Contributions of fine root production and turnover to the carbon and nitrogen cycling in taiga forests of the Alaskan interior


Abstract: Fine root production and turnover were studied in hardwood and coniferous taiga forests using three methods. (1) Using soil cores, fine root production ranged from $1574 \pm 76$ kg ha$^{-1}$-year$^{-1}$ in the upland white spruce (Picea glauca (Moench) Voss) stand to $4386 \pm 322$ kg ha$^{-1}$-year$^{-1}$ in the floodplain balsam poplar (Populus balsamifera L.) stand, accounting for 49% of total production for coniferous stands and 32% of total production for deciduous stands. Fine root turnover rates were higher in floodplain (0.090 $\pm$ 0.06 year$^{-1}$) stands than in upland (0.42 $\pm$ 0.10 year$^{-1}$) stands. Across all sites, the ratio of fine root turnover to litter fall averaged 2.2 for biomass and 2.8 for N. Both values were higher in floodplain stands than in upland stands, and in coniferous stands than in deciduous stands. (2) The C budget method showed that C allocation to fine roots varied from 150 to 425 g C m$^{-2}$-year$^{-1}$ and suggested that soil respiration was more dependent on C derived from roots than from aboveground inputs. The C allocation ratio (C to roots : C to litter fall) was inversely correlated with litter-fall C and varied from 0.3 to 69.5; there was a tendency for higher proportional belowground allocation in coniferous stands than in deciduous stands and the highest values were at the earliest successional sites. (3) Estimates of apparent N uptake ($N_{app}$) allocation to fine roots, and fine root production based on N budget calculations showed that annual aboveground N increments exceeded $N_{app}$ estimates at half the sites, indicating that the method failed to account for large amounts of N acquired by plants. This suggests that plant and (or) mycorrhizal uptake of soil organic N may be more significant to ecosystem N cycling than mineral N turnover by the soil microbial biomass.

Résumé : La production et le renouvellement des racines fines ont été étudiés dans des forêts de feuillus et de conifères de la taïga à l'aide de trois méthodes. (1) Selon la méthode des échantillons de sol, la production de racine fine a varié de $1574 \pm 76$ kg ha$^{-1}$-an$^{-1}$ dans le peuplement d'épinette blanche (Picea glauca (Moench) Voss) des hautes terres à $4386 \pm 322$ kg ha$^{-1}$-an$^{-1}$ dans le peuplement de peuplier baumier (Populus balsamifera L.) de la plaine alluviale, représentant 49% de la production totale pour les peuplements conifériens et 32% de la production totale pour les peuplements décidus. Le taux de renouvellement des racines fines était plus élevé dans les peuplements de la plaine alluviale (0.080 $\pm$ 0.06 an$^{-1}$) que dans ceux des hautes terres (0.42 $\pm$ 0.10 an$^{-1}$). Le ratio du renouvellement des racines fines sur les chutes des litières a été en moyenne, pour les différents sites, de 2,2 pour la biomasse et de 2,8 pour N. Ces valeurs étaient plus élevées dans les peuplements de la plaine alluviale comparés aux hautes terres, et dans les peuplements conifériens comparés aux peuplements décidus. (2) La méthode du bilan de C a montré que l'allocation de C aux racines fines a varié de 150 à 425 g C m$^{-2}$-an$^{-1}$, et suggère que la respiration du sol était plus dépendante du C dérivé des racines que des apports épigènes. Le ratio de l'allocation de C aux racines/chutes de litières était inversement corrélé au C des litières, et a varié de 0.3 à 69.5, avec une tendance pour une allocation plus élevée à la partie hypogée dans les peuplements conifériens que dans les peuplements décidus, avec de plus hauts niveaux dans les sites en début de succession. (3) L'estimation du prélèvement apparent de N ($N_{app}$), l'allocation de N aux racines fines, et la production de racines fines basée sur les calculs des bilans de N ont montré que les accroissements annuels de N dans la partie épigène excédaient les quantités estimées de $N_{app}$ dans la moitié des sites, indiquant que la méthode n'a pas été capable de prendre en compte les fortes quantités de N acquises par les plantes. Ceci suggère que le prélèvement de N organique du sol par la plante et (ou) les mycorhizes peut être plus important pour le recyclage de N de l'écosystème que le renouvellement de N minéral par la biomasse microbienne du sol.

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R.W. Ruess, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, U.S.A.
K. Van Cleve and J. Yarie, Forest Soils Laboratory, University of Alaska Fairbanks, Fairbanks, AK 99775, U.S.A.
L.A. Vierreck, Institute of Northern Forestry, USDA Forest Service, 308 Tanana Drive, Fairbanks, AK 99775, U.S.A.
Introduction

Fine root productivity often exceedsaboveground productivity in forest ecosystems, despite the fact that live fine root biomass constitutes only a small fraction of total stand biomass (Fogel and Hunt 1983; Grier et al. 1981; Meier et al. 1985; Vogt et al. 1986; Gower et al. 1992; Hendrick and Pregetzer 1993). This is due to the high biomass of woody tissue relative to production aboveground, coupled with high rates of growth and turnover relative to biomass belowground. Recent research has focused ontemporal and spatial patterns of fine root growth, mortality, and decomposition, relative to gradients in soil water, organic matter, nutrients and temperature, belowground consumers, and anthropogenic disturbances to these environmental factors (Aber et al. 1985; Gower et al. 1992; Pregitzer et al. 1993; Fahey and Hughes 1994). It is widely recognized that the turnover and decomposition of fine roots and associated mycorrhizae may contribute substantially more to soil carbon (C) and nutrient pools than do aboveground litter-fall inputs (Edwards and Harris 1977; Persson 1978; Vogt et al. 1983, 1986; Joslin and Henderson 1987; Raich and Nadelhoffer 1989; Arthur and Fahey 1992; Hendrick and Pregitzer 1993). However, clear relationships between aboveground and belowground production across ecosystems, and an understanding of controls over root production and turnover remain unresolved.

