

# Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada

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**Summary** Root biomass, net primary production and turnover were studied in aspen, jack pine and black spruce forests in two contrasting climates. The climate of the Southern Study Area (SSA) near Prince Albert, Saskatchewan is warmer and drier in the summer and milder in the winter than the Northern Study Area (NSA) near Thompson, Manitoba, Canada. In-growth soil cores and minirhizotrons were used to quantify fine root net primary production ( $NPP_{FR}$ ). Average daily fine root growth ( $m\ m^{-2}\ day^{-1}$ ) was positively correlated with soil temperature at 10-cm depth ( $r^2 = 0.83\text{--}0.93$ ) for all three species, with black spruce showing the strongest temperature effect. At both study areas, fine root biomass (measured from soil cores) and fine root length (measured from minirhizotrons) were less for jack pine than for the other two species. Except for the aspen stands, estimates of  $NPP_{FR}$  from minirhizotrons were significantly greater than estimates from ingrowth cores. The core method underestimated  $NPP_{FR}$  because it does not account for simultaneous fine root growth and mortality. Minirhizotron  $NPP_{FR}$  estimates ranged from  $59\ g\ m^{-2}\ year^{-1}$  for aspen stands at SSA to  $235\ g\ m^{-2}\ year^{-1}$  for black spruce at NSA. The ratio of  $NPP_{FR}$  to total detritus production (above-ground litterfall +  $NPP_{FR}$ ) was greater for evergreen forests than for deciduous forests, suggesting that carbon allocation patterns differ between boreal evergreen and deciduous forests. In all stands,  $NPP_{FR}$  consistently exceeded annual fine root turnover and the differences were larger for stands in the NSA than for stands in the SSA, whereas the difference between study areas was only significant for black spruce. The imbalance between  $NPP_{FR}$  and fine root turnover is sufficient to explain the net accumulation of carbon in boreal forest soils.

*Keywords:* boreal forests, BOREAS, carbon balance, detritus production, fine roots, root turnover, soil carbon.

## Introduction

Boreal forests comprise 8% of all terrestrial biomes but contain 40% of the total terrestrial soil carbon (C) (calculated from Schlesinger 1991). Soil C content represents the long-term net balance between detritus inputs (both above- and below-ground) and heterotrophic respiration. Scientists are interested

in the C budget of boreal forests because the net accumulation of C in vegetation and soil in these forests may partially explain the “missing” carbon sink in the global carbon budget (Tans et al. 1990, Cias et al. 1995, Francey et al. 1995, Keeling et al. 1996). Many scientists anticipate that climate warming will occur in the future with the greatest warming occurring in boreal and subarctic regions (IPCC 1995). However, the effect of climate warming on the C budget of boreal forests, especially the large amount of C stored in the soil, is unclear. Jenkinson et al. (1991) predicted that global warming would accelerate the release of  $CO_2$  from terrestrial ecosystems because of the positive effect of increased temperature on decomposition. This prediction is based on the assumption that climate change would not affect detritus production; however, empirical data indicate that total belowground carbon allocation (root production + respiration) and fine root net primary production differ among forests in contrasting climates (Vogt et al. 1986, Raich and Nadelhoffer 1989, Gower et al. 1995).

Fine root production and turnover are important processes responsible for carbon input to soil. Fine root turnover can equal or exceed aboveground detritus production in many temperate forests (Vogt et al. 1986). There are few published data on fine root dynamics in boreal forests (Ruess et al. 1996), and the role fine roots play in the carbon budget of boreal forests has not been determined, although it is commonly assumed that fine root NPP is proportional to aboveground net primary production. Therefore, information is needed on the influence of major biophysical factors, such as vegetation cover and climate, on fine root production and turnover and the contribution of fine roots to the carbon budget of boreal forests.

The objectives of this study were to compare estimates of fine root biomass and fine root net primary production obtained by different methods, examine the influence of soil temperature on fine root growth and mortality, and compare fine root biomass, NPP and turnover both (i) among three boreal forest types (jack pine, aspen and black spruce) in a similar climate and (ii) for a given forest type in two contrasting climates. We also discuss the importance of fine root NPP and turnover in the carbon budget of boreal forests. We speculate that (i) fine root biomass and NPP are greater in infertile forests (e.g., black spruce) than in fertile forests (e.g., aspen)

as has been shown for temperate forests (Vogt et al. 1986), and (ii) for a similar forest type, that fine root turnover is greater for forests in a warmer climate (Hendrick and Pregitzer 1993a).

## Methods

### Experimental design and site description

The experimental design consisted of three forest types in a southern and northern study area. Four replicate plots were established in random locations in each stand. The Southern Study Area (SSA) is located approximately 40 km north of Prince Albert, Saskatchewan, Canada, near the southern limit of the boreal forest. Soils developed from thick glacial deposits from the late Wisconsin age of the Pleistocene epoch and recent deposits of organic material. The Northern Study Area (NSA) is located 60 km northwest of Thompson, Manitoba, Canada. The soils developed from parent material deposited by Glacial Lake Agassiz. Permafrost occurs within 60 cm of the soil surface in fens and poorly drained forests and at greater depths in upland forest soils. Summers are warmer and drier, and winters are milder in the SSA than the NSA (Table 1). The average length of the growing season for the SSA and NSA are 150 and 120 days, respectively (Rowe 1972). Soil temperatures during the growing season are generally highest for the jack pine stands and lowest for the black spruce stands, with the differences being greater at the SSA than at the NSA (Steele 1996).

General stand characteristics for the six stands are provided in Table 2. The jack pine (*Pinus banksiana* Lamb.) stands at the SSA and NSA are even-aged, 65 to 70 years old (1993 age) and originated after a catastrophic fire. Clumps of green alder (*Alnus crispa* (Ait.) Pursh) with a feathermoss (*Pleurozium* spp.) ground cover occurs sporadically in the stands (Vogel 1997). Paper birch (*Betula papyrifera* Marsh.) occurs in green alder clumps at the NSA. Dominant ground cover at both study areas include bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.) and a nearly continuous cover of reindeer lichen (*Cladonia mitis* (Sandst.) Hale & Culb.). The soil is an excessively drained coarse sand with a 5-cm organic layer and is classified as a Brunisol. The soil at the NSA contains 20 to 30% (by volume) coarse fragments.

Table 1. Select climate characteristics for the Southern Study Area (SSA) and the Northern Study Area (NSA).

Climate characteristics	SSA <sup>1</sup>	NSA <sup>2</sup>
Mean January air temperature (°C)	-19.8	-25.0
Mean July air temperature (°C)	17.6	15.7
Mean annual precipitation (mm)	405	536

<sup>1</sup> Data based on 48-year average (1942–1990) from Prince Albert, Saskatchewan.

