

# Fine root production varies with climate in balsam fir (*Abies balsamea*)

Jakub Olesinski, Marek J. Krasowski, Michael B. Lavigne, John A. Kershaw, Jr., and Pierre Y. Bernier

**Abstract:** The rising global temperature will likely affect ecological processes but the extent and direction of these responses are uncertain. To reduce this uncertainty, we evaluated the environmental controls over fine root dynamics in balsam fir (*Abies balsamea* (L.) Mill.). Fine root production was measured over 5 years at two balsam fir sites in the southern part of its range and two sites in the northern part using the minirhizotron and soil-coring methods. The objective of the study was to quantify climatic effects on fine root production and on allocation of growth to foliage (NPP<sub>f</sub>) and fine roots (NPP<sub>fr</sub>). Year-end fine root biomass was greater in the south ( $800 \pm 60 \text{ g}\cdot\text{m}^{-2}$ ) than in the north ( $490 \pm 69 \text{ g}\cdot\text{m}^{-2}$ ) ( $p < 0.001$ ). Similarly, NPP<sub>fr</sub> was greater in the south ( $557 \pm 35 \text{ g}\cdot\text{m}^{-2}$ ) than in the north ( $351 \pm 41 \text{ g}\cdot\text{m}^{-2}$ ) ( $p = 0.01$ ). Differences in annual NPP<sub>fr</sub> between north and south arose because summer and autumn NPP<sub>fr</sub> was greater in the south. Fine root production did not vary interannually within regions. Annual fine root growth was correlated with air growing degree-days ( $r^2 = 0.53$ ,  $p = 0.002$ ). The allocation to NPP<sub>f</sub> relative to NPP<sub>fr</sub> did not differ significantly between regions. Our results suggest that NPP<sub>fr</sub> will increase with an increase in mean annual air temperature but that there will be no significant changes in functional equilibrium between foliage and fine roots as global warming progresses.

**Résumé :** L'augmentation de la température globale va probablement avoir un impact sur les processus écologiques mais l'ampleur et la direction de ces réactions sont incertaines. Dans le but de réduire cette incertitude, nous avons évalué les mécanismes environnementaux qui contrôlent la dynamique des racines fines chez le sapin baumier (*Abies balsamea* (L.) Mill.). La production de racines fines a été mesurée pendant 5 ans dans deux sapinières situées dans la partie sud et dans deux autres situées dans la partie nord de l'aire de répartition de l'espèce à l'aide de minirhizotrons et de carottes de sol. L'objectif de cette étude était de quantifier les effets du climat sur la production de racines fines et l'allocation de croissance foliaire (PPN<sub>f</sub>) et racinaire (PPN<sub>fr</sub>). La biomasse de racines fines à la fin de l'année était plus élevée dans le sud ( $800 \pm 60 \text{ g}\cdot\text{m}^{-2}$ ) que dans le nord ( $490 \pm 69 \text{ g}\cdot\text{m}^{-2}$ ) ( $p < 0,001$ ). De la même façon, la PPN<sub>fr</sub> était plus élevée dans le sud ( $557 \pm 35 \text{ g}\cdot\text{m}^{-2}$ ) que dans le nord ( $351 \pm 41 \text{ g}\cdot\text{m}^{-2}$ ) ( $p = 0,01$ ). La différence de PPN<sub>fr</sub> annuelle entre le nord et le sud était due à la plus grande PPN<sub>fr</sub> durant l'été et l'automne dans le sud. La production de racines fines n'a pas varié d'une année à l'autre à l'intérieur des régions. La croissance annuelle des racines fines était corrélée avec les degrés-jours de croissance basés sur la température de l'air ( $r^2 = 0,53$ ,  $p = 0,002$ ). L'allocation à la PPN<sub>f</sub> relativement à la PPN<sub>fr</sub> n'était pas significativement différente d'une région à l'autre. Nos résultats indiquent que la PPN<sub>fr</sub> va augmenter avec l'augmentation de la température annuelle moyenne de l'air mais qu'il n'y aura pas de changements importants dans l'équilibre fonctionnel entre le feuillage et les racines fines à mesure que progressera le réchauffement global.

[Traduit par la Rédaction]

## Introduction

The changing climate will affect carbon cycling (Intergovernmental Panel on Climate Change 2007) but the extent and direction are uncertain for any one site or region (Hyvönen et al. 2007). One cause of this uncertainty is our limited understanding of belowground carbon allocation as illustrated by the wide range in estimates of its contribution to total net primary production (NPP<sub>tot</sub>) of forest ecosystems; estimates range from 10% to 75% (Nadelhoffer and Reich 1992; Vogt

et al. 1996; Satomura et al. 2007). Despite its large contribution to NPP<sub>tot</sub>, our understanding of factors controlling fine root net primary production (NPP<sub>fr</sub>) is much less than of those controlling aboveground NPP. In addition, fine roots have short life spans (Withington et al. 2006), so they make large contributions to detrital carbon pools. Our ability to predict responses of forest ecosystems to global warming will improve with greater understanding of fine root production and turnover.

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Field studies using latitudinal transects and interannual variation have found different relationships between  $NPP_{fr}$  and temperature (Hendrick and Pregitzer 1993; Steele et al. 1997; Pregitzer et al. 2000); however, it is generally concluded, at least in boreal forests (Yuan and Chen 2010), that fine root biomass and annual production increase with mean annual temperature. For example, Steele et al. (1997) found a positive relationship between fine root production and annual temperature for black spruce (*Picea mariana* (Mill.) BSP) in a study that compared study areas near the northern and the southern boundaries of the boreal forest but not for jack pine (*Pinus banksiana* Lamb.) or trembling aspen (*Populus tremuloides* Michx.). Differences in soil moisture or nutrient availability or transect locations relative to the range of studied species may have confounded simple relationships between  $NPP_{fr}$  and temperature in some field studies (Pregitzer et al. 2000). Growth chamber and greenhouse studies in which moisture and nutrients are maintained in plentiful supply have consistently found a positive relationship of  $NPP_{fr}$  with temperature (Tryon and Chapin 1983; McMichael and Burke 1998; Grossnickle 2000); however, it is risky to extrapolate such studies to field conditions. Majdi and Öhrvik (2004) provided convincing evidence of a positive relationship between  $NPP_{fr}$  and temperature using experimentally warmed plots in a Norway spruce (*Picea abies* (L.) Karst.) forest. Therefore, it is most likely that rising temperatures will stimulate greater fine root production but the degree of stimulation may vary geographically and among species.

A better understanding of seasonal variation of fine root production might improve our capacity to explain relationships between annual fine root production and temperature. For example, Majdi and Öhrvik (2004) argued that  $NPP_{fr}$  is greater at warmer sites because the longer growing seasons extend periods of high fine root production in early spring and late autumn. In support of this notion, several studies found greater fine root production in spring and autumn than in summer (Hendrick and Pregitzer 1993, 1996; King et al. 2002; Puhe 2003). Steele et al. (1997) observed greater fine root production in summer at some boreal sites but that does not preclude greater fine root production in spring or autumn accounting for impacts of climate change.

