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High belowground biomass allocation in an upland black spruce (*Picea mariana*) stand in interior Alaska

Kyotaro Noguchi [a,*], Masako Dannoura [b], Mayuko Jomura [c],
Motoko Awazuhara-Noguchi [d,1], Yojiro Matsuura [e,2]

[a] *Shikoku Research Center, Forestry and Forest Products Research Institute (FFPRI), Kochi 780-8077, Japan*
[b] *Graduate School of Agriculture, Kyoto University, Kyoto 606-8502, Japan*
[c] *College of Bioresource Sciences, Nihon University, Fujisawa 252-8510, Japan*
[d] *Faculty of Human Life and Environmental Sciences, Ochanomizu University, Tokyo 112-8610, Japan*
[e] *Department of Forest Site Environment, FFPRI, Tsukuba 305-8687, Japan*

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Abstract

The root system of forest trees account for a significant proportion of the total forest biomass. However, data is particularly limited for forests in permafrost regions. In this study, therefore, we estimated the above- and belowground biomass of a black spruce (*Picea mariana*) stand underlain with permafrost in interior Alaska. Allometric equations were established using 4−6 sample trees to estimate the biomass of the aboveground parts and the coarse roots (roots >5 mm in diameter) of *P. mariana* trees. The aboveground biomass of understory plants and the fine-root biomass were estimated by destructive sampling. The aboveground and coarse-root biomasses of the *P. mariana* trees were estimated to be 3.97 and 2.31 kg m^{-2}, respectively. The aboveground biomass of understory vascular plants such as *Ledum groenlandicum* and the biomass of forest floor mosses and lichens were 0.10 and 0.62 kg m^{-2}, respectively. The biomass of fine roots <5 mm in diameter was 1.27 kg m^{-2}. Thus, the above- and belowground biomasses of vascular plants in the *P. mariana* stand were estimated to be 4.07 and 3.58 kg m^{-2}, respectively, indicating that belowground biomass accounted for 47% of the total biomass of vascular plants. Fine-root biomass was 36% of the total root biomass, of which 90% was accumulated in the surface organic layer. Thus, this *P. mariana* stand can be characterized as having extremely high belowground biomass allocation, which would make it possible to grow on permafrost with limited soil resource availability.

Keywords: Allometric equation; Coarse root; Fine root; Permafrost; Vertical distribution

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1. Introduction

The roots of forest trees play a key role not only in belowground resource acquisition but also in belowground carbon and nutrient dynamics of forest ecosystems. In general, tree roots are classified into fine and coarse roots according to diameter, where roots less than 1−5 mm in diameter are usually

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* Corresponding author. Tel.: +81 88 844 1121; fax: +81 88 844 1130.
E-mail address: kyotaro@affrc.go.jp (K. Noguchi).

[1] Present address: Hadaminami-machi, Kochi 780-0026, Japan.

[2] Present address: Bureau of International Partnership, FFPRI, Tuskuba 305-8687, Japan.

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categorized as fine roots (Finér et al., 2010; Noguchi et al., 2007). Coarse roots normally account for 20%–40% of a tree's biomass, indicating that they are one of the important components of carbon pools in forest ecosystems (Brunner and Godbold, 2007). On the other hand, fine roots are physiologically the most active part of the root system with absorptive functions and high respiration rates (Makita et al., 2009; Pregitzer, 2002). Although fine-root biomass is usually less than 10% of the tree biomass, several recent studies suggested that fine-root production accounted for more than 50% of the net primary production (NPP) in forest ecosystems (Hendrick and Pregitzer, 1993; Ruess et al., 2003). However, biomass allocation to the root system varies with forest type and environmental conditions (Vogt et al., 1996; Noguchi et al., 2007).

Boreal forests are generally characterized as having a cold environment. In particular, the environmental conditions are severe for tree growth in permafrost regions, which cover a substantial area of the boreal forest biome (Osawa and Zyryanova, 2010). Thus, elucidating the biomass and distribution of root systems in forests on permafrost would help us to not only better understand how trees adapt to this cold environment, but would also improve our knowledge of carbon and nutrient dynamics in the boreal forest biome, where a huge amount of carbon is accumulated in the soil (Tarnocai et al., 2009).

