pine model was significantly greater than the poplar model (P-value = 0.011). Each point is the mean of four measurement locations.

Soil CO_2 efflux

Soil CO_2 efflux was greater in pine than poplar (P-value = 0.001). However, it was also positively correlated with soil temperature (Figure 7) so controlling for temperature was necessary. Temperature-adjusted soil CO_2 efflux (Q_{10}=2 was used, cf. Sprugel et al., 1995) was still greater in pine (P-value = 0.011) because soil temperature was significantly lower in the pine stand compared with poplar (Figure 2; P-value = 0.013).

Discussion

Comparisons of root productivity

The greatest difference between pine and poplar fine-root activity was in production and standing crop as observed in minirhizotrons (Figures 1 and 2). Similar standing crop levels have been observed by others using nondestructive techniques. Standing root length densities of 0.45 – 1.19 mm cm^{-2} for ponderosa pine (Tingey et al., 1995) are slightly higher than

our pine values, which ranged between 0.21 and 0.36 mm cm^{-2} in 1996 (Figure 2A). Root lengths of 3.3 – 5.5 mm cm^{-2} for sugar maple (Hendrick and Pregitzer, 1993) compare favorably with our poplar values, which ranged between 2.8 and 5.6 mm cm^{-2} in 1995 through 1996 (Figure 2B). For further comparisons, data from Figure 2 can be expressed as root numbers. The values range from 0.05 to 0.08 roots cm^{-2} for pine. These are comparable with 0.05 – 0.36 roots cm^{-2} for Norway spruce (Majdi and Nylund, 1996). Our poplar root numbers ranged from 1.1 to 2.5 roots cm^{-2}, which are comparable with root numbers of 1.3 – 4.9 cm^{-2} for a mixed northern hardwood forest (Fahey and Hughes, 1994), but are low compared to the 4 – 9 roots cm^{-2} found in an oak-plametto system (Day et al., 1996). Steele et al. (1997) used both destructive and nondestructive techniques to measure live-root length and calculate growth and mortality among boreal forest species. Their results showed greater fine-root growth for aspen compared with jack pine, especially when adjusted for soil temperature. This agrees with indirect nitrogen budget technique results, where evergreen conifers have lower annual fine-root biomass production than deciduous hardwoods (Aber et al., 1985). However, other studies using destructive techniques to measure fine-root biomass production have found little difference between conifers and hardwoods (Fogel, 1985; Harris et al., 1977; McClaugherty et al., 1982; Nadelhoffer and Raich, 1992; Vogt, 1991).

Although the live-root length observed with minirhizotrons was distinctly lower for pine than for poplar, due to much lower pine root productivity, the differences in live-root biomass, from core samples, were not as distinct (Table 3). On a weight basis, pine actually had greater biomass than poplar. The greater biomass was associated with greater pine fine-root diameter and lower pine specific root length. As a result, when roots collected by coring were expressed on a length basis, pine had half the standing live-root length as poplar. This difference in root length from cores was much lower than minirhizotron measurements where pine live-root length averaged 1/15 that of poplar in the final season of observation (Figure 2). This standing crop difference may be attributed to age differences between plantations. However, available evidence suggests older conifer stands actually have greater fine-root production than younger ones (Grier et al., 1981) and fine-root biomass remains relatively constant after canopy closure (Vogt et al., 1987). In our study, both plantations were closed canopy and the younger one had greater production. Consequently, if fine-root production differences observed between our plantations are attributed to stand age differences it would be in contrast to the above reports.

The species differences may also be related to differences in response to minirhizotron installation disturbance. For instance, Joslin and Wolfe (1999) show that root elongation during the year of minirhizotron installation was much greater than after 2 years in a mature mixed hardwood forest. Our data show that root production and maximum standing crop in poplar was consistent among the three observation years suggesting no disturbance effect. Pine standing crop accumulated slowly, but even after 3 years root-length production was only 1/16 of that of poplar. So unless disturbance effects last longer than 3 years, they are unlikely to cause the differences observed between plantations. Much of the observed difference between the pine and poplar plantations appears to be the inherent speed with which roots accumulated and variable root longevity between species.