<sup>2</sup> Data based on 23-year average from Thompson, Manitoba.

The SSA and NSA aspen stands are even-aged and were 65 to 70 and 50 to 55 years-old, respectively, in 1993. Trembling aspen (*Populus tremuloides* Michx.) comprises greater than 95% of the total stand basal area at both study areas (Gower et al. 1997). Hazelnut (*Corylus cornuta* Marsh.) forms a continuous 1- to 2-m tall shrub layer at both study sites. Other shrub species present include wild rose (*Rosa acicularis* Lindl.) and willow (*Salix* spp.). The ground cover includes grasses and herbs. The soil is a 10-cm organic matter layer over a moderately drained loam to clay loam mineral soil.

The black spruce (*Picea mariana* (Mill.) BSP) stands at the SSA and NSA were 110 to 120 and 150 to 155 years-old, respectively, in 1993. Jack pine and tamarack (*Larix laricina* (Du Roi) K. Koch) occur in the better drained soils at the SSA. Black spruce seedlings, Labrador tea (*Ledum groenlandicum* Oeder), wild rose and bog cranberry (*Vaccinium* spp.) are common understory plants at both study areas. The ground cover varies from feathermoss in closed canopy areas of the stand to sphagnum (*Sphagnum fuscum* Schimp.) in open canopy areas of the stand. The soil at the SSA is a 20- to 30-cm deep organic soil layer over a sandy loam mineral soil. The soil at the NSA is a 30- to 50-cm thick organic layer over a clay mineral soil and is classified as a peaty-phase orthic gleysol.

### Plot establishment

Four plots were established in each stand in August 1993. Plot size varied depending on tree density, ranging from 15 × 15 m for the black spruce stands to 25 × 25 m for the aspen and jack pine stands at the SSA (Gower et al. 1997). All trees > 2.5 cm diameter at breast height (DBH, 1.37m) in each plot were tagged, identified by species, and DBH recorded.

### Terminology

Because the terminology used in the literature to describe fine root dynamics is inconsistent and confusing, a list of the terms used in this paper and their respective symbols, description and units is provided in Table 3.

### Fine root biomass and length

Fine root biomass ( $B_{FR}$ ) was determined in soil cores. Five soil cores (4.5 cm diameter × 30 cm deep) were collected from each plot (20 per stand) in September 1994, and stored at 3 °C until processed. Each root core was washed using a hydropneumatic elutriator system (Gillison's Variety Fabrication, Inc., Benzonia, MI) described by Smucker et al. (1982). The recovered fine root and organic material was transferred to a shallow circular (40-cm diameter) pan and all fine roots (excluding root tips) were collected. Fine roots were classified by diameter class (< 2 mm and ≥ 2 to 5 mm), woody or herbaceous vegetation, and physiological status (live or dead) based on color, texture and shape of the root (Vogt and Persson 1990). The remaining material in the pan was thoroughly mixed and a 22.5° pie-shaped divider was placed in each of four randomly selected pie-shaped sections of the pan. All root tips in each section were removed, dried at 70 °C to a constant mass and weighed. Dried fine root samples were composited by plot, and

Table 2. Stand location and characteristics for the jack pine, aspen and black spruce stands located at the Southern Study Area (SSA) and the Northern Study Area (NSA). Stand structure data are from Gower et al. (1997).

Forest type	Latitude Longitude	Trees ha <sup>-1</sup>	Basal area (m <sup>2</sup> ha <sup>-1</sup> )	Average DBH (cm)	Dominant tree height (m)
<i>Southern Study Area (SSA)</i>					
Jack pine	53.92° N 104.69° W	1190	16.9	12.9 (3.0–23.2) <sup>1</sup>	12.7
Aspen	53.63° N 106.20° W	980	33.5	20.5 (9.9–31.5)	20.1
Black spruce	53.99° N 105.12° W	6250	31.5	7.1 (2.1–21.1)	7.2
<i>Northern Study Area (NSA)</i>					
Jack pine	55.93° N 98.62° W	1280	13.3	11.1 (3.0–18.7)	10.3
Aspen	55.85° N 98.04° W	1960	26.7	12.5 (4.5–23.2)	13.8
Black spruce	55.88° N 98.48° W	5450	35.6	8.5 (2.5–18.6)	9.1

<sup>1</sup> Range of DBH.

Table 3. Symbols, definitions and units for terms related to root dynamics described in this paper.

Symbol	Description	Units
$B_{FR}$	Biomass, fine roots (< 5 mm diameter)	g m <sup>-2</sup>
$B_{CR}$	Biomass, coarse roots (> 10 mm diameter)	g m <sup>-2</sup>
$CF_{FR}$	Correction factor, converts fine root length to biomass	m g <sup>-1</sup>
$G_{FR}$	Growth, fine roots	m m <sup>-2</sup> day <sup>-1</sup>
$M_{FR}$	Mortality, fine roots	m m <sup>-2</sup> day <sup>-1</sup>
$L_{FR}$	Length, fine roots	m m <sup>-2</sup>
$NPP_{FR-C}$	Net Primary Production, fine roots using ingrowth cores	g m <sup>-2</sup> year <sup>-1</sup>
$NPP_{FR-M}$	Net Primary Production, fine root using minirhizotrons	g m <sup>-2</sup> year <sup>-1</sup>
$NPP_{CR}$	Net Primary Production, coarse roots	g m <sup>-2</sup> year <sup>-1</sup>
$T_{FR}$	Turnover, fine roots	g m <sup>-2</sup> year <sup>-1</sup>
$TI_{FR}$	Turnover Index, fine roots	year <sup>-1</sup>

dry ashed at 450 °C for 24 h to determine ash-free fine root biomass.

Fine root length ( $L_{FR}$ ) was determined using minirhizotrons. Five minirhizotrons were installed in three of the four replicate plots for a total of 15 minirhizotrons per stand. Minirhizotron tube construction and installation procedures are described by Steele (1996) and were patterned after the design developed by Hendrick and Pregitzer (1993b).

Minirhizotron images were collected with a CCD camera (Bartz Technology, Santa Barbara, CA), a high resolution videotape recorder, and a Sony Watchman LCD television. Images were recorded every 1.3 cm down the minirhizotron. A depth of view of 2 mm was used to calculate  $L_{FR}$  on an area basis (Merrill and Upchurch 1994). An index handle was used to ensure that image collection occurred at the exact same location along the face of the minirhizotron for all measurement periods.

