

COUPLING FINE ROOT DYNAMICS WITH ECOSYSTEM CARBON CYCLING IN BLACK SPRUCE FORESTS OF INTERIOR ALASKA

ROGER W. RUESS,¹ RONALD L. HENDRICK,² ANDREW J. BURTON,³ KURT S. PREGITZER,³
BJARTMAR SVEINBJORNSSÖN,⁴ MICHAEL F. ALLEN,⁵ AND GREGORY E. MAURER¹

¹Institute of Arctic Biology, University of Alaska, Fairbanks, Alaska 99775 USA

²D. B. Warnell School of Forestry, University of Georgia, Athens, Georgia 30602 USA

³School of Forestry and Wood Products, Michigan Technological University, Houghton, Michigan 49931 USA

⁴Department of Biological Sciences, University of Alaska, Anchorage, Alaska 99508 USA

⁵Center for Conservation Biology, University of California, Riverside, California 92521-0334 USA

Abstract. Fine root processes play a prominent role in the carbon and nutrient cycling of boreal ecosystems due to the high proportion of biomass allocated belowground and the rapid decomposition of fine roots relative to aboveground tissues. To examine these issues in detail, major components of ecosystem carbon flux were studied in three mature black spruce forests in interior Alaska, where fine root production, respiration, mortality and decomposition, and aboveground production of trees, shrubs, and mosses were measured relative to soil CO₂ fluxes.

Fine root production, measured over a two-year period using minirhizotrons, varied from 0.004 ± 0.001 mm·cm⁻²·d⁻¹ over winter, to 0.051 ± 0.015 mm·cm⁻²·d⁻¹ during July, with peak growing season values comparable to those reported for many temperate forests using similar methods. On average, 84% of this production occurred within 20 cm of the moss surface, although the proportion occurring in deeper profiles increased as soils gradually warmed throughout the summer. Monthly rates of production and mortality were somewhat asynchronous because mortality tended to peak during fall and be minimal during periods of peak production. Production and mortality were, however, positively correlated across all tubes and time periods. Annual fine root production averaged 2.45 ± 0.31 , 8.01 ± 1.39 , and 2.53 ± 0.27 mm·cm⁻²·yr⁻¹ (means ± 1 SE) among the three sites, when averaged across years.

Fine root survival and decomposition were measured by tracking and analyzing the fate of individual fine roots using mark–recapture techniques. Fine root survival was greatest during periods of peak root growth, and least over winter (ϕ_{time}). Roots first appearing in the middle of the growing season had higher survival rates than those first appearing early or late in the growing season, or over winter (ϕ_{cohort}), and risk of mortality decreased with root age (ϕ_{age}). Survival estimates translate to mean life spans of 108 ± 4 d during the growing season. While these values are in striking contrast to needle longevity and rates of aboveground litter decomposition, they are similar to many values found for temperate systems, supporting the notion that there are basic morphological and physiological traits of first-order roots that are common to most woody plant root systems. During the growing season, monthly fine root decomposition rates averaged 0.46 ± 0.01 per month, while decomposition rates over winter averaged 0.73 ± 0.01 per winter. These growing season estimates translate to 49 ± 2 d from the time a root was first observed as dead, to the time it disappeared. For roots that decomposed during the growing season, those with longer life spans decomposed more slowly after death. Comparing these results with other minirhizotron studies suggests that life-history traits of black spruce first-order roots are similar to those from temperate (and perhaps most) forest ecosystems.

Annual production of fine roots averaged 228 ± 75 g biomass·m⁻²·yr⁻¹, constituting ~56% of total stand production. Aboveground production of trees (50 ± 14 g biomass·m⁻²·yr⁻¹, 13%) and shrubs (40 ± 2 g biomass·m⁻²·yr⁻¹, 11%) contributed similarly to total production, while mosses (73 ± 14 g biomass·m⁻²·yr⁻¹, 20%) accounted for the largest component of aboveground production. Soil temperature had a strong control over both soil respiration ($Q_{10} = 2.21 \pm 0.31$) and root respiration ($Q_{10} = 2.30 \pm 0.37$). During the growing season (15 May to 15 September), ~56% of soil CO₂ efflux (580 ± 40 g C/m²) was derived from fine root respiration (329 ± 54 g C/m²). Although apparent rates of heterotrophic respiration (May through September) and total production did not differ, definitive estimates of net ecosystem production are impossible given the potentially large, unmeasured components of NPP (net primary production), such as root exudation and mycorrhizal production. Nevertheless, rates of fine root production, mortality, and decomposition indicate that in these black spruce ecosystems, fine roots are much more dynamic than would be predicted from patterns of aboveground processes, and that carbon, and presumably nutrients, are cycling through fine roots at rates several orders of magnitude faster than through aboveground tissues.

Key words: belowground allocation; boreal forest; decomposition; fine roots; longevity; NPP.

INTRODUCTION

The proportion of net annual production allocated to fine roots is thought to be greater in coniferous than deciduous forests, particularly in boreal ecosystems, where low soil fertility and soil temperatures are major factors limiting plant growth (Van Cleve et al. 1983, 1993, Ruess et al. 1996, 1998, Gower et al. 1997, 2001). It follows that in boreal coniferous forests, decaying fine roots account for a large percentage of carbon and nutrients cycled annually, given the recalcitrance of foliage and aboveground woody tissues relative to the rapid turnover of fine roots in these systems (Ruess et al. 1996, 1998, Gower et al. 1997, Steele et al. 1997). Boreal coniferous forests in Alaska were found to have higher ratios of total root carbon allocation to litterfall when compared with temperate forests using the carbon balance approach (Raich and Nadelhoffer 1989, Ruess et al. 1996), and rates of live fine root turnover estimated from soil cores indicated that approximately six times as much nitrogen is cycled through fine roots than through litterfall (Ruess et al. 1996). Thus, while boreal coniferous forests are unproductive relative to many other temperate forests (Van Cleve et al. 1983, Gower et al. 1997, 2001), these systems are dynamic, in that a disproportionate amount of the annual nutrient budget and soil CO₂ efflux appear to be derived from fine root processes.

Black spruce (*Picea mariana* L.) is the most abundant tree species within boreal forests throughout Canada and the United States, and as such, constitutes one of the largest continuous vegetation types in North America (Gower et al. 2001). Throughout the 140 000 km² Tanana River basin in interior Alaska, ecosystems dominated by black spruce account for ~63% of the region's forested area (Mead 1995). These ecosystems are characterized by cold, permafrost-dominated soils with low nutrient availability, poor drainage, and low rates of net aboveground primary production (Van Cleve et al. 1981, 1983, 1993). The low litter quality of aboveground vascular and nonvascular plants, combined with cold soils and a short growing season contribute to the slow turnover of soil organic matter in black spruce ecosystems (Flanagan and Van Cleve 1983). This explains, in part, why high latitude ecosystems store ~40% of the Earth's reactive soil carbon, despite accounting for only ~24% of the land area (McGuire et al. 1995). The fate of this stored carbon and the nature and magnitude of net ecosystem responses of boreal forests to climate change are poorly understood (Van Cleve et al. 1986, Goulden et al. 1998, Randerson et al. 1999, Chapin et al. 2000). Recent warming throughout interior Alaska over the past several decades has been linked to permafrost thaw (Osterkamp and Romanovsky 1999, Jorgenson et al. 2001), changes in the growth rates of white spruce (Barber et al. 2000), increases in aerial extent of fire (Kasischke et al. 1999), and expansion of boreal forest into tundra.

Because of reduced albedo, winter and spring energy exchanges of boreal coniferous forests are substantially greater than for either tundra or deciduous forests, thus, a northern expansion of boreal forest or shift to earlier successional stands will have significant, albeit potentially offsetting effects on global atmospheric carbon exchange (Betts 2000, Eugster et al. 2000).

Modeling boreal forest net ecosystem production and projecting responses to climate change are limited by uncertainties regarding many ecosystem parameters, notably moss and shrub production, and the production, respiration, longevity, and decomposition rate of fine roots and associated mycorrhizae (Gower et al. 2001, McGuire et al. 2001). The only estimates of fine root production and turnover from permafrost-dominated, late-successional forests in Alaska are those derived from soil cores and indirect budgeting methods (Ruess et al. 1996). Minirhizotron observations in permafrost-free forests in interior Alaska have found relatively short fine root life spans (<150 d) and rapid decomposition rates (<100 d) for both early successional (Ruess et al. 1998) and white spruce (R. Hendrick and R. Ruess, *unpublished data*) forests. Several recent studies have pointed out that a large proportion of the fine root length and biomass is comprised of very small diameter roots with rapid turnover rates (Eissenstat et al. 2000, Wells and Eissenstat 2001, Pregitzer et al. 2002). Thus, while coring methods suggest a decline in root turnover with increasing latitude (Gill and Jackson 2000), such approaches typically ignore variability in fine root life span associated with the position of an individual root on the branching fine root system (Nadelhoffer 2000, Pregitzer et al. 2002). If fine roots in Alaskan black spruce forests are as dynamic as those reported for other Alaskan systems, there may be a more striking contrast among the turnover of active vegetation pools than was previously appreciated. This may partially explain the high belowground allocation estimated previously for these forests using C and N budgeting approaches (Ruess et al. 1996).

The purpose of this study was to better understand the dynamics of fine roots in black spruce ecosystems of interior Alaska. In particular, we were interested in the magnitude of fine root production relative to aboveground production, and in assessing the contributions of live and decomposing roots to soil respiratory fluxes and ecosystem-level C cycling. To accomplish this, we measured net annual aboveground (tree, shrub, and moss) production and fine root production, the contributions of root respiration to total soil respiration, and patterns of fine root longevity and decomposition at a group of permafrost-dominated lowland black spruce sites along the Tanana River in interior Alaska.

METHODS

Study sites

Research was conducted in three black spruce stands located along the floodplain of the Tanana River, ~30

TABLE 1. Stand characteristics and vegetation biomass of study sites.

Stand characteristics	Study site		
	5A	5C	5D
Site characteristics			
Stand age (yr)	200	170	160
Growing season soil temperature (°C)†	5.1 ± 0.2 (0.0–8.9)	5.6 ± 0.2 (1.1–8.1)	3.0 ± 0.2 (0.0–4.9)
Maximum depth of thaw (cm)‡	140–200	40–65	30–45
Total soil C to 50 cm (g/m²)§	10 000 ± 500	9900 ± 1100	12 200 ± 1200
Total soil N to 50 cm (g/m²)§	330 ± 10	340 ± 40	550 ± 60
Vegetation structure			
Trees (basal area , density¶)			
<i>Picea mariana</i>	11.22, 1556	11.90, 1778	11.87, 2578
<i>Larix laricina</i>	1.33, 44	0	0.92, 533
<i>Alnus crispa</i>	0	0.32, 533	0
<i>Salix</i> sp.	0.02, 44	0	0
Shrubs (percent cover)			
<i>Ledum groenlandicum</i>	19.5	11.5	4.6
<i>Vaccinium vitis-idaea</i>	12.1	16.8	0.7
<i>V. uliginosum</i>	0.7	0.7	14.4
<i>Empetrum nigrum</i>	7.7	0.6	10.3
Bryophytes (percent cover)	>95	>95	>95
Aboveground biomass#			
<i>Picea mariana</i>	2884	3058	3050
<i>Larix laricina</i>	485	0	217
<i>Alnus crispa</i>	0	16	0
<i>Salix</i> sp.	1	0	0
<i>Ledum groenlandicum</i>	91	53	21
<i>Vaccinium vitis-idaea</i>	28	40	2
<i>V. uliginosum</i>	2	2	34
<i>Empetrum nigrum</i>	34	3	46
Total cryptogams††	163	112	224
Belowground biomass			
Live fine root biomass (<1 mm)	1589	2196	1545

† Soil temperature measured at 6 cm below the base of the live moss layer from 15 May to 15 September 1999; range is listed below mean in parentheses.