Minirhizotron observations were limited in time, while core samples represent net accumulation over the life of the stand. For pine, the average live-root length continued to increase on minirhizotron surfaces through the third growing season; poplar standing crop appeared to stabilize in the first year. If root accumulation on minirhizotron surfaces continued at the same rate in subsequent years, pine root standing crop would be half that of poplar and equivalent to the difference observed in cores within one or two more growing seasons. Consequently if root production and turnover are slow as in pine, it can take several years to reach representative live-root length on minirhizotron surfaces; therefore, inconsistent species differences in standing crop between techniques, appear to be affected by minirhizotron observation time.

Comparisons of root survival/longevity

Greater pine fine-root longevity compared with poplar resulted in a greater percentage of roots surviving between seasons (Figure 4), contributing to the accumulation of fine-roots observed with minirhizotrons. Life-table survival estimates indicate that 36% of pine roots remain after 700 days compared with only 6% of poplar roots. Long-lived roots are responsible for standing crop accumulation and are, perennial by definition. Pine retains a much larger percentage of these perennial roots than poplar.

Fine-root lifespan for both species was controlled by a number of root characteristics, such as soil depth, root diameter and month of appearance. Greater root lifespan occurred with depth in the soil profile. Similar results have been found for sugar maple (Hendrick and Pregitzer, 1992) and Norway spruce (Majdi and Nylund, 1996), both using minirhizotron observations. However, relatively shorter root lifespan in lower horizons has been found using sequential coring techniques (Schoettle and Fahey, 1994). Greater lifespan at depth may be caused by soil environment. At greater depth, soil is cooler in summer, higher in soil moisture and carbon dioxide concentration, and lower in nitrogen. Each of these factors favors greater root longevity. At low temperature and higher carbon dioxide concentration, root respiration would be lower (Burton et al., 1997; Qi et al., 1994; Sprugel et al., 1995), so the cost of maintaining roots at these depths would be much less. During winter, the insulating properties of upper soil layers protect deeper roots from extreme temperatures. Increased moisture content with depth protects deeper roots from dry soil conditions that cause mortality (Kolesnikov, 1971; Lamont, 1995; Schoettle and Fahey, 1994). Lastly, the typical pattern of decreasing organic content and nutrient concentrations with depth will encourage increased longevity because low nutrient concentrations tend to extend fine-root lifespan (Majdi and Nylund, 1996; Pregitzer et al., 1995). The tendency for each of these soil factors to favor greater root longevity with depth makes it highly probable that increased longevity is due to soil environment. However, differences in diameter with depth may also be a contributing factor, especially in pine.

Little is known about the influence of root diameter on fine-root longevity. Gholz et al. (1986) inferred from sequential coring that pine root longevity increases with diameter. Root longevity is also inversely related to root branch order in kiwi (Reid et al., 1993), which implies that diameter is directly related to longevity, because diameter tends to decrease with increasing root order (Pregitzer et al., 1997). There is also evidence that species with smaller diameter fine roots have shorter root lifespans (Eissenstat and Yanai, 1997). Yet we are not aware of any direct observations showing that root lifespan is positively related to initial root diameter. In this study, the roots of both pine and poplar less than 0.5 mm initial diameter had much shorter lifespans than those greater than 0.5 mm (Figure 5), suggesting that the initial root diameter classes defined here represent different functional root classes.

Two functional fine-root classes can be defined: 'pioneer' roots or 'feeder' roots (Eissenstat and Yanai, 1997). Poplar roots less than 0.5 mm in this study met many of the criteria for feeder roots because they were smaller in diameter and length, had few lateral roots and had shorter lifespans. Those greater than 0.5 mm diameter are better characterized as pioneer roots because of larger diameter and length, more lateral roots and longer lifespans. These functional differences help explain the similarity between the percentage of larger diameter roots (Figure 3) and the percentage surviving after 700 days (Figure 4).