Video images were analyzed with Optimas<sup>®</sup> software (Bothwell, WA) installed on a computer equipped with a TARGA+ video board (Truevision, Inc., Indianapolis, IN). The length and diameter of each root in each 1.8 × 1.3 cm image were recorded and each root was classified as woody or herbaceous and live or dead based on appearance and diameter. The length of fine roots in each category was summed for each 5-cm soil depth for each minirhizotron and the average fine root length for each class was calculated for the five minirhizotrons in each plot. Differences in  $L_{FR}$  between measurement dates for each depth were used to calculate fine root growth ( $G_{FR}$ , m m<sup>-2</sup> day<sup>-1</sup>) and fine root mortality ( $M_{FR}$ , m m<sup>-2</sup> day<sup>-1</sup>). Minirhizotron data were converted from length (m m<sup>-2</sup>) to a dry matter basis (g m<sup>-2</sup>) using conversions factors ( $CF_{FR}$ ) of 7.1 m g<sup>-1</sup> for bog pine for jack pine (Finer 1991), 51.0 m g<sup>-1</sup> for aspen (M. Coleman, U.S. Forest Service, NCFES, Rhinelander, WI, unpublished data) and 15.0 m g<sup>-1</sup> for black spruce (S. Steele, unpublished data). Herbaceous  $G_{FR}$  and  $M_{FR}$  may have been overestimated because the overstory  $CF_{FR}$  was used for all understory fine roots in each stand.

#### Fine root phenology

Roots on the minirhizotron surface were measured in October 1994 (approximately 4 months after the minirhizotrons were

installed) and June, July, September, and October 1995 to determine  $G_{FR}$  and  $M_{FR}$ . Average daily  $G_{FR}$  and  $M_{FR}$  were calculated by dividing the total  $G_{FR}$  or  $M_{FR}$  for each measurement interval by the number of days between measurements. The phenology of  $G_{FR}$  was correlated to soil temperature at 10-cm soil depth in each stand. Soil temperature was measured continuously with a micrometeorological system (Campbell Scientific Inc., Logan, UT) that was located near an eddy covariance flux tower in each forest type. Soil temperature data were retrieved from BORIS—the BOREAS Information System.

#### *Fine root net primary production and turnover*

Annual fine root net primary production ( $NPP_{FR}$ ) was estimated by means of ingrowth cores and minirhizotrons. To calculate  $NPP_{FR}$  from the minirhizotron data ( $NPP_{FR-M}$ ),  $G_{FR}$  was summed for the five measurement periods during 1994–95 and the cumulative value multiplied by the  $CF_{FR}$  to convert  $L_{FR}$  to  $B_{FR}$ . Similarly, fine root turnover ( $T_{FR}$ ) was calculated from minirhizotron data by summing  $M_{FR}$  for the five measurement periods during 1994–95 and multiplying the cumulative value by the  $CF_{FR}$  to convert  $L_{FR}$  to  $B_{FR}$ .

Ingrowth cores ( $NPP_{FR-C}$ ) were also used to estimate  $NPP_{FR}$  because numerous scientists have used this method (Nadelhoffer and Raich 1992). Ingrowth cores were installed on April 28–30, 1994, in the jack pine and aspen stands at the SSA and on May 28 to June 4 at the SSA black spruce stand and all of the NSA stands. The later sampling date was required at these sites because the soil was still frozen in late April 1994. Ten soil cores (10 cm diameter  $\times$  30 cm depth) were collected at each plot and the soil was composited by horizon for each plot and sieved to remove roots. The root-free soil was placed in each hole, by soil horizon, and the forest floor was replaced. It was impossible to sieve the thick organic layer at the black spruce stands, therefore, we sieved only the mineral soil and replaced the organic layer with commercially available sphagnum. To mimic the chemical and hydrological characteristics of the surrounding peat we collected water from free-standing pools in the stand and saturated each sphagnum core.

In June 1995 and 1996, five ingrowth cores were collected from each plot with a 5 cm diameter  $\times$  30 cm deep corer. Samples were stored in plastic bags at 3 °C until processed. Cores were washed using a hydropneumatic elutriator system and all roots were collected. Live roots were sorted and classified as herbaceous or woody. Samples were dried at 70 °C to a constant mass and weighed. Dried root tissue from each plot was composited, ground in a Wiley mill to pass a 1-mm screen and dry ashed in a muffle furnace at 450 °C for 24 h to determine ash content. To calculate  $NPP_{FR-C}$  for each year, live  $B_{FR}$  in the ingrowth core was divided by the number of years the ingrowth cores were in the ground.

#### *Fine root turnover index*

Fine root turnover index ( $TI_{FR}$ ), or the fraction of live roots that die each year, was calculated from the minirhizotron data by the methods of Cheng et al. (1991) and Hendrick and Pregitzer

(1992). Cheng et al. (1991) calculated  $TI_{FR}$  as the sum of the average daily  $M_{FR}$  for a measurement period (1 year) normalized by the average of the initial and final  $L_{FR}$ . Hendrick and Pregitzer (1992) calculated  $TI_{FR}$  as the ratio of  $M_{FR}$  to initial  $L_{FR}$ .

#### *Coarse root biomass and net primary production*

Allometric equations were used to estimate coarse root biomass from stem DBH. An equation developed for subalpine balsam fir (*Abies balsamea* (L.) Mill) (Foster 1985) was used for black spruce, a trembling aspen equation (Ruark and Bockheim 1987) was used for trembling aspen and balsam poplar, and a jack pine equation (S.J. Steele, unpublished data) was used for jack pine. Although use of non-species-specific allometric equations is not desirable, it was justified on the basis that coarse root biomass equations appear to be relatively constant among species (Santantonio et al. 1977) and the need to construct complete root net primary production budgets. Coarse root biomass estimates derived from a site-specific jack pine equation (S.J. Steele, unpublished data) and a general equation (data composited from Crow 1970, Morrison 1974 and Steele 1996) differed by only 9%, suggesting that the generalized species-specific equations were satisfactory, at least for jack pine.

Coarse root NPP was estimated as the sum of the biomass increments for all of the trees in the plot. Coarse root detritus production was negligible because no trees in the plots died during the study. Annual coarse root biomass increment was calculated from estimates of annual radial stem wood increment and allometric equations for all trees in one to two variable radius plots (10 basal area factor prism) located inside each of the four fixed area plots.

