Total belowground carbon and nitrogen partitioning of mature black spruce displaying genetic × soil moisture interaction in growth

John E. Major, Kurt H. Johnsen, Debby C. Barsi, and Moira Campbell

Abstract: Total belowground biomass, soil C, and N mass were measured in plots of 32-year-old black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) from four full-sib families studied previously for drought tolerance and differential productivity on a dry and a wet site. Stump root biomass was greater on the wet than on the dry site; however, combined fine and coarse root biomass was greater on the dry than on the wet site, resulting in no site root biomass differences. There were no site differences in root distribution by soil depth. Drought-tolerant families had greater stump root biomass and allocated relatively less to combined coarse and fine roots than drought-intolerant families. Fine roots (<2 mm) made up 10.9% and 50.2% of the belowground C and N biomass. Through 50 cm soil depth, mean total belowground C mass was 187.2 $\mathrm{Mg{\cdot}ha^{-1}}$, of which 8.9%, 3.4%, 0.7%, and 87.0% were from the stump root, combined fine and coarse roots, necromass, and soil, respectively. Here, we show that belowground C sequestration generally mirrors (mostly from stump roots) aboveground growth, and thus, trends in genetic and genetic × environment productivity effects result in similar effects on belowground C sequestration. Thus, tree improvement may well be an important avenue to help stem increases in atmospheric CO_2.

Résumé : La biomasse souterraine totale ainsi que la masse de C et de N dans le sol ont été mesurées dans des places échantillons où croissaient des épinettes noires (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) âgées de 32 ans. Quatre descendances biparentales étudiées précédemment pour leur tolérance à la sécheresse et leurs différences de productivité selon qu'elles croissaient dans une station sèche ou humide étaient représentées. La biomasse des racines de souche était plus importante dans la station humide que dans la station sèche. Cependant, la biomasse combinée des racines fines et des grosses racines était plus grande dans la station sèche que dans la station humide, de telle sorte qu'il n'y avait pas de différence entre les stations dans la biomasse des racines. Il n'y avait pas de différence entre les stations dans la distribution des racines en fonction de la profondeur dans le sol. La biomasse des racines de souche étaient plus importante chez les descendances tolérantes à la sécheresse qui allouaient relativement moins de ressources aux racines fines et aux grosses racines combinées que les descendances intolérantes. Les racines fines (<2 mm) contenaient respectivement 10,9% et 50,2% de la biomasse souterraine de C et de N. Dans les premiers 50 cm de sol, C avait une masse totale moyenne de 187,2 $\mathrm{Mg{\cdot}ha^{-1}}$, dont respectivement 8,9%, 3,4%, 0,7% et 87,0% provenaient des racines de souche, des racines fines et des grosses racines combinées, de la nécromasse et du sol. Dans cet article, nous démontrons que la séquestration du C dans le sol reflète (surtout dans les racines de souche) la croissance aérienne et, par conséquent, que les tendances des effets de nature génétique et génétique × environnement sur la productivité se traduisent par des effets similaires sur la séquestration de C dans le sol. Par conséquent, l'amélioration des arbres pourrait bien être une importante façon de favoriser les augmentations de CO_2 atmosphérique dans la tige.

[Traduit par la Rédaction]

Introduction

Efforts to reduce atmospheric CO_2 are being explored both by reducing emissions and by sequestering more C. Forests are important C sinks because they sequester C both in situ (biomass and soil) and ex situ (products) (Johnsen et al. 2001*b*); these sinks can be manipulated by active forest management. The role of forests in C sequestration and the use and development of process models have highlighted the need for more accurate information for above- and, particularly, belowground parameters for our most dominant and important forest and reforestation species (Johnsen et al. 2001*a*). Because belowground forestry research is difficult, it has often been neglected, and total and component belowground sequestration information is severely lacking for mature trees and particularly mature pedigreed trees. Also, tremendous variation exists in the amount of root biomass and C in the soil (Vogt et al. 1998). In a published review of the C-based model

Received 15 May 2012. Accepted 21 September 2012. Published at www.nrcresearchpress.com/cjfr on 31 October 2012.

J.E. Major and M. Campbell. Natural Resources Canada, Canadian Forest Service-Atlantic Forestry Centre, Fredericton, NB E3B 5P7, Canada.
K.H. Johnsen. USDA Forest Service, Southern Research Station, 3041 Cornwallis Road, Research Triangle Park, NC 27709, USA.
D.C. Barsi. Natural Resources Canada, Canadian Forest Service-Headquarters, 580 Booth Street, Ottawa, ON K1A 0E4, Canada.

Corresponding author: John E. Major (e-mail: jmajor@nrcan.gc.ca).

Can. J. For. Res. **42**: 1939–1952 (2012) doi:10.1139/x2012-145 Published by NRC Research Press

CBM-CFS2, estimates of belowground biomass ranged from 5 to 80 Mg·ha^{-1} (Li et al. 2003) for moderate aboveground softwood biomasses of 130 Mg·ha^{-1} and from 15 to 130 Mg·ha^{-1} for a 260 Mg·ha^{-1} aboveground biomass. Soil coring is the most commonly used method for collecting root biomass data but it generally underestimates root biomass, as stump roots are often only estimated using a single, often generalized allometric equation (Vogt et al. 1998). As such, there is a scarcity of mature-aged belowground biomass data as well as unquantified environmental and genetic variation even for dominant forest tree species.

For stump root estimates, most reports rely on other studies, with different conditions and even different species. Few studies have excavated mature tree roots of northern conifers. Haynes and Gower (1995) uprooted seven red pine (*Pinus resinosa* Ait.) trees, Ostonen et al. (2005) uprooted seven 40-year-old Norway spruce (*Picea abies* (L.) Karst.) trees, and Steele et al. (1997) empirically estimated fine roots of jack pine (*Pinus banksiana* Lamb.) and black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenb.) but had to estimate coarse root biomass using allometric equations from another species. There are published studies on coarse root inventory of balsam fir (*Abies balsamea* (L.) Mill.), but they provided no information on the fine roots or soil properties (Baskerville 1965, 1966; Lavigne and Krasowski 2007). We know of no other complete belowground root and C inventory of Canadian spruce (*Picea* spp.) trees.

Although traditional forest genetics research has clearly shown that tree genotypes can vary greatly in aboveground volume growth, it is not at all certain that these aboveground growth increases will result in overall increases in C sequestration. This is because trade-offs can exist between above- and belowground C sinks. This has been seen with irrigation and fertilization experiments in a review by Litton et al. (2007). Such growth "strategies" can be genetically controlled. Thus, a genetically superior aboveground volume-producing genotype may well divert less C belowground than a slower aboveground volume-producing genotype. Working with 1-year-old seedlings, considerable variation in genetically controlled allocation differences was observed among red spruce (*Picea rubens* Sarg.), black spruce, and hybrid spruce to meet various breeding or sequestration objectives (Major et al. 2003*a*, 2003*b*).

A standard quantitative genetic analysis of an F1, 7 × 7 black spruce diallel planted in 1973 on three sites at the Petawawa Research Forest, Ontario (Morgenstern 1974), indicated important genetic, environment, and genetic × environment interaction effects in aboveground growth characteristics (Boyle 1987; Major and Johnsen 1996). Four families (2 × 2 breeding structure) that exhibited this growth variation between two sites were selected for further examination (Table 1). One female parent (59) produced progeny that displayed relatively high productivity on both sites, whereas the other female parent (63) produced progeny that had high growth rates on one site but not on another, less productive site (Fig. 1). Multiple lines of evidence strongly support that site variation was largely due to differences in soil moisture availability (Johnsen and Major 1995; Major and Johnsen 1996, 2001). In addition, under drying conditions, it was found that drought-tolerant families (progeny of female 59) generated lower osmotic potential, greater turgor, greater photosynthesis, and lower ^{13}C discrimination than drought-intolerant families (progeny of female 63) (Flanagan and Johnsen 1995; Major and Johnsen 1996, 1999; Johnsen et al. 1999). Sampled for ^{13}C:^{12}C across half the diallel, drought tolerance was found to be under strong genetic control, highly heritable (heritability coefficient 0.54, the highest of all traits measured) and demonstrating a strong genetic correlation (−0.97) to growth (Johnsen et al. 1999). Thus, there were important genetic and site components of varying aboveground productivity that we also selected for belowground biosequestration studies. The families being assessed here have well-documented differences in aboveground growth, and mechanisms contributing to this variation are well understood. We directly address the question do drought-tolerant families allocate more resources belowground than drought-intolerant families?

Table 1. Parentage of the four full-sib families (7122, 7125, 7143, and 7146) of black spruce (*Picea mariana*).

Male	Female 59	Female 63
52	7122	7125
62	7143	7146

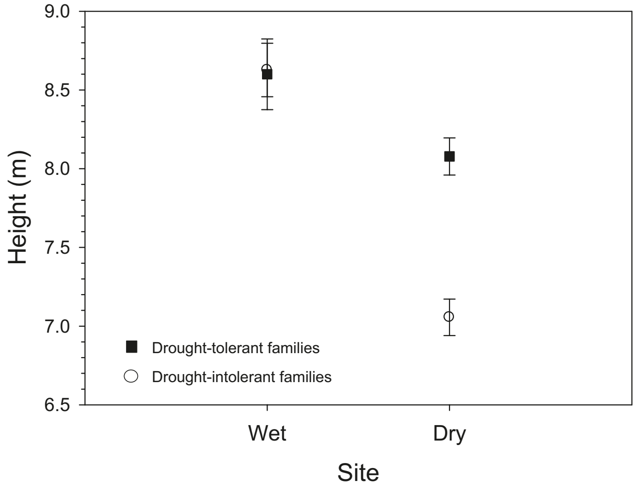


Fig. 1. Height of drought-tolerant and -intolerant black spruce (*Picea mariana*) families (mean and SD) from two sites located at the Petawawa Research Forest, Ontario. Drought-tolerant families are progeny of female 59 (solid symbols) and drought-intolerant families are progeny from female 63 (open symbols). Dry and wet sites refer to sites 2 and 3, respectively.