‡ Mean maximum depth of thaw measured in August.

§ Total soil C and N include live and dead moss, and fibric, humic, and mineral horizons to a depth of 50 cm below the live moss surface ($n = 5$ soil cores/site).

|| Basal area, m²/ha.

¶ Density, stems/ha.

Aboveground and belowground biomass, g biomass/m².

†† Sum of green mosses and lichens.

km southwest of Fairbanks, Alaska (64°48' N, 147°52' W). Our sites are part of a larger network of successional forested stands under long-term study by the Bonanza Creek Long-term Ecological Research Program (BNZ LTER). Black spruce represents the terminal stage of floodplain succession initiated by alluvial processes and initial colonization by several willow species (*Salix* sp.) (0–15 yr), followed typically by a mixture of alder (*Alnus tenuifolia*) and balsam poplar (*Populus balsamifera*) (15–25 yr), mature balsam poplar (25–100 yr), and mature white spruce (*Picea glauca*) (80–175 yr) (Van Cleve et al. 1991, 1993, Viereck et al. 1993a). Black spruce (100–250 yr) dominates older terraces (>1000 yr) throughout the Tanana floodplain on cold, poorly drained soils underlain by permafrost (Viereck 1970, Viereck et al. 1993a). The increased insulation of the soil surface, provided by a continuous moss cover and thick organic mat, coupled

with dominance by species with low litter decomposability, are responsible for permafrost development, impeded drainage, and slow nutrient cycling rates in these systems (Viereck 1970, Viereck et al. 1993a).

Our study sites (designated by the BNZ LTER as 5A, 5C, and 5D) are open stands of black spruce with occasional individuals of tamarack (*Larix laricina*), paper birch (*Betula papyrifera*), and some *Salix* species. Density of mature black spruce trees ranges from 1556 (site 5A) to 2578 trees/ha (site 5D), with a total basal area of trees ranging from 11.2 to 12.8 m²/ha, respectively, of which 94% is black spruce on average (Table 1). Average heights of dominant black spruce trees range from 6 to 10 m, many of which are ~200 years old, although occasional younger trees occur. A low shrub layer is conspicuous at all sites, comprised mainly of *Ledum groenlandicum*, *Vaccinium vitis-idaea*, *V. uliginosum*, and *Empetrum nigrum*, with *Betula glandu-*

losum occurring at the coldest, most mesic site (5D). *Hylocomium splendens*, *Pleurozium schreberi*, and *Aulacomnium palustre* dominate the nearly continuous moss cover, and the lichens *Peltigera aphthosa* and *Cladonia gracilis* are common at all three sites. Additional information concerning these and other BNZ LTER sites can be found on the BNZ web page.⁶

Soils at the sites are in the Tanana series and are classified as Pergelic Cryaquepts (Viereck et al. 1983). The forest floor consists of 15–18 cm of moss and decaying fibrous moss and other material above 10 cm of black humus. Total soil C and N content to a 50 cm depth averaged $10\,700 \pm 700$ and 400 ± 70 g/m², respectively (Table 1). Soils remain frozen throughout the winter, and begin to thaw in late May. The active layer thickness is highly variable among years at all sites, and typically reaches a maximum thaw depth by mid to late July, depending on site. At 5A, the frozen layer may persist at a depth of 140 cm, while in other years most of the seasonal frost melts, except at isolated patches, and the average active layer thickness may be as much as 200 cm. Depth of thaw typically varies from 40 to 65 cm, and from 30 to 45 cm at 5C and 5D, respectively. In 1999, soil temperatures were recorded with three HOBO (Onset Computer Corporation, Pocasset, Massachusetts, USA) data loggers per site, buried 6 cm below the bottom of the live moss layer (Table 1.)

Regional climate of interior Alaska is characterized by an intensely cold snow period averaging 214 d, with annual temperature extremes ranging from -50 to 35°C . Average daily air temperatures range from -24.9°C in January to 16.4°C in July, with an average annual temperature of -3.3°C . Potential evapotranspiration (466 mm) exceeds annual precipitation (269 mm), 65% of which falls during the growing season, which typically extends from mid-May to early September (Viereck et al. 1993b).

Aboveground production

At each site, the diameter (at 1.37 m height) of each tree within a 30×30 m plot was measured, and the aboveground biomass of each tree was estimated from allometric equations established by Van Cleve et al. (1983) for interior Alaskan stands. Increment cores were taken from an average of 10 trees per site, and the radial increment growth was measured on each core using a Velmex measurement system (Velmex, Bloomfield, New York, USA) linked to a Leica Stereo Zoom 7 microscope (± 0.001 mm resolution; Leica, Wetzlar, Germany). The mean annual diameter increment for the past 10 years (1990s) was used to estimate mean diameter growth. Total tree increment growth was then estimated as the product of tree density and mean tree growth at each site. Total tree production was the sum of aboveground increment growth + detritus produc-

tion. Detritus production was estimated from Van Cleve et al. (1983) after adjusting for the lower basal area at our sites. Aboveground production of understory shrub species was estimated from percent cover during the 1999 growing season, after establishing species-specific relationships between percent cover and current annual growth and woody biomass on 20 plots. These relationships were established at 5A and used at all three sites. Current annual increment to wood in *Ledum groenlandicum* was assumed to be 10% of annual shoot production (Shaver 1986), but was ignored for the smaller shrubs. Production and biomass data for cryptogams were obtained from a companion study of feather moss biomass and growth at each site during 1998 and 1999. In each stand, 20 to 40 plots ($50 \text{ cm} \times 50 \text{ cm}$) were established, and in each, 10 shoots of either *Hylocomium splendens* or *Pleurozium schreberii* were tagged for monitoring of extension growth and branching. Biomass was estimated in the fall of each year, when 25 randomly located samples of forest floor vegetation (vascular plants and cryptogams) were collected in each stand using a 22 cm diameter corer. Vegetation was sorted by species, bryophytes separated into green and brown mass, and dried at 65°C . Feather mosses comprised the majority of the cryptogam mass, and for estimation of total cryptogam productivity, all cryptogam mass was assigned to the two feather mosses in proportion to their abundance in the sample. Two conversion factors for productivity were obtained, biomass per unit length of moss shoot for each species, and the number of shoots per unit biomass.

Fine root production and mortality

Fine root production and mortality were measured using minirhizotrons. At each site, a 30×30 m plot was established and five minirhizotron tubes (2 m in length, 5.6 cm outer diameter) were installed randomly throughout the plot at an average angle of 21° to the soil surface, providing an average viewable tube surface extending to 51 cm vertical depth. Each tube was permanently scribed with 120, 1.4×1.2 cm frames every 1.2 cm along the tube, which was sealed permanently at the bottom. Each tube extended approximately 20 cm out of the soil, where it was painted black and then repainted white, and capped between measurements. Tubes were installed during August, the time of maximum thaw depth, during 1991 (5A) and 1992 (5C and 5D). Images of each frame were taken at approximately monthly intervals throughout the growing season beginning the summer following installation using a Bartz color micro-video camera (Bartz Technology, Santa Barbara, California, USA) and stored on Hi8 video tape. Images were then digitized using a PC-based interactive image analysis program (ROOTS) (Michigan State University, East Lansing, Michigan, USA), and production and mortality of fine roots were calculated as extension growth of live roots, and live to dead or missing roots, respectively

⁶ URL: <http://www.lter.uaf.edu/>

(Hendrick and Pregitzer 1992, 1993, Ruess et al. 1998). Due to a personnel change, we did not identify dead roots at one site (5C), and digitized mortality conservatively as live to missing. This site was not included in our survival analyses. Programs used for production and mortality computations can be downloaded from the BNZ LTER website (see footnote 6). Here we report monthly production and mortality throughout the growing season as mm fine root per cm² minirhizotron tube per day (mm·cm⁻²·d⁻¹). These values are based on 201.6 cm² of viewing image per tube. We assumed that fine root production and mortality between the fall and spring sampling periods occurred sometime during fall or over winter, and for estimations of annual production, include these overwinter values as previous year's growth. Annual values for fine root production and mortality were simply the sum of growth and mortality across all actual sampling intervals throughout the year. This characterization is somewhat arbitrary, because we don't know how much growth and mortality actually occurred during late fall vs. early spring. In order to translate annual production values to a ground area basis, we assumed a depth of view of 2 mm for the minirhizotron camera (Merrill and Upchurch 1994). We used the specific root length value (SRL = 44.02 m/g) reported for first-order white spruce roots by Pregitzer et al. (2002) taken from Tanana River floodplain white spruce stands. Those first-order white spruce roots had a mean diameter (0.23 mm) very similar to the mean diameter of all black spruce roots digitized from our sites (5A, 0.220 ± 0.009 mm; 5C, 0.201 ± 0.008 mm; 5D, 0.253 ± 0.010 mm). Production was calculated for each minirhizotron tube separately, to account for the fact that tube angle, and thus tube depth, varied slightly among tubes.

Fine root survival and decomposition

Fine root survival and decomposition rates were obtained from minirhizotron data using a parameter estimation program developed for the analysis of marked animal populations, Program MARK (White and Burnham 1999). Because the condition and fate of individual roots are followed, known survival of individuals can be estimated in much the same manner as is done for marked animal populations (Lebreton et al. 1992), without disturbing the root/mycorrhizal association. Following an earlier protocol (Ruess et al. 1998), encounter history files were created that included a listing for each individual root, coded for every time period as either "1" (alive), or "0" (dead or missing). MARK was then used to generate fine root survival estimates (noted as phi, ϕ) after constructing models incorporating direct effects of time of year, age, cohort (when the root first appeared), and site, along with their interactions, on fine root longevity. The most parsimonious models were identified using the information-theoretic Akaike's Information Criterion (AIC), and likelihood ratio tests (LRT). The identification of mod-

els follows the notation of Lebreton et al. (1992). For example, a model including both site and time effects (abbreviated as $\phi_{\text{time} \times \text{site}}$) can be compared statistically with a reduced model including only time effects (ϕ_{time}), which can be compared to the most reduced model (ϕ_0). In this manner, the effects of time, cohort, age of the root, site, and their interactions were evaluated. We also tested for differences in survival between growing season and overwinter periods (abbreviated as ϕ_{season}), and for site differences for growing season (abbreviated as $\phi_{\text{site} \times \text{growing season}}$) and overwinter periods (abbreviated as $\phi_{\text{site} \times \text{winter}}$) separately. Mean life span (MLS) of roots imaged during the growing seasons was computed from survival estimates outputted from models adjusted for interval lengths ($\text{MLS} = -1/\ln(\phi)$), which varied from 20 to 35 d during the growing season. The standard error of MLS was calculated using the "delta method" as described by Seber (1982).