Seasonal differences in poplar root longevity indicate high early-spring root mortality, which could be due to frost damage, carbohydrate competition with growing leaves or root herbivory. Peaks in the hazard function (Figure 6) shows that significant root loss occurred either prior to the late February – May period and was only recorded at the first post-winter observations or it occurred during this period. Root disappearance of winter-kill roots may be delayed due to the preserving effect of frozen soils. If most root mortality was prior to the hazard peak, it would suggest that the peak was due to frost damage, which is plausible because there are multiple reports of increased tree-root winter mortality in temperate climates (Head, 1973; Kolesnikov, 1971; Steele et al., 1997; Vogt and Bloomfield, 1991).

If the peak hazard occurred during late February – May, rather than earlier, it would suggest there may be internal competition for carbohydrates (Head, 1973). There is some evidence of increased root mortality during bud burst (Kolesnikov, 1971) and during flowering, fruit set and grain storage periods (Eissenstat and Yanai, 1997). Stored reserves in deciduous species are used for spring leaf flush and new root growth is thought to be dependent upon current photosynthate (Dickson, 1991), nonetheless, availability of assimilates for root processes is limited during leaf flushing.

Root herbivory could also explain the seasonal hazard peak. Although root herbivory is poorly understood, it is seasonally dependent on environmental conditions and insect life cycles (Brown and Gange, 1991; Head, 1973). For instance, the population of an introduced root feeding weevil (*Polydrusus* sp.) is quite high at the Harshaw Forestry Research Farm. The final and most consumptive larval stage of this beetle occurs during spring (Drooz, 1985; William J. Mattson, Jr., pers. comm.), which may explain increased mortality at this time. Clearly, the cause of

peak root mortality, indicated by consistent timing of hazard peaks, warrants further study.

Soil CO_2 efflux and species differences

Root respiration may account for half of soil CO_2 efflux (Anderson, 1992), so it is reasonable to expect the level of belowground activity due to growth and maintenance of roots to have a large influence on soil CO_2 efflux. Based on soil CO_2 efflux measurements, belowground activity of pine was higher than that of poplar (Figure 7). Greater pine soil CO_2 efflux can be attributed to maintenance of greater fine-root biomass in pine compared with poplar (Table 3); however, according to minirhizotron measurements, fine-root production, and thus growth respiration, of pine is expected to be much lower than for poplar. Similarly, maintenance respiration for coarse diameter pine roots is expected to be less than that of finer poplar roots (Sprugel et al., 1995). Therefore, even though greater fine-root biomass may explain greater soil CO_2 efflux in pine, there is reason to consider other possibilities.

Soil CO_2 efflux also contains a microbial component that, to a large extent, consists of symbiotic and saprophytic fungi. In our study, fungal hyphae occurred on minirhizotron surfaces in the organic layers of both the pine and poplar stands. However, the density of hyphae was greater in pine than in poplar. Although no direct quantification of soil hyphae was attempted, this qualitative observations suggest that greater soil CO_2 efflux for pine stands may also be attributed to greater fungal activity. Observed fungal hyphae are suspected to be symbiotic because many of the sporocarps observed were known mycorrhizal fungi from the genera *Telephora*, *Boletus*, *Lacaria* and *Aminita*. Quantification of hyphae through soil dilution techniques (Jones et al., 1990) or ergoserol methods (Nylund and Wallander, 1992) would be necessary to conclusively demonstrate differences in fungal activity in these two stands.

Nonetheless, autotrophic and heterotrophic components contributing to soil CO_2 efflux appear to be distinct in these two forest types. These distinctions in belowground activities suggest that strategies for tissue deployment and resource acquisition for conifers and hardwoods are as unique belowground as they are above.

Acknowledgements

Tina Scupian digitized minirhizotron images. Bill Gerrish assisted in field data collection and Raymond Lange helped with root separation from soil cores. Marianne K. Burke, Stith T. Gower, Paul T. Rygiewicz and an anonymous reviewer provided valuable comments on earlier drafts. Support was provided by funds from the USDA Forest Service Northern Global Change Program and the North Central Research Station Physiological Processes work unit(NC-4152).