A positive relationship between  $NPP_{fr}$  and temperature might occur because a greater proportion of  $NPP_{tot}$  is partitioned to roots without greater  $NPP_{tot}$  at warmer sites or because  $NPP_{tot}$  is greater at warmer sites without a difference in the proportional allocation to fine roots. The principle of a functional balance between foliage and root biomass (Thornley and Johnson 1990) can be used to address the problem of carbon partitioning. This principle argues that the relative amounts of foliage and fine roots depend on supplies of resources in the environment. Helmisaari et al. (2007) did not find differences in the relative amounts of fine roots and foliage among climatically different sites for Norway spruce or Scots pine (*Pinus sylvestris* L.); however, they did not compare foliage and fine root annual production. Better understanding of effects of temperature on allocation to fine roots will help with predicting impacts of global warming.

We investigated fine root production over 5 years at two northern balsam fir (*Abies balsamea* (L.) Mill.) sites and one southern site and over 4 years at another southern site in eastern Canada. The objectives were (i) to quantify regional

differences and interannual variability in fine root production and to evaluate the roles of climatic variables in explaining these differences, (ii) to compare seasonal distribution of fine root production between the northern and southern areas, and (iii) to determine if the proportion of  $NPP_{tot}$  allocated to foliage and fine roots differs between northern and southern areas. Comparisons of northern and southern areas are used to draw inferences about potential impact of global warming on fine root production.

## Methods

### Study sites

A site in central Quebec (Forêt Montmorency (N-FM)) and one in northwestern New Brunswick (Green River (N-GR)) were chosen as the northern sites (Table 1). The sites were previously described by Bernier et al. (1999) and Lavigne et al. (2003). N-FM is located in the Laurentian Highlands at 700 m elevation on a 20%–30% northeastern slope. The soil is a well-drained humo-ferric podzol with a sandy loam texture and 21% stone content. Balsam fir dominates the stand (91% of basal area). N-GR is located at an elevation of 475 m on a 5% southeastern slope. The soil is a ferro-humic podzol with a silt loam texture in the top 25 cm and a sandy loam texture at greater depths and a stone content of 32%. The stand originated after a clearcut in the 1950s and was precommercially thinned in 1976. Balsam fir dominates the stand (80% of basal area).

Two southern sites are in southcentral New Brunswick (Table 1). The Nashwaak Lake (S-NL) site is located at an elevation of 341 m on a 5% northern slope. The soil is a well-drained humo-ferric podzol with a silty loam texture in the top 18 cm and sandy clay loam at greater depths, a stone content of 31%, and a hardpan at 45–50 cm depth. The stand is dominated by balsam fir (85% of basal area). Grand John (S-GJ) is located in almost flat terrain adjacent to a brook at an elevation of 270 m. The balsam fir stand (90% of basal area) is on a well-drained humo-ferric podzol with silty loam texture in the top 28 cm and silty clay loam at greater depths and 22% stone content.

### Monitoring climate and soil moisture

Climate was monitored at the N-FM, N-GR, and S-NL sites with sensors mounted on towers and attached to data loggers (CR-10; Campbell Scientific, Edmonton, Alberta). We used thermocouples to measure air temperature ( $T_a$ ) at 1.5 m above ground and soil temperatures ( $T_s$ ) at 2, 5, 10, 20, and 30 cm depths at two locations per site.  $T_a$  and  $T_s$  were logged half hourly, 24 h, year round. Annual and growing season means were calculated based on daily averages. Precipitation was measured above the canopy with TE525M tipping bucket rain gauges (Texas Electronics, modified by Campbell Scientific for use with their data loggers). Growing season was defined as a period from 1 May to 31 October. Climate was not monitored at S-GJ, so we estimated air temperature from S-NL data using adiabatic lapse rate (decrease of temperature with increasing altitude at a rate of 0.64 °C·100 m<sup>-1</sup>).  $T_s$  at S-GJ was assumed to be the same as at S-NL because we found that  $T_s$  varied less than  $T_a$  among sites, soil properties at both sites were similar, and sites were only 27 km apart.

**Table 1.** Geographical location, mean annual air temperature, and basic stand characteristics at studied balsam fir (*Abies balsamea*) sites along a climatic transect ranging from southern Quebec to central New Brunswick.

Site	Location	Mean annual air temperature (°C) <sup>a</sup>	Age in 2004 (years)	Mean tree diameter at breast height (cm) <sup>b</sup>	Mean tree height (m)	Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	Number of trees (ha <sup>-1</sup> )
N-FM	47°19'00"N, 71°06'00"W	0.3	74	17	17	45	2100
N-GR	47°44'10"N, 68°09'00"W	2	54	18	16	37	2300
S-NL	46°28'19"N, 67°05'60"W	3.4	39	16	13	43	2800
S-GJ	46°15'19"N, 66°55'52"W	3.4	74	19	19	54	1900

<sup>a</sup>1971–2000 climate normals for the nearest Environment Canada weather station.

<sup>b</sup>Arithmetic mean diameter.

### Minirhizotron observations

The procedures used to collect and process minirhizotron images were described in detail by Olesinski et al. (2011) and they are briefly summarized below. Five acrylic minirhizotron tubes (5.1 cm in diameter) were installed each at N-GR and N-FM in the summer and autumn of 1997, and 10 acrylic tubes were installed each at S-NL and S-GJ sites in the summer of 2003. At N-FM, tubes were inserted at angles to the ground ranging from 53° to 63°, at N-GR from 28° to 45°, and at the southern sites from 45° to 50°. Two minirhizotron tubes at S-NL and one tube at S-GJ had to be excluded from monitoring due to damage by wildlife or frost heaving. Insulation was inserted into tubes from mid-November to mid-May. The maximum vertical depth of observations from the soil surface was 68 cm at N-GR, 107 cm at N-FM, 72 cm at S-NL, and 78 cm at S-GJ.

Collection of minirhizotron images began in spring 1998 at N-FM and N-GR and in spring 2004 at S-NL and S-GJ. Collections were approximately monthly, beginning when sites became accessible in spring (late May – early June) and ending when snow made sites inaccessible in autumn (late October – mid-November). Images (18 mm × 15 mm) were collected with a portable minirhizotron image acquisition system (Bartz Technologies Ltd., Santa Barbara, California). This system consisted of a digital camera that was moved from the lowest to the uppermost position along a tube in 15 mm steps using an indexed handle so that images were taken from the same positions on each date. Only data from 2004–2008 were used in this study except for the S-NL site where only data from 2004–2007 were used because soil moisture was manipulated in 2008 at this site.