Data sets were modeled as "live recaptures" with all recapture parameters fixed at 1, since we were assured of "recapturing" a root unless it had decomposed. We were confident in this known-fate approach, because it is unlikely that many roots would appear, die and completely decompose between sampling periods. The exception to this is perhaps the overwinter period. In addition to modeling fine root longevity, we also estimated the probability that dead fine roots would decompose between successive time periods by modeling the "survival" of dead roots. This was accomplished by recoding the data to create encounter history files which identified dead roots as "1," and roots at time of first disappearance as "0." Fine root decomposition estimates were then simply taken as 1 - (dead root survival). A similar model selection approach to that used for fine root longevity was used to determine factors affecting fine root decomposition (Ruess et al. 1998). To evaluate the effects of root longevity on decomposition rate, we wrote a separate dBASE program that estimated the life span of every root. Roots were assumed to have been born half way through the period prior to first appearance. Similarly, the death or disappearance of a root was assumed to have occurred half way through the period prior to final appearance as live. Age at death was then entered as a continuous individual covariate in MARK to examine both linear and nonlinear constraints on dead to missing survival analysis (Schmutz and Ely 1999). Individual covariates were standardized in MARK to have a mean between 0 and 1, to ensure that the numerical optimization algorithm identified the correct parameter estimates. We then tested the hypothesis that age at death, in combination with other factors, influenced decomposition rate using LRTs with more reduced models.

Fine root respiration

Fine root respiration was measured in the field as CO₂ production throughout the 1999 growing season at each site (Burton et al. 2002). Black spruce roots

(<1 mm diameter, ~2 g fresh weight) were excised from the near-surface fibric horizon, brushed free of soil and organic material, and placed immediately in an aluminum cuvette (5.4 cm diameter \times 15 cm in length) coupled to a LICOR-6200 photosynthesis system (LICOR, Lincoln, Nebraska, USA). The cuvette contained a solid aluminum plug (263 cm³), and was cooled on ice prior to measurements to facilitate equilibration of the cuvette to ambient soil temperatures. Both soil and cuvette temperatures were monitored and cuvette temperature was adjusted to ambient soil temperature prior to measurements by burying the cuvette closer to or away from the permafrost layer. This enabled root respiration to be measured at ambient soil temperatures, so that thermal acclimation responses throughout the growing season could be incorporated into our seasonal temperature response relationship (Tjoelker et al. 1999). Cuvette CO₂ concentration was adjusted to 1000 ppm and respiration rates were measured after stabilized readings were observed, which typically took 10 min. Root respiration was measured on four to five root samples collected at locations selected randomly at each site during each sampling period. After measurements, roots were placed on ice and transported to the laboratory, where samples were washed free of adhering soil and organic matter, dried at 60°C for 48 h, and analyzed for total N on a LECO 2000 CNS autoanalyzer (St. Joseph, Michigan, USA).

Respiration rates (nmol CO₂·g fine root dry mass⁻¹·s⁻¹) collected from all sites throughout the season were related to soil temperatures (TSOIL, °C) using nonlinear regression (PROC NLIN; SAS 1999). The slope, k , of the nonlinear regression ($R_{FR} = a \cdot e^{-k(TSOIL)}$) was used to estimate Q_{10} , ($Q_{10} = e^{10k}$), and the standard error of Q_{10} , $SE(Q_{10})$, was derived as $SE(Q_{10}) = SE(k) \times 10Q_{10}$. An estimate of total growing season (15 May to 15 September) fine root respiration (g C·m⁻²·growing season⁻¹) was obtained by combining this equation with daily soil temperature means, and live fine root biomass values obtained from soil cores. During late July 1999, soil cores (5 cm diameter \times 20 cm length) were taken from each site and hand sorted into live and dead roots. Because of the large amount of organic debris and the extreme fineness of the roots, soil cores were washed through a series of successively smaller sieves (800, 400, 250, and 125 μ m) after sorting out the larger fine root fragments. The largest fractions were sorted completely, while the smaller fractions were subsampled. Because each core required approximately one week to sort, we were limited to processing only five cores per site.

Soil respiration

Soil respiration (μ mol CO₂·m⁻²·s⁻¹) was measured throughout the growing season at all sites during 1998 and 1999 using a LICOR 6000-09 Soil Respiration System (LICOR, Lincoln, Nebraska, USA). Ten sampling locations were randomly located at each site and

marked with lathe stakes at the beginning of each season. During sampling periods (five times each growing season), an undisturbed location was randomly selected within 2 m of each stake and the top layer of live moss was carefully removed immediately prior to soil respiration measurements to eliminate the influences of either moss photosynthesis or respiration on fluxes. This method has been employed previously (Schlentner and Van Cleve 1985) and recently shown to be effective in eliminating moss influences (O'Connell et al., 2003a). Due to the density of fine root growth within the upper fibric surface soil layers, we elected not to install soil rings for the LICOR-6009 chamber. For each measurement, the LICOR-6009 chamber was inserted 1.3 cm into the dead moss layer, and CO₂ was drawn down 40 μ mol/mol below ambient and allowed to increase 10 μ mol/mol prior to logging four flux measurements as determined by a 10 μ mol/mol change in CO₂ within the chamber. The flux reading taken closest to ambient CO₂ concentration was that used in analyses. Soil temperature was recorded at the time of measurement using the LICOR temperature probe positioned to 6 cm below the lower limit of live moss, within the humic layer. Seasonal relationships between the soil respiration and temperature were generated by nonlinear regression by combining data across sampling dates and sites, using the mean of the ten sampling stations from each of the three sites at each time period. We scaled instantaneous measurements (μ g CO₂·C·m⁻²·s⁻¹) to estimates of growing season efflux (15 May–15 September) by summing daily respiration estimates predicted from the nonlinear relationship using daily soil temperature means measured for each site. The relationship between soil respiration and soil temperature did not differ among sites or between years; therefore, one exponential relationship was generated using data from all sites and both years. Seasonal soil temperature data from each site was then used with this equation to estimate seasonal soil CO₂ efflux for each site.

Statistical analyses

Variations in fine root production and mortality among sites and time periods were analyzed by ANOVA (PROC GLM; SAS 1999) using a cross-nested model (Neter et al. 1996). Effects of site, date, tube within site, site \times date, and date \times tube within site were tested using site, date, and tube as class variables, and tube within site, and date \times tube within site as random effects. The error term for testing for effects of site was provided by tube within site, and the error term for effects of date and site \times date was date \times tube within site. Significant date and site effects were further described using linear contrasts in a model similar to the original but with the date \times tube within site source removed to prevent model saturation. Data were square-root, or $\log(X + 1)$ transformed where necessary to meet ANOVA assumptions. Unless otherwise

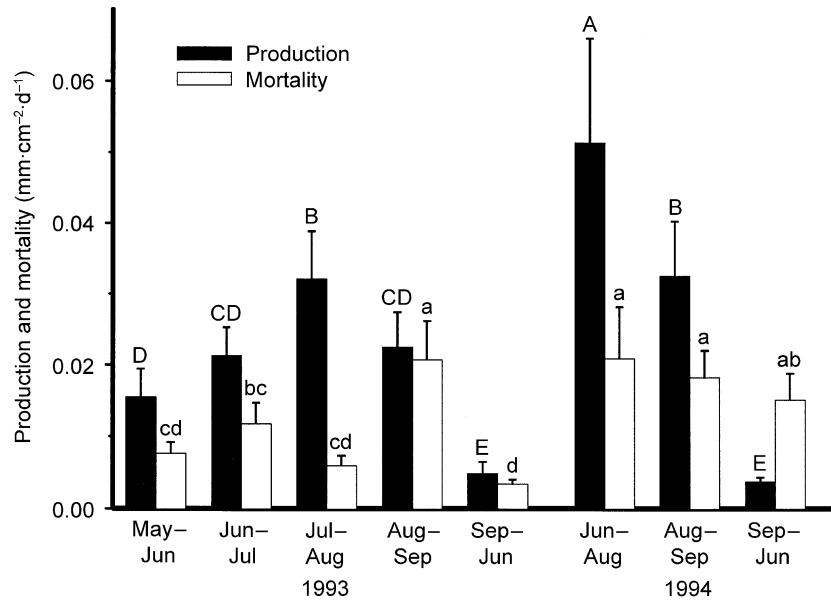


FIG. 1. Fine root production and mortality measured over two growing seasons (1993–1994), averaged across three floodplain black spruce forests. All values are expressed as mm root length per cm² minirhizotron tube per day (+1 SE), including overwinter values. Bars with different uppercase letters (production) or lowercase letters (mortality) are different at $P < 0.05$.

stated, data presented are means (± 1 SE) of untransformed data.

RESULTS

Fine root production and mortality

Fine root production varied by over an order of magnitude among sampling dates (Fig. 1). On average, $78 \pm 1\%$ of the fine root production was derived from “new root production,” as opposed to only 22% that was contributed by growth of preexisting roots. Although monthly rates of production and mortality appear to be somewhat asynchronous due to the fact that mortality tended to peak during fall and be low during periods of peak production, production and mortality were positively correlated across all tubes and time periods ($r^2 = 0.46$, $P < 0.0001$). The slope of this relationship differed significantly from unity, suggesting that even after 2 years, root colonization along the minirhizotron tubes had not yet fully equilibrated.

Fine root production varied among dates for 1993 ($F_{4,48} = 12.17$, $P < 0.0001$) and 1994 ($F_{2,24} = 29.33$, $P < 0.0001$), and also among sites for both 1993 ($F_{2,12} = 3.62$, $P = 0.06$) and 1994 ($F_{2,12} = 11.51$, $P < 0.01$). Similar differences were found in mortality among dates for 1993 ($F_{4,48} = 10.38$, $P < 0.0001$) but not for 1994 ($F_{2,24} = 0.98$, $P = 0.39$), and among sites in 1994 ($F_{2,12} = 5.49$, $P < 0.05$), but not 1993 ($F_{2,12} = 1.32$, $P = 0.30$). Fine root production was significantly greater at 5C, the site with the highest aboveground production, compared with 5A and 5D. Significant site \times date interactions both years (data not shown), particularly for productivity, were due to the fact that productivity

differences among dates were greatest at the most productive site (5C), and least at 5D, the coldest, wettest site.

Fine root production and mortality were concentrated in surface organic layers, including the dead moss layer, which was ~ 5 cm thick. When averaged across all dates and sites, the proportion of production by “soil” layer averaged $24 \pm 3\%$ (0–10 cm), $57 \pm 2\%$ (10–20 cm), $13 \pm 2\%$ (20–30 cm), $5 \pm 1\%$ (30–40 cm), $0 \pm 0\%$ (40–50 cm), $1 \pm 0\%$ (50–60 cm), and $1 \pm 0\%$ (60–70 cm). We define “0 cm” as the surface of the live moss layer; therefore, most of the 0–10 cm layer is within the live and dead moss layer. As expected, production and mortality increased with depth as the growing season progressed and deeper organic layers thawed. For example, during 1993, proportional production in the top two 20-cm soil layers (0–20 and 20–40 cm, respectively) varied as follows: May to June (84 ± 4 , $15 \pm 4\%$), June to July (80 ± 6 , $19 \pm 6\%$), July to August (75 ± 6 , $23 \pm 6\%$), and August to September (71 ± 7 , $28 \pm 7\%$). This pattern was most dramatic at 5D, the coldest site, where values ranged from 82 ± 10 and $16 \pm 8\%$ during May to June, to 41 ± 11 and $59 \pm 11\%$ during August to September, for the 0–20 and 20–40 cm layers, respectively.