#### *Statistical analysis*

The plot was treated as the experimental unit in all statistical analyses. Fine root mass, NPP and phenology data were tested for homogeneity of variance by Levene's test. When required, a square root transformation was used to correct for nonhomogeneous variance. Analysis of variance was used to test for species and study area effects. Fisher's protected multiple range test (LSD,  $\alpha = 0.10$ ) was used to compare treatment means. Kruskal-Wallis Rank Sum test, a non-parametric means comparison analysis was used when transformations did not correct for unequal variance among stands (Snedecor and Cochran 1980). The  $L_{FR}$  was highly variable among the fifteen minirhizotrons at each site. Based on  $L_{FR}$  data for September 1995, 148 to 488 minirhizotrons would be required in the stands to estimate fine root length to within 10% of the mean with a 95% confidence interval. Large spatial variation is a common problem of all of the current methods used to quantify fine root dynamics, justifying the use of an alpha value of 0.10.

**Results**

*Fine and coarse root biomass*

Live fine root biomass (< 5 mm diameter) ranged from 286 g m<sup>-2</sup> for the SSA jack pine stand to 827 g m<sup>-2</sup> for the NSA black spruce stand (Table 4). Dead roots comprised from 24 to 47% of total fine root biomass. There were few differences in live fine root biomass among the forest types at each study area. Live fine root biomass was significantly lower (*P* = 0.01) for jack pine than for aspen and black spruce at the SSA, but it did not differ among forest types at the NSA.

Live very fine (< 2 mm diameter) root biomass in soil cores was significantly greater at the NSA than at the SSA for jack pine (*P* = 0.0002) and aspen stands (*P* = 0.07), but not for black spruce (*P* = 0.11) (Table 4).

At both study areas, coarse root biomass was lowest in the jack pine stands and highest in the aspen stands, ranging from 977 g m<sup>-2</sup> for NSA jack pine stand to 2121 g m<sup>-2</sup> for SSA aspen stand (Table 4). Total live root biomass ranged from 1519 g m<sup>-2</sup> for the NSA jack pine stand to 2778 g m<sup>-2</sup> for the SSA aspen stand.

*Fine root length*

Fine root length was greatest in the upper 10 cm of soil and generally decreased with soil depth in all forests (Figure 1). For example, jack pine, aspen and black spruce contain, on average, 45, 62 and 69%, respectively, of the total fine root length in the upper 10 cm of soil. Fine root length did not differ significantly (*P* > 0.10) among forest types at the NSA or SSA, although it was lowest for jack pine at both study areas, corroborating fine root biomass data estimated from soil cores. Fine root length ranged from 1036 m m<sup>-2</sup> for NSA jack pine to 3606 m m<sup>-2</sup> for NSA aspen (Figure 2).

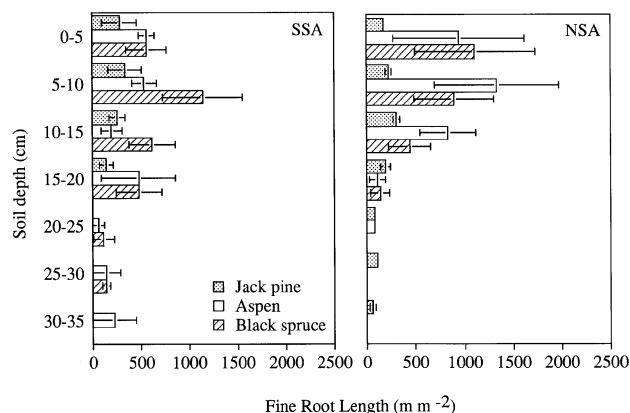


Figure 1. Vertical fine root length distribution in jack pine, aspen and black spruce stands at the Southern Study Area (SSA) and Northern Study Area (NSA).

*Phenology of fine root growth and mortality*

Average daily fine root growth (m m<sup>-2</sup> day<sup>-1</sup>) was negligible during the winter, reached a maximum during the spring or summer, depending on forest type, and decreased in the fall (Figure 3). The phenology of fine root growth differed among species and between sites but 83 to 93% of the observed variation within a species was explained by soil temperature at 10 cm depth (Figure 4). From June to mid-July, average daily fine root growth was significantly greater (*P* = 0.07) for aspen and black spruce than for jack pine at the SSA and was significantly greater (*P* = 0.01) for aspen than for jack pine and black spruce at the NSA. Black spruce average daily fine root growth and soil temperature from June through July were significantly greater (*P* = 0.04) at the SSA than at the NSA.

Table 4. Live and dead root mass (± 1 standard error) for jack pine, aspen and black spruce stands at the SSA and NSA. All values are ash-free dry mass, g dry mass m<sup>-2</sup>. Samples were collected in September 1994. Means followed by similar letters indicate no significant difference ( $\alpha$  = 0.10) within a study area. Asterisk indicates use of the rank sum test.

Forest type	Live			Dead			Live coarse	Total live
	< 2 mm	2–5 mm	Total	< 2 mm	2–5 mm	Total		
<i>Southern Study Area (SSA)</i>								
Jack pine	90 a*	196 b	286 b	133 a*	118 a	257 a	1303	1589
	(6)	(31)	(63)	(6)	(58)	(58)	(119)	
Aspen	79 a	578 a	657 a	80 b	270 a	357 a	2121	2778
	(17)	(107)	(104)	(21)	(89)	(83)	(120)	
Black spruce	77 a	514 a	591 a	58 b	185 a	243 a	1677	2268
	(16)	(126)	(126)	(17)	(41)	(36)	(164)	
<i>Northern Study Area (NSA)</i>								
Jack pine	205 a*	338 a*	543 a*	122 a*	54 a*	187 a	977	1520
	(14)	(94)	(108)	(14)	(27)	(34)	(93)	
Aspen	158 a	486 a	644 a	61 a	141 a	204 a	2019	2663
	(29)	(81)	(74)	(15)	(50)	(62)	(107)	
Black spruce	170 a	657 a	827 a	153 a	104 a	257 a	1936	2763
	(45)	(117)	(113)	(53)	(6)	(56)	(292)	

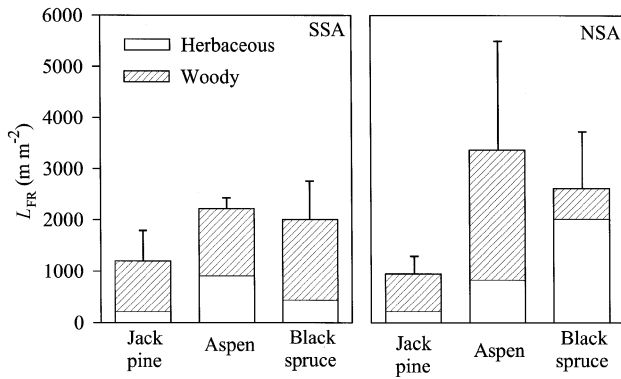


Figure 2. Average fine root length ( $\text{m m}^{-2}$ ) to soil depth of 20 cm for jack pine, aspen and black spruce stands at the Southern Study Area (SSA) and Northern Study Area (NSA) in September 1995. Data are plot means for herbaceous and woody species fine roots. Standard error bars are for total fine root length.