We analyzed images with WinRhizotron MF 2005a (Regent Instruments, Quebec, Quebec). Fine roots were defined as those of ≤2 mm in diameter. We recorded dates of appearance and maximum diameter of fine roots intersecting the tubes as explained in Bernier and Robitaille (2004). Dates of birth of roots in minirhizotron images were calculated as midpoints between the observation date of first appearance and the previous observation date. Less than 8% of annual root production occurred between the last observation date in autumn and the first observation date in spring. Because it was impossible to collect images in winter and early spring, it was assumed that these roots began growth in early spring when soil water became available; therefore, all of these roots were assumed to have been produced early in the new growing season.

### Root cores

Five samples of organic and mineral soil layers were collected annually in late October – mid-November after the last monthly minirhizotron measurement at most sites except N-FM where cores were collected in October 2004, September 2005, and August 2006–2008. We used a 10 cm × 10 cm template to collect the organic layer samples at most sites and a stainless steel corer of 8 cm diameter to collect the mineral soil layer sample. At N-FM, a steel corer of 4.7 cm in diameter was used to collect organic and mineral soil samples. Soil cores were processed in the laboratory in the following steps. (1) Roots were separated into “herbaceous” (very thin, translucent, easy to break when bent, and wiry) and “woody” (sturdy, difficult to break when bent, and opaque). (2) Herba-

**Table 2.** Definitions and descriptions of abbreviations of aboveground and belowground dynamics used in this article.

Abbreviation	Description	Units
$A_{fr}$	Sum of year-end fine root cross-sectional areas as seen in minirhizotrons	mm <sup>2</sup>
$A_{fr-cum}$	Cumulative frequency of year-end fine root cross-sectional areas with depth as seen in minirhizotrons	%
$a_p$	Fine root cross-sectional areas of roots that were produced in an observational period	mm <sup>2</sup>
$A_p$	Sum of $a_p$ for a calendar year	mm <sup>2</sup>
$A_{ps}$	Sum of $a_p$ for a season of the year	mm <sup>2</sup>
$B_f$	Foliage biomass estimated using empirical equations	g·m <sup>-2</sup>
$B_{fr}$	Year-end standing crop of fine root biomass (detrended, averaged for a site)	g·m <sup>-2</sup>
$B_{rc}$	Observed year-end fine root biomass in root cores	g·m <sup>-2</sup>
$NPP_f$	Foliage net primary production	g·m <sup>-2</sup>
$NPP_{fr}$	Fine root net primary production	g·m <sup>-2</sup>
$NPP_{sfr}$	Seasonal fine root net primary production	g·m <sup>-2</sup>
$P_c$	Cone production	g·m <sup>-2</sup>
$P_{fi}$	Branch foliage biomass observed for each foliage age class	g
$P^*_{fi}$	Detrended annual branch-level foliage biomass for each foliage age class	g

ceous roots contributed <5% of all fine roots collected in cores and were discarded. (3) Remaining roots of ≤2 mm in diameter, measured at the thicker end, were divided into live and dead categories based on external appearance and an endurance test. Roots that appeared dark, shriveled, or partly decomposed were gently tugged and, if broken easily, were considered dead. (4) All roots were separated from soil by hand without sieving or elutriation, oven dried for 24 h at 60 °C, and weighed. We aimed to collect samples to the depth that included 90% of fine roots found in minirhizotron tubes, but obstructions sometimes prevented sampling to that depth. We explain below how we accounted for variable sampling depths in our site estimates of fine root biomass.

### Estimation of fine root standing crops

#### Standing crops in minirhizotron tubes ( $A_{fr}$ )

We calculated the cross-sectional area of each fine root from its diameter. For each date, we summed cross-sectional areas for roots that first appeared in minirhizotron images ( $a_p$ ) (Table 2). We then used the cross-sectional area of all roots on the last measurement date of each year ( $A_{fr}$ ) in our calculations of standing crops by averaging tube-level data by site.

#### Standing crops in soil cores ( $B_{rc}(90\%)$ )

We adjusted fine root biomass in soil cores that did not reach the depth of 90% of fine roots as seen in minirhizotron tubes in the following steps. First, we calculated the cumulative frequency of living fine roots ( $A_{fr-cum}$ ) with depth ( $D$ ) at the end of the growing season for each site and year. Second, the cumulative frequency was converted to percentage of  $A_{fr}$  and related to depth for each site using the following equation:

$$[1] \quad A_{fr-cum} = \frac{a}{1 + e^{-\left(\frac{D-x_0}{b}\right)}}$$

where  $a$ ,  $b$ , and  $x_0$  are site-specific coefficients estimated by

nonlinear regression using Sigstastat v. 3.5 (Systat Software Inc., San Jose, California).

Finally, for soil cores that did not reach the depth that included 90% of fine roots as seen with minirhizotrons, we estimated root biomass to the 90% depth by reworking eq. 1 and incorporating core-observed fine root biomass as shown below:

$$[2] \quad B_{rc}(90\%) = B_{rc}(D) \frac{0.9}{A_{fr-cum}(D)}$$

where  $B_{rc}$  is fine root biomass in root cores and  $D$  is depth of the core.

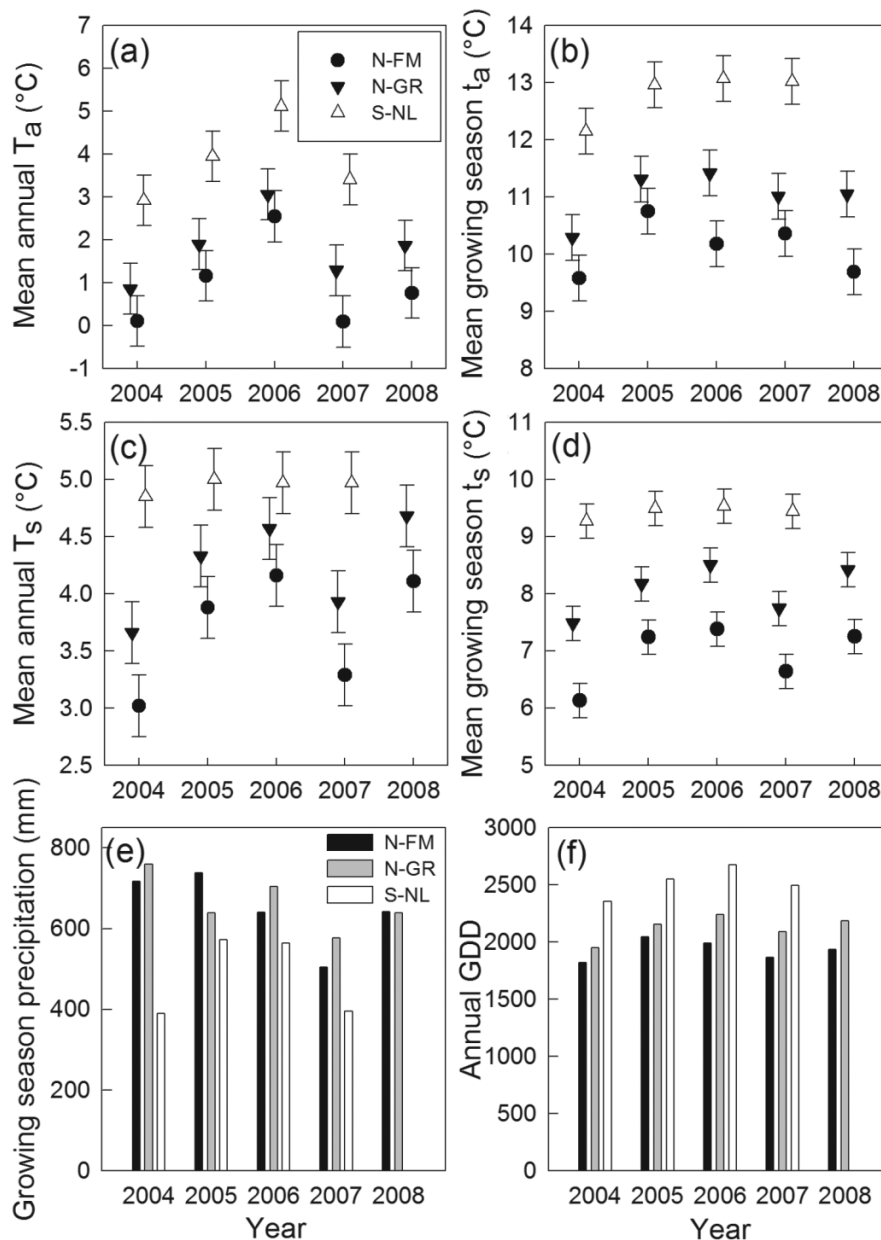
#### Year-end standing crops in biomass ( $B_{fr}$ )