There are several reasons why taiga ecosystems may have lower levels of fine root mass and production, but higher ratios of belowground to aboveground production compared with temperate forest ecosystems. Rates of nutrient cycling and primary production are generally lower in taiga ecosystems than in temperate forest ecosystems because of extreme environmental factors (Van Cleve et al. 1991). These include drastic seasonal fluctuations in day length and temperature, a short growing season, low soil temperatures, and the occurrence of permafrost. Whereas nutrient availability and fine root biomass may be inversely correlated across forest ecosystems (Keyes and Grier 1981; Nadelhoffer et al. 1985; Santantonio and Herrman 1985; Vogt et al. 1987), on a global scale, fine root mass and production typically decline across both broad-leaved and needle-leaved forests with increasing latitude (Vogt et al. 1986). Nevertheless, increased biomass allocation to roots and lower rates of tissue turnover are typically associated with low soil temperatures and declining soil nutrient availability in arctic and subarctic ecosystems (Shaver and Chapin 1991). Since forest floor turnover rates are lower in cold-dominated soils with poor litter quality (Flanagan and Van Cleve 1983; Vogt et al. 1986), one would also expect fine root decomposition to be lower in taiga ecosystems.

Within interior Alaskan taiga forests, net aboveground primary production (AGNPP), biomass turnover, soil fertility, and nutrient cycling rates vary dramatically across the successional transition from hardwoods to conifers (Van Cleve et al. 1983, 1991). One would expect lower rates of root growth and turnover, but higher proportional allocation to roots and higher overall root biomass across these ecosystem types, paralleling changes in aboveground growth patterns and nutrient cycling processes.

The purpose of this study was to measure fine root production and biomass allocation to fine roots and to evaluate the contribution of fine roots to the cycling of C and N across a successional sequence of forested sites within the Alaskan interior. A series of comparative methods was used, which included (1) maximum—minimum (max.—min.) and increment methods using soil cores (Fairley and Alexander 1983), (2) a C budget method (Raich and Nadelhoffer 1989), and (3) a nitrogen (N) budget method (Nadelhoffer et al. 1985). Estimates of fine root production and turnover were compared with measurements of aboveground biomass, production, and litter fall to determine patterns of C allocation within these taiga forest ecosystems and to compare these patterns with similar measures in temperate forest ecosystems.

Study sites

Research was conducted within the Bonanza Creek Experimental Forest at sites established by the Bonanza Creek Long Term Ecological Research (BNZ LTER) program. These sites were selected to represent transitional periods in ecosystem structure associated with functional changes of particular significance in forest development both in uplands, where succession is triggered by fire, and along the floodplain of the Tanana River, where succession follows alluvial bar formation (Van Cleve et al. 1991, 1993a). In the upland sites included (i) early successional stands of post-burn vegetation (UP1), 5–8 years; (ii) birch–aspen (Betula papyrifera Marsh. – Populus tremuloides Michx.) stands (UP2), 75–80 years; and (iii) white spruce (Picea glauca (Moench) Voss) stands (UP3), 105–155 years. Along the floodplain of the Tanana River, sites included (i) open willow (Salix spp.) (FP1), 5–10 years; (ii) balsam poplar–thinleaf alder (Populus balsamifera L. – Alnus tenuifolia Nutt.) (FP2), 20–40 years; (iii) balsam poplar (FP3), 80–100 years; (iv) white spruce (FP4), 200–300 years; and (v) black spruce (Picea mariana (Mill.) BSP) stands (FP5), 150–250 years. Details of the vegetation at each of these successional stages have been described previously, as has the importance of state factor control and herbivory in the regulation of ecosystem processes (Bryant and Chapin 1986, Van Cleve et al. 1991).

Regional climate is characterized by an intensely cold snow period averaging 214 days and annual temperature extremes ranging from −50°C to 35°C. Average daily temperatures range from −24.5°C in January to 17.5°C in July, with an average annual temperature of −3.5°C. Potential evapotranspiration (466 mm) exceeds annual precipitation (269 mm), 65% of which falls during the growing season (Viereck et al. 1993). Throughout the region, slope and aspect have dramatic effects on modifying local microclimate and ecosystem processes.

Methods

Aboveground biomass and production

Basal area (BA) was determined by measuring the BA at breast height of each tree (>2.5 cm) within a 50 × 60 m plot at each of the three replicate sites within each successional stage. Aboveground live biomass and productivity of overstory trees were calculated as the sum of biomass and productivity measurements on each plot. Aboveground biomass (kg ha⁻¹) was expressed as the average of 3 years of measurements (1989, 1992, and 1993). Yearly AGNPP was calculated on an individual
Soil coring

Fifteen soil cores (5 x 30 cm) were taken monthly (June–September) from randomly located points within one 25 x 25 m permanent plot at each site during 1990 and 1991. Sites sampled included birch–aspen (UP2a) and white spruce (UP3a) stands in the uplands, and alder–poplar (FP2a), poplar (FP3a), white spruce (FP4a), and black spruce (FP5a) along the Tanana River floodplain. The black spruce site was cored only in 1990. Logistical demands of root sorting restricted sampling to one replicate stand per site, and one plot per stand. We recognize that cores collected from this plot do not constitute true replicates; nevertheless, we assume that the mean for this 625 m² plot is representative of the stand.