The biomass of forest trees is often estimated by means of allometric equations based on the relationship between the stem diameter and biomass (e.g., Mack et al., 2008). In general, however, available allometric equations for root biomass are limited compared with those for aboveground biomass. As for forests in permafrost regions, several recent studies established root biomass allometric equations and estimated the coarse-root biomass (Kajimoto et al., 1999, 2006), which showed that the belowground biomass allocation of larch forests was greater than that in other forests in non-permafrost regions. In interior Alaska, north-facing slopes and bottomlands underlain with permafrost are usually dominated by black spruce (*Picea mariana*) forests (Viereck et al., 1983), for which an earlier study showed that root biomass accounted for 30%–45% of the total biomass (Van Cleve et al., 1981). However, this data was obtained by the excavation method (block sampling), not by allometric equations. Sets of allometric equations are available for root biomass calculations in southern *P. mariana* forests in Canada, but it is unclear whether these equations can be applied to the stands in interior Alaska because patterns of biomass allocation can vary with environmental conditions (Bond-Lamberty et al., 2002; Ouimet et al., 2008; Rencz and Auclair, 1980). Therefore, in order to study the belowground biomass of *P. mariana* forests in interior Alaska, it is necessary to establish allometric equations specific to the site.

On the other hand, the biomass and dynamics of fine roots in *P. mariana* stands in interior Alaska have been reported (Ruess et al., 1996, 2003). These studies showed that fine-root production accounted for nearly 60% of the total NPP of the stands, suggesting that those *P. mariana* stands have characteristics of high biomass allocation to fine roots. Fine-root biomass in the four *P. mariana* stands ranged from approximately 220–2200 g m^{-2}, but three of them were more than 1500 g m^{-2}. This suggested that fine roots may also be an important component of the carbon pool in those *P. mariana* forests. In addition, information on other fine-root characteristics such as morphology (e.g., diameter size) and spatial distribution is still limited for *P. mariana* forests in interior Alaska. These characteristics of fine roots can also vary with environmental conditions and the elucidation of these characteristics would help us better understand how forest trees respond to unfavorable environmental conditions (Makita et al., 2011; Ostonen et al., 2007; Tateno et al., 2004).

In this study, therefore, we estimated the belowground biomass of both coarse and fine roots and compared it with the aboveground biomass at an upland *P. mariana* stand in interior Alaska. In addition, we examined the biomass distribution of fine roots in different diameter classes and their pattern of vertical distribution. Taken together, this paper discusses the pattern of belowground biomass allocation in *P. mariana* stands in permafrost regions compared with other forests in non-permafrost regions.

2. Materials and methods

2.1. Study site

This study was conducted at a black spruce (*P. mariana*) stand on a north-facing slope in the Poker Flat Research Range (PFRR; 65°07'N, 147°28'W) of the University of Alaska, Fairbanks. PFRR is located approximately 50 km northeast of Fairbanks and is adjacent to the Caribou Poker Creek Research Watershed (CPCRW), where the mean annual temperature and mean annual precipitation are −2.5 °C and 400 mm, respectively (Petrone et al., 2006). Stand age of this study site was more than 180 years according to the tree rings at stem base. Stand density of dominant *P. mariana* trees (>1.3 m in height) was 4300 trees ha^{-1}. Mean diameter at breast height (DBH) and mean height of the *P. mariana* trees were 5.5 cm and 4.8 m, respectively. Understory vegetation was comprised mainly of shrubs such as *Ledum groenlandicum*, *Vaccinium vitis-idaea*, and *V. uliginosum* with *Equisetum* spp. The forest floor was under continuous cover of a moss—lichen complex (*Pleurozium schreberi*, *Hylocomium splendens*, *Cladina stellaris*, *Cladina rangiferina*). Reddish sphagnum moss (*Sphagnum warnstorfii*) patches were partly developed. According to a soil survey conducted in August 2005, the soil type of this stand was Typic Haplorthels (Soil Survey Staff, 1998) and the permafrost table was observed at a depth of 33 cm in the mineral soil horizon, on which a thick organic layer (living moss—lichen and undecomposed organic matter) of 28 cm was formed.