We regressed  $A_{fr}$  and corresponding  $B_{rc}(90\%)$  for all sites and years and used this relationship to estimate standing crop in biomass for each site and year ( $B_{fr}$ ). Because minirhizotron tubes have been in place for less than 2 years in the south, linear trends in  $B_{fr}$  over time were observed (see also Bernier and Robitaille 2004; Krasowski et al. 2010). To eliminate artifacts resulting from differences in timing of tube installation in the north and south, we removed these trends at all sites with following steps: (1) we fitted a quadratic regression equation ( $B_{fr} = b_0 + b_1 \text{Year} + b_2 \text{Year}^2$ ) to north and south separately and then calculated residuals, (2) we fitted a quadratic equation to the root core data for each region as we had done for  $B_{fr}$  ( $B_{rc}(90\%) = b_0 + b_1 \text{Year} + b_2 \text{Year}^2$ ), and (3) we calculated detrended  $B_{fr}$  values by adding residuals from step 1 to the predicted values from step 2, thus preserving interannual variability of the original estimates.

#### Estimation of fine root production

Annual fine root production for the ecosystem ( $NPP_{fr}$ , g·m<sup>-2</sup>·year<sup>-1</sup>) was calculated by site and year in the following manner. The ratios of cross-sectional areas of roots produced annually ( $A_p$ ) to cross-sectional area of year-end standing crops ( $A_{fr}$ ) were calculated and multiplied by the detrended  $B_{fr}$  to estimate the  $NPP_{fr}$ .

**Fig. 1.** (a) Mean annual air temperature at 1.5 m, (b) mean growing season (1 May – 31 October) air temperature at 1.5 m, (c) mean annual soil temperature at 5 cm depth, (d) mean growing season soil temperature at 5 cm depth, (e) growing season precipitation, and (f) sum of annual growing degree-days (GDD) (0 °C threshold) measured at two northern balsam fir (*Abies balsamea*) sites and a southern site in eastern Canada. Error bars denote standard error.



We also estimated seasonal fine root production ( $NPP_{Sfr}$ ,  $g \cdot m^{-2} \cdot season^{-1}$ ) in spring, summer, and autumn. Growth observed in monthly images collected up to late June or early July were assigned to spring. Observations taken up to late August or early September were assigned to summer. The remaining observations were assigned to autumn. We computed ratios of cross-sectional areas of roots produced seasonally ( $A_{ps}$ ) to  $A_p$  and multiplied these ratios by annual  $NPP_{fr}$ .

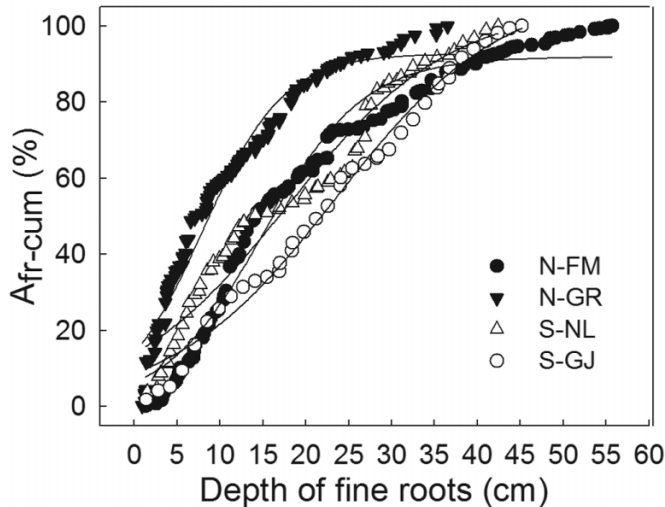
#### Estimation of foliage production

We collected a sample of branches, dissected the branches, and developed equations for estimating  $NPP_f$  for the previous 5 years at each site to compare foliage and fine root production.

#### Estimation of foliage production on sample branches

We collected one branch per tree from eight codominant trees at each of the four sites late in the 2008 growing season. Each branch was collected at a height approximately equal to one-third the depth of the canopy from the top of the tree. In the laboratory, branches were dissected into shoots produced in 2008, 2007, 2006, 2005, 2004, and all older shoots and weighed fresh. A sample of shoots was selected from each shoot age class weighed fresh, oven dried for 48 h at 70 °C, separated into foliage and stems, and reweighed. We used conventional computations for stratified sampling to estimate oven-dried foliar biomass by shoot age class for each branch.

**Fig. 2.** Distribution of fine roots in soil at northern and southern balsam fir (*Abies balsamea*) sites in eastern Canada. Patterns of cumulative frequency of fine roots in soil were used to adjust biomass values obtained from root cores using eq. 1. ( $r^2 = 0.97$ ,  $p < 0.0001$  for N-FM,  $r^2 = 0.96$ ,  $p < 0.0001$  for N-GR,  $r^2 = 0.95$ ,  $p < 0.0001$  for S-NL,  $r^2 = 0.98$ ,  $p < 0.0001$  for S-GJ).