Our hypothesis was that there would be greater root biomass on the dry site than on the wet site and greater root biomass deeper in the dry site soil profile than in the wet site soil profile. It was also hypothesized that drought-tolerant families would have a larger root system than drought-intolerant families, particularly on the dry site. Full stump root systems were displaced with an air spade, and soil cores were used to quantify soil C, N, and fine and coarse root biomass by soil depth. Our objectives were to (1) quantify the main components of belowground biomass (soil, stump root, fine and coarse roots, necromass, and other buried mass), (2) calculate component and total belowground C and N mass, (3) examine the relative contribution of each component to the total belowground C and N pools, and (4) examine genetic and site variation in root and soil parameters and their possible relationship to aboveground drought tolerance and site productivity differences.

Materials and methods

Plant material and location

A complete 7 × 7 diallel cross black spruce experiment was started at the Petawawa Research Forest (46°N, 77°30′W), Ontario, in 1970 (Morgenstern 1974; Boyle 1987). The seven parental trees used for the diallel cross were from a plantation at the Petawawa Research Forest, but the exact origin of the trees is unknown, except that they were grown from seed collected in the Lake Simcoe–Rideau region in Ontario (Morgenstern 1974). The diallel seeds were germinated 21 March 1971, and seedlings were grown for 2 years in a greenhouse before being planted at three field sites at the Petawawa Research Forest in 1973. At each site, trees from a full-sib family were planted in either nine-tree (site 3) or 16-tree (site 2) square (1.83 m × 1.83 m) spacing. At site 3, there were three replicate blocks, and at site 2, there were four replicate blocks. Family plots were randomized within each block at each site.

As previously reported (Major and Johnsen 1996, 1999, 2001; Johnsen and Major 1999) and discussed above, the primary difference between sites studied was water availability. Site 2 will be referred to as the "dry" site and site 3 as the "wet" site. The two sites are located within 5 km of each other and thus are expected to receive similar rainfall; the dry site has a deep sandy substrate, and the wet site has a hard pan layer about 30–40 cm below the surface that restricts drainage (S. Brown and R. Ponce-Hernandez, unpublished). A subset of four full-sib families that displayed differences in drought tolerance were used and comprised a two female parent × two male parent breeding structure (Table 1). Progeny of female 59 (families 7122 and 7143) are referred as "drought-tolerant" families and progeny of female 63 (families 7125 and 7146) are referred to as "drought-intolerant" families. We note that labels of "wet" and "dry" sites, as well as "tolerant" and "intolerant" families, are relative to this particular study and do not necessarily reflect where these sites, or families, exactly fit along the larger scale environmental and genetic variation spectra within black spruce as a species.

Methodology

The number of trees sampled on the dry site was one tree per plot × four families × four blocks or 16 trees and the number of trees sampled on the wet site was one tree per plot × four families × three blocks or 12 trees for a grand total of 28 trees. Tree No. 1 (corner tree) from each plot was sampled; if it was missing, then the tree in an adjacent corner was used. Trees were cut at the top of the root butt swell, and a 1 m × 1 m frame was placed around the root stump; an air spade (Lavigne and Krasowski 2007) was used to remove the soil from around the stump in this area. Once cleared of soil, the stump and coarse roots were cut along the 1 m × 1 m frame. No tap roots were encountered. We will refer to this component as "stump root" biomass. The stump root biomass was cleaned and dried to a constant mass at 65 °C for 4 days. Stump root wood subsamples were removed for C and N analysis. Fine and coarse roots as well as soil and stones were sampled using 10.16 cm diameter soil cores to a depth of 50 cm by 10 cm increments. Full sampling methodology and design as well as fine and coarse root results are described in Major et al. 2012*a*. Soil was dried, ground, and subsampled for C and N analyses. Roots and belowground wood were then ground, and C and N concentrations were determined for all subsamples and root categories using an elemental analyzer (CNS-2000; LECO Corporation, St. Joseph, Michigan). At the time of sampling, basal area was approximately 36 $m^2 \cdot ha^{-1}$, density was 2900 $trees \cdot ha^{-1}$, live crown length was approximately 50%, and leaf area index was approximately 5.0 (Major et al. 2012*b*).

Calculations

The within-plot soil core subsamples were averaged together after all measurements were taken for analysis. Soil bulk density was estimated as the soil dry mass divided by the soil volume. Soil dry mass is equal to soil sample mass minus rock mass. Volume of soil is equal to volume extracted minus volume of rocks. Concentration and biomass data were used to scale estimates up to the stand level. Soil samples by depth were scaled up by using the soil mass (grams) per unit area from the 10.16 cm round core (or 81.072 cm^2), and thus, to arrive at megagrams per hectare, soil core mass (grams) was multiplied by 1.2335. The trees were planted at 1.83 m × 1.83 m. Thus, to arrive at stump root mass megagrams per hectare, stump root biomass (grams) was multiplied by 0.0029893.

Statistical analysis

The ANOVA model for testing overall mass traits includes the following effects: site (S), soil depth (D), female (F), and male (M), all considered fixed. The ANOVA model used is as follows:

$$\begin{aligned} Y_{ijklm} = \mu &+ \mathrm{S}_i + \mathrm{D}_j + \mathrm{F}_k + \mathrm{M}_l + \mathrm{SD}_{ij} + \mathrm{SF}_{ik} \\ &+ \mathrm{SM}_{il} + \mathrm{DF}_{jk} + \mathrm{DM}_{jl} + \mathrm{FM}_{kl} + \mathrm{SDF}_{ijk} \\ &+ \mathrm{SFM}_{ijl} + \mathrm{DFM}_{jkl} + \mathrm{SDFM}_{ijkl} + e_{ijklm} \end{aligned}$$

The ANOVA model for stump root traits includes the following effects: site (S), female (F), and male (M), all considered fixed. The ANOVA model used is as follows:

$$\begin{aligned} Y_{ijkl} = \mu &+ \mathrm{S}_i + \mathrm{F}_j + \mathrm{M}_k + \mathrm{SF}_{ij} + \mathrm{SM}_{ik} \\ &+ \mathrm{FM}_{jk} + \mathrm{SFM}_{ijk} + e_{ijkl} \end{aligned}$$

Effects were considered statistically significant at the $\alpha = 0.10$ level, although individual *p* values are provided so that readers can make their own interpretations. The general linear model from Systat (Chicago, Illinois) was used for analysis. Full description of the ANOVA model is included in the supplementary section of the online version.[1]

Results

Here, we present the significant and biologically meaningful effects in these sometimes complicated analyses, which include genetic (progeny of female, progeny of male), site, and soil depth effects as well as their interactions. A complete presentation of the four main effects and their interactions of the two ANOVA models and the additional quantification

---

[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/x2012-145.

documentation are available in the supplementary section of the online version.

Soil properties

Soil C concentration had a nonsignificant site effect (p = 0.185) but significant soil depth ($p < 0.001$) and site × soil depth interaction (p = 0.004) effects (Table 2). In the top depth (0–10 cm), the dry site had 18.8% C and the wet site had 11.1% C (Fig. 2*a*). In the lower depths, soil C was substantially lower (<5%) for both sites, and the wet site had greater or equal soil C concentration, thus the significant site × soil depth interaction.

Soil N concentration had a nonsignificant site effect (p = 0.296) but had significant soil depth ($p < 0.001$) and female × male (family) (p = 0.066) effects (Table 2; Fig. 2*b*). The female × male (family) effect was the result of drought-tolerant families showing no differences with both males but drought-intolerant families expressing large differences, depending on the male parent.

Soil C:N ratio showed significant site (p = 0.005), soil depth ($p < 0.001$), and site × soil depth interaction ($p <$ 0.001) effects (Table 2). Overall, the dry site had a lower C:N ratio than the wet site, with 23.7 and 28.8, respectively. The site × soil depth interaction was a result of rank changes with depth. At the 0–10 cm soil depth, the dry site had greater soil C:N ratio than the wet site, whereas at the lower depths, the wet site had greater C:N ratios than the dry site (Fig. 2*c*).

Soil bulk density had significant site ($p < 0.001$), soil depth ($p < 0.001$), male (p = 0.010), site × soil depth (p = 0.051), site × female (p = 0.023), and site × male interaction (p = 0.028) effects (Table 2). Overall, the dry site had greater soil bulk density than the wet site with an average of 1.12 and 1.00 g·cm^{-3} (Fig. 2*d*). The site × soil depth effect is a magnitude effect, as there were no rank changes. The female × site effect was a result of rank change between sites.

Soil C and N mass

Soil C mass had significant soil depth ($p < 0.001$) and site × soil depth interaction ($p < 0.001$) effects (Table 2). Although not statistically significant, the dry site had greater soil C mass than the wet site, with 167.5 and 158 Mg C·ha^{-1}, respectively (Fig. 3*a*). The site × soil depth interaction was due to site rank change along soil depth. At 0–10 cm soil depth, the dry site had substantially greater C mass than the wet site. At the 10–20 cm soil depth, site C mass was similar. At the lower three soil depths, the wet site had greater soil C mass than the dry site.

Soil N mass had significant site (p = 0.001) and soil depth ($p < 0.001$) effects (Table 2). The dry site had greater soil N mass than the wet site, with 7.05 and 5.65 Mg·ha^{-1}, respectively (Fig. 3*b*). Dry site soil N mass was consistently greater than wet site soil N mass at each soil depth.