2.2. Above- and belowground biomass of *P. mariana* trees

In this study, the biomass of aboveground components and coarse roots (roots >5 mm in diameter) of *P. mariana* trees was estimated using the allometric relationship between the stem diameter and the dry weight of the sample trees. In August 2007, a 20 × 20-m plot was established and six trees were selected for destructive sampling. Since diameter at breast height (1.3 m, DBH) in the plot ranged from 1 to 15 cm, we selected four sample trees >1.3 m in height, for which DBH evenly varied in 4-cm intervals between 2 and 14 cm. As for sample trees 0.5—1.3 m in height, two trees with a height close to the minimum and maximum in this range were selected. Those sample trees were cut at the ground surface with a handsaw, and the fresh weight of the stems, branches, leaves, and cones was measured. Dead branches were not included in the measurement. Then, subsamples of each aboveground component were taken, where disk samples were prepared at 1-m intervals from a 0.3-m height for the stems. Those subsamples were weighed for fresh weight and their dry/fresh weight ratio was analyzed after drying at 70 °C. Then, the dry weight of those aboveground parts was determined by their fresh weight and the dry/fresh weight ratio of the subsamples. Belowground parts (roots) of the sample trees were also harvested after their aboveground parts were removed. The roots were carefully excavated by hand, and were classified in terms of diameter (5—20 mm, 20—50 mm and >50 mm in diameter). Then, their fresh weight was measured and subsamples were taken for each diameter class. Similar to the aboveground parts, the dry weight of the roots was determined by their fresh weight and dry/fresh weight ratio of the subsamples. Then, the relationship between the stem diameter and dry weight of the sample trees was analyzed, and allometric equations were established based on the natural logarithmic data. Correction factors (CF) for the equations were determined following Sprugel (1983).

To estimate the biomass in the *P. mariana* stand, the DBH of all trees >1.3 m in height in the study plot was determined and the basal diameter (D_0) of those trees was indirectly estimated using the following equation based on the DBH-D_0 relationship of the four harvested sample trees >1.3 m in height.

$$D_0 = 0.778 + 1.32 \times \mathrm{DBH}\left(N = 4, R^2 = 0.999, P < 0.001\right)$$

To estimate the biomass of the smaller *P. mariana* trees 0.5—1.3 m in height, the D_0 of smaller trees in a 3 × 16-m subplot was determined. Then, the biomass of *P. mariana* per unit stand area was estimated using the obtained D_0 and DBH values subjected to the abovementioned allometric equations.

2.3. Aboveground biomass of understory vascular plants

To estimate the aboveground biomass of understory vascular plants and the biomass of fine roots <5 mm in diameter, a 16-m line transect was established along the slope, on which eight 0.5 × 0.5-m plots were placed at 2-m intervals. In July 2006, the aboveground parts of the understory vascular plants in those plots were harvested by cutting their stems at the level of the forest floor vegetation surface (mosses and lichens). The samples were dried at 70 °C and then weighed.

2.4. Soil coring

Eight soil core samples were collected along the abovementioned 16-m line transect in July 2006. A sampling location was set at the center of each 0.5 × 0.5-m plot where the aboveground biomass of the understory vascular plants was examined. A soil auger 4.8 cm in inner diameter (18.1 cm^{-2} in area; Split-tube sampler, Eijkelkamp, Netherlands) was knocked into the soil to the depth where the auger was hindered by permafrost. The depth from the surface of ground vegetation to that of the mineral soil was measured during the core sampling. The core samples were divided into layers of living moss and lichen, organic matter, and mineral soil and were placed in plastic bags. Mineral soil cores were further divided at a depth of 10 cm when possible. The samples were transported to the laboratory at a cool temperature (with refrigerant) and were stored in a freezer at −30 °C until processed. Fine roots were collected from the core samples by using tweezers in tap water. In the case of mineral soil samples, a 0.5-mm metal sieve was used for efficient removal of soil. The fine roots were then divided by diameter classes of <1 mm, 1–2 mm, and 2–5 mm. Living fine roots were separated from dead ones based mainly on their resilience. Samples of the fine roots and living mosses and lichens were dried at 70 °C and then weighed.