Our method of scaling up branch samples to estimate annual canopy foliage production depends on the assumption that there is no time-related trend in canopy foliar biomass during the study period, an assumption that does not exclude the possibility of interannual variation in canopy foliage biomass. We selected stands in the stem exclusion stage of stand development (Oliver and Larson 1996) because such stands remain at or near the site-dependent carrying capacity for canopy foliage biomass (Satoo and Madgwick 1982) to meet this condition. It follows from this assumption that foliage biomass should be distributed approximately equally among recent shoot age classes on sample branches so that the branches also demonstrate no time-related trend in foliage biomass as is expected of the canopy. This condition for sample branches does not decrease the importance of interannual variation. We selected the canopy position for sampling to meet this condition based on results of earlier studies of branch allocation dynamics with this species (Lavigne et al. 2005; Bernier et al. 2007). Further, we tested whether our branch data met this condition by using regression to test for time trends in annual age class foliar biomass. Linear trends were observed only at the two southern sites. For these sites, we used the slope of the linear relationship to detrend by adjusting estimates prior to and subsequent to 2006 (selected because it was the midpoint of the study period) to values comparable with those predicted for 2006 using the following equation:

$$[3] \quad P^*f_i = Pf_i[1 + b(i - 2006)]$$

where  $P^*f_i$  is the detrended foliar production of year  $i$ ,  $i$  takes on values 2004, 2005, 2007, and 2008, and  $b$  is the slope of the linear trend. For each site, we calculated ratios of annual age class foliage biomass to branch total foliar biomass ( $Rf$ ) using adjusted values for southern sites.

### Estimation of canopy foliage production

Repeated measurements of diameter at breast height in permanent sample plots and measurements of sapwood width obtained from increment cores collected from trees sampled for branches were used to make yearly estimates of sapwood cross-sectional area for each tree in the permanent sample plots. Foliar biomass ( $B_f$ ) for each year at each site was then calculated using the equations of Lavigne et al. (2005) relating sapwood cross-sectional area and foliage biomass. We multiplied  $B_f$  by  $Rf$  to estimate  $NPP_f$  at each site for 2004–2008.

### Estimation of cone production

Thirty litter traps ( $0.12 \text{ m}^2$ ) were installed at S-NL in early spring of 2004. Litter was collected in early spring, mid-summer, and late autumn each year. The litter was sorted into foliage, twigs, and reproductive structures. Using these data, annual production of reproductive structures ( $P_c$ ) was estimated for each year.

### Relating fine root production and biomass allocation to climate

The  $NPP_{fr}$ ,  $NPP_{S_{fr}}$ , and  $NPP_f/NPP_{fr}$  for all sites and years were plotted against mean annual air and soil temperatures and their growing degree-days (GDD) ( $0^\circ \text{C}$  threshold). We used simple linear regression to test for relationships between  $NPP_{fr}$ ,  $NPP_{S_{fr}}$ ,  $NPP_f/NPP_{fr}$ , and climatic variables using SigmaStat v. 3.5 software.

### Experimental design and statistical analysis

In our analyses, we considered N-FM and N-GR as sites nested within the northern region (described as “north”) and S-NL and S-GJ as sites nested within the southern region (described as “south”) and investigated differences between regions. We assessed interannual variation and differences between regions in  $NPP_{fr}$  and  $NPP_f$  using the restricted maximum likelihood method of the mixed procedure in SAS v. 9.1 (SAS Institute Inc., Cary, North Carolina) with the repeated measures option and adjusted for autocorrelation. The minirhizotron tube and the sample branch were considered to be the experimental units. We report the outcomes of analyses of variance by presenting  $F$  values with degrees of freedom in subscript and corresponding probabilities ( $p$  values) of the null hypothesis being true at a significance level of  $\alpha = 0.05$ . The least square means option of the mixed procedure with Bonferroni adjustment was used to distinguish significant differences among means.

Simulated analysis of variance using the Monte Carlo method (Metropolis and Ulam 1949) was performed to assess differences in  $NPP_f/NPP_{fr}$  among sites. Simulated analysis of variance was used because sample branches were not assigned to particular minirhizotron tubes. The Monte Carlo method randomly assigned sampling branches to tubes and the process was repeated 100 times. Simulated  $p$  values were calculated as

$$[4] \quad p = 1 - f$$

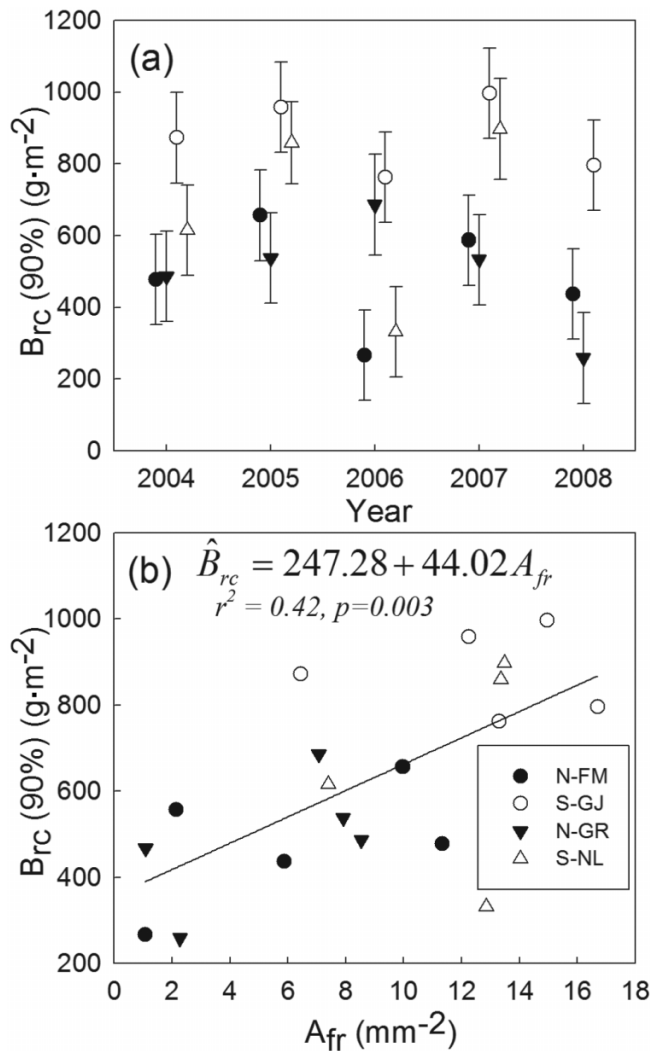
where  $f$  is the frequency of significance.

**Table 3.** Average soil core depth, the depth above which 90% roots were found in minirhizotrons, and the magnitude of adjustment applied to the root cores collected on the last measurement date each year using eq. 2.