Stump root biomass

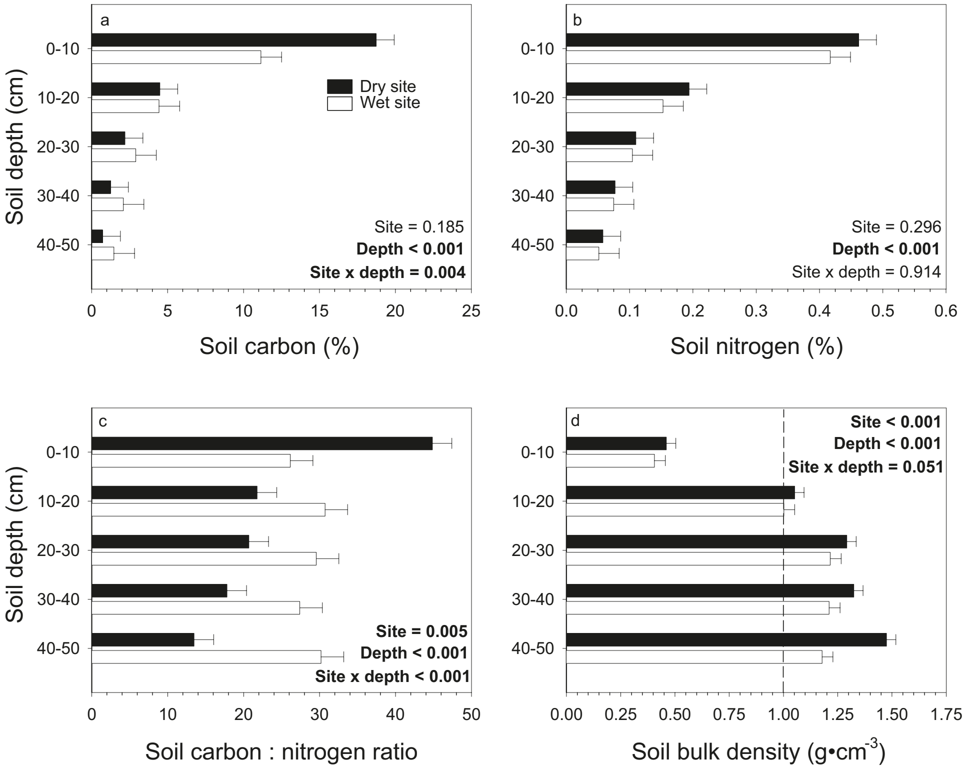
Stump root biomass showed a significant female effect (p = 0.026) (Table 3). The overall stump root biomass for the drought-tolerant and -intolerant families was 33.9 and 26.8 Mg·ha^{-1}, respectively (Fig. 4*a*). Although site was not statistically significant (p = 0.152), for the record, the overall stump root biomass for the dry and wet sites was 28.2 and 32.6 Mg·ha^{-1}, respectively.

Table 2. Soil property ANOVAs, including source of variation, degrees of freedom (df), mean square values (MS), p values, and coefficient of determination (R^2).

Source of variation	df	C (%) MS	C (%) p	N (%) MS	N (%) p	C:N ratio MS	C:N ratio p	Soil bulk density (g·cm^{-1}) MS	Soil bulk density (g·cm^{-1}) p	Soil C mass (Mg·ha^{-1}) MS	Soil C mass (Mg·ha^{-1}) p	Soil N mass (Mg·ha^{-1}) MS	Soil N mass (Mg·ha^{-1}) p
Site (S)	1	39.423	0.185	0.014	0.296	884.661	**0.005**	0.481	**<0.001**	117.480	0.347	2.727	**0.001**
Depth (D)	4	900.585	**<0.001**	0.676	**<0.001**	819.111	**<0.001**	3.735	**<0.001**	7393.494	**<0.001**	5.271	**<0.001**
Female (F)	1	1.020	0.830	0.003	0.653	6.255	0.809	0.001	0.825	40.692	0.579	0.022	0.747
Male (M)	1	1.293	0.809	0.032	0.117	2.794	0.872	0.204	**0.010**	46.444	0.554	0.193	0.341
S×D	4	92.046	**0.004**	0.003	0.914	1286.565	**<0.001**	0.073	**0.051**	1592.907	**<0.001**	0.154	0.573
S×F	1	2.493	0.738	0.000	0.903	0.469	0.947	0.157	**0.023**	60.922	0.498	0.001	0.934
S×M	1	0.260	0.914	0.004	0.555	75.793	0.401	0.147	**0.028**	18.585	0.708	0.131	0.433
D×F	4	2.387	0.979	0.007	0.704	90.513	0.497	0.009	0.882	21.998	0.955	0.292	0.244
D×M	4	2.987	0.969	0.009	0.566	129.284	0.309	0.013	0.778	171.000	0.276	0.058	0.893
F×M	1	3.801	0.679	0.043	**0.066**	193.451	0.181	0.000	0.981	33.243	0.616	0.122	0.448
S×D×F	4	0.374	0.999	0.010	0.517	11.369	0.980	0.039	0.265	54.873	0.796	0.155	0.569
S×D×M	4	2.549	0.977	0.001	0.990	56.318	0.715	0.023	0.546	24.195	0.946	0.106	0.734
S×F×M	1	0.075	0.954	0.002	0.673	17.254	0.688	0.045	0.219	1.188	0.924	0.298	0.238
D×F×M	4	7.853	0.840	0.040	**0.016**	63.599	0.665	0.023	0.541	9.951	0.989	0.131	0.650
S×D×F×M	4	0.148	1.000	0.000	0.998	120.940	0.344	0.009	0.872	60.449	0.765	0.054	0.905
Error	100	22.091		0.013		106.442		0.030		131.606		0.211	
R^2			0.671		0.716		0.547		0.854		0.761		0.581

Note: p values <0.10 are in bold print.

Fig. 2. Vertical distribution of (*a*) soil C concentration, (*b*) soil N concentration, (*c*) soil C:N ratio, and (*d*) soil bulk density for the dry and wet sites (note: p values <0.10 are in bold print).



Stump root C concentration showed a significant but small difference between sites ($p = 0.086$) (Table 3). The dry site had 55.2% and the wet site had 56.1% C (Fig. 4*b*). There were no significant sources of variation for stump root N concentration (Fig. 4*c*), but note that the overall mean stump root N concentration was extremely low at 0.063% N. There were no significant sources of variation for stump root C:N ratio (Table 3; not shown), but note that overall mean stump root C:N ratio was extremely high at 980.

Stump root C mass showed significant site ($p = 0.086$) and female ($p = 0.027$) effects (Table 3). The dry site had lower stump root C mass than the wet site, with 15.2 and 18.2 Mg·ha^{-1}, respectively (Fig. 4*d*). Drought-tolerant families had greater stump root C mass than drought-intolerant families, with 18.6 and 14.8 Mg·ha^{-1}, respectively. Stump root N mass did not show any significant sources of variation (Table 3). The overall mean value was 19.7 kg·ha^{-1} (not shown).

Total root biomass

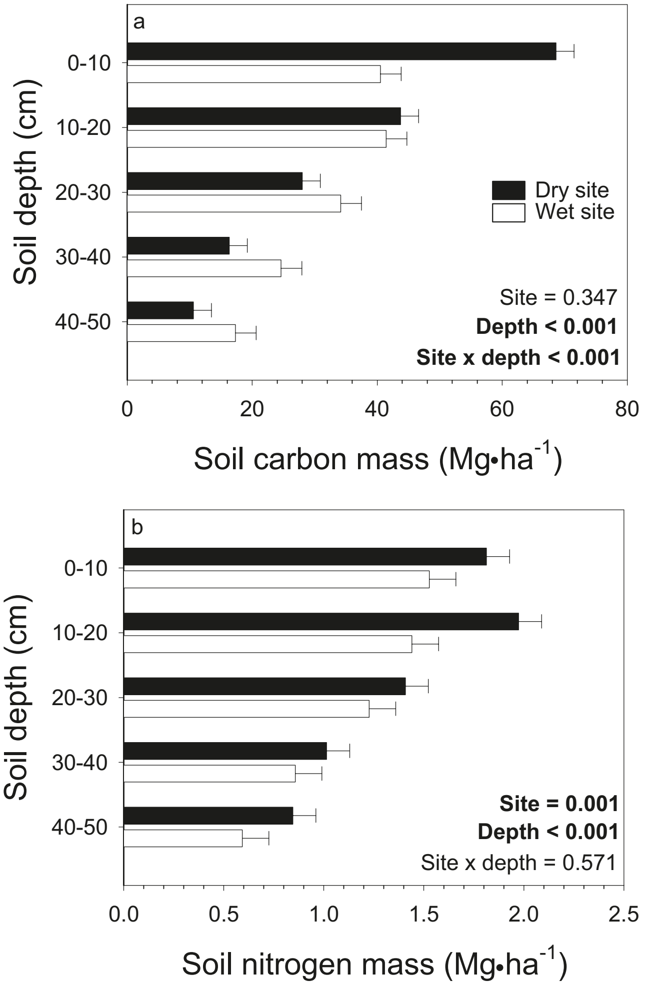
Total root biomass had significant soil depth ($p < 0.001$), female ($p = 0.013$), depth × female ($p = 0.026$), and depth × female × male ($p = 0.076$) effects (Table 4). Overall site effect was not significant ($p = 0.972$); however, it should be noted that the two main components — total combined fine and coarse roots ($p = 0.091$) and stump root ($p = 0.152$) — were significant and near significant, but site rank was reversed (Fig. 5*a*), and thus, effects were compensatory. Parallel results were observed with total root C mass (Table 4). Overall, total stump root biomass and total combined fine and coarse root biomass were 30.4 and 12.4 Mg·ha^{-1}, respectively.

Drought-tolerant families had greater total root biomass than drought-intolerant families, with 46.0 and 38.9 Mg·ha^{-1}, respectively (Table 4; Fig. 6*a*). Note that the component stump root biomass had a significant female effect ($p = 0.026$) (Table 3), with drought-tolerant families greater than drought-intolerant families. The other component, combined fine and coarse roots, did not have a female effect ($p = 0.756$), and the mean was 12.4 Mg·ha^{-1} (Fig. 6*a*). The female × depth effect had some rank changes, but there were also magnitude effects: drought-tolerant families had greater root biomass than drought-intolerant families for the top two depths, but it was similar for the bottom three depths, with some minor rank changes. Total root C mass had the same significant effects and responses as total root biomass.

Total root N mass had significant soil depth ($p < 0.001$), female ($p = 0.094$), male ($p = 0.006$), site × male ($p = 0.009$), depth × male ($p = 0.006$), and site × depth × male ($p = 0.001$) effects (Table 4). Total root N mass was not significant for site ($p = 0.613$). However, unlike total root biomass and C mass, the components were not significant for site (Fig. 5*b*). Average total root N mass was 63.0 kg·ha^{-1}.