3. Results

3.1. Allometric equations for estimating biomass of *P. mariana* trees

The basal diameter (D_0) and the diameter at breast height (DBH) of the *P. mariana* sample trees ranged from 1.6 to 19.4 cm and from 2.3 to 14.0 cm, respectively (Fig. 1). The aboveground and coarse root (roots >5 mm in diameter) biomasses of the sample trees ranged from 0.08 to 50.3 kg and from 0.05 to 30.8 kg, respectively. The ratio of aboveground to coarse-root biomass (top/root ratio) ranged from 1.6 to 2.5. From this data, allometric equations were established for estimating the biomasses of the aboveground components and the coarse roots of *P. mariana* trees from D_0 and DBH (Tables 1 and 2). Both procedures gave similar results for the biomass of stems, branches, leaves, and coarse roots, although the biomass estimated from D_0 was 1%–4% larger than that estimated from DBH (Table 3). Although the equations using D_0 made it possible to estimate the biomass of small *P. mariana* trees less than 1.3 m in height, the contribution of small trees to the biomass accumulation was negligible (<2%) in our study plot.

3.2. Biomass of *P. mariana* and understory plants

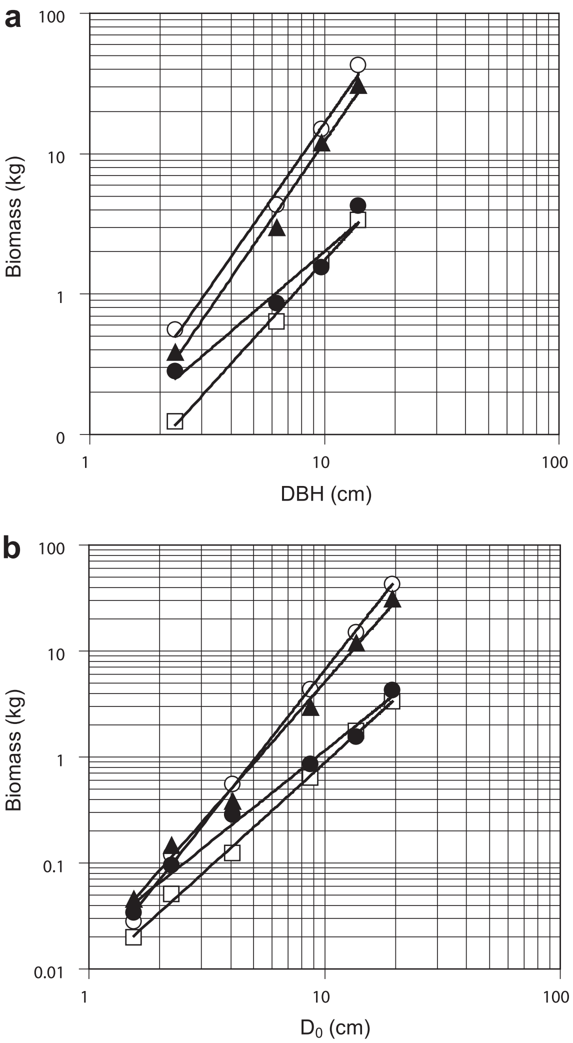

Fig. 1. Relationships between stem diameter (a, DBH; b, D_0) and biomass of *P. mariana* tree components. Open circle, closed triangle, closed circle and open square indicate data on stem, coarse root (>5 mm in diameter), leaf, and branch, respectively. Equations for regression lines are shown in Tables 1 and 2 for DBH-biomass and D_0-biomass, respectively.