Site	Average core depth (cm)	Depth above which 90% of roots were found (cm)	Proportion of samples not reaching the 90% rooting depth
N-FM	48 (30–50)	55	0.01
N-GR	30 (14–50)	37	0.09
S-NL	30 (18–56)	43	0.2
S-GJ	32 (20–47)	46	0.25

**Note:** The range of variation in coring depth is given in parentheses ( $n = 20$ ).

**Fig. 3.** (a) Year-end fine root standing crops ( $B_{rc}(90\%)$ ) obtained from root cores at northern and southern balsam fir (*Abies balsamea*) sites in eastern Canada. Error bars denote standard errors ( $n = 5$ ). (b) Relationship between sum of cross-sectional areas ( $A_{fr}$ ) of fine roots intersecting minirhizotron tube observation areas at the last date of measurements each year and adjusted fine root biomass ( $B_{rc}(90\%)$ ) measured in root cores at corresponding dates.

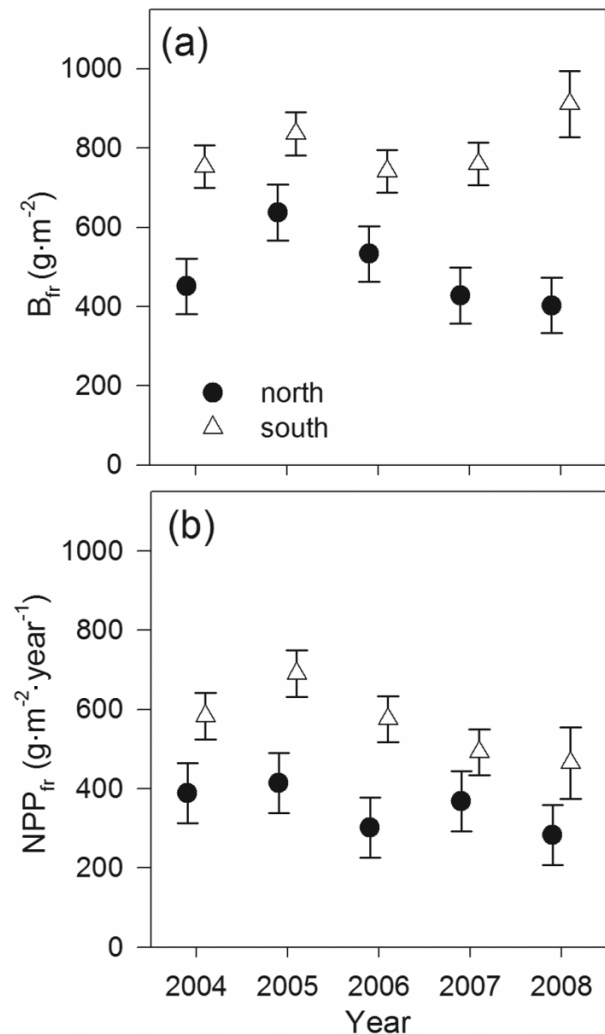


## Results

### Climate

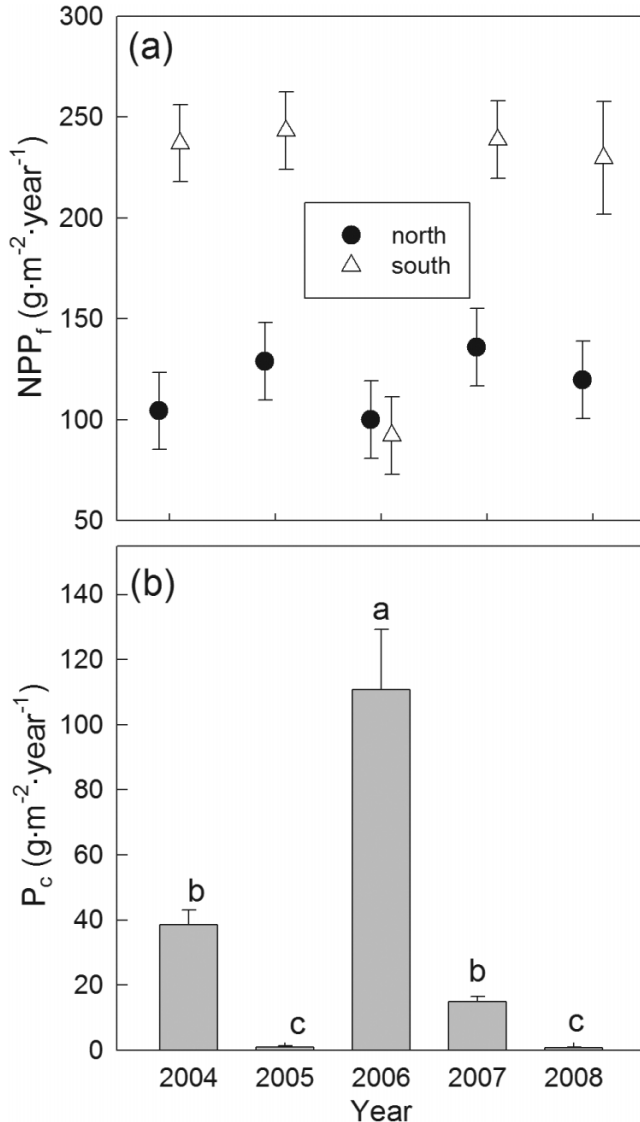
Mean annual air temperature ( $T_a$ ) and mean growing season air temperature ( $t_a$ ) were greatest at S-NL ( $3.82 \pm 0.36$  and  $12.72 \pm 0.18$  °C, respectively) and lowest at N-FM

**Fig. 4.** Interannual variation in (a) year-end fine root standing crops ( $B_{fr}$ ) and (b) fine root production ( $NPP_{fr}$ ) at northern and southern balsam fir (*Abies balsamea*) sites in eastern Canada. Error bars denote standard errors ( $n = 10$  in the north,  $n = 17$  in the south).



( $0.92 \pm 0.45$  and  $10.11 \pm 0.21$  °C, respectively) (Figs. 1a and 1b). Similarly, mean annual soil temperature ( $T_s$ ) and mean growing season soil temperature ( $t_s$ ) were greatest at S-NL ( $5.09 \pm 0.15$  and  $9.59 \pm 0.16$  °C, respectively) and lowest at N-FM ( $3.69 \pm 0.23$  and  $6.93 \pm 0.21$  °C, respectively) (Figs. 1c and 1d). Mean growing season precipitation was greatest at N-GR ( $663.7 \pm 31.1$  mm) and least at S-NL ( $480.5 \pm 50.8$  mm) (Fig. 1e). Mean sum of GDD was greatest at S-NL ( $2519 \pm 67$ ) and least at N-FM ( $1931 \pm 91$ ) (Fig. 1f).

**Fig. 5.** (a) Interannual variation in foliage production ( $NPP_f$ ) in studied balsam fir (*Abies balsamea*) sites along a climatic transect in eastern Canada. Error bars denote standard errors ( $n = 16$ ). (b) Interannual variation in cone production ( $P_c$ ) at the S-NL site located in central New Brunswick. Error bars denote standard errors ( $n = 30$ ). Significant differences among means ( $\alpha = 0.05$ ) are indicated by letters.