The total root N mass female effect was due to drought-tolerant families having greater stump root N mass than drought-intolerant families, with 66.8 and 59.4 kg·ha^{-1}, respectively (Fig. 6*b*). Note that the total combined fine and coarse roots was not significantly different for females ($p = 0.626$). The overall proportions of stump root N mass and combined fine and coarse N mass were 19.71 and 43.38 kg·ha^{-1} (31.2% and 68.8%), respectively.

Fig. 3. Vertical distribution of (*a*) soil C mass and (*b*) soil N mass for the dry and wet sites (note: *p* values <0.10 are in bold print).



Total root biomass allocation by root category and depth

Total root biomass allocation by root category and soil depth is shown in Fig. 7*a*. The average root biomass was 31.5, 9.4, 0.6, 0.3, and 0.9 Mg·ha^{-1} for soil depths 0–10, 10–20, 20–30, 30–40, and 40–50 cm, respectively, for a total of 42.7 Mg·ha^{-1}. Total root biomass allocation by root size was 3.71, 0.95, 1.80, 5.82, and 30.35 Mg·ha^{-1} for root sizes <1, 1–2, 2–5, and >5 mm and stump root (or 8.7%, 2.2%, 4.2%, 13.6%, and 71.2%), respectively (Fig. 7*a*, inset).

Total root N mass allocation by root category and soil depth is shown in Fig. 7*b*. For soil depth, the average root N mass was 46.5, 11.4, 2.6, 1.1, and 1.4 kg·ha^{-1} for soil depths 0–10, 10–20, 20–30, 30–40, and 40–50 cm, respectively, for a total of 63.0 kg·ha^{-1} (Fig. 5*b*). Total root N mass allocation by root size was 28.19, 3.39, 4.07, 7.63, and 31.3 kg·ha^{-1} for root sizes <1, 1–2, 2–5, and >5 mm and stump root (or 44.8%, 5.4%, 6.5%, 12.1%, and 31.3%), respectively (Fig. 7*b*, inset).

Total belowground C and N mass allocation

Total belowground C mass displayed a nonsignificant site effect ($p = 0.494$) but significant soil depth ($p < 0.001$) and site × soil depth ($p < 0.001$) effects (Table 4). The site × soil depth effect was due to rank change with depth. In the top layer (0–10 cm), the dry site had greater C mass than the wet site, with 86.0 and 58.5 Mg·ha^{-1}, respectively (Fig. 8*a*). At 10–20 cm, the sites had similar values at approximately 48 Mg·ha^{-1}. The remaining depths had declining values, but the wet site had greater values than the dry site. Across both sites and all depths, average total belowground organic C mass was 187.2 Mg·ha^{-1} and was partitioned as follows: 16.7, 6.4, 1.4, and 162.7 Mg C·ha^{-1} (or 8.9%, 3.4%, 0.7%, and 87.0%) for the stump root, fine and coarse roots, necromass, and soil mass, respectively (Fig. 8*b*).

The total belowground N mass showed only significant site ($p < 0.001$) and soil depth ($p < 0.001$) effects (Table 4). The dry site had greater total N mass than the wet site, with 7135 and 5724 kg·ha^{-1}, respectively (Fig. 8*c*). Across both sites and all depths, average total belowground N mass of 6430 kg·ha^{-1} was partitioned as follows: 19.7, 43.4, 14.6, and 6352 kg·ha^{-1} (or 0.31%, 0.67%, 0.23%, and 98.76%) for the stump root, fine and coarse roots, necromass, and soil mass (Fig. 8*d*), respectively.

Discussion

Soil mass

Direct soil C content comparisons with other studies can be difficult due to different depths of organic matter and mineral soil, species mix, age, fire, and management history, among other factors. The averaged total soil C mass of our study was approximately 163 Mg·ha^{-1}. In much older (110–155 years) black spruce stands in the province of Saskatchewan, Canada, there was approximately 400 Mg·ha^{-1} soil C mass, which was far greater than in the 84-year-old aspen (*Populus* sp.) and 88-year-old jack pine stands from the same study area, which had 36 and 21 Mg·ha^{-1}, respectively (Gower et al. 1997; Howard et al. 2004; Kalyn and van Rees 2006). However, it should be noted the black spruce stands selected by Gower et al. (1997) were restricted to black spruce–feathermoss stands, which had 20–50 cm of peat layer over mineral soil. The high C concentrations and depth of peat inflate the C content of those soils (Smith et al. 2000). In a recent study of a three-age black spruce chronosequence in Newfoundland with different aboveground disturbances, the soil C mass was more comparable (Moroni et al. 2010). The authors found that belowground soil C pools averaged 150 Mg C·ha^{-1} (45 cm soil depth) with little or no effects of stand age or aboveground disturbance. Soil C mass for a subboreal spruce in central British Columbia was also comparable, with 135, 133, and 109 Mg·ha^{-1} for hygric, (wet) subhygric, and mesic sites (well drained) sites (0–47 cm depth), respectively (Bois et al. 2009).

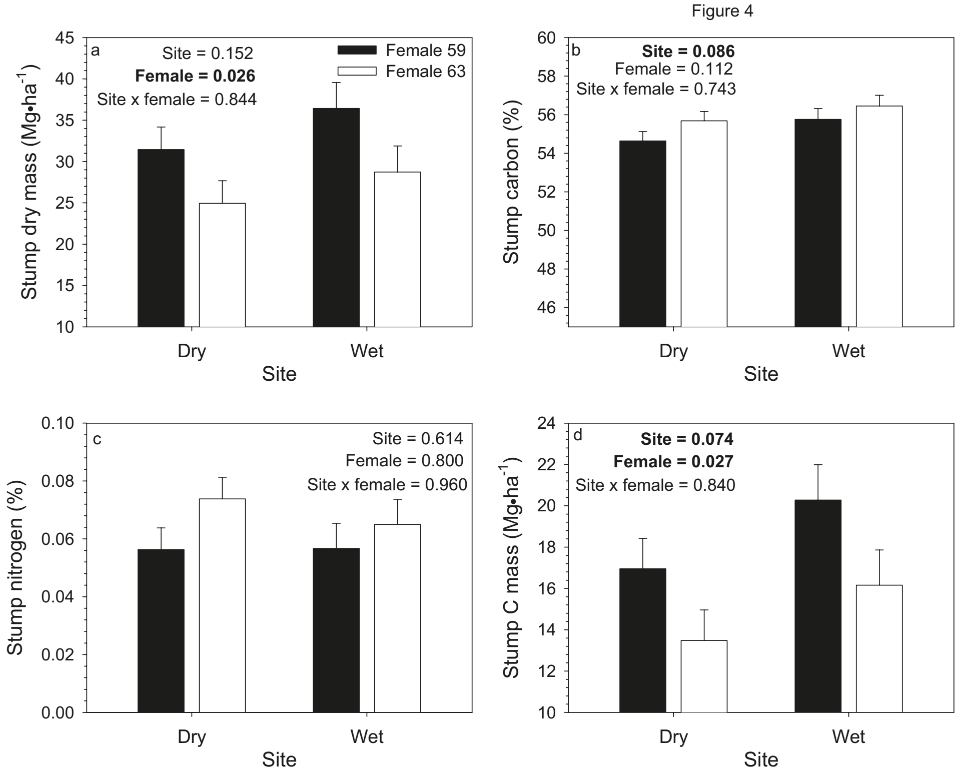
For the top layer (0–10 cm), our dry and wet sites had soil C concentrations of 18.8% and 11.1%, respectively; this was due in part to the depth of organic matter horizon (OM). Our mean OM depth was 7.9 and 5.8 cm for the dry and wet sites, respectively, which partly explains the variation in C concentration between the sites. Needle biomass, and presumably the input of needle litter into the soil, was higher on the wet versus dry site, particularly for the drought-tolerant families (Major et al. 2012*b*). Fine root turnover has been found to be greater or equal on dry sites compared with wet sites (Santantonio and Hermann 1985; Chen et al. 2002). In our study, fine root mass (<2 mm) was greater on the dry than on the wet site (Major et al. 2012*a*), and if root turnover is greater or equal, inputs from these roots would result in greater OM inputs into the 0–10 cm

Table 3. Black spruce (*Picea mariana*) stump property ANOVAs, including source of variation, degrees of freedom (df), mean square values (MS), p values, and coefficient of determination (R^2).

Source of variation	df	Stump dry mass (Mg·ha^{-1})		Stump C (%)		Stump N (%)		C:N ratio		Stump C mass (Mg·ha^{-1})		Stump N mass (kg·ha^{-1})	
		MS	p	MS	p	MS×10^{-4}	p	MS	p	MS	p	MS	p
Site (S)	1	132.191	0.152	6.091	**0.086**	1.19	0.614	82 825	0.420	61.984	**0.074**	39.462	0.541
Female (F)	1	345.036	**0.026**	5.150	0.112	0.30	0.800	44 869	0.551	98.873	**0.027**	180.183	0.198
Male (M)	1	0.015	0.988	1.016	0.470	11.44	0.128	42 041	0.563	1.950	0.742	109.088	0.313
S×F	1	2.379	0.844	0.0.206	0.744	0.01	0.960	19 435	0.694	0.726	0.840	3.889	0.847
S×M	1	89.171	0.235	5.131	0.113	1.44	0.579	30 186	0.624	14.277	0.376	10.300	0.754
F×M	1	99.809	0.210	0.713	0.544	0.00	1.000	2 036	0.899	29.861	0.205	16.641	0.690
S×F×M	1	24.667	0.527	3.629	0.179	1.71	0.545	154 043	0.274	11.179	0.433	0.278	0.959
Error	20	59.565		1.873		4.53		121 976		17.424		101.758	
R^2			0.374		0.378		0.163		0.139		0.391		0.146

Note: p values <0.10 are in bold print.

Fig. 4. Black spruce (*Picea mariana*) stump root (*a*) biomass, (*b*) C concentration, (*c*) N concentration, and (*d*) C mass by female and site (note: p values <0.10 are in bold print).



layers on the dry site. Needle litter is more recalcitrant than fine root biomass. Therefore, the conditions on the dry site appear to have, on balance, increased the input of more recalcitrant biomass and (or) reduced the oxidization of the OM, via frequent desiccation, allowing it to build up to a higher level. A study of black spruce in peat bogs in eastern Quebec, which had distinguished just two layers, organic and mineral, and these averaged 38% and 2.0% C concentration, respectively (Smith et al. 2000). Even given differences in OM depth between our sites, the OM on our sites had substantially lower C concentrations than peat.