Annual fine root production averaged 2.45 ± 0.31 , 8.01 ± 1.39 , and 2.53 ± 0.27 mm·cm⁻²·yr⁻¹ at 5A, 5C, and 5D, respectively, when averaged across years. Averaged across sites, annual production and mortality values differed slightly for 1993 (4.01 ± 0.92 vs. 2.10 ± 0.38 mm·cm⁻²·yr⁻¹, respectively) ($t_{18,6} = 1.91$, $P = 0.07$), but not for 1994 (4.66 ± 1.00 vs. 5.51 ± 1.36

TABLE 2. Aboveground and belowground net primary production of Tanana River black spruce study sites.

Component	Study Site			Mean \pm 1 SE
	5A	5C	5D	
Aboveground net primary production [†]				
Trees (<i>Picea mariana</i>)				
AG annual increment	28	56	24	36 \pm 10
Litterfall [‡]	11	22	9	14 \pm 4
Shrubs [§]				
<i>Ledum groenlandicum</i>	22	13	5	13 \pm 5
<i>Vaccinium vitis-idaea</i>	11	15	10	12 \pm 2
<i>Vaccinium uliginosum</i>	1	1	13	5 \pm 4
<i>Empetrum nigrum</i>	7	1	9	6 \pm 3
<i>Alnus</i> sp.	0	13	0	4 \pm 4
Cryptogams	101	65	53	73 \pm 14
Total aboveground NPP	179	184	123	162 \pm 20
Fine root production [¶]	186	374	126	228 \pm 75
Total net primary production	365	558	249	391 \pm 90

[†] All net primary production values, obtained from a 10-yr tree core average during the 1990s, g biomass·m⁻²·yr⁻¹.

[‡] Litterfall was estimated as a percentage of total AG annual increment using values from Van Cleve et al. (1983) (see *Methods*).

[§] Aboveground production values for shrubs were estimated during 1999. Values for *L. groenlandicum* include estimates of both shoot and wood production, while values for other shrubs only include current annual shoot growth.

^{||} Cryptogam production data are means across 1998 and 1999.

[¶] Fine root production values are means across 1993 and 1994.

mm·cm⁻²·yr⁻¹, respectively) ($t_{25,7} = 0.50$, $P = 0.62$). Assuming a 0.2 cm depth of view for the minirhizotron camera and a specific root length of 44.02 m/g (see *Methods: Fine root production and mortality*), these averages across sites translate to 213 \pm 41 and 244 \pm 43 g fine root biomass·m⁻²·yr⁻¹ for 1993 and 1994, respectively ($t_{28} = 0.47$, $P = 0.64$; Table 2).

Fine root survival and decomposition

Fine root survival was affected significantly by time period (ϕ_{time}), which, based on Akaike's Information Criterion (AIC) scores, was the most parsimonious single-factor model (Table 3). Fine root survival (ϕ_{time}) was greatest during periods of peak root growth, and least during overwinter periods at both sites (Fig. 2a). Monthly survival during the growing season averaged 0.76 \pm 0.01 month⁻¹, while survival during overwinter periods averaged 0.47 \pm 0.01 winter⁻¹ (ϕ_{season}). Overwinter survival was lower at 5D, the colder, wetter site (0.43 \pm 0.02 winter⁻¹), when compared with 5A, the warmer, drier site (0.47 \pm 0.02 winter⁻¹) (ϕ_{site}). Mean life span was estimated for growing season intervals only, using time-adjusted models constructed to produce an estimate for growing season and overwinter survival periods separately for each site (designated as $\phi_{\text{site} \times \text{growing season}}$), where site effects were tested against the nested model (ϕ_{season}) (see *Methods: Fine root survival and decomposition*). This produced mean life span estimates of 109 \pm 5 d and 124 \pm 6 d for fine roots at 5A and 5D, respectively. These values are conservative estimates of life span because they do not

include overwinter periods. However, time-adjusted survival estimates can not truly be computed for overwinter periods because we have no way of knowing exactly when roots died, only that they were found dead (or missing) when tubes were imaged in the spring. Nevertheless, we can set an upper bound for life span from a single-factor, time-adjusted model that includes all time periods, which assumes that roots that die over winter do so immediately before the imaging date. This model indicates a marginally significant effect of site on fine root survival (LRT, $\chi_1^2 = 3.55$, $P = 0.06$), and yields life span estimates of 233 \pm 8 and 214 \pm 8 d for 5A and 5D, respectively.

Other single-factor models were also significant. For example, roots that first appeared during the middle of the growing season generally had higher survival rates than those first appearing during the early or late growing season, or during overwinter periods (ϕ_{cohort}). Age models indicated that risk of mortality decreased with root age, from an average survival of 0.64 \pm 0.01 month⁻¹ to 0.78 \pm 0.02 month⁻¹ over the first four age groups (ϕ_{age}). Other significant interactions indicated that there were similar, but distinct effects at the two sites for both cohort ($\phi_{\text{site} \times \text{cohort}}$) and age ($\phi_{\text{site} \times \text{age}}$) (data not shown).

Survival estimates for dead roots indicated significant effects of age, time (Fig. 2b), cohort, site, and their interactions on fine root decomposition rates. Strong age effects (ϕ_{age}) showed that dead roots decomposed rapidly after they were first identified as being dead (25 \pm 1 d), but more slowly thereafter (89

TABLE 3. Results of MARK survival modeling, and comparisons between models for (a) fine root survival, (b) fine root decomposition, and (c) live-to-missing transitions.

Model	np	AIC	LRT comparison	P
a) Fine root survival rate				
(1) ϕ_0	1	6661		
(2) ϕ_{time}	8	5974	(2) vs. (1) $\chi^2_7 = 700.8$	<0.0001
(3) ϕ_{season}	2	6247	(3) vs. (1) $\chi^2_1 = 416.5$	<0.0001
(4) ϕ_{cohort}	8	6352	(4) vs. (1) $\chi^2_7 = 323.7$	<0.0001
(5) ϕ_{age}	8	6611	(5) vs. (1) $\chi^2_7 = 64.2$	<0.0001
(6) ϕ_{site}	2	6656	(6) vs. (1) $\chi^2_1 = 7.3$	<0.01
(7) $\phi_{\text{time} \times \text{site}}$	16	5904	(7) vs. (2) $\chi^2_8 = 86.1$	<0.0001
(8) $\phi_{\text{time} \times \text{age}}$	36	5929	(8) vs. (2) $\chi^2_{28} = 102.3$	<0.0001
(9) $\phi_{\text{site} \times \text{growing season}}$	3	6131	(9) vs. (3) $\chi^2_1 = 117.9$	<0.0001
(10) $\phi_{\text{site} \times \text{winter}}$	3	6132	(10) vs. (3) $\chi^2_1 = 116.8$	<0.0001
(11) $\phi_{\text{site} \times \text{cohort}}$	16	6308	(11) vs. (4) $\chi^2_8 = 60.0$	<0.0001
(12) $\phi_{\text{site} \times \text{age}}$	16	6582	(12) vs. (5) $\chi^2_8 = 45.3$	<0.0001
b) Fine root decomposition rate				
(1) ϕ_0	1	2993		
(2) ϕ_{age}	8	2679	(2) vs. (1) $\chi^2_7 = 328.1$	<0.0001
(3) ϕ_{time}	8	2726	(3) vs. (1) $\chi^2_7 = 281.3$	<0.0001
(4) ϕ_{cohort}	8	2823	(4) vs. (1) $\chi^2_7 = 184.0$	<0.0001
(5) ϕ_{season}	2	2833	(5) vs. (1) $\chi^2_1 = 162.4$	<0.0001
(6) ϕ_{site}	2	2973	(6) vs. (1) $\chi^2_1 = 22.2$	<0.0001
(7) $\phi_{\text{time} \times \text{age}}$	36	2487	(7) vs. (2) $\chi^2_{28} = 296.1$	<0.0001
(8) $\phi_{\text{age} \times \text{site}}$	14	2664	(8) vs. (3) $\chi^2_6 = 26.9$	<0.0001
(9) $\phi_{\text{time} \times \text{site}}$	16	2677	(9) vs. (3) $\chi^2_8 = 64.9$	<0.0001
(10) $\phi_{\text{site} \times \text{cohort}}$	16	2748	(10) vs. (4) $\chi^2_8 = 91.6$	<0.0001
(11) $\phi_{\text{site} \times \text{growing season}}$	3	2796	(11) vs. (5) $\chi^2_1 = 38.3$	<0.0001
c) Fine root live-to-missing transitions				
(1) ϕ_0	1	18 630		
(2) ϕ_{site}	3	18 524	(2) vs. (1) $\chi^2_2 = 110.2$	<0.0001
(3) ϕ_{season}	8	16 683	(3) vs. (1) $\chi^2_7 = 1949.1$	<0.0001
(4) $\phi_{\text{site} \times \text{summer}}$	8	16 519	(4) vs. (3) $\chi^2_1 = 168.1$	<0.0001

Notes: The number of estimated parameters (np), and the Akaike Information Criterion (AIC) are included. Comparison of nested models uses the likelihood ratio test (LRT) and lists χ^2_{df} and the P value. Models in panel (c) differ from those in panels (a) and (b) in that all time intervals, including winter, are adjusted for actual length to establish an upper limit for mean life span. Only models mentioned in *Results* are included. For model notation, see *Methods* and refer to Ruess et al. (1998).

± 7 , 67 ± 7 , and 84 ± 17 d for the next three “age” classes of dead roots). During the growing season, monthly decomposition rates averaged 0.46 ± 0.01 month⁻¹, while decomposition rates over winter averaged 0.73 ± 0.01 winter⁻¹ (ϕ_{season}). Models estimating growing season survival rates of dead roots for each site ($\phi_{\text{site} \times \text{growing season}}$), showed that fine roots decomposed in 62 ± 4 d at 5A, and 37 ± 2 d at 5D. Again, an upper bound for decomposition rate was set by including overwinter periods in a time-adjusted model. This showed that from the time fine roots were first seen as dead, they disappeared in 143 ± 6 d and 97 ± 4 d at 5A and 5D, respectively (AIC = 3340, LRT: $\chi^2_1 = 41.4$, $P < 0.0001$). Thus, while roots lived longer at the colder, wetter site (5D), once dead, fine roots decomposed faster at this site.