#### Distribution of fine roots in the soil

Vertical distributions of fine roots are shown in Fig. 2. The depth for the cumulative frequency of 90% of fine roots was 33 cm at S-NL, 30 cm at N-GR, 45 cm at N-FM, and 37 cm at S-GJ. Fewer than 10% of cores required adjustment in  $B_{rc}$  at N-FM and N-GR, but 20%–25% of cores required adjustment at S-NL and S-GJ (Table 3). Difficulties in reaching the 90% rooting depth at S-NL and S-GJ were due to high stone content at both sites.

#### Relating minirhizotron estimates to biomass

The  $B_{rc}(90\%)$  tended to be higher at southern sites ( $775 \pm 77 g \cdot m^{-2}$ ) than at northern sites ( $489 \pm 74 g \cdot m^{-2}$ ) (Fig. 3a), but this trend was not constant among years (region  $\times$  year

$F_{[4,84]} = 2.82, p = 0.03$ ). The  $B_{rc}(90\%)$  was lower in 2006 than in 2005 and 2007. The relationship between  $A_{fr}$  and  $B_{rc}(90\%)$  (eq. 4) is shown in Fig. 3b. Biomass of fine roots estimated with the relationship shown in Fig. 3b was used to calculate  $B_{fr}$  and consequently detrended  $B_{fr}$  and  $NPP_{fr}$  as described in the Methods:

$$[5] \quad B_{fr} = 247.2807 + 44.0168A_{fr} \quad (r^2 = 0.42, p = 0.003)$$

#### Year-end fine root standing crop and annual fine root production

The  $B_{fr}$  was higher in the south ( $800 \pm 60 g \cdot m^{-2}$ ) than in the north ( $490 \pm 69 g \cdot m^{-2}$ ) ( $F_{[1,91]} = 16.33, p < 0.001$ ), and it varied among years ( $F_{[4,91]} = 3.15, p = 0.02$ ). Regional differences were greater than the differences observed interannually (Fig. 4a). Annual  $NPP_{fr}$  was higher in the south ( $557 \pm 35 g \cdot m^{-2}$ ) than in the north ( $351 \pm 41 g \cdot m^{-2}$ ) ( $F_{[1,91]} = 14.48, p = 0.01$ ), but it did not vary among years ( $F_{[4,91]} = 1.8, p = 0.13$ ) (Fig. 4b).

#### Foliage production and biomass allocation

The  $NPP_f$  was greater in the south than in the north in all years except 2006 (region  $\times$  year interaction  $F_{[4,148]} = 4.52, p = 0.002$ ) (Fig. 5a). We found interannual variation in the south because  $NPP_f$  was lower in 2006 than in other years. In contrast,  $NPP_f$  did not vary among years in the north.

The  $NPP_f/NPP_{fr}$  was 0.37 in the north and 0.36 in the south. These values were not statistically different ( $p = 0.64$ ). Moreover,  $NPP_f/NPP_{fr}$  did not differ significantly among years in the north and south ( $p = 0.84$ ).

#### Cone production

$P_c$  was significantly higher in 2006 than in other years ( $F_{[4,135]} = 42.92, p < 0.001$ ) (Fig. 5b). Cone production tends to be synchronized throughout the range for balsam fir (Bakuzis and Hansen 1965; D. Simpson, personal communication) and was therefore assumed to be high in 2006 at all sites. High cone production contrasted with low  $NPP_f$  at S-NL in 2006. Because of the influence of cone production, we excluded estimates of fine root production and foliage production in 2006 from analyses of climatic effects.

#### Relationships between annual $NPP_{fr}$ , $NPP_f/NPP_{fr}$ , and climate

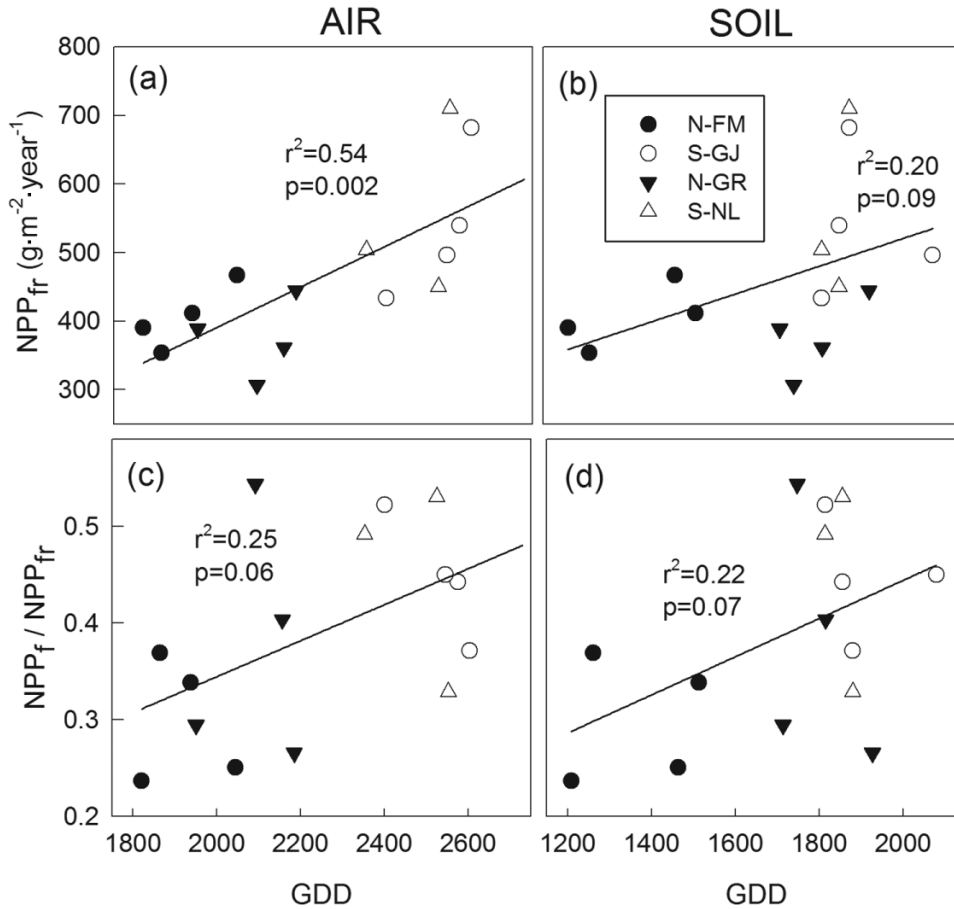
We found a significant positive relationship between annual  $NPP_{fr}$  and air GDD ( $r^2 = 0.53, p = 0.002$ ) (Fig. 6a). In addition,  $NPP_{fr}$  tended to increase with soil GDD ( $r^2 = 0.14, p = 0.17$ ) (Fig. 6b).  $NPP_f/NPP_{fr}$  also tended to increase with increasing air GDD ( $r^2 = 0.18, p = 0.11$ ) (Fig. 6c) and soil GDD ( $r^2 = 0.24, p = 0.06$ ) (Fig. 6d).