Mean soil N concentration ranged from 0.45% in the top layer to 0.2% in the 10–20 cm layer and <0.1% in the remaining depths, and these N levels parallel where OM is higher and where most of the fine roots are found (Major et al. 2012*a*). In the study of peat bog black spruce that distinguished only two layers, organic and mineral averaged 1.0% and 0.07% N, respectively (Smith et al. 2000). As with C content, peat has a higher N concentration than mineral soil. In a study of 37-year-old boreal black spruce in Manitoba, the soil N concentration was 0.20%, 0.14%, and 0.04% for A, B, and C horizons, respectively (Bond-Lamberty et al. 2006).

Table 4. Black spruce (*Picea mariana*) total live root and below ANOVAs, including source of variation, degrees of freedom (df), mean square values (MS), p values, and coefficient of determination (R^2).

		Total live root mass (Mg·ha^{-1})		Total live root C mass (Mg·ha^{-1})		Total live root N mass (kg·ha^{-1})		Total below C mass (Mg·ha^{-1})		Total below N mass (Mg·ha^{-1})	
Source of variation	df	MS	p	MS	p	MS	p	MS	p	MS	p
Site (S)	1	0.012	0.972	0.654	0.615	5.809	0.613	105.841	0.379	2.728	**<0.001**
Depth (D)	4	4719.440	**<0.001**	1393.965	**<0.001**	9777.192	**<0.001**	14878.846	**<0.001**	5.628	**<0.001**
Female (F)	1	61.360	**0.013**	18.592	**0.008**	64.592	**0.094**	118.716	0.352	0.025	0.730
Male (M)	1	0.437	0.831	0.398	0.695	175.674	**0.006**	37.200	0.601	0.204	0.327
S×D	4	0.726	0.989	1.059	0.799	8.295	0.831	1519.361	**<0.001**	0.152	0.579
S×F	1	0.841	0.768	0.076	0.863	31.614	0.239	56.236	0.521	0.002	0.921
S×M	1	4.940	0.475	0.878	0.560	161.341	**0.009**	13.032	0.757	0.138	0.419
D×F	4	27.837	**0.026**	8.611	**0.013**	33.209	0.216	42.642	0.868	0.298	0.233
D×M	4	3.215	0.854	0.625	0.913	85.703	**0.006**	183.887	0.255	0.060	0.885
F×M	1	19.537	0.157	4.948	0.168	43.784	0.166	16.558	0.728	0.111	0.469
S×D×F	4	2.243	0.919	0.470	0.947	36.610	0.174	54.232	0.808	0.160	0.554
S×D×M	4	5.753	0.664	1.256	0.743	112.968	**0.001**	20.140	0.963	0.112	0.711
S×F×M	1	21.798	0.135	6.361	0.119	0.010	0.983	16.657	0.727	0.296	0.238
D×F×M	4	21.031	**0.076**	5.313	**0.091**	4.886	0.928	8.392	0.993	0.132	0.645
S×D×F×M	4	17.441	0.132	5.120	0.102	16.129	0.583	92.241	0.608	0.055	0.901
Error	100	9.588		2.566		22.516		135.753		0.210	
R^2			0.958		0.961		0.953		0.845		0.594

Note: p values <0.10 are in bold print.

Wet site soil C:N ratio averaged 30:1, with similar values across the depths on the wet site and on the dry site starting at 45:1 on the top and declining in value with depth to about 15:1 in the bottom layer. Again, recurring desiccation of the upper soil layers of the dry site may be reducing OM oxidation. Lower in the soil profile, the wet site may retain C due to a hardpan layer, which was found on the wet site and is the physical reason why more water is retained on the wet site (S. Brown and R. Ponce-Hernandez, unpublished); clay is often associated with a hardpan layer, and clay particles can act to stabilize organic matter (Six et al. 2002). In a black spruce bog site without an alder (*Alnus* sp.) understorey, the C:N ratio was 54:1 in the top layer and 27:1 at the 20–30 cm depth (their lowest; Bhatti et al. 1998).

Soil N mass from our study was approximately 6.3 Mg ha^{-1}, at the mid- to higher end of estimates for comparable sites in the literature. Soil mass for two 10 cm horizons in eastern Quebec black spruce plots averaged 1.4 and 1.0 Mg·ha^{-1} for the organic and mineral soils, respectively (Smith et al. 2000). In a study of N dynamics of boreal black spruce in a seven-age, 3- to 151-year-old chronosequence in Manitoba, soil N content ranged from 3.2 to 5.2 Mg·ha^{-1} for the mineral soil and was an average of 0.6 Mg·ha^{-1} for the forest floor, and each was unaffected by stand age (Bond-Lamberty et al. 2006).

Total root biomass and partitioning

Our total root biomass was on average 42.5 Mg·ha^{-1}, 30.2 Mg·ha^{-1} from stump root and 12.4 Mg·ha^{-1} from fine and coarse roots. In a 40-year-old Norway spruce study, the total scaled mean root biomass (derived from a harvest of seven trees) was 48.3 Mg·ha^{-1} (Ostonen et al. 2005), the stump root making up 26.2 Mg·ha^{-1} or 54.4% of the total root biomass. In contrast, in highly productive 10-year-old loblolly pine (*Pinus taeda* L.) forests (in Georgia; Samuelson et al. 2008), total root biomass was estimated at 50 Mg·ha^{-1}.

Most of the roots in our study were found in the 0–20 cm depth. This was expected for the wet site, but on the dry site, with its sandy soil, it was suspected that that a tap root might form. These results on these two distinct sites planted with the same full-sib families provide strong evidence that black spruce has a strong, genetically (species) determined shallow root system. Total root biomass and C mass showed no differences between sites; however, there were underlying offsetting site differences that combined to produce these results. The dry site had lower stump root biomass than the wet site but also had greater fine and coarse root biomass than the wet site, resulting in no difference overall between sites.

In a review of forest types, it was estimated that fine root (<2 mm) C mass accounts for about 10%–20% of the total amount of tree root C mass (Jackson et al. 1997; Brunner and Godbold 2007). Comeau and Kimmins (1989), examining fine root (<5 mm) biomass across moisture conditions, found that it accounted for between 8% and 19% of belowground biomass. Depending on the definition, <2 or <5 mm, fine roots in our study accounted for either 10.9% or 15.1% (4.66 or 6.46 Mg·ha^{-1}) of total root biomass, respectively. On average, for the two black spruce stands in Manitoba and Saskatchewan, fine roots <2 and <5 mm averaged 4.7% and 28.0%, respectively, of the total belowground biomass (Steele et al. 1997). It should be noted that their >5 mm coarse root estimates were calculated using an allometric equation derived from subalpine balsam fir (*Abies lasiocarpa* (Hook.) Nutt.) (Foster 1985).

Total belowground sequestration and allocation

In a general review, it was estimated that roots can account for between 4% and 20% of the C mass in forest soils (Brunner

Fig. 5. Vertical distribution of black spruce (*Picea mariana*) (*a*) total root biomass by site and (*b*) total root N mass by site. Note that the solid and open parts of the bar graphs represent the stump root and fine and coarse root biomass, respectively (note: *p* values <0.10 are in bold print).

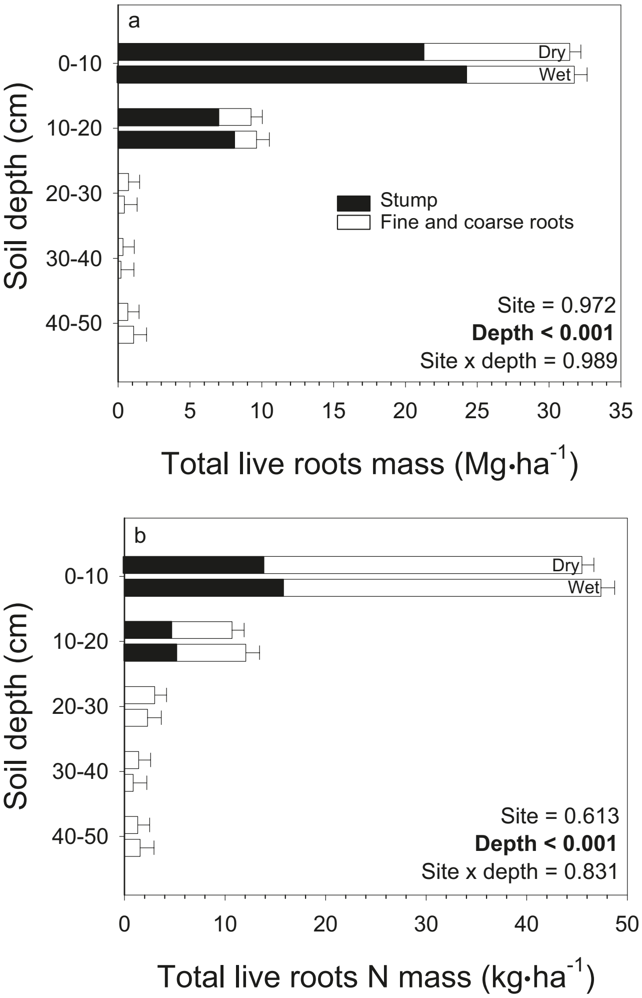
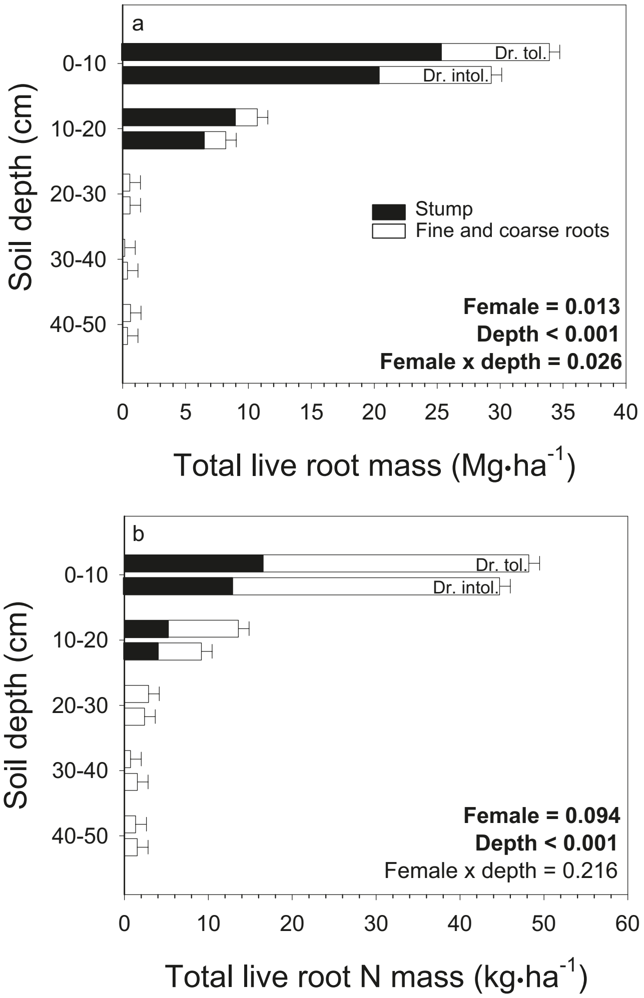


Fig. 6. Vertical distribution of black spruce (*Picea mariana*) (*a*) total root biomass by female and (*b*) total root N mass by female. Note that the solid and open parts of the bar graphs represent the stump root and fine and coarse root biomass, respectively (note: *p* values <0.10 are in bold print).