Soil cores were stored in polyethylene bags at 4°C until processed, at which time fine roots (< 2 mm) and coarse roots (> 2 mm) were washed free of soil through a series of sieves ranging in size from 0.5 to 5 mm, and sorted into live and dead on the basis of brittleness, and texture and color of the cortex. Roots were then dried at 60°C, weighed, and a subsample was analyzed for total N on a LECO CNS 2000 Auto-Analyzer. Root biomass data were square-root transformed, and differences between sites and years were determined by ANOVA using a general linear models procedure (SAS Institute Inc. 1985).

Annual fine root production was estimated from differences between maximum and minimum live fine root biomass within the growing season (max–min. method), and annual turnover rates were calculated as the ratio of production to live biomass. Fine root N turnover was the product of fine root N mass and fine root biomass turnover. Additional fine root production estimates were obtained from changes, statistically significant and otherwise, in monthly values of live and dead fine root biomass using a decision matrix (monthly increment method) (McClougherty et al. 1982; Fairley and Alexander 1983).

Carbon budget

Total C allocation to roots was estimated as the difference between total soil respiration and litter-fall C using the C budget method (Raisch and Nadelhoffer 1989). This method relies on the assumption that heterotrophic soil respiration (R_h) is balanced by the sum of aboveground litter-fall C inputs (P_l) and belowground C inputs from root turnover, sloughing, and exudates. Since total soil respiration (R_s) is the sum of root respiration (R_r) and R_h, the difference between R_s and P_l is assumed to equal the total annual C allocation to roots. The method likely overestimates proportional belowground allocation at upland post-burn sites where residual soil C persists following fire, and at early stage floodplain sites where organic materials are deposited during sandbar formation. Nevertheless, the method provides a powerful insight into the magnitude and significance of belowground C allocation patterns and fluxes from two comparatively simple field measures.

Total soil respiration was measured during the 1990, 1991, and 1992 growing seasons within three replicate stands of open willow, alder–poplar, poplar, and white spruce along the Tanana River floodplain and within three replicate stands of post-burn vegetation, birch–aspen, and white spruce in the uplands. The field methodology consisted of five, 14-L plastic buckets spaced systematically at each site (Schlenzter and Van Cleve 1985). Every 2 weeks from 1 June to 15 September, one 10 cm diameter soil core containing 40 g of over-dried soda lime was placed beneath each bucket. After 24 h, cans were retrieved, oven-dried at 100°C, and weighed for accumulation of CO_2 (Edwards 1982). Results were increased by a factor of 1.41 to allow for water loss during the drying process. Total soil respiration was the sum of bimonthly increments recorded throughout the summer. Annual calculations were made assuming that soil respiration began and ended at zero on 15 May and 1 October, respectively.

Total litter-fall biomass was measured at these same sites from 1990 to 1992. At each site, three 0.25-m³ litter trays were placed on the forest floor in early summer and emptied in late fall and again in early spring the following year. Coarse and fine litter fall were dried at 60°C, weighed, summed over both collection dates, and assumed to contain 45% C. Additional data points where litter fall and total soil respiration were collected simultaneously from these similar sites were obtained from Schlenzter and Van Cleve (1985), Van Cleve et al. (1983), and K. Van Cleve (unpublished data).

Nitrogen budget

The N budget method assumes that annual allocation to fine roots (N_s) is equal to the difference between apparent N uptake (N_u) and the sum of N increments to aboveground foliage (N_f) and to perennial weed and bark (N_w) (Nadelhoffer et al. 1985). We estimated N_u as the sum of net N mineralized plus inputs via precipitation and fixation, minus losses due to leaching and denitrification, and assumed no net change in mineral N between seasons. Fine root turnover rate was calculated as annual N allocation to fine roots divided by fine root N mass, and fine root production was calculated as the product of fine root N biomass and fine root turnover. Sites included in the calculations were floodplain alder–poplar, poplar, white spruce, and black spruce, and upland birch–aspen, and white spruce. Three replicate stands of each successional stage were used and averaged for all but the fine root data, which were obtained from one stand, representative of each stage, as described above.

For the deciduous sites, N_s was leaf litter-fall N averaged over 1990, 1991, and 1992. For coniferous stands, N_s was the sum of N_i values calculated separately for deciduous and coniferous trees. For deciduous trees, N_s was calculated as above. For coniferous trees, total annual N increments to needles were calculated using data from Van Cleve et al. (1983), linearly scaled for differences in total AGNPP. N resorption was calculated as the difference between live needle N and litter needle N divided by live needle N, and was subtracted from annual N increment to needles to obtain an estimate of N_s for coniferous stands. N_i as a function of total AGNPP from Van Cleve et al. (1983) was used to calculate N_s for all sites, and annual belowground N allocation to perennial wood was assumed to be 10% of N_i.