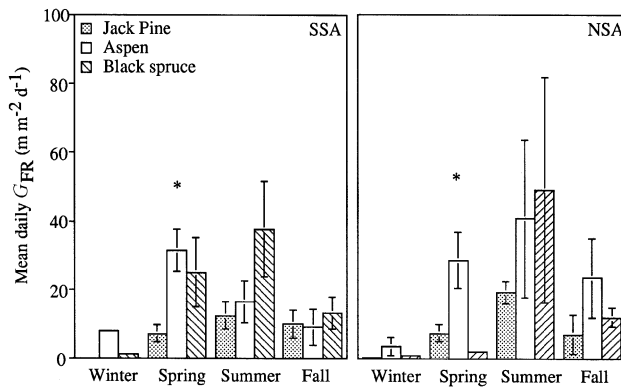


Figure 3. Average daily fine root growth ( $G_{FR}$ )  $\pm$  1 standard error for jack pine, aspen and black spruce at the Southern Study Area (SSA) and Northern Study Area (NSA). Measurement periods for winter, spring, summer and fall were October 1994–May 1995, June 1995–July 1995, July 1995–September 1995, and September 1995–October 1995, respectively. Asterisk indicates species differences at  $\alpha = 0.10$ .

The phenology of fine root mortality also varied with season. Average daily fine root mortality ( $\text{m m}^{-2} \text{day}^{-1}$ ) was minimal during the winter, low in the spring and reached a maximum in the summer or fall depending on forest type. Average daily fine root mortality was significantly lower ( $P = 0.01$ ) for jack pine than for aspen or black spruce at the SSA during the first measurement interval (Figure 5). Average daily fine root mortality was significantly greater ( $P \leq 0.07$ ) for aspen than for jack pine or black spruce at the NSA during the summer and fall and it was significantly greater ( $P = 0.08$ ) for black spruce than for the other species in the SSA during the fall.

For a similar forest type, fine root mortality occurred earlier in the growing season at the SSA than at the NSA. For example, aspen fine root mortality was greater ( $P = 0.02$ ) at the SSA than at the NSA ( $4.4$  and  $1.3 \text{ m m}^{-2} \text{day}^{-1}$ , respectively) during

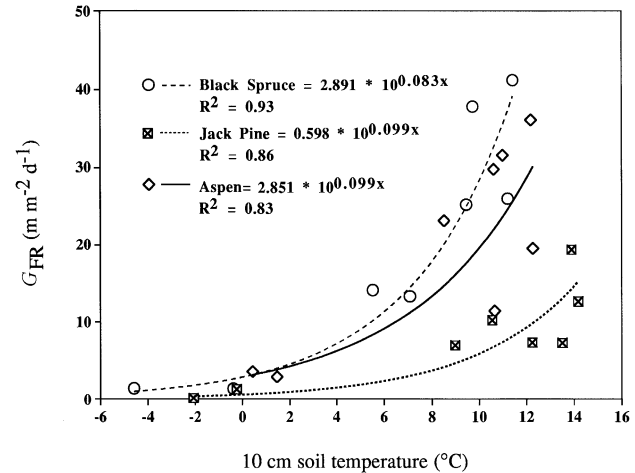


Figure 4. Relationship between average daily fine root growth ( $G_{FR}$ ) and soil temperature at a depth of 10 cm for jack pine, aspen and black spruce. Each value is the average for each measurement period at each study area.

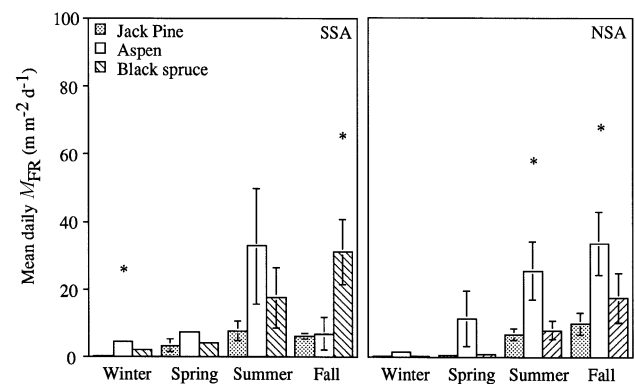


Figure 5. Average daily fine root mortality ( $M_{FR}$ )  $\pm$  1 standard error for jack pine, aspen and black spruce at the Southern Study Area (SSA) and Northern Study Area (NSA) during four measurement intervals. Measurement periods are defined in Figure 3. Asterisk indicates species differences at  $\alpha = 0.10$ .

the first sampling period, whereas maximum aspen fine root mortality was delayed in the NSA compared to the SSA and occurred earlier in the fall ( $P = 0.08$ ,  $30.9$  and  $8.8 \text{ m m}^{-2} \text{day}^{-1}$ , respectively). Black spruce fine root mortality was greater ( $P = 0.04$ ) at the SSA than at the NSA during the second sample period, also suggesting that fine root phenology differed between the two study areas.

#### Fine root net primary production

**Ingrowth cores** Estimates of fine root NPP from ingrowth cores ranged from  $29 \text{ g m}^{-2} \text{year}^{-1}$  for the SSA jack pine stand to  $93 \text{ g m}^{-2} \text{year}^{-1}$  for the SSA aspen stand for the first year and from  $43 \text{ g m}^{-2} \text{year}^{-1}$  for the NSA aspen to  $92 \text{ g m}^{-2} \text{year}^{-1}$  for the SSA aspen for the second year (Table 5).

There were few consistent  $\text{NPP}_{FR-C}$  patterns between the 2 years either among forest types at a study area or between

Table 5. Woody and herbaceous fine root net primary production ( $NPP_{FR-C}$ ) and woody coarse root net primary production ( $NPP_{CR}$ ) ( $\pm$  standard error) for jack pine, aspen and black spruce at the Southern Study Area (SSA) and Northern Study Area (NSA). All values are ash-free, g dry mass  $m^{-2} year^{-1}$ . Within each column, values followed by the same letter are not significantly different ( $\alpha = 0.1$ ) within a study area. Asterisk indicates use of the rank sum test. Mean annual  $NPP_{FR-C}$  and total NPP include both woody and herbaceous roots.