The aboveground and coarse-root biomasses of *P. mariana* trees were estimated to be 3.97 and 2.31 kg m^{-2}, respectively (Table 4). The aboveground biomass of understory vascular plants was 0.10 ± 0.02 kg m^{-2}, of which the biomass of *L. groenlandicum* and *Vaccinium vitis-idaea* accounted for 77% and 16%, respectively (data not shown). The biomass of forest floor mosses and lichens determined by core sampling was 0.62 ± 0.12 kg m^{-2}. The depth from the surface of the forest floor vegetation to that of the mineral soil ranged from 25 to 40 cm (Table 5). Although we tried to take 20-cm-long mineral soil cores, we were only able to reach 4–18 cm at six of the eight sampling locations due to permafrost. The biomass of fine roots <5 mm in diameter was 1.27 ± 0.25 kg m^{-2}, of which 57% was roots <1 mm in diameter (Tables 4 and 5). Most of those roots (90%) were concentrated in the surface organic layer (including the layer of living moss and lichen). Fine-root density in the surface organic layer (2.06 kg m^{-3}) was significantly higher than that in the

Table 1
Allometric equations for estimating biomass (kg) of stems, branches, leaves and coarse roots (>5 mm in diameter) of *P. mariana* trees from DBH (cm).

	a	b	R^2	CF[a]	SEE[b]
Stem	−2.71 (0.30)	2.39 (0.15)	0.99	1.02	0.203
Branch	−3.71 (0.18)	1.85 (0.09)	0.995	1.02	0.120
Leaf	−2.60 (0.44)	1.43 (0.22)	0.96	1.04	0.294
Aboveground	−1.96 (0.28)	2.17 (0.14)	0.99	1.02	0.187
Root	−3.12 (0.33)	2.44 (0.17)	0.99	1.02	0.222

Regression equations are expressed as "$\log_n$ (biomass) = a + b * $\log_n$ (DBH)".
Values in parentheses are standard errors.
Four sample trees were used to establish the equations.
[a] Correction factor of Sprugel (1983).
[b] Standard error of estimates of the regression.

Table 3
Biomass of tree components of *P. mariana* estimated by two sets of allometric equations shown in Tables 1 and 2.

Height class	Component	Biomass	
		Estimates 1 kg m^{-2}	Estimates 2 kg m^{-2}
>130 cm	Stem	3.11	3.24
	Branch	0.34	0.34
	Leaf	0.44	0.44
	Root	2.31	2.34
<130 cm	Stem	–	0.02
	Branch	–	0.01
	Leaf	–	0.03
	Root	–	0.03

Estimates 1: Allometric equations in Table 1 were used.
Estimates 2: Allometric equations in Table 2 were used.

mineral soil (0.39 kg m^{-3}) for roots <1 mm in diameter (one-way ANOVA, $F = 13.5$, $P = 0.002$; Fig. 2). Since fine roots 1–2 and 2–5 mm in diameter were not present in five and six mineral soil cores, respectively, the significance of vertical distribution was not tested for these diameter classes.

Taken together, the total biomass including forest floor mosses and lichens was 8.27 kg m^{-2} in this *P. mariana* stand (Table 4). The above- and belowground biomasses of vascular plants were estimated to be 4.07 and 3.58 kg m^{-2}, respectively, indicating that belowground biomass accounted for 47% of the total biomass of vascular plants.

4. Discussion

In this study, allometric equations were established for estimating the biomass of aboveground components and coarse roots (roots >5 mm in diameter) of *P. mariana* trees using basal diameter (D_0) or diameter at breast height (DBH). The equations showed that the biomass of stems, branches, leaves, and coarse roots can be predicted by D_0 or DBH ($R^2 = 0.96$ or more), although the number of sample trees used for the equations was small (n = 4–6; Fig. 1). We also compared the allometric equations for stem and coarse-root biomasses to those reported earlier (Fig. 3). In general, allometric relationships between DBH and biomass are site specific (e.g., Kajimoto et al., 2006) and the allometric equations are likely to vary among studies for *P. mariana* stands (Fig. 3). The variations appeared to be larger for roots than for stems as indicated by the slope (exponent coefficient) of the equations, which ranged from 1.21 to 2.87 and from 2.03 to 2.58 for roots and stems, respectively. Some of the previous studies used an allometric equation for *Abies balsamea* to estimate the root biomass of *P. mariana* trees (Steele et al., 1997; Bond-Lamberty et al., 2004; Wang et al., 2003). However, the data in Fig. 3 suggest that the root biomass may have been underestimated if the equation for *Abies balsamea* had been used for estimating the root biomass of *P. mariana* at our study site in interior Alaska.