We used net N mineralization data from Van Cleve et al. (1993b) for floodplain alder–poplar, poplar, and white spruce sites. In that study, net N mineralization in both forest floor and mineral soil was measured monthly throughout the growing season and over winter for 3 successive years (1986–1989) using the buried bag technique (Eno 1968). Measures of net N mineralization, using similar techniques, from upland birch–aspen and white spruce stands, and floodplain black spruce stands, were obtained from Pare (1990), Gordon (1986), and K. Van Cleve (unpublished data). Annual N fixation inputs were based on ecosystem N mass accumulation over the age of the stand (Van Cleve et al. 1993a). Wet deposition inputs were taken as 0.20 g N m⁻² y⁻¹⁻¹ (Van Cleve and Powers 1995). Denitrification and leaching losses were ignored in the calculations. We recently found that these values for N fixation inputs and losses due to denitrification and leaching may seriously underestimate actual fluxes, but that the balance
Table 1. Aboveground (AG) biomass and production, and litter fall, of overstory trees for floodplain and upland sites (mean ± SE, n = 3 for each site).

<table>
<thead>
<tr>
<th></th>
<th>AG biomass (kg/ha)</th>
<th>AG production (kg·ha⁻¹·year⁻¹)</th>
<th>Total litter fall (kg·ha⁻¹·year⁻¹)</th>
<th>Foliage litter fall (kg·ha⁻¹·year⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Floodplain</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alder – balsam poplar</td>
<td>124 233 ± 23 529</td>
<td>9667 ± 994</td>
<td>3446 ± 27</td>
<td>2662 ± 51 (100)</td>
</tr>
<tr>
<td>Balsam poplar</td>
<td>129 933 ± 38 420</td>
<td>6467 ± 1740</td>
<td>2046 ± 184</td>
<td>1578 ± 163 (51)</td>
</tr>
<tr>
<td>White spruce</td>
<td>143 867 ± 18 476</td>
<td>3667 ± 233</td>
<td>1716 ± 537</td>
<td>959 ± 215 (26)</td>
</tr>
<tr>
<td>Black spruce*</td>
<td>30 515 ± 375</td>
<td>685 ± 5</td>
<td>687 ± 146</td>
<td>573 ± 113</td>
</tr>
<tr>
<td>Upland</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Birch–aspen</td>
<td>159 933 ± 11 848</td>
<td>8100 ± 321</td>
<td>2996 ± 50</td>
<td>1966 ± 31 (88)</td>
</tr>
<tr>
<td>White spruce</td>
<td>143 433 ± 5 808</td>
<td>4533 ± 897</td>
<td>1879 ± 328</td>
<td>1367 ± 214 (36)</td>
</tr>
</tbody>
</table>

*Average percent contribution of deciduous litter fall to total foliage litter fall is in parentheses.

From Van Cleve et al. (1983).

Fig. 1. Basal area of forest stands (n = 3) used in soil core study. FP2, floodplain thinleaf alder – balsam poplar; FP3, floodplain balsam poplar; FP4, floodplain white spruce; FP5, floodplain black spruce; UP2, upland birch–aspen; UP3, upland white spruce.

Fig. 2. Relationship of foliage and total litter fall (averaged 1990–1992) to aboveground biomass production (averaged 1989–1992) (n = 3). Site abbreviations follow Fig. 1.

between these fluxes is nearly identical with rates of ecosystem N mass accumulation calculated by Van Cleve et al. (1993b) (R.W. Ruess, unpublished).

Results

Aboveground biomass and production
Values for stand BA (Fig. 1), aboveground biomass, litter fall, and AGNPP (Table 1) fall within the range of values reported previously for similar Alaskan taiga forest communities (Van Cleve et al. 1983). AGNPP and biomass were positively correlated ($r^2 = 0.33, P < 0.05$). Upland and floodplain white spruce stands had nearly identical amounts of aboveground biomass and rates of AGNPP and litter fall. White spruce stands had proportionately more woody litter fall than deciduous stands, and on average, 71% of white spruce needle litter fall occurred during the winter sampling period (data not shown). Seasonal patterns and percent deciduous–evergreen contributions were not available for black spruce stands. There was a positive relationship between litter fall and aboveground biomass production across all sites (Fig. 2). The ratio of AGNPP to biomass was over twice as high in deciduous stands (6.0 ± 0.9%·year⁻¹) as in coniferous stands (2.6 ± 0.3%·year⁻¹) and was highest in the alder-poplar stands (7.8%·year⁻¹).

Soil cores
Significant differences in live fine root biomass were found among sites (P < 0.001), with averages ranging from 2205 ± 259 to 8317 ± 469 kg·ha⁻¹ at the floodplain black spruce...
Table 2. Biomass (kg/ha) of live and dead fine roots, and coarse (live + dead) roots, at floodplain and upland sites averaged over 4 months (June–September) and two growing seasons (1990–1991).

<table>
<thead>
<tr>
<th></th>
<th>Floodplain</th>
<th>Upland</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Alder – balsam poplar</td>
<td>Balsam poplar</td>
</tr>
<tr>
<td>Live fine root</td>
<td>4 716 ± 371b</td>
<td>4 690 ± 448b</td>
</tr>
<tr>
<td>Dead fine root</td>
<td>17 160 ± 798b</td>
<td>24 653 ± 1 715a</td>
</tr>
<tr>
<td>Coarse root</td>
<td>4 883 ± 533cd</td>
<td>6 788 ± 812bc</td>
</tr>
</tbody>
</table>

Note: Means (±SE) within rows followed by different letters indicate significant intersite differences at $P < 0.05$.

Fig. 3. Relationship between coarse and fine root biomass for 1990 and 1991. Broken line represents unity. Site abbreviations follow Fig. 1.

Fig. 4. Landscape patterns in fine root production (max.–min. method) in relationship to live fine root biomass for 1990 and 1991. Broken line represents unity. Site abbreviations follow Fig. 1.