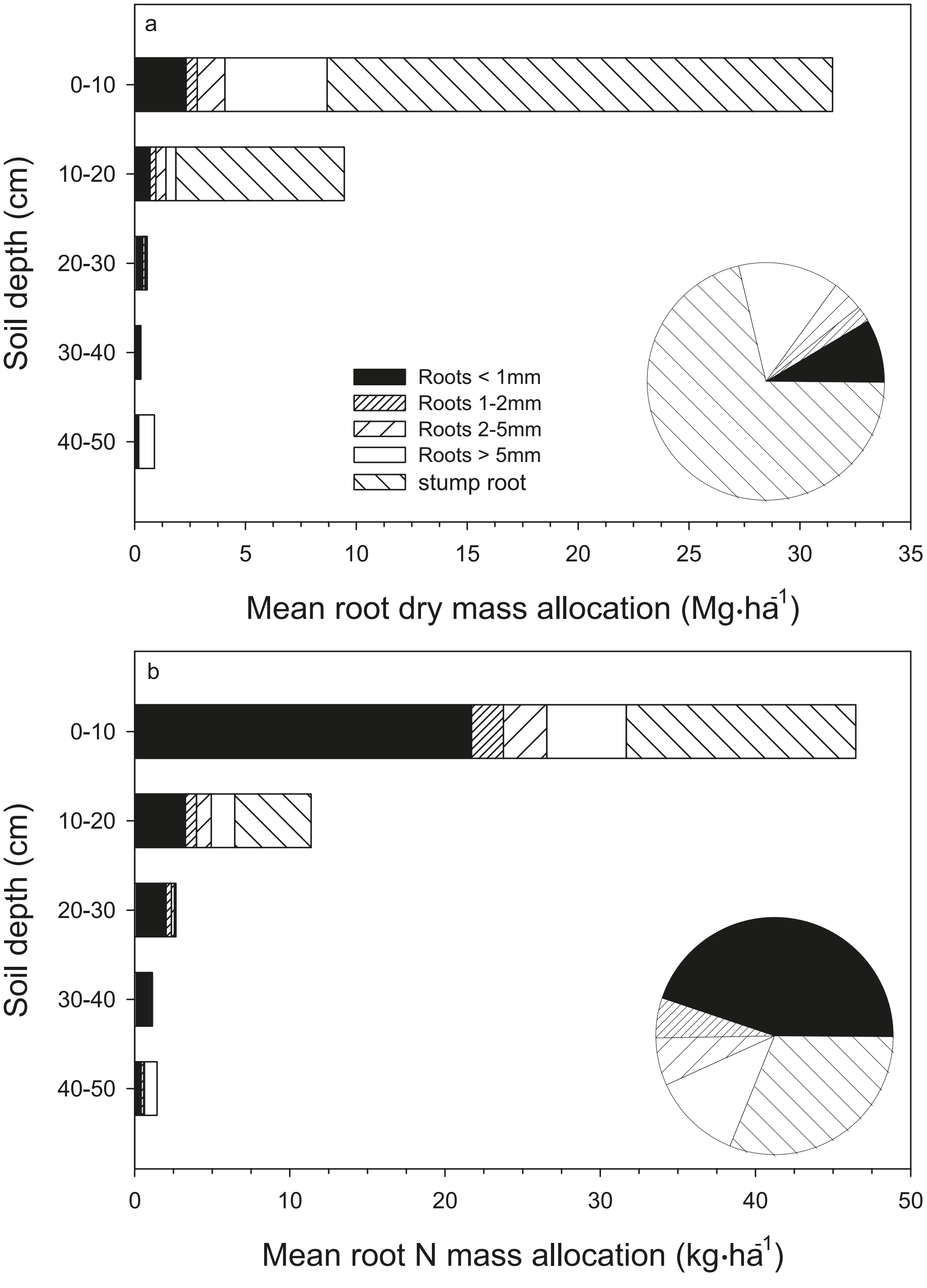
and Godbold 2007). Our total belowground C mass was, on average, 187.2 Mg·ha^{-1}, of which 12.3% was contained in root biomass. In an intensive study of 23-year-old amabilis fir (*Abies amabilis* Douglas ex J. Forbes), total belowground C mass was 167.7 Mg·ha^{-1} (Grier et al. 1981). Our stump root and combined fine and coarse root C mass was 16.7 and 6.4 Mg·ha^{-1}, respectively, which is comparable to the amabilis fir stand, which had 7.8 and 4.6 Mg C·ha^{-1} for coarse (>5 mm) and fine (<5 mm) roots, respectively (Grier et al. 1981). Although their study is one of the more encompassing ones, they did rely on a published allometric equation to estimate coarse root biomass. Also, their stand was younger, smaller, had a higher density, and was a naturally regenerated stand. Their mineral and organic matter soil C mass was 155.3 Mg·ha^{-1} (91.5%) (Grier et al. 1981), comparable to our study.

Our total belowground N mass was, on average, 6.43 Mg·ha^{-1}, of which 6.35 Mg·ha^{-1} or 98.8% was from the soil N mass. In a 140-year-old Norway spruce mixed forest, Finér et al. (2003), coring only 20 cm into the mineral soil, found 0.094, 0.045, and 2.26 N Mg·ha^{-1} (3.9%, 1.8%, and 94.2%) for stump root, fine and coarse roots, and soil pools, respectively. In a study of N dynamics of boreal black spruce in a chronosequence (seven stands, 3–151 years old) in Manitoba, the soil N content varied (3.23–5.18 Mg·ha^{-1}), and this did not vary significantly with age (Bond-Lamberty et al. 2006). Their soil and fine roots were on average 4.8 and 0.05 Mg·ha^{-1}, respectively. Their soil represented approximately 99% of the belowground N, which is virtually the same as our estimate, but the above study did not include stump root; our stump root contributed 0.31% of the total belowground N mass.

Site effects

Total root biomass (stump root, fine and coarse roots) did not display a site difference, but their two main components had significant site and compensatory differences. Stump root biomass was 28.2 and 32.6 Mg·ha^{-1} for the dry and wet sites, respectively, but the combined fine and coarse root biomass was 14.2 and 10.6 Mg·ha^{-1}, respectively, resulting in a near equal root biomass mean of 42.8 Mg·ha^{-1}. Thus, the dry site

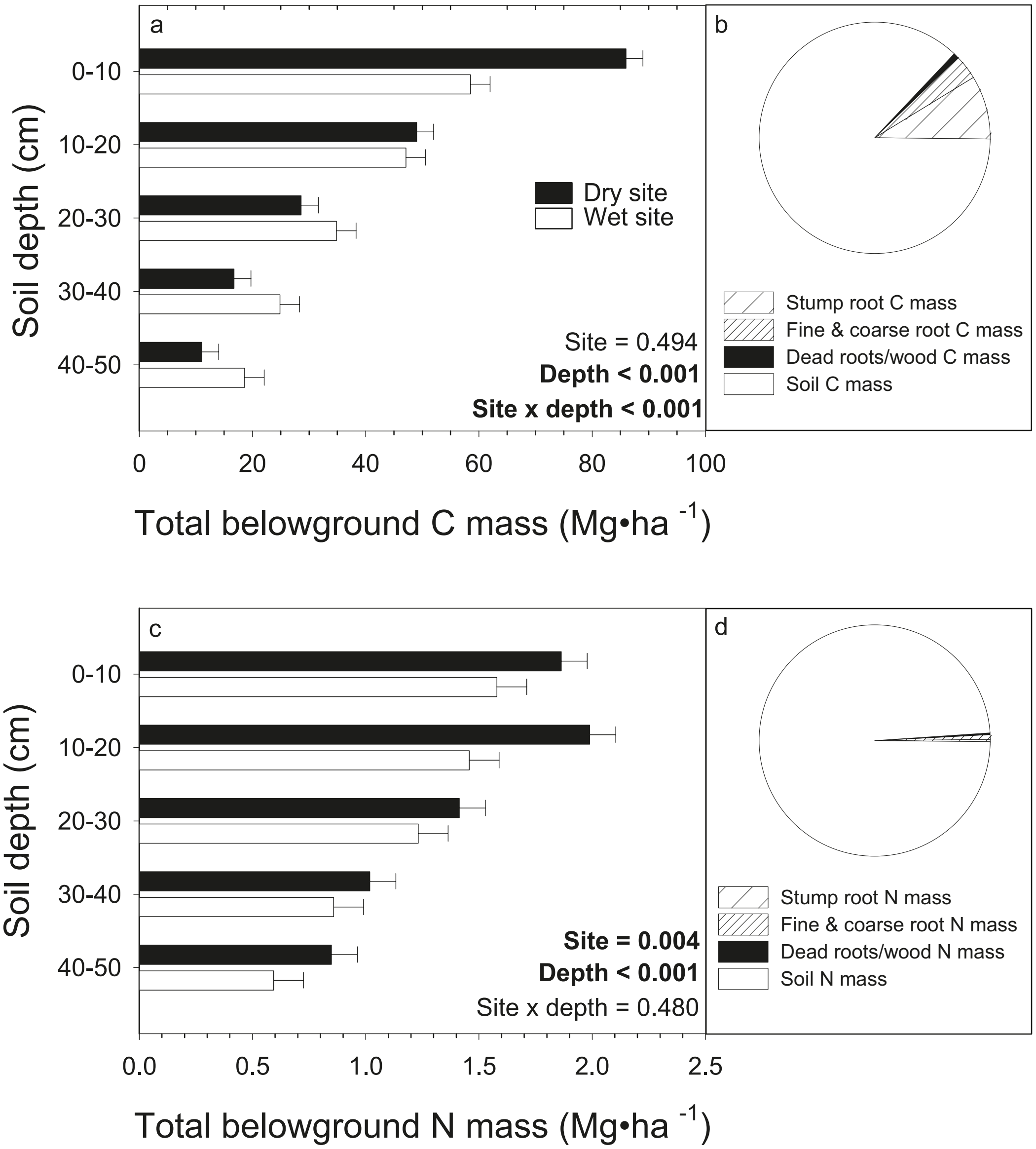
Fig. 7. (*a*) Vertical distribution of black spruce (*Picea mariana*) root biomass by root size class; inset, proportion by root size class. (*b*) Vertical distribution of root N mass by root size class; inset, proportion of root N mass by root size class.