#### Seasonal variation in fine root production

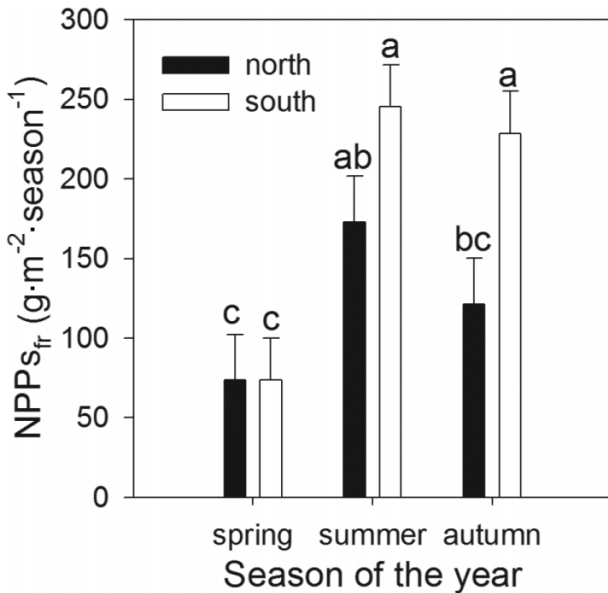
There were significant differences between regions in  $NPP_{fr}$  (region  $\times$  season interaction  $F_{[2,372]} = 4.86, p = 0.01$ ). In both regions,  $NPP_{fr}$  was as great in autumn as in summer, but  $NPP_{fr}$  was greater in the south than in the north in both of these seasons (Fig. 7). Seasonal production was lowest in spring in both regions and, interestingly, spring  $NPP_{fr}$  in the north was similar to that in the south. Thus,



**Fig. 6.** Relationships between mean annual fine root production ( $NPP_{fr}$ ) and (a) air and (b) soil growing degree-days (GDD) and foliage to fine root production ratio ( $NPP_f/NPP_{fr}$ ) and (c) air and (d) soil GDD at two northern and southern balsam fir (*Abies balsamea*) sites in eastern Canada. GDD threshold was 0 °C. Year 2006 was excluded from the analyses.



**Fig. 7.** Seasonal fine root production ( $NPP_{sfr}$ ) at two northern and two southern balsam fir (*Abies balsamea*) sites in eastern Canada. Error bars denote standard errors ( $n = 10$  in the north,  $n = 17$  in the south). Significant differences in means ( $\alpha = 0.05$ ) are indicated by letters.



summer and autumn were responsible for regional differences in annual  $NPP_{fr}$ .

**Discussion**

We found both year-end fine root biomass and annual fine root production to be greater in the south than in the north, which we attributed to differences in air temperature. Transect studies and regional comparisons have been used to investigate climatic effects on NPP and biomass, but most studies focused on aboveground NPP (e.g., Gower et al. 1997; Peng and Apps 1998, 1999). The few transect studies comparing belowground NPP and biomass have not found common trends. Similar to our findings, Steele et al. (1997) found greater fine root NPP in their southern boreal forest study area than their northern study area for black spruce, jack pine, and trembling aspen and suggested that this was due to soils that were warmer for a longer period in the south. Yuan and Chen (2010) found that fine root NPP increased with mean annual air temperature in a review of studies from the boreal biome. In a synthesis of fine root biomass studies for European beech (*Fagus sylvatica* L.), Scots pine, and Norway spruce, Finér et al. (2007) did not find significant differences in fine root biomass between the boreal and temperate zones because of large variation within climatic zones due to stand age and site productivity differen-

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ces. We were able to attribute significant differences between study areas in both fine root biomass and production to temperature because we selected mature stands on mesic sites, thereby minimizing these non-climate-related sources of variation.

To our knowledge, this is the first study finding that differences in summer and autumn fine root NPP between study areas were responsible for climate-related differences in annual fine root NPP and that there were no temperature-related differences in spring NPP between study areas. Our findings suggest that climate is more favorable for fine root production in summer and autumn at the southern sites; however, climate was also more favorable for greater fine root NPP in spring in the south. Therefore, it is not only climatic suitability that is responsible for greater autumn fine root NPP in the south but also the seasonal coordination of growth among tree components. Our finding of the role of autumn fine root NPP contrasts with findings that early spring climatic conditions are responsible for differences in aboveground NPP (Parmesan and Yohe 2003; Monson et al. 2005). This suggests that the seasonality effect on coordination of the allocation of growth to aboveground and belowground components may be affected by the overall climate with more aboveground NPP in spring and more belowground NPP in autumn in a warmer climate compared with a cooler one.

We used annual foliage to fine root production ratios to investigate climatic control over the functional balance in balsam fir. The ratio of NPP is a better measure of the allocation of growth between foliage and fine roots than is the ratio of their biomass because the NPP ratio reflects allocation of growth over a year, whereas the biomass ratio is confounded by differences in longevity between fine roots and foliage. Several studies have reported foliage to fine root biomass ratios (e.g., Vanninen and Mäkelä 1999; Helmisaari et al. 2007), but we are not aware of any other study using foliage to fine root NPP ratios to investigate climatic control over biomass allocation. In a synthesis study, Gower et al. (1994) found that, on the global scale, fine root and foliage production in pine forests was positively correlated with mean annual temperature; however, they did not report relationships between foliage to fine root NPP ratios and temperature. Our results suggest that northern balsam fir ecosystems will increase foliage and fine root production in response to increasing temperatures, and consequently, the functional balance in balsam fir may not change as climate change progresses providing all other climatic variables are held constant.

The impact of cone production in 2006 on annual foliage production was evident in the branch growth data at all sites and in fine root biomass as measured in root cores at most sites but not in our minirhizotron data. In fact, substantial reductions in foliage production during heavy seed years in balsam fir forests have been previously reported (Morris 1951; Bernier et al. 2001). Regardless, inclusion of low production rates in 2006 due to cone production would have confounded relationships with climatic variables, and therefore, we excluded 2006 estimates from our analyses of climatic effects on  $NPP_{fr}$  and  $NPP_f/NPP_{fr}$ .

In conclusion, our results suggest that annual  $NPP_{fr}$  will increase in balsam fir forests in a warming climate. However, increased variability in annual precipitation may cause re-

duced  $NPP_{fr}$  in some years, confounding a simple relationship with temperature. Our previous study (Olesinski et al. 2011) found that  $NPP_{fr}$  was enhanced in the year following a drought, suggesting that occasional drought years may not negate a long-term relationship between  $NPP_{fr}$  and temperature. In addition, the increasing  $NPP_{fr}$  in the northern forest will be accompanied by proportional increases in  $NPP_f$  leading to no significant changes in functional balance between foliage and fine roots as global temperatures continue to rise.

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