References

Aber J D, Melillo J M, Nadelhoffer K J, McClaugherty C A and Pastor J 1985 Fine root turnover in forest ecosystems in relation to quantity and form of nitrogen availability: A comparison of two methods. Oecologia 66, 317–321.

Anderson J M 1992 Responses of soils to climate change. Adv. Ecol. Res. 22, 163–210.

Black K E, Harbron C G, Franklin M, Atkinson D and Hooker J E 1998 Differences in root longevity of some tree species. Tree Physiol. 18, 259–264.

Brown V K and Gange A C 1991 Effects of root herbivory on vegetation dynamics. *In* Plant Root Growth: An Ecological Perspective. Ed. D Atkinson. pp 453–470. Blackwell Scientific, Oxford.

Burton A J, Zogg G P, Pregitzer K S and Zak D R 1997 Effect of measurement CO_2 concentration on sugar maple root respiration. Tree Physiol. 17, 421–427.

Day F P, Weber E P, Hinkle C R and Drake B G 1996 Effects of elevated atmospheric CO_2 on fine root length and distribution in an oak-palmetto scrub ecosystem in central Florida. Global Change Biol. 2, 143–148.

Dickson R E 1991 Assimilate distribution and storage. *In* Physiology of Trees, Ed. A S Raghavendra. pp 51–85. John Wiley and Sons, Inc., New York.

Drooz A T 1985 Insects of Eastern Forests, USDA Forest Service Miscellaneous Publication No. 1426 Eissenstat D M and Yanai R D 1997 The ecology of root lifespan. Adv. Ecol. Res. 27, 1–60.

Enslin W R, Pregitzer K S and Hendrick R L 1994 MSU ROOTS: A PC-based program to quantify plant roots. Center for Remote Sensing, Michigan State University, East Lansing, MI, USA.

Fahey T J and Hughes J W 1994 Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. J. Ecol. 82, 533–548.

Fogel R 1985 Roots as primary producers in below-ground ecosystems. *In* Ecological Interactions in Soil. Eds. AH Fitter, D Atkinson, DJ Read and M Usher. pp 23–36. Blackwell Scientific, Oxford.

Gholz H L, Hendry L C and Cropper W P 1986 Organic matter dynamics of fine roots in plantations of slash pine (*Pinus elliotti*) in north Florida. Can. J. For. Res. 16, 529–538.

Grier C C, Vogt K A, Keyes M R and Edmonds R L 1981 Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washingtion Cascades. Can. J. For. Res. 11, 155–167.

Harris W F, Kinerson R S and Edwards N T 1977 Comparison of belowground biomass of natural deciduous forest and loblolly pine plantations. Pedobiologia 17, 369–381.

Head G C 1973 Shedding of roots. *In* Shedding of Plant Parts, Ed. T T Kozlowski. pp 237–292. Academic Press, New York.

Hendrick R L and Pregitzer K S 1992 The demography of fine roots in a northern hardwood forest. Ecology 73, 1094–1104.

Hendrick R L and Pregitzer K S 1993 The dynamics of fine root length, biomass and nitrogen content in two northern hardwood ecosystems. Can. J. For. Res. 23, 2507–2520.

Jackson R B, Mooney H A and Schulze E D 1997 A global budget for fine root biomass, surface area and nutrient contents. Proc. Natl. Acad. Sci. 94, 7362–7366.

Jones M D, Durall D M and Tinker P B 1990 Phosphorus relationships and production of extramatrical hyphae by two types of willow ectomycorrhizas at different soil phosphorus levels. New Phytol. 115, 259–267.

Joslin J D and Wolfe M H 1999 Disturbances during minirhizotron installation can affect observation data. Soil. Sci. Soc. Am. J. 63, 218–221.

Kalbfleisch J D and Prentice R L 1980 The statistical analysis of failure time data. John Wiley & Sons, Inc., New York.

Kleinbaum D G and Kupper L L 1978 Applied regression analysis and other multivariable methods. Duxbury Press, Boston, MA, USA. 556 p.

Kolesnikov V 1971 The root system of fruit plants. MIR Publishers, Moscow. 269 p. (translated from Russian by L. Aksenova).