had 66.5% and 33.5% allocated to stump root and combined fine and coarse roots, respectively, whereas the wet site had 75.4% and 24.6% partitioned to stump root and combined fine and coarse roots, respectively.

Comeau and Kimmins (1989), working with approximately 70- to 80-year-old lodgepole pine (*Pinus contorta* Douglas ex Loudon), found that there were more fine roots (<5 mm) in dry than in wet sites in both absolute and percentage values of biomass, consistent with what we found. Similarly, they also found that the coarse roots (>5 mm) including stump were greater on the wet than on the dry site. On their dry sites, the roots <5 and >5 mm including stumps averaged 6.4 and 26.9 Mg·ha^{-1}, respectively, which represent 19.2% and 80.8% belowground root biomass. On their wet sites, however, the roots <5 and >5 mm including stumps averaged 5.1 and 61.2 Mg·ha^{-1}, which represent 7.7% and

Fig. 8. (*a*) Vertical distribution of black spruce (*Picea mariana*) total belowground C mass by site, (*b*) proportion of C mass by belowground class, (*c*) vertical distribution of total belowground N mass by site, and (*d*) proportion of N mass by belowground class (note: *p* values <0.10 are in bold print).



92.3% of belowground root biomass. What is also interesting in the comparison is that Comeau and Kimmins (1989) found that over half (55%) of the total net primary production for the dry site goes to fine and coarse roots (<5 mm) but that only 35% of wet site net primary production goes to fine and coarse roots (<5 mm).

Fine roots, however, appear to be more responsive to environmental factors than coarse roots. In a review of C allocation with varied belowground resource availability, there was a decrease in belowground C partitioning with increased fertilization and irrigation, (Litton et al. 2007) across three genera (*Eucalyptus* spp., radiata pine (*Pinus radiata* D. Don), and loblolly pine). Most of the C reallocation went to stem wood, but some went to foliage, depending on species and other factors. On average, 60% less was partitioned to fine roots, and there was a 21.5% increase to wood and 11.2% to foliage (Litton et al. 2007). For loblolly pine, fertilization and water decreased C partitioning belowground by 77% but increased partitioning by 28% to wood and 29% to foliage (Maier et al. 2004). Albaugh et al. (1998), studying 11-year-old loblolly pine, found that fertilization lowered fine root (<2 mm) mass absolutely and relatively with approximately 6% or 0.8 Mg·ha^{-1} fine roots compared with nonfertilized plots, which had 15.1% or 1.0 Mg·ha^{-1}.

Genetic effects

Total root biomass (stump root, coarse and fine roots) did show a female effect, mostly due to stump root biomasses of 33.9 and 26.8 Mg·ha^{-1} for the drought-tolerant and -intolerant families, respectively. The coarse and fine root biomass values were almost identical, with 12.06 and 12.08 Mg·ha^{-1} for drought-tolerant and -intolerant families, respectively, resulting in a total root biomass of 46.0 and 38.9 Mg·ha^{-1}, respectively. This produced a partitioning difference of 26.3% and 31.1% for fine and coarse roots for drought-tolerant and -intolerant families, respectively. We hypothesized that there might be a female difference in fine and coarse roots, but in absolute terms, there were no female differences, and in relative terms, the tolerant families had fewer fine and coarse roots than intolerant families. In a seedling study, provenances of black spruce from the very far north (Yukon) grew slower but allocated more biomass to roots than southern Ontario populations (Johnsen and Seiler 1996). In one of the few genetic quantifications of biomass variation in partitioning of field-grown trees, Oleksyn et al. (1999), using a 12-year-old Scots pine (*Pinus sylvestris* L.) provenance test, found regional differences among northern, central, and southern populations in a common-garden plot in central Poland. Trees from all three regions allocated similar amounts to fine roots ($<$2 mm), approximately 2.3 Mg·ha^{-1}. However, allocation to roots $>$2 mm was 5.4, 9.1, and 2.9 Mg·ha^{-1} for northern, central, and southern populations, respectively. Total root biomass accounted for 22%, 19%, and 28% of total stand biomass for northern, central, and southern populations, respectively. Thus, the largest trees, the central population (grown on a centrally located site), have partitioned less to fine roots, suggesting that, in agreement with our study, genotypes can produce faster growth by allocating less biomass to fine roots, at least under some environmental conditions.

In most cases, there is much more genetic variation within a population than among populations (Morgenstern 1996). From this diallel, the genetic variation was very large, and these four families fall within the upper fifth percentile for productivity and drought tolerance (Johnsen et al. 1999).Tree improvement has been shown to increase aboveground growth and C sequestration. However, it is plausible that aboveground growth could come at the expense of belowground growth, and thus, genetically improved trees may provide little or no benefit with respect to C sequestration. Here, we show that belowground C sequestration generally mirrors (mostly from stump roots) aboveground growth, and thus, trends in genetic and genetic × environment productivity effects result in similar effects on belowground C sequestration. It appears that, both environmentally (site) and genetically, stump root variation reflects variation in aboveground growth; basically, these roots are extensions of the stem. Genetic variation in stump root biomass will also impact multirotation C sequestration to some degree because the stump roots will most likely persist as necromass in the following rotation, which has been quantified in tap roots of temperate loblolly pine (Ludovici et al. 2002; Maier et al. 2012), an impact that will likely persist longer in northern climates with short growing seasons and frozen soils. Note that we found only minor amounts of necromass, but it was common for the stumps to be removed from the site before establishing such a genetic experiment.

Belowground forestry research is difficult, often neglected, and time consuming, and consequently, total component empirical belowground sequestration information is severely lacking, particularly for mature trees. The benefits of using a genetic study on multiple sites is that the biological variation can be more accurately partitioned, and thus, environmental effects as well as genetic and genetic × environmental effects can be more accurately ascertained. Here, we show that belowground C sequestration generally mirrors (mostly from stump roots) aboveground growth, and thus, trends in genetic and genetic × environment productivity effects result in similar effects on belowground C sequestration. Thus, tree improvement may well be an important avenue to help stem increases in atmospheric CO$_2$.

Acknowledgments

We gratefully acknowledge useful comments received from Jakub Olesinski and Martin Moroni and two anonymous reviewers. In addition, the technical skills of Pete Anderson, Lance Kress, Stephanie West, Soren Johnsen, and Jenny Johnsen are thankfully acknowledged.

References

Albaugh, T.J., Allen, H.L., Dougherty, P.M., Kress, L.W., and King, J.S. 1998. Leaf area and above- and belowground growth responses of loblolly pine to nutrient and water additions. For. Sci. **44**: 317–328.

Baskerville, G.L. 1965. Estimation of dry weight of tree components and total standing crop in conifer stands. Ecology, **46**(6): 867–869. doi:10.2307/1934021.

Baskerville, G.L. 1966. Dry-matter production in immature balsam fir stands: roots, lesser vegetation, and total stand. For. Sci. **12**: 49–53.

Bhatti, J.S., Foster, N.W., and Hazlett, P.W. 1998. Fine root biomass and nutrient content in a black spruce peat soil with and without alder. Can. J. Soil Sci. **78**(1): 163–169. doi:10.4141/S96-097.

Bois, C.H., Janzen, D.T., Sanborn, P.T., and Fredeen, A.L. 2009. Contrasting total carbon stocks between ecological site series in a subboreal spruce research forest in central British Columbia. Can. J. For. Res. **39**(5): 897–907. doi:10.1139/X09-018.

Bond-Lamberty, B., Gower, S.T., Wang, C., Cyr, P., and Veldhuis, H. 2006. Nitrogen dynamics of a boreal black spruce wildfire chronosequence. Biogeochemistry, **81**(1): 1–16. doi:10.1007/s10533-006-9025-7.

Boyle, T.J.B. 1987. A diallel cross in black spruce. Genome, **29**(1): 180–186. doi:10.1139/g87-031.

Brunner, I., and Godbold, D.L. 2007. Tree roots in a changing world. J. For. Res. **12**(2): 78–82. doi:10.1007/s10310-006-0261-4.

Chen, H., Harmon, M.E., Sexton, J., and Fasth, B. 2002. Fine-root decomposition and N dynamics in coniferous forests of the Pacific Northwest, USA. Can. J. For. Res. **32**(2): 320–331. doi:10.1139/x01-202.

Comeau, P.G., and Kimmins, J.P. 1989. Above- and below-ground biomass and production of lodgepole pine on sites with differing soil moisture regimes. Can. J. For. Res. **19**(4): 447–454. doi:10.1139/x89-070.