Forest type	Woody $NPP_{FR-C}$		Herbaceous $NPP_{FR-C}$		Annual mean $NPP_{FR-C}$	$NPP_{CR}$ 1994–95	Total NPP 1994–95
	1994–95	1995–96	1994–95	1995–96			
<i>Southern Study Area (SSA)</i>							
Jack pine	24 b (2)	59 a (13)	5 b* (1)	9 b (3)	48 ab (20)	22 (3)	51
Aspen	73 a (16)	53 a (7)	20 a (6)	39 a (14)	92 a (1)	32 (4)	125
Black spruce	66 a (5)	35 a (8)	13 a (2)	11 b (4)	62 (17)	25 (6)	104
<i>Northern Study Area (NSA)</i>							
Jack pine	29 a (3)	59 a (11)	9 a* (2)	23 a (3)	60 (22)	27 (3)	65
Aspen	45 a (4)	27 b (1)	8 a (4)	15 a (2)	48 a (6)	51 (8)	104
Black spruce	53 a (9)	40 b (8)	7 a (1)	18 a (4)	59 a (1)	21 (1)	81

study areas for a forest type. Herbaceous  $NPP_{FR-C}$  did not differ significantly ( $P = 0.50$ ) among forest types in the NSA, but it was significantly greater ( $P = 0.01$ ) for aspen and black spruce stands (except for 1995–96) than for jack pine stands at the SSA, reflecting the greater amount of aboveground understory biomass in the aspen and black spruce stands (Gower et al. 1997).

All components of  $NPP_{FR-C}$  (i.e., woody, herbaceous and total) were significantly greater ( $P \leq 0.10$ ) for jack pine at the NSA than at the SSA, but were significantly lower ( $P = 0.04$ ) for black spruce at the NSA than at the SSA. Fine root NPP was significantly greater ( $P = 0.01$ ) for aspen at the SSA than at the NSA for both years.

*Coarse root NPP*

Coarse root NPP ranged from 21  $g m^{-2} year^{-1}$  for the NSA black spruce stand to 51  $g m^{-2} year^{-1}$  for the NSA aspen stand and was greatest for the aspen stands at both study areas (Table 5). Except for the aspen stand at the NSA,  $NPP_{CR}$  comprised 26 to 31% of total (fine + coarse) root NPP.

*Minirhizotrons*

Fine root NPP from minirhizotrons ( $NPP_{FR-M}$ ) ranged from 57  $g m^{-2} year^{-1}$  for the SSA aspen stand to 235  $g m^{-2} year^{-1}$  for the SSA black spruce stand (Figure 6). Fine root NPP was significantly lower for aspen than for jack pine or black spruce at the SSA. Black spruce  $NPP_{FR-M}$  was greater ( $P = 0.10$ ) at the SSA than at the NSA. Except for the SSA aspen stand, fine root net primary production was greater than turnover in each stand, but the difference was statistically significant for only black spruce (Figure 7). Fine root turnover did not differ between study areas for jack pine and aspen, but it was significantly

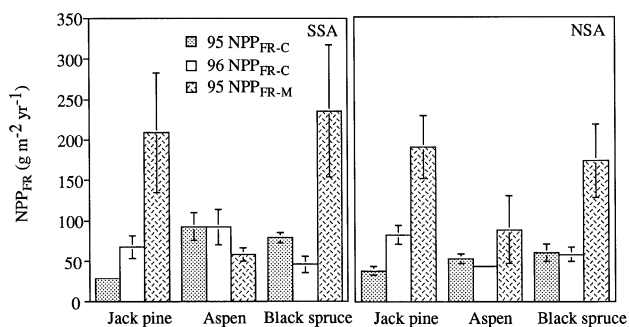


Figure 6. Comparison of annual fine root NPP obtained from ingrowth cores for 1995 (95  $NPP_{FR-C}$ ) and 1996 (96  $NPP_{FR-C}$ ), and minirhizotrons (95  $NPP_{FR-M}$ ) for jack pine, aspen and black spruce at both the Southern Study Area (SSA) and Northern Study Area (NSA).

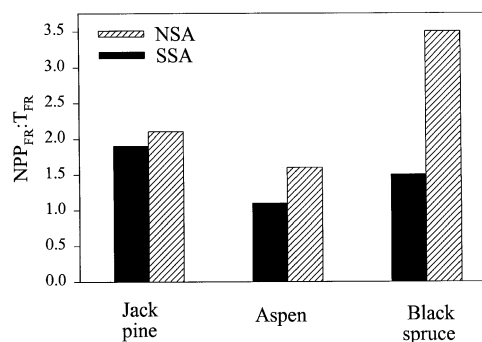


Figure 7. Fine root net primary production ( $NPP_{FR}$ ):fine root turnover ( $T_{FR}$ ) ratio for jack pine, aspen and black spruce at the Southern Study Area (SSA) and Northern Study Area (NSA).

greater ( $P = 0.04$ ) at the SSA than at the NSA for black spruce. Fine root mortality was significantly greater ( $P = 0.05$ ) for aspen than for jack pine or black spruce at the NSA.

#### Fine root turnover index

Annual  $TI_{FR}$  ranged from 1.4 for SSA jack pine and NSA black spruce to 3.3 for NSA black spruce (Figure 8). Fine root turnover did not differ consistently between study areas for a similar species or among species at each of the two study areas. In general, the Hendrick and Pregitzer (1992) method yielded higher estimates of  $TI_{FR}$  than the Cheng et al. (1991) method.

## Discussion

#### Method comparisons: fine root biomass and NPP

Live fine root biomass estimates from soil cores were within the range of values reported for other boreal forests, but the fine root biomass estimates from minirhizotrons were lower than estimates for other boreal forests (Table 6). The soil core and minirhizotron methods also yield different estimates of fine root biomass in agricultural crops (Gregory 1979, Bragg et al. 1983, Vos and Groenwold 1983, Cheng et al. 1990, Samson and Sinclair 1994). Minirhizotrons underestimate fine root biomass and length for some time after the minirhizotrons are installed because fine roots must recolonize the disturbed soil around the minirhizotrons (Hendrick and Pregitzer 1993b).