In order to evaluate the effects of root age on decomposition rate, we first estimated survival of dead roots as a function of season (growing season vs. winter), site (5A and 5D), age at death, age at death squared, and all interactions. The most parsimonious model was a nonlinear one that included season, age, age², and age \times season (AIC = 2598, LRT: $\chi^2_1 = 12.60$,

$P < 0.001$). We only present data for roots that decompose during the growing season, because of the uncertainty of knowing if roots that disappear over winter do so in the fall, during winter or during spring. The model shows that decomposition time increases only slightly with age for roots that live less than a year, but increases substantially for roots living longer than a year (Fig. 3). For example, roots that are 2, 8, and 18 mo old at the time of death, decompose in 41, 50, and 156 d, respectively.

Live to missing survival estimates were made from models that included roots from all three study sites. These models showed that from the time of first observation, live roots died and disappeared in 239 ± 15 d at 5A, 118 ± 3 d at 5C, and 193 ± 10 d at 5D ($\phi_{\text{site} \times \text{growing season}}$). Fixing an upper time estimate for this transition yielded similar values for 5A (369 ± 15 d) and 5D (360 ± 19 d), but a significantly smaller estimate for 5C (189 ± 4 d).

Soil respiration

Soil respiration data for the 1998 and 1999 growing seasons are presented for all sites in Table 4. Differ-

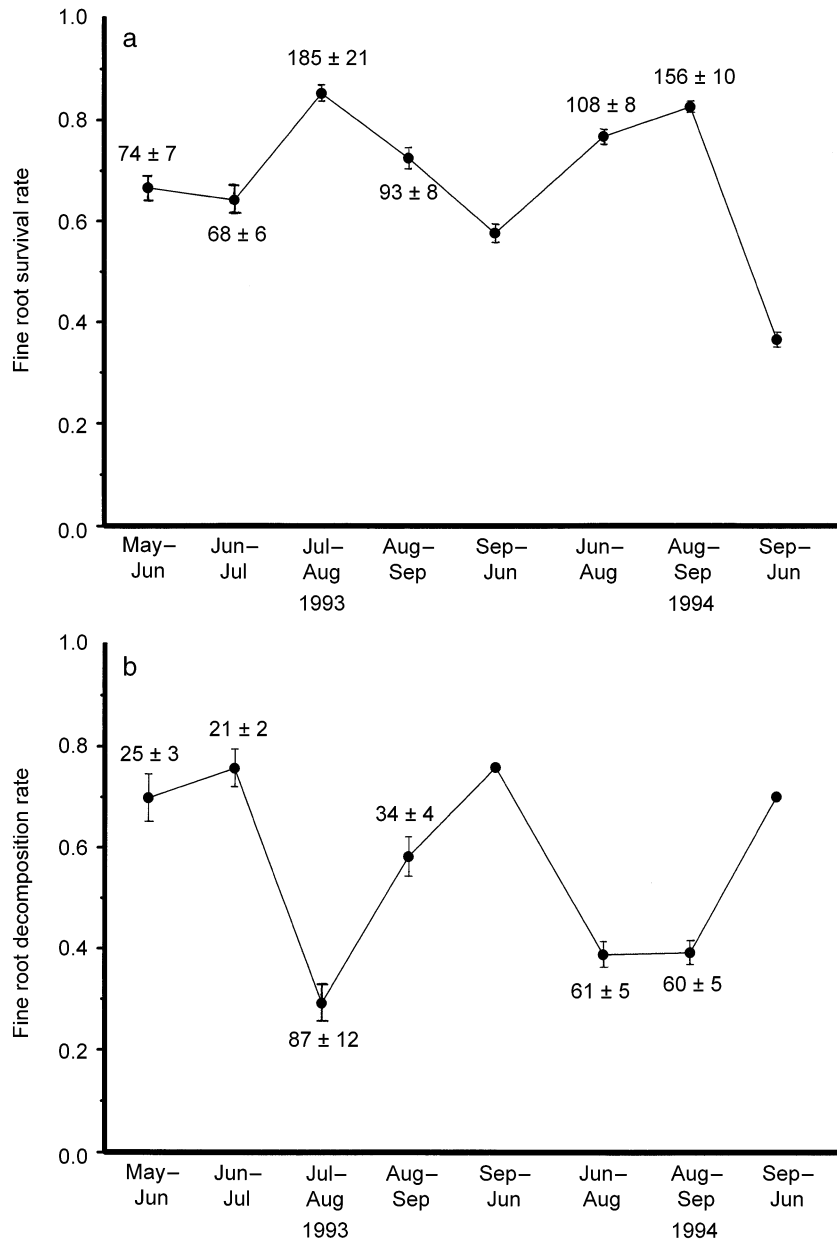


FIG. 2. Estimates (means \pm 1 SE) of (a) fine root survival and (b) decomposition for each time interval (ϕ_{time}) during 1993 and 1994 (from MARK). Growing season estimates represent monthly survival and decomposition rates, while overwinter survival estimates are those reflecting the entire overwinter period. Values above data points are mean life spans (MLS) in days (\pm 1 SE) calculated from survival estimates ($\text{MLS} = -\ln[1/\phi_{\text{time}}]$). These time models represent the most parsimonious single-factor model for both survival and decomposition, significantly different from the null model (ϕ_0) as follows: (a) ($\text{LRT}_{\text{survival}}$, $\chi^2_7 = 700.8$, $P < 0.0001$), (b) ($\text{LRT}_{\text{decomposition}}$, $\chi^2_7 = 281.3$, $P < 0.0001$). MLS was not measured for overwinter periods for either survival or decomposition, due to the fact that we are uncertain when roots died or disappeared; we only know that these had occurred by the times tubes were imaged in the spring. See *Methods* and *Results* for model notations, and other model results.

ences among sites were significant for 1999 ($F_{2,10} = 3.67$, $P = 0.06$), but not for 1998 ($F_{2,11} = 1.56$, $P = 0.25$) due to strong site differences in soil temperature during 1999 ($F_{2,10} = 21.39$, $P < 0.001$). Soil respiration did not vary between years ($F_{1,21} = 1.26$, $P = 0.27$), despite higher average soil temperatures measured with

the LICOR probe in 1999 ($10.1 \pm 1.0^\circ\text{C}$) compared to 1998 ($7.0 \pm 1.2^\circ\text{C}$; $F_{1,21} = 5.09$, $P < 0.05$). Soil respiration increased with temperature across sites during both years, although Q_{10} values for 1998 ($Q_{10} = 2.33 \pm 0.47$) and 1999 ($Q_{10} = 2.18 \pm 0.50$) were indistinguishable ($t = 4.32$, not significant) (Fig. 4). Daily soil

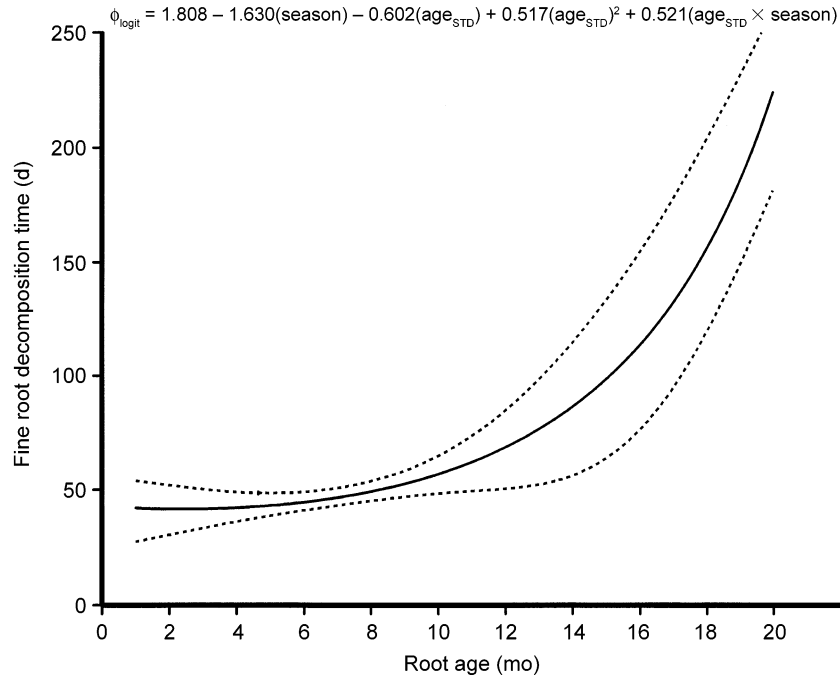


FIG. 3. Relationship between fine root decomposition time (d) and root age at death (mo) for roots that died during the growing season, modeled as a quadratic logit function (from MARK) ($\phi_{\text{logit}} = \beta_0 + \beta_1[\text{season}] + \beta_2[\text{age}_{\text{STD}}] + \beta_3[\text{age}_{\text{STD}}]^2 + \beta_4[\text{age}_{\text{STD}} \times \text{season}]$). Season = 1 for growing season periods; 0 for overwinter periods. This relationship is for growing season periods only. Survival estimates (ϕ) used for decomposition time calculations were derived from the logit expression as $\phi = e^{\phi_{\text{logit}}}/e^{(1 + \phi_{\text{logit}})}$, and mean life span of dead roots (MLS = decomposition time in days) = $-1/\ln(\phi)(30)$.

temperature averages obtained from loggers at each site were used with the generalized temperature response across both years and sites (SOILRESP = $2.985e^{0.0792(\text{TSOIL})}$, $F_{2,25} = 160.7$, $P < 0.0001$, $Q_{10} = 2.21 \pm 0.31$) to estimate growing season (15 May to 15 September) soil efflux for each site. This yielded total seasonal soil efflux estimates of 616, 624, and 501 g $\text{CO}_2\text{-C/m}^2$ for 5A, 5C, and 5D, respectively.

Fine root respiration

Fine root respiration ranged from 0.44 to 4.79 nmol $\text{CO}_2\text{-g fine root dry mass}^{-1}\text{-s}^{-1}$, averaging 1.9 ± 0.1 nmol $\text{CO}_2\text{-g fine root dry mass}^{-1}\text{-s}^{-1}$ across all sites and time periods. Fine root respiration was positively correlated with soil temperature over an ambient temperature range of 2.9 to 14.9°C across all sites and time periods (FRRESP = $0.924e^{0.0834(\text{TSOIL})}$, $Q_{10} = 2.30 \pm 0.37$, $F_{2,66} = 219.9$, $P < 0.0001$) (Fig. 5a). Roots with respiration rates higher than predicted by this relationship had significantly higher total nitrogen concentrations, indicating that at a given temperature, fine root N content had strong effects on respiration rates (Fig. 5b).

Only slightly more than half of the live biomass in soil cores (56%) was sorted as root fragments greater than 1 cm in length; the remainder was recovered from the 850 μm (23%), 400 μm (13%), 250 μm (6%), and 125 μm (2%) sieve fractions. We used average live fine root biomass for each site to produced estimates for

total growing season (15 May to 15 September) fine root respiration of 430, 315, and 243 g C/m^2 for 5A, 5C, and 5D, respectively.