Deciduous stands had significantly higher live fine root biomass than coniferous stands. Live fine root biomass at upland and floodplain white spruce stands was nearly identical, while the upland birch–aspen stand had nearly twice the live fine root biomass as either of the floodplain deciduous stands. Dead fine roots constituted the largest percentage of total fine root biomass, ranging from 62% to 95% of total fine root biomass at the upland birch–aspen and floodplain white spruce sites, respectively. With the exception of the black spruce stand, dead fine root biomass was significantly higher at floodplain stands than at upland stands. Live coarse root biomass also varied among sites ($P < 0.0001$) and was positively correlated with live fine root biomass, exceeding live fine root biomass in most instances (Fig. 3). Neither total fine root biomass nor live fine root biomass was correlated with aboveground biomass.

All three root biomass components (Table 2) showed significant intra- and inter-seasonal variation (both $P < 0.0001$), and on average, variation between years was significantly greater than that within years. Live fine root biomass showed the greatest intra- and inter-seasonal variation, and live coarse root biomass showed the least. Live fine root biomass was significantly greater in 1990 at all sites except upland birch–aspen; in general, upland sites showed less interseasonal variation in all root biomass components than floodplain sites. Live fine root biomass typically increased from June to July, and from August to September, with levels higher in September than June at all sites.

There was no relationship between the max.–min. and monthly increment estimates of fine root production ($r^2 = 0.10, P = 0.33$); monthly increment values averaged 4.5 times values based on the max.–min. method. As expected from the interseasonal patterns in live fine root biomass, there were large differences in both fine root production estimates between the 2 years of study. There were apparent differences between upland and floodplain stands in the relationship between fine root production (max.–min. method) and live fine root biomass (Fig. 4). These landscape patterns are also evidenced by significantly higher annual turnover rates of live fine roots at floodplain (0.90 ± 0.06 year$^{-1}$) than at upland sites (0.43 ± 0.10 year$^{-1}$) (Table 3, $P < 0.05$). Fine root production and AGNPP were weakly correlated ($r^2 = 0.33, P = 0.23$); however, fine root production and total primary production (aboveground + belowground) were positively correlated ($r^2 = 0.55, P = 0.09$), with a tendency for lower ratios of fine root to AGNPP at upland sites for both coniferous and deciduous stands.

Live fine root turnover rates were, on average, over an order of magnitude greater than forest floor turnover rates reported by Van Cleve et al. (1983) (Table 3). Total fine root turnover averaged 0.14 year$^{-1}$ across all sites, and except
Table 3. Fine root production (max.-min. method) and turnover, fine root nitrogen content and turnover, and foliage litter-fall nitrogen at floodplain and upland sites.

<table>
<thead>
<tr>
<th>Biomass</th>
<th>Nitrogen</th>
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<tbody>
<tr>
<td></td>
<td>Fine root production (kg·ha⁻¹·year⁻¹)</td>
</tr>
<tr>
<td>Floodplain</td>
<td></td>
</tr>
<tr>
<td>Alder - balsam poplar</td>
<td>3551±2167</td>
</tr>
<tr>
<td>Balsam poplar</td>
<td>4386±322</td>
</tr>
<tr>
<td>White spruce</td>
<td>2477±1088</td>
</tr>
<tr>
<td>Black spruce</td>
<td>2324</td>
</tr>
<tr>
<td>Upland</td>
<td></td>
</tr>
<tr>
<td>Birch-aspen</td>
<td>2755±50</td>
</tr>
<tr>
<td>White spruce</td>
<td>1574±76</td>
</tr>
</tbody>
</table>

aLive fine root turnover = fine root production/live fine root biomass.
bTotal fine root turnover = fine root production/live + dead fine root biomass.
cForest floor turnover = litter fall/forest floor mass (Van Cleve et al. 1983).
dLive fine root N turnover = live fine root N X live fine root turnover.

for poplar, were also higher than forest floor turnover rates. Live fine root turnover was higher in floodplain stands than in upland stands (3184 ± 490 vs. 2165 ± 581 kg·ha⁻¹·year⁻¹; P < 0.05), and in deciduous stands than in coniferous stands (3564 ± 481 vs. 2124 ± 274 kg·ha⁻¹·year⁻¹; P < 0.05). These values of live fine root biomass turnover averaged 2.2 times foliage litter fall across all sites and were 2.1 times higher in floodplain sites than in upland stands (P = 0.19) and 1.4 times higher in coniferous stands than in deciduous stands (P = 0.41).

Live fine root N turnover was positively correlated with foliage litter-fall N (r² = 0.46, P = 0.12). The ratio of fine root N turnover to foliage litter-fall N (both as kg N·ha⁻¹·year⁻¹) averaged 2.8 across all sites and, similar to biomass turnover, was significantly higher in floodplain stands than in upland stands (P = 0.09) and in coniferous stands than in deciduous stands (P < 0.05).

Carbon budget

Soil respiration rates (Rₘ) averaged 1.3 to 80.3 times total aboveground litter-fall C (Pₘ) across all years and sites. Soil respiration rates were not statistically related to total litter-fall C (r² = 0.001, P = 0.91), but were positively correlated with C allocation to fine roots, calculated as Rₘ/Pₘ (Fig. 5). The latter relationship is confounded by the fact that allocation to fine roots is derived, in part, from soil respiration. Nevertheless, we believe this pattern is consistent with our soil core data, even though allocation to fine roots was not correlated with max.-min. or monthly increment fine root production estimates. However, assuming that approximately 50% of belowground C allocation is lost as respiratory CO₂ (Edwards and Harris 1977; Ewel et al. 1987), and that fine root biomass is 45% C by weight, this range of values for C allocation to fine roots is similar to the range of values calculated by the max.-min. method.