Fine root NPP estimates from ingrowth cores were lower than most values reported for boreal forests (Table 6), including the estimates from the minirhizotrons (Figure 6). Many scientists have found that estimates of  $NPP_{FR}$  from ingrowth cores are lower for the first year than for subsequent years (Persson 1979, Yin et al. 1989, Conlin and Lieffers 1993, Messier and Puttonen 1993). The low values for the first year presumably reflect the slow rates of root recolonization in the root-free cores. Our second-year  $NPP_{FR}$  estimates from ingrowth cores were also low compared to values for other boreal forests. Vogt and Persson (1990) suggested that ingrowth cores

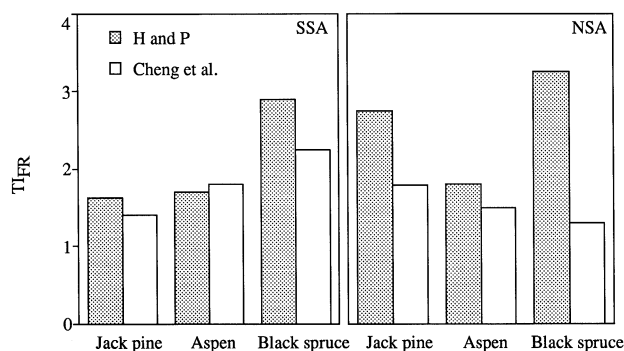


Figure 8. Comparison of annual fine root turnover index for jack pine, aspen and black spruce at the Southern Study Area (SSA) and Northern Study Area (NSA) using minirhizotron data calculated according to the formulae proposed by Cheng et al. (1991) (Cheng et al.) and Hendrick and Pregitzer (1992) (H and P).

should be left in the ground for more than one growing season to obtain reliable estimates of  $NPP_{FR}$ ; however, leaving ingrowth cores in the soil for an extended period of time will confound  $NPP_{FR}$  estimates because fine root growth and mortality occur simultaneously in these stands. We conclude that the ingrowth core method provides an estimate of the minimum amount of biomass allocated to fine root NPP.

Our estimates of  $NPP_{FR}$  from the minirhizotron were similar to values for other boreal forests (Table 6) and were two to four times greater than estimates from ingrowth cores, except for the aspen stands (Figure 6). Sequential coring and ingrowth cores underestimate  $NPP_{FR}$  when fine root growth and mortality occur simultaneously (Vogt et al. 1986, Kurz and Kimmins 1987, Hendrick and Pregitzer 1993b). The minirhizotron data clearly show that fine root growth and mortality occur concurrently in these forests, especially during the summer (Figures 3 and 5). Therefore, minirhizotrons provide more accurate estimates of  $NPP_{FR}$  than ingrowth cores for these boreal forests. It is unclear why  $NPP_{FR}$  estimates for the aspen stands were substantially smaller than values for boreal aspen forests in Alaska (Ruess et al. 1996). It is conceivable that the corer used to install the minirhizotrons compacted the clay soil even though a coring tube was used that was designed to compact the soil inside rather than outside the corer. The Hendrick and Pregitzer (1993b) method of calculating  $TI_{FR}$  produced similar or larger values than the Cheng et al. (1991) method. The method proposed by Hendrick and Pregitzer (1993b) is sensitive to recolonization of fine roots along the minirhizotrons, whereas the method developed by Cheng et al. avoids this problem because it accounts for specific growth and death rates and includes both initial and final fine root length.

#### Influence of soil temperature on fine root distribution and phenology

Fine roots were concentrated in the upper 10 cm of soil as has been reported for other boreal forests (cf. Pulling 1918, Kimmins and Hawkes 1978, Persson 1979, Strong and La Roi 1983, Tryon and Chapin 1983). The sharp decrease in soil temperature below the soil surface, especially for boreal forest soils with permafrost, is probably responsible for the large concentration of fine roots near the surface. Fine root growth of boreal trees is positively and exponentially correlated to soil temperature (Tryon and Chapin 1983). Also, the warmer soil near the surface stimulates decomposition, resulting in greater nutrient availability (Flanagan and Van Cleve 1983).

Soil temperature also strongly influenced the phenology of fine root growth, as shown by the strong positive exponential relationships between average daily fine root growth and soil temperature (Figure 5). Fine root growth occurred earlier in the SSA than in the NSA because the soil warms to a critical minimum threshold earlier at the SSA than at the NSA. Differences in fine root phenology among species at each study area also related to differences in soil thermal environments. The low thermal conductivity of the deep organic surface layer in the black spruce forests caused soil temperature to lag behind air temperature. As a result, fine root growth began later in the black spruce than in the upland species. Tryon and Chapin



Table 6. Fine root biomass, net primary production and belowground:total detritus production percent for boreal forests of the world.

Dominant species	Location	Fine root mass (g m <sup>-2</sup> )	Total root mass (g m <sup>-2</sup> )	NPP <sub>FR</sub> (g m <sup>-2</sup> year <sup>-1</sup> )	NPP <sub>FR</sub> : total detritus (%)	Source
Evergreen						
<i>Picea abies</i>	Llomantsi, Finland	–	–	344	86	Finer 1989
<i>Picea glauca</i>	Alaska, USA	305 <sup>2</sup>	998	157 <sup>2,4</sup>	46	Ruess et al. 1996
<i>Picea glauca</i>	Alaska, USA	288 <sup>2</sup>	917	248 <sup>2,4</sup>	59	Ruess et al. 1996
<i>Picea mariana</i>	Alaska, USA	220 <sup>2</sup>	738	232 <sup>2,4</sup>	77	Ruess et al. 1996
<i>Picea mariana</i>	Saskatchewan, Canada	133 <sup>3,7</sup> , 591 <sup>3,8</sup>	2268	235 <sup>2,7</sup> , 66 <sup>2,5</sup>	69 <sup>7</sup>	this study
<i>Picea mariana</i>	Manitoba, Canada	175 <sup>3,7</sup> , 827 <sup>3,8</sup>	2763	174 <sup>2,7</sup> , 53 <sup>2,5</sup>	52 <sup>7</sup>	this study
<i>Pinus banksiana</i>	Saskatchewan, Canada	168 <sup>3,7</sup> , 286 <sup>3,8</sup>	2763	209 <sup>2,7</sup> , 24 <sup>2,5</sup>	62 <sup>7</sup>	this study
<i>Pinus banksiana</i>	Manitoba, Canada	133 <sup>3,7</sup> , 543 <sup>3,8</sup>	1519	190 <sup>2,7</sup> , 29 <sup>2,5</sup>	66 <sup>7</sup>	this study
<i>Pinus sylvestris</i>	Llonamtsi, Finland	–	–	122	52	Finer 1989
<i>Pinus sylvestris</i>	Llomantsi, Finland	–	–	256	66	Finer 1989
<i>Pinus sylvestris</i>	Tammela, Finland	344 <sup>1</sup>	1244	171 <sup>1,6</sup>	69	Mälkönen 1974
<i>Pinus sylvestris</i>	Jädraås, Sweden	26 <sup>2</sup>	50	183 <sup>2,5</sup>	–	Persson 1983
<i>Pinus sylvestris</i>	Jädraås, Sweden	122 <sup>2</sup>	313	159 <sup>2,5</sup>	–	Persson 1983
<i>Pinus sylvestris</i>	Jädraås, Sweden	–	–	484 <sup>1,6</sup>	75	Linder & Axelsson 1982
Evergreen, average				226	64	
Deciduous						
<i>Betula pubescence</i>	Llomantsi, Finland	–	–	89	53	Finer 1989
<i>Betula papyrifera</i>	Alaska, USA	832 <sup>2</sup>	2090	276 <sup>2,4</sup>	48	Ruess et al. 1996
<i>Populus balsamifera</i>	Alaska, USA	472	960	355	51	Ruess et al. 1996
<i>Populus balsamifera</i>	Alaska, USA	469 <sup>2</sup>	1148	439 <sup>2,4</sup>	68	Ruess et al. 1996
<i>Populus tremuloides</i>	Saskatchewan, Canada	43 <sup>3,7</sup> , 657 <sup>3,8</sup>	2778	58 <sup>2,7</sup> , 73 <sup>2,5</sup>	25 <sup>7</sup>	this study
<i>Populus tremuloides</i>	Manitoba, Canada	66 <sup>3,7</sup> , 644 <sup>3,8</sup>	2663	88 <sup>2,7</sup> , 45 <sup>2,5</sup>	30 <sup>7</sup>	this study
Deciduous, average				218	46	