In this study, we estimated above- and belowground biomasses using allometric equations specific to our study site, together with destructive sampling for the biomass of understory plants and fine roots. The aboveground biomass of *P. mariana* trees in our study site was similar to that previously reported (Table 4; Ruess et al., 2003). In addition, the biomass of the low shrub layer was small, whereas the biomass of forest floor mosses and lichens accounted for a significant proportion of the biomass of understory vegetation (Table 4), which is also similar to that in other *P. mariana* stands in interior Alaska (Ruess et al., 2003; Van Cleve et al., 1981). Thus, these results suggest that our study site is likely a typical *P. mariana* stand in this region. The estimated total root biomass,

Table 2
Allometric equations for estimating biomass (kg) of stems, branches, leaves and coarse roots (>5 mm in diameter) of *P. mariana* trees from D_0 (cm).

	a	b	R^2	CF[a]	SEE[b]
Stem	−4.62 (0.13)	2.82 (0.07)	0.998	1.02	0.149
Branch	−4.77 (0.10)	2.02 (0.05)	0.997	1.01	0.117
Leaf	−3.96 (0.19)	1.78 (0.10)	0.99	1.05	0.218
Aboveground	−3.49 (0.09)	2.48 (0.05)	0.999	1.01	0.106
Root	−4.22 (0.20)	2.54 (0.10)	0.99	1.05	0.226

Regression equations are expressed as "$\log_n$ (biomass) = a + b * $\log_n$ (D_0)".
Values in parentheses are standard errors.
Six sample trees were used to establish the equations.
[a] Correction factor of Sprugel (1983).
[b] Standard error of estimates of the regression.

Table 4
Aboveground and belowground biomass in an upland *P. mariana* stand in interior Alaska.

		Biomass kg m^{-2}	Ratio %
Aboveground	*P. mariana*	3.97	48
	Understory	0.10	1
	Mosses and lichens	0.62	7
	Aboveground total	4.69 (4.07)[a]	–
Belowground	Coarse root	2.31	28
	Fine root	1.27	15
	Belowground total	3.58	–
Total		8.27	100

[a] The data in parenthesis is aboveground biomass excluding those of moss and lichens.

on the other hand, was approximately 3.6 kg m^{-2}, which accounted for 47% of the total biomass (excluding forest floor mosses and lichens; Table 4). An earlier study on *P. mariana* stands in interior Alaska also showed high belowground biomass allocation (29% and 43% in upland and muskeg stands, respectively), whereas root biomass (1.04 and 1.25 kg m^{-2} in upland and muskeg stands, respectively) was one-third of that in our study site (Van Cleve et al., 1981). The larger biomass in our study site might be due to greater stand age (~180 vs. ~60 years). Rencz and Auclair (1978) also showed high belowground biomass allocation in a *P. mariana* – *Cladonia alpestris* woodland in Quebec, Canada, where the root/total biomass ratio was approximately 35%. In contrast, *P. mariana* forests (>70 years in stand age) in Saskatchewan and Manitoba, Canada, showed lower biomass allocation to belowground (approximately 15%–20%) and similar or much larger aboveground biomass (approximately 1.8–7.2 kg m^{-2} in carbon (C) content; O'Connell et al., 2003; Wang et al., 2003) compared with that in our study site (Table 4). A recent review by Brunner and Godbold (2007) reported that the amount of C in total roots accounted for 27% of the total C in forest trees. Thus, our data together with previous reports suggests that biomass allocation to root systems would be larger in *P. mariana* forests in interior Alaska than is generally recognized.