Total C allocation to roots was inversely correlated with total litter fall C (r² = 0.44, P < 0.001), and the ratio of root to aboveground litter-fall C allocation, ranging from 0.3 to 69.5, decreased with increasing litter fall C (Fig. 6).

Nitrogen budget

Estimates of apparent N uptake (Nₘ), N allocation to fine roots, and fine root production based on N budget calculations are listed in Table 4. Annual aboveground N increments exceeded Nₘ estimates at half the sites; thus fine root production could not be estimated for these sites using
Table 4. Nitrogen budgets for floodplain and upland forest sites.

<table>
<thead>
<tr>
<th></th>
<th>Floodplain</th>
<th></th>
<th>Upland</th>
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<tbody>
<tr>
<td></td>
<td>Alder – balsam poplar</td>
<td>Balsam poplar</td>
<td>White spruce</td>
<td>White spruce</td>
</tr>
<tr>
<td>$N_{al}$</td>
<td>3.25</td>
<td>1.49</td>
<td>1.03</td>
<td>0.15</td>
</tr>
<tr>
<td>$N_{wb}$</td>
<td>1.09</td>
<td>0.91</td>
<td>0.44</td>
<td>0.23</td>
</tr>
<tr>
<td>$N_{al} + N_{wb}$</td>
<td>4.34</td>
<td>2.40</td>
<td>1.47</td>
<td>0.38</td>
</tr>
<tr>
<td>$N_{min}$</td>
<td>1.50</td>
<td>1.60</td>
<td>1.00</td>
<td>0.57</td>
</tr>
<tr>
<td>$N_{fix}$</td>
<td>5.76</td>
<td>0.43</td>
<td>0.15</td>
<td>0.15</td>
</tr>
<tr>
<td>$N_{pp}$</td>
<td>0.20</td>
<td>0.20</td>
<td>0.20</td>
<td>0.20</td>
</tr>
<tr>
<td>$N_{f}$</td>
<td>7.46</td>
<td>2.23</td>
<td>1.35</td>
<td>0.92</td>
</tr>
<tr>
<td>$N_{fr}$</td>
<td>3.12</td>
<td>—</td>
<td>—</td>
<td>0.54</td>
</tr>
<tr>
<td>$N_{fm}$</td>
<td>5.14</td>
<td>4.64</td>
<td>3.11</td>
<td>1.50</td>
</tr>
<tr>
<td>Fine root turnover rate (year$^{-1}$)</td>
<td>0.61</td>
<td>—</td>
<td>—</td>
<td>0.35</td>
</tr>
<tr>
<td>Fine root production (g m$^{-2}$ year$^{-1}$)</td>
<td>287.7</td>
<td>—</td>
<td>—</td>
<td>77.2</td>
</tr>
</tbody>
</table>

Note: Nitrogen fluxes are in g N m$^{-2}$ year$^{-1}$. $N_{al}$, N allocation to aboveground foliage; $N_{wb}$, N allocation to belowground foliage; $N_{min}$, N mineralization; $N_{fr}$, N fixation input; $N_{pp}$, N immobilization in precipitation; $N_{f}$, apparent N uptake = $N_{fix} + N_{al} + N_{pp}$; $N_{fm}$, N allocation to fine root = $N_{f} - (N_{al} + N_{wb})$; $N_{fr}$, fine root N mass = fine root mass × %N content of fine roots/100.

Fig. 6. Root to litter-fall carbon allocation calculated by the carbon budget method in relation to total litter-fall carbon. Site abbreviations follow Fig. 5.

This method. Fine root production based on the N budget method was 23% and 3 times higher than estimates obtained from the max.–min. method at floodplain alder–poplar and black spruce sites, respectively, but within 6% of max.–min. values for upland birch–aspen stands. Although $N_{f}$ was highly correlated with foliage litter fall ($r^2 = 0.95, P < 0.01$), the method appears to underestimate actual rates of plant N uptake, for reasons listed below.

Discussion

Averaged across all sites, our estimates of the fine root contribution to total stand production ranged from 41% (max.–min. method) to 68% (monthly increment method) and suggest that relative to temperate forests, these taiga forests have a higher proportion of total ecosystem fixed C allocated below ground. The fact that fine root production (max.–min. method) accounted for an average of 32% total stand production for deciduous stands and 49% total stand production for coniferous stands is consistent with the observation that evergreen trees appear to allocate a greater proportion of photosynthate to fine roots than deciduous trees (Vogt et al. 1986). A similar contrast between deciduous and coniferous stands was found using the monthly increment method (from 57% to 78% of total stand production, respectively). Methodological uncertainties and inconsistencies associated with quantifying fine root dynamics complicate cross-ecosystem comparisons, and as reviewed elsewhere, the max.–min. values are likely the most conservative of any of the measures we used (McClougherty et al. 1982; Aber et al. 1985; Fairley and Alexander 1985; Kurz and Kimmins 1987; Santantonio and Grace 1987; Hendrick and Pregitzer 1992, 1993; Nadelhoffer and Raich 1992; Hendricks et al. 1993; Publicover and Vogt 1993). These methodological difficulties notwithstanding, our high end value of fine root production as a percentage of total productivity for coniferous stands is similar to that reported for subalpine Pacific silver fir (Abies amabilis (Dougl. ex Loud.) Dougl. ex J. Forbes) stands in the Washington Cascades using similar techniques (Vogt et al. 1980, 1983; Grier et al. 1981; Meier et al. 1983), while even our more conservative estimate exceeds values reported for other coniferous forests (Persson 1978: Keyes and Grier 1981; Aber et al. 1985; Arthur and Fahey 1992; Gower et al. 1992). Similarly, ratios of fine root production
(max.–min. method) to total stand production for our hardwood stands were, on average, greater than those reported for temperate hardwood forests using similar methods (McClaugherty et al. 1982; Aber et al. 1985). Our values of fine root production also exceed the average of 1000 kg ha\(^{-1}\) year\(^{-1}\) reported by Vogt et al. (1986) for a limited number of mostly Siberian boreal forests.