<sup>1</sup> Root diameter size class < 1 mm.

<sup>2</sup> Root diameter size class < 2 mm.

<sup>3</sup> Root diameter size class < 5 mm.

<sup>4</sup> Fine root NPP estimated by min–max method.

<sup>5</sup> Fine root NPP estimates from ingrowth cores.

<sup>6</sup> Fine root NPP estimated using carbon budget approach from Linder and Axelsson 1982.

<sup>7</sup> Minirhizotron estimate.

<sup>8</sup> Soil core estimate.

(1983) also found that fine root growth began earlier in aspen and birch stands than in black spruce and white spruce stands. The smaller amount of fine root growth of jack pine than black spruce during the spring and summer (Figure 3) was a consequence of the smaller initial fine root length (Table 4). When fine root growth was expressed on a per unit fine root length basis, fine root growth was similar or greater for jack pine than for black spruce (Steele 1996).

Frozen soils prevent water uptake by overwintering fine roots and inhibit the growth of new fine roots, resulting in low water availability in the early spring. The lack of available water is an important constraint on the carbon balance of overstory trees because irradiance and air temperatures are often sufficient for photosynthesis by boreal evergreen conifers in early spring (Frolking et al. 1996). Jarvis et al. (1997) reported higher Bowen ratios (ratio of sensible to latent heat) for the black spruce forest in the SSA in the spring, when the soil was frozen, than in the summer or fall. A large Bowen ratio

indicates a reduction in transpiration and photosynthetic activity of the canopy.

#### *Role of fine root production and turnover in C budgets of boreal forests*

Fine root net primary production and subsequent turnover is a major carbon input to forest soils. The fine root NPP:total detritus production (aboveground litterfall + NPP<sub>FR</sub>) ratio ranged from 0.27 to 0.69 and these values are similar to other boreal forests (Table 6). The fine root NPP:total detritus production ratios were greater for the two conifer species than for the deciduous species at both study areas. A similar pattern was seen when data for other boreal forests were included—fine root NPP comprised 64% of total detritus production in boreal conifer forests versus 46% for boreal deciduous forests (Table 6). These data suggest that the relative contribution of fine root production to total detritus production differs between boreal evergreen and deciduous forests. Vogt et al. (1986)

reported a similar pattern for temperate evergreen and deciduous forests.

Fine root turnover index estimates varied depending on the method used, but in general were smaller for jack pine than for black spruce. Our values are larger than the range of  $0.33 \text{ year}^{-1}$  for birch/aspens to  $1.05 \text{ year}^{-1}$  for black spruce stands in Alaska (Ruess et al. 1996). The influence of climate on fine root longevity is unclear (Eissenstat and Yanai 1996). Hendrick and Pregitzer (1993a) reported that sugar maple (*Acer saccharum* Marsh) fine root lifespan was shorter at a southern site than at a northern site in Michigan because the warmer soil at the southern site caused higher root respiration costs and more rapid fine root mortality than at the northern site. Our study provided mixed support for Hendrick and Pregitzer's theory. Fine root turnover index for jack pine was significantly greater at the SSA than at the NSA, but there was no clear trend for aspen or black spruce fine root turnover index between study areas. A better understanding of the environmental and biological factors that influence fine root mortality is needed given the importance of fine roots in the carbon budget of boreal forests.

North temperate and boreal forests are thought to be the "missing carbon sink" that could explain the imbalance between the global sources and sinks of atmospheric  $\text{CO}_2$  (Cias et al. 1995, Francey et al. 1995, Keeling et al. 1996). Little is known about the process(es) causing carbon to accumulate in these terrestrial ecosystems (Cias et al. 1995). Harden et al. (1997) estimated that the NSA black spruce stand sequestered 40 to  $60 \text{ g C m}^{-2} \text{ year}^{-1}$  over the past 90 years, but they did not identify the process(es) responsible for the net C accumulation in the soil. We speculate that the greater fine root production than turnover and slow decomposition rates of fine roots may account for, in part, the accumulation of carbon in these boreal forest soils. The greatest difference between fine root production and turnover occurs for forests in the NSA (Figure 7) and specifically for the black spruce stand, where Harden et al. (1997) measured high soil C accumulation rates. Unfortunately, they did not measure soil carbon accumulation rates at any of the other stands where we measured root dynamics. Cold soil temperatures and anaerobic conditions in the black spruce stands adversely affect decomposition (Flanagan and Van Cleve 1983) and cause mean residence times of forest floor organic matter to range from tens to hundreds of years (Van Cleve et al. 1983, Gower et al. 1997, Harden et al. 1997, Trumbore et al. 1997). Furthermore, fine roots decompose more slowly than other plant tissues of similar size because of the high concentration of suberin, a lignin-like structural constituent found exclusively in roots, which does not decompose readily (Aber and Melillo 1992). Additional data on fine root production and turnover for boreal forests are needed to determine if the patterns reported in this study are representative for boreal forests and to determine the sensitivity of fine root dynamics to climatic variation.

In summary, fine root production and turnover is a significant component of the carbon cycle of boreal forests. Future studies examining the effects of climate change on soil carbon budgets of boreal forests should consider the effects of altered

soil temperatures on fine root production, turnover and their balance.

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