The biomass of fine roots in forests is normally considered to account for only a small proportion of total tree biomass. As for boreal forests, a recent review showed that the mean fine-root biomass (<2 mm in diameter) of 81 stands was approximately 530 g m^{-2} (Finér et al., 2010). Brunner and Godbold (2007) reported that fine-root C accounted for 5% of total forest tree C and 20% of total root C in boreal forests. In *P. mariana* forests in interior Alaska, however, the biomass allocation to fine roots is likely to be much larger; the estimated biomass of fine roots <2 mm in diameter (919 g m^{-2}) accounted for 12% of the total biomass and 26% of the total root biomass in this study (Tables 4 and 5). In addition, a recent paper estimated the biomass of fine roots <1 mm in diameter to be approximately 1500–2200 g m^{-2} (Ruess et al., 2003), which is 2–3 times larger than that in our study site (Table 5). Although their study did not examine coarse-root biomass, the data suggests high biomass allocation especially to fine roots, considering that those stands had an aboveground biomass of vascular plants (approximately 3.2–3.5 kg m^{-2}) similar to that in our study site (Table 4). On the other hand, biomass allocation to fine roots in southern *P. mariana* forests seems to be much smaller; the biomass of fine roots <2 mm in diameter was 77 and 170 g m^{-2} in *P. mariana* forests in Saskatchewan and Manitoba, respectively, and accounted for 3% and 6%, respectively, of the total root biomass (Steele et al., 1997).

As has been reported, *P. mariana* forests in interior Alaska are usually established on north-facing slopes or bottomlands underlain with poorly drained permafrost (Viereck et al., 1983) and this is also the case in our study site, where the permafrost table was observed at approximately 30 cm. In contrast, soils under *P. mariana* forests in Saskatchewan and Manitoba were reported to be permafrost free. Even where permafrost is present, the permafrost table is much lower (100–150 cm in depth; Wang et al., 2003) than that in interior Alaska. A permafrost biome is also present in Siberia, which is dominated by larch forests (Osawa and Zyryanova, 2010). In their series of studies, Kajimoto et al. (1999) elucidated that root biomass (1.67 kg m^{-2}) accounted for 43% of the total biomass in a *Larix gmelinii* stand in

Table 5
Biomass of fine roots in different diameter classes in the *P. mariana* stand. Data shown are mean ± SE ($n = 8$).

	Depth cm	Biomass		
		Diam. <1 mm g m^{-2}	Diam. 1–2 mm g m^{-2}	Diam. 2–5 mm g m^{-2}
Organic	33 ± 2	703 ± 181	151 ± 26	289 ± 89
Mineral	12 ± 3	28 ± 9	37 ± 29	66 ± 61
Total	45 ± 3	731 ± 184	188 ± 40	355 ± 126

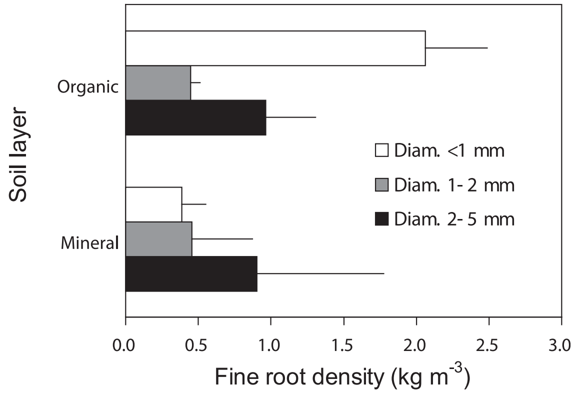

Fig. 2. Vertical distribution of fine-root density in different diameter classes. Data shown are mean + SE ($n = 8$).

central Siberia, and the belowground biomass allocation of the *Larix* species was greater than that of *Pinus sylvestris* growing in discontinuous or non-permafrost regions in Siberia (Kajimoto et al., 2006). Helmisaari et al. (2007), on the other hand, suggested that fine-root biomass in northern forests was larger than that in southern forests in their study of *Picea abies* and *P. sylvestris* forests across southern (60°37'N latitude) to northern (69°35′N latitude) Finland. Although their northernmost study sites were located at higher latitudes than that of our study site (65°07'N), the biomass of fine roots <2 mm in diameter was larger in our *P. mariana* stand (919 g m^{-2}; Table 5) than the largest fine-root biomass that they observed in *P. abies* (552 g m^{-2}) and *P. sylvestris* (493 g m^{-2}) forests (Helmisaari et al., 2007). Thus, the high belowground biomass allocation observed in this study might be the result of environmental conditions particular to permafrost ecosystems, where soil temperature and soil resource availability would be much lower than that in permafrost-free ecosystems. In this study, more than 95% of the biomass of fine roots <1 mm in diameter was in the surface organic layer (Table 5), where fine-root density was also significantly greater than that in the mineral soil (Fig. 3). These results would also suggest extremely poor soil resource availability in our study site compared with other non-permafrost forests with more moderate vertical fine-root distribution in the mineral soil (Helmisaari et al., 2007; Makita et al., 2011; Steele et al., 1997; Ugawa et al., 2010).