Finér, L., Mannerkoski, H., Piirainen, S., and Starr, M. 2003. Carbon and nitrogen pools in an old-growth, Norway spruce mixed forest in eastern Finland and changes associated with clear-cutting. For. Ecol. Manage. **174**(1–3): 51–63. doi:10.1016/S0378-1127(02)00019-1.

Flanagan, L.B., and Johnsen, K.H. 1995. Genetic variation in carbon isotope discrimination and its relationship to growth under field conditions in full-sib families of *Picea mariana*. Can. J. For. Res. **25**(1): 39–47. doi:10.1139/x95-005.

Foster, J.R. 1985. Coarse root biomass in subalpine balsam fir forest. For. Sci. **31**: 952–956.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., and Stow, T.K. 1997. Carbon distribution and aboveground net primary production in aspen, jack pine and black spruce stands in Saskatchewan and Manitoba, Canada. J. Geophys. Res. **102**(D24): 29029–29041.

Grier, C.C., Vogt, K.A., Keyes, M.R., and Edmonds, R.L. 1981. Biomass distribution and above- and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. Can. J. For. Res. **11**(1): 155–167. doi:10.1139/x81-021.

Haynes, B.E., and Gower, S.T. 1995. Belowground carbon allocation in unfertilized and fertilized red pine plantations in northern Wisconsin. Tree Physiol. **15**(5): 317–325. PMID:14965955.

Howard, E.A., Gower, S.T., Foley, J.A., and Kucharik, C.J. 2004. Effects of logging on carbon dynamics of jack pine forest in Saskatchewan, Canada. Glob. Change Biol. **10**(8): 1267–1284. doi:10.1111/j.1529-8817.2003.00804.x.

Jackson, R.B., Mooney, H.A., and Schulze, E.-D. 1997. A global budget for fine root biomass, surface area, and nurtrient contents. Proc. Natl. Acad. Sci. U.S.A. **94**(14): 7362–7366. doi:10.1073/pnas.94.14.7362. PMID:11038557.

Johnsen, K.H., and Major, J.E. 1995. Gas exchange of 20-year-old black spruce families displaying a genotype × environmental interaction in growth rate. Can. J. For. Res. **25**(3): 430–439. doi:10.1139/x95-048.

Johnsen, K.H., and Major, J.E. 1999. Shoot water relations of mature black spruce families displaying a genotype × environment interaction in growth rate: I. Family and site effects over three growing seasons. Tree Physiol. **19**(6): 367–374. doi:10.1093/treephys/19.6.367. PMID:12651558.

Johnsen, K.H., and Seiler, J.R. 1996. Growth, shoot phenology and physiology of diverse seed sources of black spruce: I. Seedling responses to varied atmospheric CO_2 concentrations and photoperiods. Tree Physiol. **16**(3): 367–373. doi:10.1093/treephys/16.3.367. PMID:14871738.

Johnsen, K.H., Flanagan, L.B., Huber, D.A., and Major, J.E. 1999. Genetic variation in growth, carbon isotope discrimination, and foliar N concentration in *Picea mariana*: analyses from a half-diallel mating design using field-grown trees. Can. J. For. Res. **29**: 1727–1735. doi:10.1139/x99-144.

Johnsen, K.H., Samuelson, L., Teskey, R.O., McNulty, S., and Fox, T. 2001*a*. Process models as tools in forestry research and management. For. Sci. **47**: 2–8.

Johnsen, K.H., Wear, D., Oren, R., Teskey, R.O., Sanchez, F., Will, R., Butnor, J., Markewicz, D., Richter, D., Rials, T., Allen, H.L., Seiler, J., Ellsworth, D., Maier, C., Samuelson, L., Katul, G., and Dougherty, P. 2001*b*. Carbon sequestration via southern pine forestry. J. For. **99**: 14–21.

Kalyn, A.L., and van Rees, K.C.J. 2006. Contribution of fine roots to ecosystem biomass and net primary production in black spruce, aspen, and jack pine forests in Saskatchewan. Agric. For. Meteorol. **140**(1–4): 236–243. doi:10.1016/j.agrformet.2005.08.019.

Lavigne, M.B., and Krasowski, J.M. 2007. Estimating coarse root biomass of balsam fir. Can. J. For. Res. **37**(6): 991–998. doi:10.1139/X06-311.

Li, Z., Kurz, W.A., Apps, M.J., and Beukema, S.J. 2003. Belowground biomass dynamics in the Carbon Budget Model of the Canadian Forest Sector: recent improvements and implications for the estimation of NPP and NEP. Can. J. For. Res. **33**(1): 126–136. doi:10.1139/x02-165.

Litton, C.M., Raich, J.W., and Ryan, M.G. 2007. Carbon allocation in forest ecosystems. Glob. Change Biol. **13**(10): 2089–2109. doi:10.1111/j.1365-2486.2007.01420.x.

Ludovici, K.H., Zarnoch, S.J., and Richter, D.D. 2002. Modeling in-situ pine root decomposition using data from a 60-year old chronosequence. Can. J. For. Res. **32**(9): 1675–1684. doi:10.1139/x02-073.

Maier, C.A., Albaugh, T.J., Allen, H.L., and Dougherty, P.M. 2004. Respiratory carbon use and carbon storage in mid-rotation loblolly pine (*Pinus taeda* L.) plantations: the effect of site resources on the stand carbon balance. Glob. Change Biol. **10**(8): 1335–1350. doi:10.1111/j.1529-8817.2003.00809.x.

Maier, C.A., Johnsen, K.H., Dougherty, P., McInnis, D., Anderson, P., and Patterson, S. 2012. Effect of harvest residue management on tree productivity and carbon pools during early stand development in a loblolly pine plantation. For. Sci. **X**: xx–xx. [In press.]

Major, J.E., and Johnsen, K.H. 1996. Family variation in photosynthesis of 22-year-old black spruce: a test of two models of physiological response to water stress. Can. J. For. Res. **26**(11): 1922–1933. doi:10.1139/x26-217.

Major, J.E., and Johnsen, K.H. 1999. Shoot water relations of mature black spruce families displaying a genotype × environment interaction in growth rate. II. Temporal trends and response to varying soil water conditions. Tree Physiol. **19**(6): 375–382. doi:10.1093/treephys/19.6.375. PMID:12651559.

Major, J.E., and Johnsen, K.H. 2001. Shoot water relations of mature black spruce families displaying a genotype × environment interaction in growth rate. III. Diurnal patterns as influenced by vapor pressure deficit and internal water status. Tree Physiol. **21**(9): 579–587. doi:10.1093/treephys/21.9.579. PMID:11390302.

Major, J.E., Mosseler, A., Barsi, D.C., Campbell, M., and Rajora, O.P. 2003*a*. Morphometric allometric, and developmentally adaptive traits in red spruce and black spruce. I. Species and seed source variation. Can. J. For. Res. **33**(5): 885–896. doi:10.1139/x03-049.

Major, J.E., Mosseler, A., Barsi, D.C., Campbell, M., and Rajora, O.P. 2003*b*. Morphometric, allometric, and developmentally adaptive traits in red spruce and black spruce. II. Seedling and mature tree assessment of controlled intra- and inter-specific hybrids. Can. J. For. Res. **33**(5): 897–909. doi:10.1139/x03-067.

Major, J.E., Johnsen, K.H., Barsi, D.C., and Campbell, M. 2012*a*. Fine and coarse root parameters from mature black spruce displaying genetic × soil moisture interaction in growth. Can. J. For. Res. **42**(11): 1926–1938. doi:10.1139/x2012-144.

Major, J.E., Johnsen, K.H., Barsi, D.C., and Campbell, M. 2012*b*. Needle parameter variation of mature black spruce families displaying a genetic × environment interaction in growth. Trees (Berl.), **X**: xx–xx. [Submitted.]

Morgenstern, E.K. 1974. A diallel cross in black spruce, *Picea mariana* (Mill.) B.S.P. Silvae Genet. **23**: 67–70.

Morgenstern, E.K. 1996. Geographic variation in forest trees: genetic basis and application of knowledge in silviculture. University of British Colimbia Press, Vancouver, B.C.

Moroni, M.T., Shaw, C.H., and Otahal, P. 2010. Forest carbon stocks in Newfoundland boreal forests of harvest and natural disturbance origin I: field study. Can. J. For. Res. **40**(11): 2135–2145. doi:10.1139/X10-154.

Oleksyn, J., Reich, P.B., Chalupka, W., and Tjoelker, M.G. 1999. Differential above- and below-ground biomass accumulation of European *Pinus sylvestris* populations in a 12-year-old provenance experiment. Scand. J. For. Res. **14**: 7–17.

Ostonen, I., Lohmus, K., and Pajuste, K. 2005. Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: comparison of soil core and ingrowth core methods. For. Ecol. Manage. **212**(1–3): 264–277. doi:10.1016/j.foreco.2005.03.064.

Samuelson, L.J., Butnor, J., Maier, C., Stokes, T.A., Johnsen, K.H., and Kane, M. 2008. Growth and physiology of loblolly pine in response to long-term resource management: defining growth potential in the southern United States. Can. J. For. Res. **38**(4): 721–732. doi:10.1139/X07-191.

Santantonio, D., and Hermann, R.K. 1985. Standing crop, production and turnover of fine roots on dry, moderate, and wet sites of mature Douglas-fir in western Oregon. Ann. For. Sci. **42**(2): 113–142. doi:10.1051/forest:19850201.

Six, J., Conant, R.T., Paul, E.A., and Paustian, K. 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant Soil, **241**(2): 155–176. doi:10.1023/A:1016125726789.

Smith, C.K., Coyea, M.R., and Munson, A.D. 2000. Soil carbon, nitrogen, and phosphorus stocks and dynamics under disturbed black spruce forests. Ecol. Appl. **10**(3): 775–788. doi:10.1890/1051-0761(2000)010[0775:SCNAPS]2.0.CO;2.

Steele, S.J., Gower, S.T., Vogel, J.G., and Norman, J.M. 1997. Root biomass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. **17**(8–9): 577–587. doi:10.1093/treephys/17.8-9.577. PMID:14759831.

Vogt, K.A., Vogt, D.J., and Bloomfield, J. 1998. Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant Soil, **200**(1): 71–89. doi:10.1023/A:1004313515294.