DISCUSSION

Fine root production

One of the most interesting findings from this study is the relatively high rate of fine root production in floodplain black spruce forests, particularly in reference to aboveground growth. We found rates of root length production (average RLP = 0.023 ± 0.003 mm-cm $^{-2}\text{-d}^{-1}$; peak growing season RLP = 0.051 ± 0.015 mm-cm $^{-2}\text{-d}^{-1}$) that are comparable to values reported for many temperate forests using similar methods. This includes peak growing season RLP estimates from studies on managed sweetgum (*Liquidambar styraciflua*) (0.033 mm-cm $^{-2}\text{-d}^{-1}$ (<25 cm), Price and Hendrick 1998), slash pine (*Pinus elliotti*) (0.016 mm-cm $^{-2}\text{-d}^{-1}$ (<25 cm), Schroeer et al. 1999), sugar maple (*Acer saccharum*) (0.026 to 0.036 mm-cm $^{-2}\text{-d}^{-1}$ (<30 cm), Hendrick and Pregitzer 1997), and red pine (*Pinus resinosa*) (0.0044 mm-cm $^{-2}\text{-d}^{-1}$ (<85 cm), (Coleman et al. 2000). Part of the difficulty in comparing RLP among studies is the fact that not only does production typically decrease significantly with depth, but also, there is no standard depth distribution for reporting fine root production. Averaged across all sites and time periods, we found RLP to be greatest in the

TABLE 4. Soil respiration ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) (mean \pm 1 SE, and range) measured at three black spruce sites during the 1998 and 1999 growing seasons.

Season	Site			Q_{10}
	5A	5C	5D	
1998				
Mean	5.45 ± 0.99	7.46 ± 1.85	4.22 ± 0.88	2.23 ± 0.47
Range	3.96–9.16	4.19–11.21	1.49–6.67	
1999				
Mean	8.00 ± 1.63	7.98 ± 0.69	4.65 ± 0.59	2.18 ± 0.50
Range	5.16–12.18	6.24–9.61	3.26–6.68	

Note: Q_{10} values were derived from data across all sites for each year.

10–20 cm fibric layer ($0.063 \pm 0.008 \text{ mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$), second highest within the live and dead moss layer at the surface (0–10 cm = $0.026 \pm 0.004 \text{ mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$), but less in deeper humic (20–30 cm = $0.014 \pm 0.002 \text{ mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) and mineral (30–40 cm = $0.004 \pm 0.001 \text{ mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) profiles. Peak values were recorded for the 10–20 cm depth during the 1994 growing season ($0.153 \pm 0.040 \text{ mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$). Thus, it appears that RLP of interior black spruce is as high or higher than has been recorded for many temperate hardwoods, such as that reported by Burton et al. (2000), who found peak growing season values ranging from 0.033 to $0.067 \text{ mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$ among four sugar maple sites in Michigan. This is a striking result, given the very slow growth of aboveground tissues, and the low growing-season soil temperatures and N mineralization rates (Flanagan and Van Cleve 1983, Van Cleve et al. 1983). Clearly, black spruce roots are adapted to rapid growth under these conditions, as reported by Tryon and Chap-

in (1983), who studied the growth of roots against vertical Plexiglas plates, and found elongation rates of black spruce were higher than midsuccessional Alaskan forest species.

One possible explanation for these high RLP values is that minirhizotron tubes were not equilibrated with

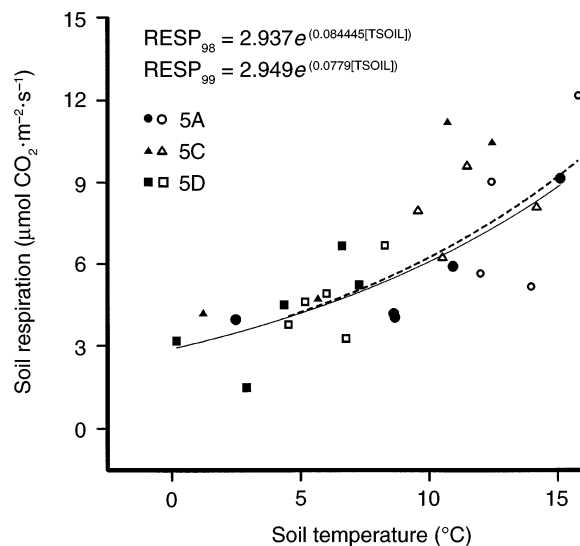


FIG. 4. Relationship between soil respiration rate ($\mu\text{mol CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and soil temperature ($^{\circ}\text{C}$), measured 10 cm below the moss surface throughout the growing seasons of 1998 ($P < 0.001$) and 1999 ($P < 0.001$) at three floodplain black spruce stands. Each point represents the mean of 10 sampling points at each time period.

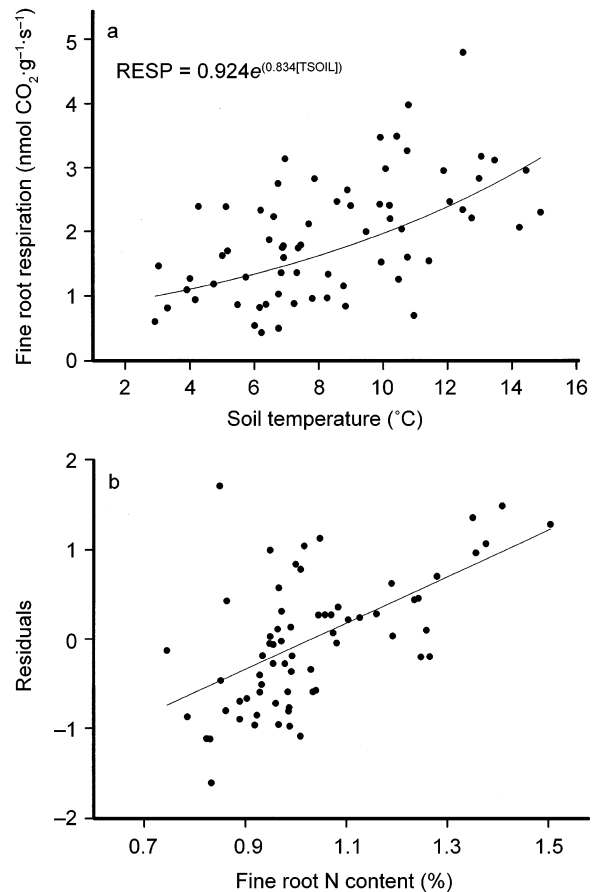


FIG. 5. (a) Relationship between fine root respiration rate ($\text{nmol CO}_2\cdot\text{g}^{-1}\cdot\text{s}^{-1}$) and soil temperature ($^{\circ}\text{C}$), measured 10 cm below the moss surface, across three floodplain black spruce stands throughout the 1999 growing seasons ($P < 0.001$). Each point represents one fine root sample. (b) Relationship between residuals of graph in (a) and fine root nitrogen content (%) ($Y = 2.60 \times \text{ROOTN} - 2.68$, $r^2 = 0.28$, $P < 0.001$).

root growth dynamics in bulk soil (Joslin and Wolfe 1999, Burton et al. 2000, Wells and Eissenstat 2001). This is suggested by the imbalance between annual production and mortality during 1993. As noted, we did not distinguish dead roots at one site (5C), where mortality was conservatively estimated from disappearance. Since a large percentage of roots were first observed as dead, this would lead to an underestimation of mortality when averaged across the three sites. Minirhizotron tubes not fully equilibrated could show elevated fine root growth if installation disturbances stimulate fine root growth, or lower rates if tube colonization was not fully complete. But annual fine root production and mortality were statistically indistinguishable during 1994, suggesting that minirhizotron tubes had reached equilibration by the end of the study period. To examine this further, we digitized one tube from each site for two time periods during the 1999 growing season, after an additional 5 yr of tube stabilization. Expressed on a whole-tube basis, root length production ($0.169 \pm 0.040 \text{ mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) and mortality ($0.120 \pm 0.027 \text{ mm}\cdot\text{cm}^{-2}\cdot\text{d}^{-1}$) did not differ ($t_4 = 1.0$, $P = 0.38$). Moreover, this check verifies that for brief periods during a very short growing season, rates of root length production, particularly in surface soil layers, are as high as have been recorded for many temperate forests.

Fine root growth in black spruce stands peaks approximately one month later than that found for early successional floodplain forests within the same region (Ruess et al. 1998). This is likely a function of slower soil warming during spring and early summer in black spruce stands due to a continuous moss cover and the presence of permafrost (Viereck 1970). We previously suggested that this lag in peak fine root growth behind leaf out and the initiation of shoot growth appears to increase with latitude (Ruess et al. 1998). Maximum rates of fine root growth coincide with canopy development during spring in northern hardwood ecosystems (Hendrick and Pregitzer 1992), but become progressively more delayed in boreal forests where root elongation rates are closely tied with accumulative soil heat sums (Tryon and Chapin 1983, Steele et al. 1997; O'Connell et al. 2003b; R. Hendrick and R. Ruess, unpublished data). We assigned production occurring between fall and spring sampling dates to previous year's annual growth, out of convenience for calculating annual increments. However, we suspect that most of the production during this period occurred in the spring and early summer while surface soils were still close to freezing. Thus, while soil temperature plays a dominant role in regulating belowground dynamics in these systems, fine root growth in black spruce is highly adapted to low temperatures, and may be tightly synchronized with soil warming in the spring.

Fine root production accounted for $70 \pm 3\%$ of vascular plant production, and $56 \pm 5\%$ of total stand production in these floodplain black spruce ecosystems.

Aboveground growth of trees ($13 \pm 1\%$) and shrubs ($11 \pm 2\%$) contributed similarly to total production, while mosses ($20 \pm 5\%$) accounted for the largest component of aboveground production. The significant contributions of bryophytes to total production has been noted for other boreal forests (Oechel and Van Cleve 1986, Gower et al. 1997; O'Connell et al. 2003b). Estimates for fine root contributions to total production for 5A (51%) and 5D (51%) were somewhat less than for 5C (67%), due to higher and more variable rates of root production among minirhizotron tubes at 5C ($374 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, $\text{cv} = 54\%$) compared with 5A ($186 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, $\text{cv} = 32\%$) and 5D ($126 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, $\text{cv} = 34\%$). Nevertheless, this variation among stands is fairly low, given the number of assumptions that are included in calculations of belowground production (Johnson et al. 2000). These estimates are greater than those reported by Gower et al. (1997) for black spruce in Manitoba and Saskatchewan, where fine root production comprised 41–46% of total stand production. Like ours, their estimates also included contributions by bryophytes. Estimates of allocation to fine root production are greater in black spruce than we previously found for floodplain white spruce, where fine roots accounted for $38 \pm 10\%$ of vascular plant production (R. Hendrick and R. Ruess, unpublished data). In that study, allocation to fine roots increased across a gradient of decreasing mean growing season temperatures. Proportional allocation to fine roots is thought to be greater in coniferous forests than deciduous forests (Ruess et al. 1996, Gower et al. 1997, 2001), and it has been argued that fine root production constitutes a greater percentage of total production in boreal forests, where soils are nutrient poor and soil temperatures low (Ruess et al. 1996). The most critical assumptions affecting our estimates of annual fine root production ($\text{g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) are (1) the SRL estimate of 44.02 m/g is accurate, (2) RLP measures are representative of long-term values, and (3) the minirhizotron depth of view is 0.2 cm, beyond which fine roots are evenly distributed. Extensive study of white spruce fine root morphology in nearby forests (Pregitzer et al. 2002), and the similarity of black spruce and white spruce fine roots, suggests that our estimated SRL values are reasonable. With respect to our RLP values being representative of long-term values, there are simply too few data from this or other ecosystems to assess the extent of interannual variability in RLP. However, there were no exceptional climate or disturbance events, or deviations in aboveground growth as evidenced in the increment cores, to suggest that belowground production was especially low or high during the measurement period. Finally, while depth of view is likely to deviate from 0.2 cm along a minirhizotron tube, there is precedent for using this value in observational studies (e.g., Atkinson 1992, Merrill and Upchurch 1994, Smit et al. 2000). Moreover, an attempt to extrapolate minirhizotron length data to biomass values from one of

our previous studies (Atkinson 1992) eventually proved to underestimate actual values, and thus the contribution of roots to ecosystem productivity, by >20% (Hendrick and Pregitzer 1993). And while root densities along minirhizotrons do not always correlate perfectly with those in bulk soil (Smit et al. 2000), Hendrick and Pregitzer (1996) showed that the relationship is often better than commonly assumed. Because minirhizotron root length densities are often less than those of bulk soil, especially near the surface, this would again result in conservative estimates of root productivity at our sites.