Rates of fine root turnover for taiga forest ecosystems do not appear to be notably different from those reported for temperate forests. Hendrick and Pregitzer (1993) reviewed literature values for standing crop and production of fine roots in temperate hardwood forests and found a wide range in production to biomass ratios depending on methodology. Using the max.–min. method, live fine root turnover rates for our deciduous stands ranged from 0.33 year\(^{-1}\) (upland birch–aspen) to 0.94 year\(^{-1}\) (floodplain balsam poplar). These values are, on average, 18% greater than expected from the inverse relationship between root turnover and latitude reported for deciduous forests by Vogt et al. (1986), and are generally consistent with those reported for temperate deciduous forests. Fine root turnover rates in coniferous stands were comparable to those from deciduous forests (Table 3).

Relative to litter-fall inputs, however, these fine root turnover values for taiga forests exceed those reported elsewhere. Our estimates of the ratio of root turnover to foliage litter fall averaged 2.2 and 2.8 for biomass and N, respectively, with both ratios approximately 40% greater in coniferous stands than in deciduous stands. These values generally exceed literature values for both temperate hardwood (McClaugherty et al. 1982; Nadelhoffr et al. 1985; Hendrick and Pregitzer 1993; Burke and Rynal 1994) and temperate coniferous forests (Edwards and Harris 1977; Persson 1978; Keyes and Grier 1981; Vogt et al. 1986; Arthur and Fahey 1992; Gower et al. 1992) with the exception of the Pacific silver fir studies cited above.

The ratios of dead to live fine root biomass that we found are notably higher than those reported for temperate coniferous forests (Vogt et al. 1986; Arthur and Fahey 1992) or temperate hardwood forests (McClaugherty et al. 1982; Fahey et al. 1988; Burke and Rynal 1994) and suggest that in more cold-dominated taiga forests, the rate of fine root decomposition relative to growth and mortality is extremely low. Reports from temperate hardwood and coniferous forests indicate that fine roots often represent only a small percentage of total ecosystem biomass (Gower et al. 1992; Hendrick and Pregitzer 1993). We found that live fine root biomass accounted for between 2% and 7% of total stand biomass, while total fine root biomass accounted for between 11% and 29% of total stand biomass. Ratios of dead to live fine roots averaged 5.9 for coniferous stands and 5.5 for deciduous stands. Biomass of dead roots was over 80% greater at floodplain sites, perhaps because of the higher rates of both fine root production and turnover, but also slower rates of fine root decomposition on the colder floodplain soils. In addition to low soil temperatures, poor root substrate quality likely contributes to the high accumulation of dead roots in these ecosystems also, as well as explains the rate of dead root accumulation with successional time. Similar patterns in forest floor turnover rates across this successional sequence have been linked with the chemical characteristics of decaying litter (Flanagan and Van Cleve 1983) and N mineralization in the forest floor (Van Cleve et al. 1993c). However, at this stage, we know little about the chemical nature of fine roots or how the large annual influx of dead roots affects soil nutrient processes.

Landscape differences in belowground allocation and turnover were greater in many cases than differences between deciduous and coniferous forests. For example, we found higher rates of AGNPP and litter fall in upland white spruce than in floodplain white spruce, but higher rates of fine root production and turnover in floodplain white spruce than in upland white spruce. A similar landscape pattern was found when comparing upland birch–aspen with floodplain balsam poplar. The upland birch–aspen stand had higher aboveground biomass and rates of AGNPP and litter fall than the floodplain poplar stand, but the latter had higher rates of fine root growth and turnover. Proportional allocation of total production to fine roots was over 50% higher in floodplain forests than in upland forests for both deciduous and coniferous stands.

Pronounced landscape differences in site characteristics and soil biophysical properties between upland and floodplain forests may have important, but complex, controls over patterns of fine root growth, turnover, and decomposition. In general, upland soils are warmer, have higher rates of nutrient turnover and a longer snow-free period, and experience distinctively different histories of organic matter development than their floodplain counterparts (Van Cleve et al. 1991; Van Cleve and Powers 1993). Soil temperatures are 3°C and 2°C colder for floodplain balsam poplar and white spruce than upland birch–aspen and white spruce, respectively; coniferous stands are wetter in upland sites, while deciduous stands are wetter along the floodplain of the Tanana River (LTER climatological data base). Apparent N uptake (Table 4) is perhaps our best approximation of landscape differences in plant-available N for these stands. This value was over twice as high for upland birch–aspen as for floodplain balsam poplar and 25% higher in upland white spruce than in floodplain white spruce. Phosphorus availability is also higher in upland soils, primarily because of the predominance of calcium and magnesium phosphate complexes on floodplain soils. This pattern of higher fine root growth and turnover, and greater proportional allocation to belowground production, on lower fertility sites agrees with other soil core studies of fine root growth relative to natural soil fertility gradients (Keyes and Grier 1981; Santantonio and Hermann 1985; Vogt et al. 1987), but is in contrast with budgetary methods showing a positive relationship between soil fertility and fine root turnover (Nadelhoffr et al. 1985; Hendricks et al. 1993). Using the C budget method, we found no apparent pattern in belowground allocation distinguishing upland and floodplain landscapes for either coniferous or deciduous forests, and N budget calculations were not possible for all stands. Our two white spruce sites offer the most meaningful comparison relative to this issue, simply because these stands are of nearly identical age, species composition, BA, and total net production. We emphasize, however, that soil fertility is one of many factors distinguishing these sites and
that landscape patterns in belowground allocation may be a function of a complex of interacting site factors.