Lamont B B 1995 Mineral nutrient relations in Mediterranean regions of California, Chile and Australia. *In* Ecology and Biogeography of Mediterranean Ecosystems of Chile, California and Australia. Eds. M T K Arroyo, P H Zedler and M D Fox. pp 211–238. Springer-Verlag, New York.

Landsberg J J and Gower S T 1997 Applications of physiological ecology to forest management. Academic Press, New York. 354 p.

Lee E T 1992 Statistical methods for survival data analysis. John Wiley & Sons, Inc., New York. 482 p.

Majdi H 1996 Root sampling methods – applications and limitations of the minirhizotron technique. Plant Soil 185, 255–258.

Majdi H and Nylund J E 1996 Does liquid fertilization affect fine root dynamics and lifespan of mycorrhizal short roots? Plant Soil 185, 305–309.

McClaugherty C A, Aber J D and Melillo J M 1982 The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. Ecology 63, 1481–1490.

Nadelhoffer K J and Raich J W 1992 Fine root production estimates and belowground carbon allocation in forest ecosystems. Ecology 73, 1139–1147.

Nylund J-E and Wallander H 1992 Ergosterol analysis as a means of quantifying mycorrhizal biomass. *In* Techniques for Mycorrhizal Research. Eds. J R Norris, D J Read and A K Varma. pp 537–548. Academic Press, London.

Pregitzer K S, Zak D R, Curtis P S, Kubiske M E, Teeri J A and Vogel C S 1995 Atmospheric CO_2, soil nitrogen and turnover of fine roots. New Phytol. 129, 579–585.

Pregitzer K S, Kubiske M E, Yu C K and Hendrick R L 1997 Relationships among root branch order, carbon, and nitrogen in four temperate species. Oecologia 111, 302–308.

Qi J, Marshall J D and Mattson K G 1994 High soil carbon dioxide concentrations inhibit root respiration of Douglas fir. New Phytol. 128, 435–442.

Reid J B, Sorensen I and Petrie R A 1993 Root demography in kiwifruit (*Actinidia deliciosa*). Plant Cell Environ. 16, 949–957.

Ruess R W, Van Cleve K, Yarie J and Viereck L A 1996 Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior. Can. J. For. Res. 26, 1326–1336.

SAS Institute Inc. 1989 SAS/STAT users guide, Version 6, 4th edn. Vol. 2. SAS Institute Inc, Cary, NC, USA. 846 p.

Schoettle A W and Fahey T J 1994 Foliage and fine root longevity in pines. Ecol. Bull. 43, 136–153.

Snedecor G W and Cochran W G 1980 Statistical methods, 7th edn. The Iowa State University Press, Ames, Iowa, USA. 507 p.

Sprugel D G, Ryan M G, Brooks J R, Vogt K A and Martin T A 1995 Respiration from the organ level to the stand. *In* Resource Physiology of Conifers. Eds. W K Smith and T M Hinckley. pp 255–299. Academic Press, New York.

Steele S J, Gower S T, Vogel J G and Norman J M 1997 Root mass, net primary production and trunover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. 17, 577–587.

Tingey D T, Johnson M G, Phillips D L and Storm M J 1995 Effects of elevated CO_2 and nitrogen on ponderosa pine fine roots and associated fungal components. J. Biogeogr. 22, 281–287.

Vogt K 1991 Carbon budgets of temperate forest ecosystems. Tree Physiol. 9, 69–86.

Vogt K A and Bloomfield J 1991 Tree root turnover and senescence. *In* Plant Roots: The Hidden Half. Eds. Y Waisel, A Eshel and U Kafkafi. pp 287–306. Marcel Dekker, New York.

Vogt K A, Vogt D J, Moore E E, Fatuga B A, Redlin M R and Edmonds R L 1987 Conifer and angiosperm fine-root biomass in relation to stand age and site productivity in Douglas-fir forests. J. Ecol. 75, 857–870.

Vogt K A, Vogt D J, Palmiotto P A, Boon P, O'Hara J and Asbjornsen H 1996 Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187, 159–219.

Section editor: R Aerts