Aboveground production of black spruce trees in the floodplain stands we studied (50 ± 14 g biomass·m⁻²·yr⁻¹) is lower than the range of 72 to 148 g biomass·m⁻²·yr⁻¹ (mean \pm 1 SE = 113 ± 17) previously reported for interior Alaskan black spruce stands (Van Cleve et al. 1983). Part of this discrepancy is due to the fact that sites considered by Van Cleve et al. (1983) included black spruce growing on north-facing slopes within the surrounding uplands adjacent to the Tanana River, which can be twice as productive as floodplain, or low-lying muskeg stands (Van Cleve et al. 1981, Viereck et al. 1986). Black spruce forests studied by Van Cleve et al. (1983) were also younger (95 yr old) and more dense (density = 14 000 stems/ha, BA = 25 m²/ha, AG biomass = 5094 \pm 2107 g/m²) than our stands (Table 1). Because we don't know how biomass allocation to fine roots and ectomycorrhizae vary with stand age or site conditions, we are somewhat hesitant to extrapolate our results more broadly to the black spruce ecosystem throughout interior Alaska. Thus, we are uncertain whether the higher allocation to root production in our stands relative to those studied by Gower et al. (1997) represents an actual latitudinal pattern in belowground allocation, or is more characteristic of older, more senescent stands. Nevertheless, our sense is that many of the characteristics of fine root growth and the role of fine roots in carbon and nutrient cycling that we found for our stands apply broadly to black spruce within interior Alaska.

Fine root longevity and decomposition rate

A general characteristic regarding the root systems of woody plants appears to be that the smallest diameter fine roots have life spans typically less than a year. This conclusion derives from minirhizotron studies conducted across a diverse range of forested ecosystems from warm temperate, cold temperate, and boreal climates, such as red pine (291 d) and hybrid poplar (149 d) plantations in Wisconsin (Coleman et al. 2000), sugar maple in Michigan (75–500 d; Hendrick and Pregitzer 1992, Burton et al. 2000), northeastern hardwoods (314 d; Tierney and Fahey 2001), apple (36 to 114 d; Wells and Eissenstat 2001), eastern citrus groves (150–300 d; Eissenstat et al. 2000), early successional Alaskan forests (Ruess et al. 1998), and Alaskan white spruce forests (R. Hendrick and R. Ruess, unpublished

data). Fine root longevity has been shown to be influenced by a number of factors, including root age and birth date, time of year, soil climate and nutrient availability, the degree of mycorrhizal infection, aboveground pathogens, and vertebrate herbivory (Hendrick and Pregitzer 1992, Grime 1994, Kosola et al. 1995, Pregitzer et al. 1997, Ruess et al. 1998, Burton et al. 2000, Eissenstat et al. 2000, Tierney and Fahey 2001, King et al. 2002). However, functionally, fine root longevity may be most closely associated with morphological and physiological properties of fine roots, such as diameter and SRL, N content, respiration, nutrient uptake capacity, and mycorrhizal status, in much the same manner as is seen for leaf life span and associated leaf traits (Yanai et al. 1995, Pregitzer et al. 1997, 2002, Reich et al. 1998a, b, Eissenstat et al. 2000, Wells and Eissenstat 2001, King et al. 2002). The smallest diameter, most distal fine roots on lateral branches, hereafter referred to as first-order roots, often constitute a high percentage of fine root biomass and length in forested ecosystems (Hendrick and Pregitzer 1993, Pregitzer et al. 2002). These first-order roots are considered relatively inexpensive to build because of their high SRL and low structural content, but costly to maintain due to their high N content and respiration rates (Eissenstat and Yanai 1997, Pregitzer et al. 1997, 2002). It is logical that these traits would also be associated with short life span (Reich et al. 1992). Eissenstat et al. (2000) found shorter life spans in fine roots of apple compared to citrus, which were associated with higher SRL, and greater succulence and fragility in apple, and Wells and Eissenstat (2001) found a positive relationship between mean root diameter and survivorship in apple trees, as did King et al. (2002) in loblolly pine.

Minirhizotron studies collectively show that there are basic morphological and phenological traits of first-order roots that are common to most woody plant root systems. For example, we found that fine root survival was greatest during periods of peak root growth, and least during overwinter periods (ϕ_{time}). Variation in survival among time periods has been found by nearly all studies that have looked, and although low overwinter survival appears to be a characteristic of high latitudes (Ruess et al. 1998; R. Hendrick and R. Ruess, unpublished data), it is certainly not unique to high latitudes (Price and Hendrick 1998, Coleman et al. 2000, Wells and Eissenstat 2001). Our finding that roots first appearing during the middle of the growing season had higher survival rates than those first appearing during the early or late growing season, or over winter (ϕ_{cohort}), and the result that the risk of mortality decreases with age (ϕ_{age}), also appear to be general traits of very fine, short-lived roots (Hendrick and Pregitzer 1993, Ruess et al. 1998, Coleman et al. 2000, Tierney and Fahey 2001). We hesitate to conclude taxonomic differences in longevity from published minirhizotron studies because all woody plant fine roots viewed using minir-

rhizotrons are not always functionally similar, as emphasized by studies that have followed root cohorts of different diameters, morphologies, and life spans (Coleman et al. 2000, Tierney and Fahey 2001, Wells and Eissenstat 2001). Clearly, there is a need for a more systematic cross-ecosystem synthesis of fine root demography using common field and analytical methods. Nevertheless, as we point out above, the average diameter of fine roots digitized in this study (0.204 ± 0.010 mm), suggests that they were most likely first-order roots. Thus, while permafrost-dominated Alaskan black spruce ecosystems are dominated by plants with extremely slow-growing aboveground tissues, the life history of very fine roots in these systems is very similar to that observed in temperate forests.

It has been suggested that fine root longevity should increase at high latitudes where soils are colder and typically have low nutrient availability (Nadelhoffer et al. 1985, Eissenstat 1992, Hendricks et al. 1993, Grime 1994, Eissenstat and Yanai 1997, Gill and Jackson 2000, Burton et al. 2000, Nadelhoffer 2000). However, our data from black spruce stands, and other Alaskan forests we have investigated (Ruess et al. 1998; R. Hendrick and R. Ruess, *unpublished data*) show that mean life spans of fine roots in Alaskan boreal forests are not dissimilar from those reported for many temperate forests. Our survival estimates of black spruce fine roots translate to mean life spans of 108 ± 4 d during growing season intervals (ϕ_{season}). Relative to other Tanana floodplain forest types we have studied over the same time periods, using the same minirhizotron techniques, mean life span of black spruce fine roots is 20% greater than that of white spruce forests (MLS = 99 ± 2 d; R. Hendrick and R. Ruess, *unpublished data*), and over 50% greater than that measured for early successional stands dominated by willows (MLS = 74 ± 3 d; Ruess et al. 1998). So while variation in fine root longevity among Alaskan ecosystem types doesn't parallel the magnitude of differences in growth and phenological characteristics of aboveground tissues (Van Cleve et al. 1991), there do appear to be significant differences in fine root life span that are correlated with other physiological/morphological growth traits. These may be a function of general plant growth traits (Flanagan and Van Cleve 1983), or driven by differences in soil climate and/or chemistry (Van Cleve et al. 1983), or both. These results suggest that variation among species in the longevity of first-order roots may indeed be correlated with other physiological/morphological growth traits of the whole plant.

The notion that fine root longevity, litter quality, and decomposition rate are intercorrelated functional traits associated with other plant growth characteristics is compelling (Hendricks et al. 2000, Nadelhoffer 2000, Zak et al. 2000), given the strong relationships reported for aboveground tissues (Reich et al. 1992, 1998a, b). Hendricks et al. (2000) found a positive relationship between fine root nitrogen and soil nitrate availability,

both within and among a range of temperate deciduous and coniferous forests. One hypothesis resulting from their study was that higher ratios of acid-insoluble C to total N in fine roots growing on lower nutrient soils would translate to slower rates of fine root decomposition. Because condensed tannin and lignin concentrations increase with root age, factors that increase average root lifespan would similarly affect fine root decomposability and rates of nutrient cycling (Zak et al. 2000). Here, we found that, during the growing season, monthly fine root decomposition rates averaged 0.46 ± 0.01 month⁻¹, while decomposition rates over winter averaged 0.73 ± 0.01 winter⁻¹ (ϕ_{season}). These growing-season estimates translate to 49 ± 2 d from the time a root was first observed as dead, to the time it disappeared. We also found that for roots that decomposed during the growing season, fine roots with longer life spans decomposed more slowly after death (Fig. 3). Our relationship shows that there was essentially no variation in decomposition rate among fine roots that lived less than a year, but that decomposition rate decreased appreciably after that. For example, roots that lived for 8 mo decomposed three times as fast (50 d) as those that lived for 18 mo (156 d). We don't know how the magnitude of this difference would impact nutrient cycling rates, given that life-span of roots dying during the growing season (108 ± 4 d), and the value set as the conservative upper limit when over-winter was included in the analyses (122 ± 4 d) (see *Results: Fine root longevity and decomposition rate* for explanation), are both less than 8 mo. Despite the fact that we observed very few fine roots living 18 mo, they surely exist, and likely have life-spans, and presumably decomposition rates, that are characteristic of higher order, larger diameter roots with significantly higher C:N ratios. If we assume that the morphology and chemistry of black spruce and white spruce roots are identical, then the first-order roots we observed would constitute 32% of the mass, and contain 39% of the nitrogen from all first through fourth order fine roots (calculated from Pregitzer et al. 2002). This biomass proportion is not dissimilar from the ratio of biomass calculated independently from minirhizotron images (mean ± 1 SE across all dates = 718 ± 117 g/m²; assuming SRL = 44.02 m/g and depth of view = 0.2 cm), to the total fine root biomass (<1 mm diameter) sampled from cores (1714 ± 187 g/m², $n = 15$). Thus, while minirhizotrons clearly demonstrate that a large proportion of C fixed in these systems is cycling rapidly through first-order fine roots, there is a significant mass of fine roots less than 1 mm diameter about which we know very little. We would predict that while production of these larger diameter fine roots is substantially less than those we studied, they could easily live several years, and once dead, decompose slowly due to high C:N ratios and high concentrations of secondary chemicals (Gaudinski et al. 2001, Silver and Miya 2001).