The C budget method indicated that while soil respiration was independent of total litter-fall C, C allocation to fine roots and soil respiration were highly correlated. This suggests that soil respiratory fluxes are more dependent on C derived from roots than from aboveground inputs. We found a pronounced increase in the C allocation ratio (C to roots : C to litter fall) with decreasing litter-fall C, with a tendency for higher proportional belowground allocation in coniferous stands than in deciduous stands, and highest levels at the earliest successional sites. A subset of these sites was used by Raich and Nadelhoffer (1989) in their summary of global patterns; both data sets emphasize that these taiga forests have the highest recorded ratios of belowground : litter fall C allocation.

The range of belowground allocation values derived from the C budget method is similar in magnitude to that calculated from the max.–min. soil coring method. It appears, therefore, that the methods underestimate belowground allocation to the same degree. Our soil respiration measurements did not include late-fall, winter, and early break-up respiratory fluxes. A more important consideration is the underestimation of soil respiration rates by the static chamber method for efflux levels above 0.2 g CO₂·m⁻²·h⁻¹ (Nay et al. 1994). The average efflux across all of our measurements was 0.45 ± 0.1 g CO₂·m⁻²·h⁻¹ (median = 0.45), suggesting that our C budget estimates of fine root production and the proportion of respiratory fluxes derived from roots are conservative.

For the most part, N budget calculations failed to account for large amounts of N acquired by plants. For example, to reach fine root production values equal to those calculated from the max.–min. method, apparent N uptake (Table 4) would need to be doubled at floodplain black spruce and upland white spruce stands, and tripled at floodplain balsam poplar and white spruce stands. There are several reasons why our buried bag method underestimated N mineralization, including the elimination of live root rhizosphere–microbial interactions and associated fauna (Griffiths 1994). However, there may be other, more significant processes omitted from the N budget calculations. First, the method assumes a constant fine root N content and no N resorption from senescent roots (Hendrick and Pregitzer 1993). A more significant factor in these highly organic soils may be the dependency of plants on soluble organic N, known to play an important role in arctic ecosystems (Kieland 1994). Another important N source unaccounted for by the method involves the growth dynamics and turnover of mycorrhizae. Estimates of biomass and N allocation to mycorrhizae indicate that mycorrhizal growth and maintenance can consume substantial amounts of plant resources (Fogel and Hunt 1983; Vogt et al. 1983; Fahey 1992; Rygiewicz and Andersen 1994). The uptake of N to support this mycorrhizal mass is not included in the N budget calculations. The buried bag technique likely underestimates N derived from the decomposition of dead fine roots and mycorrhizae, because of the disturbance of the hyphal links between active mycorrhizae and decaying roots and mycorrhizae (Fahey 1992; Fahey and Hughes 1994). Perhaps more significant is the direct incorporation of mycorrhizal and fine root decay products by living mycorrhiza–root associations, essentially short-circuiting N turnover via non-mycorrhizal soil microorganisms (Finlay and Soderstrom 1992). Using minihizotron imaging tubes, we have observed extensive fine root–mycorrhiza proliferation within buried organic layers and decomposing forest floor litter (personal observations). Interior Alaska taiga soils are generally regarded as having low decomposition rates due to low temperatures, but more importantly to a high C:N ratio organic matter composed of slowly decomposing complex organic chemicals with a high potential for microbial immobilization of mineralized nutrients (Flanagan and Van Cleve 1983; Van Cleve et al. 1991). Thus, direct internal cycling of nutrients within active mycorrhizospheres surrounding decaying roots and mycorrhizae or litter fall would facilitate nutrient transfer to plants and prevent potential immobilization by soil microorganisms.

Conclusions

Relative to temperate forests, Alaskan interior forests have comparable rates of fine root production and turnover, but a significantly higher proportion of total ecosystem fixed C allocated below ground. This results in a disproportional amount of soil C and soil respiratory fluxes being derived from the rapid turnover of fine roots, and approximately 3 times as much N being cycled through fine roots compared with aboveground litter fall. Compared with temperate forests, fine root decomposition in these forests is slow relative to rates of production and turnover, but nevertheless appears to exceed forest floor turnover. The rate at which fine roots decompose, become incorporated into soil organic matter, and (or) supply C or N to soil organisms and plants depends in large part on fine root litter quality and decomposability. The shortcomings of the N budget method suggest that other factors, such as soil organic N or N cycling mediated by mycorrhizae, may provide important N sources to plants. Given the apparent significance of fine roots to the N and C economy of these ecosystems, the dynamics of fine root turnover and decay remains a critical question for future research.

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