Fine roots and soil CO₂ efflux

The ratio of net ecosystem production (NEP) to total ecosystem respiration (Valentini et al. 2000), and the contribution of fine root respiration (R_{FR}) to total soil CO₂ efflux (R_S) (Raich and Nadelhoffer 1985, Ruess et al. 1996, Hogberg et al. 2001) are both thought to increase with increasing latitude in forested ecosystems. We believe these two observations are functionally coupled. Our estimate of R_{FR}/R_S (0.57) is greater than (Malhi et al. 1999, 0.24, *Picea mariana*, Canada), similar to (Hogberg et al. 2001; 0.52–0.56, *Pinus sylvestris*, Sweden), but less than (Ryan et al. 1997, 0.74, *Picea mariana*, Manitoba; O'Neill 2000, 0.85, *Picea mariana*, Alaska) recent estimates from other high-latitude forests. O'Connell et al. (2003a) used trenched plots to measure R_{FR} throughout the year in *Sphagnum* and feather moss black spruce stands at the southern BOREAS site, and found that R_{FR}/R_S ranged from 0.63 to 0.69 during the growing season, and from 0.16 to 0.21 during winter, respectively. They concluded that their forests were net C sinks during the growing season, but on an annual basis, stands were sources of C to the atmosphere at a rate similar to NPP, due to the magnitude of overwinter respiration. Rayment and Jarvis (2000) reported that annual CO₂ efflux at their southern BOREAS site was an order of magnitude greater than net ecosystem uptake, and six times greater than NPP. We only estimated NEP during the growing season, but could not detect an imbalance between soil heterotrophic respiration ($R_H = R_S - R_{FR} = 251 \pm 36$ g C·m⁻²·yr⁻¹) and total NPP (196 ± 45 g C·m⁻²·yr⁻¹) (paired $t = 0.98$, not significant). Given that we didn't measure soil respiration at the season "shoulders," an alternative interpretation of this result is that these older floodplain stands are responding to climate warming in interior Alaska (Goulden et al. 1998; O'Connell et al. 2003a). However, there are many uncertainties associated with plot-based measurements of NEP (Clark et al. 2001; O'Connell et al. 2003a). One issue is simply the fact that while we measured most of the component fluxes over multiple years, they were not all measured over the same years. Several other uncertainties specific to our calculation of NEP deserve discussion.

First, for reasons we don't completely understand, our R_S measurements are higher, and in some cases, substantially higher than those measured in other black spruce ecosystems. O'Neill (2000) reported midseason (July) R_S values for a 150-yr-old black spruce stand near Tok, Alaska that ranged from 6.18 ± 2.29 to 9.53 ± 3.09 μmol CO₂·m⁻²·s⁻¹ (mean ± 1 SD) over 2 yr, values not dissimilar from averages we found over 2 yr for July (6.86 ± 0.71 μmol CO₂·m⁻²·s⁻¹) and August (8.42 ± 1.29 μmol CO₂·m⁻²·s⁻¹). However, their overall relationship between R_S (converted to μmol CO₂·m⁻²·s⁻¹) and soil temperature ($R_S = 2.170e^{0.08711(T_{SOIL})}$) produces an efflux at 10°C (5.19 μmol CO₂·m⁻²·s⁻¹) that is 21% less than the value es-

timated from our equation (6.59 μmol CO₂·m⁻²·s⁻¹). Our efflux at 10°C is approximately twice as high as that reported by Jarvis et al. (1997) (3.2 μmol CO₂·m⁻²·s⁻¹), and O'Connell et al. (2003a; 3.34 μmol CO₂·m⁻²·s⁻¹), who both worked in BOREAS black spruce stands. Jarvis et al. (1997) estimated annual R_S at 896 g C·m⁻²·yr⁻¹. Growing season R_S from our stands (580 ± 40 g C/m²) is similar to the annual R_S reported for feather-moss black spruce stands by O'Connell et al. (2003a; 564 ± 10 g C/m²); however, they found that ~57% of this annual R_S occurred during winter. Because our soils freeze to permafrost during winter, we would expect substantially less overwinter CO₂ efflux relative to their sites. Our growing season R_S is also higher than the 2-yr growing season average of 369 g C·m⁻²·yr⁻¹ for Tanana upland and floodplain black spruce stands reported by Schlentner and Van Cleve (1985) using the soda-lime method. Part of this discrepancy could be accounted for by methodological differences, given the tendency of the soda-lime method to underestimate higher flux rates. For example, Nay et al. (1994) found that the soda-lime method underestimated dynamic chamber rates at fluxes above 2.52 μmol CO₂·m⁻²·h⁻¹, and by 57% at the highest efflux value measured (4.86 μmol CO₂·m⁻²·h⁻¹). During side-by-side comparisons in various floodplain and upland stands near Fairbanks, our LICOR-6009 (LICOR, Lincoln, Nebraska, USA) gave readings that were 23% lower than a PP Systems Ciras-I with a SRC-1 soil respiration chamber (PP Systems, Haverhill, Massachusetts, USA) ($r^2 = 0.87$, $P < 0.001$; $t_{intercept} = 1.42$, $P = 0.20$, $n = 10$), but approximately the same as another closed system (J. Vogel, unpublished data), similar in design to that used by O'Connell et al. (2003a) ($r^2 = 0.85$, $P < 0.01$; $t_{intercept} = -0.12$, $P = 0.91$, $n = 10$). In summary, it appears that while the LICOR 6200–6009 system produced temperature sensitivity responses ($Q_{10} = 2.21 \pm 0.31$) similar to many values derived in black spruce ecosystems, the magnitude of R_S at 0°C (β_0 of the exponential equation) is higher than expected from other studies.

There are at least two other aspects of our NEP estimates that deserve mention. First, in older, senescent, black spruce stands that are losing a substantial proportion of basal area through tree mortality, there may be time lags between detrital inputs and decomposition rates, and therefore, no reason to expect a balance between NPP and R_H . Data on average aboveground tree biomass relative to stand age for Alaska forests (Yarie and Billings 2002) indicate that 120–140-yr-old black spruce stands lose, on average, 19%, 12%, and 54% of the aboveground tree biomass over the three subsequent 20-yr periods, respectively. The 200-yr-old stands we studied had approximately half the aboveground tree C (1499 ± 29 g C/m²) reported for the 100-yr-old stands by Van Cleve et al. (1983) (2547 ± 1054 g C/m²). Part of this difference is likely due to landscape variation in NPP among black spruce ecosystems

as mentioned above, but their stands also had much higher stem densities. Although we know little about the timing or residence time of this detrital input, it could easily influence soil C efflux decades later because of lags in maximum wood decomposition rates.

The second issue, perhaps of more significance, is our omission of C allocation to ectomycorrhizal growth and respiration from NPP calculations. It is generally agreed that while estimations of C allocation to mycorrhizae vary by over an order of magnitude (Allen 1992), we have a very crude understanding of the actual values. Ectomycorrhizal hyphae supported by first-order roots would be expected to have fairly short life spans, and lose perhaps half their C through respiration (Rygiewicz and Anderson 1994). Mycorrhizal infection of tips of first-order white spruce fine roots growing along the Tanana River floodplain is nearly 100%, and rhizomorph density per square centimeter of minirhizotron tube is higher in these forests relative to other temperate coniferous stands examined (K. Treseder and J. Lansing, *personal communication*). Thus, we would expect C allocation to ectomycorrhizal growth and respiration to contribute significantly to the C balance of these black spruce systems. For example, if ectomycorrhizal production were 20% of fine root growth, then C allocation to ectomycorrhizal hyphae could be as high as $67 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$, assuming 50% respiratory losses. While it is difficult to imagine how plot-based estimates of NEP can be made without the inclusion of these fluxes, it's also difficult to imagine how these fluxes can be more precisely estimated.

CONCLUSION

Rates of fine root production, life span, and decomposition rate reported here indicate that, in these black spruce ecosystems, carbon and presumably nutrients are cycling through fine roots at rates more than two orders of magnitude faster than through aboveground tissues. For example, Van Cleve et al. (1981) reported forest floor residence times of 99 and 111 yr for upland and muskeg black spruce, respectively, and later reported a mean residence time of 178 yr for black spruce forest floor averaged across both upland and floodplain sites (Van Cleve et al. 1983). In contrast, our mean life span for live fine roots ranged from 108 ± 4 to 225 ± 6 d, and decomposition time for dead roots ranged from 49 ± 2 to 122 ± 4 d, depending on estimation assumptions. Findings from this study, and from early successional (Ruess et al. 1998) and white spruce (R. Hendrick and R. Ruess, *unpublished data*) forests along the Tanana floodplain all emphasize that first-order roots in these boreal forests are highly dynamic. The rapid growth, death, and disappearance of such a large proportion of total ecosystem production is a striking contrast to our previous understanding of these low nutrient, permafrost-dominated, late successional ecosystems (Van Cleve et al. 1983, 1993, Viereck et al. 1993a). Our results also support previous C budget

results that suggested roots and root-derived products account for the largest fraction of labile C cycling in these ecosystems. The fate of fine root C and N following root disappearance remains a key question in the dynamics of C and element cycling. In particular, how much fine root N is cycled directly back to live roots via ectomycorrhizae (Michelsen et al. 1996), vs. that decomposed by free-living heterotrophs and subsequently taken up in organic forms (Kielland 1994; McFarland et al. 2002), or sequestered for longer periods of time in soil organic matter (Perakis and Hedin 2001) needs to be carefully studied. Data indicate that while there may well be subtle differences in fine root longevity across these Alaskan ecosystem types, first-order roots are behaving in fundamentally similar ways across a broad range of species and site conditions. It also suggests that implications for variation in functional traits of aboveground tissues on ecosystem-level nutrient cycling processes may not necessarily translate to variation among first-order roots, which appear to be extremely dynamic irrespective of ecosystem type. It is perfectly reasonable that longevity differences across higher orders of fine roots are correlated with differences in substrate quality that affect decomposition rates. However, we contend that the largest and most dynamic portion of the fine root system is comprised of very fine root tips with short life spans and fast decomposition rates. Flanagan and Van Cleve (1983) showed that across the sequence of successional forest ecosystems in interior Alaska, variations in the chemical composition of litter and soil organic matter were strong predictors of forest floor turnover rates. They reported that mass loss of decaying black spruce needles was <10% after 2 yr, and that the residence time of forest floor biomass was ~ 50 yr. Thus, while strong differences in aboveground litter quality and forest floor turnover contribute to significant differences in nutrient cycling rates among successional forests within interior Alaska, these fluxes may constitute only a small fraction of the nutrients and C that are cycling annually. Nevertheless, we suspect that the high secondary chemical content of aboveground litter serves an important role in rate regulation, and potentially the fate of decomposing fine roots as a portion of this pool is sequestered into complex constituents of soil organic matter. Mechanisms characterizing these processes, and the extent to which ectomycorrhizal fungi subvert these pathways through direct uptake of nutrients from decaying fine roots remain critical challenges for future studies in these forests.

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