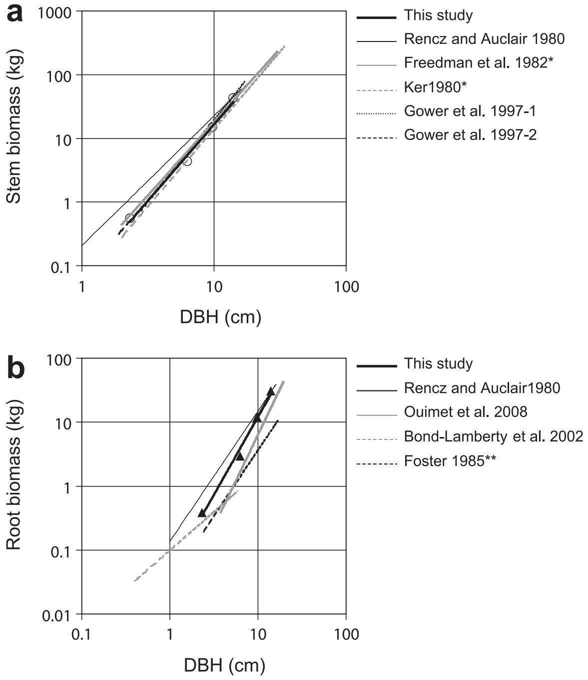

Fig. 3. Allometric equations to estimate biomass of stem (a) and root (b) of *P. mariana* trees. Locations of study sites of the published papers are as follows: Rencz and Auclair 1980, Quebec; Freedman et al., 1982 and Ker 1980, Nova Scotia; Gower et al. 1997-1, Manitoba; Gower et al. 1997-2, Saskatchewan; Ouimet et al., 2008, Quebec; Bond-Lamberty et al., 2002, Manitoba; Foster 1985, new Hampshire. (*Reviewed by Ter-Mikaelian and Korzukhin, 1997. **Data on *Abies balsamea*.)

In summary, our study showed that belowground biomass allocation was extremely high at a *P. mariana* stand in interior Alaska, which may be related to the environmental conditions associated with permafrost. Although permafrost regions cover a substantial area of the boreal forest biome, recent reports suggest that permafrost may be vulnerable to climate changes such as global warming and the changing fire regimes observed in the last several decades (Hinzman et al., 2006; Osawa et al., 2010; Osawa and Zyryanova, 2010). In future studies, therefore, it is necessary to elucidate the root dynamics under various permafrost conditions to better understand and predict future changes in the permafrost forest ecosystems.

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References

Bond-Lamberty, B., Wang, C., Gower, S.T., 2002. Aboveground and belowground biomass and sapwood area allometric equations for six boreal tree species of northern Manitoba. Can. J. For. Res. 32, 1441–1450.

Bond-Lamberty, B., Wang, C., Gower, S.T., 2004. Net primary production and net ecosystem production of a boreal black spruce wildfire chronosequence. Glob. Change Biol. 10, 473–487.

Brunner, I., Godbold, D.L., 2007. Tree roots in a changing world. J. For. Res. 12, 78–82.

Finér, L., Ohashi, M., Noguchi, K., Hirano, Y., 2010. Factors causing variation in fine root biomass in forest ecosystems. For. Ecol. Manage. 261, 265–277.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J., 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-Atmos 102, 29029–29041.

Helmisaari, H.-S., Derome, J., Nöjd, P., Kukkola, M., 2007. Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. Tree Physiol. 27, 1493–1504.

Hendrick, R.L., Pregitzer, K.S., 1993. The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. Can. J. For. Res. 23, 2507–2520.

Hinzman, L.D., Viereck, L.A., Adams, P.C., Romanovsky, V.E., Yoshikawa, K., 2006. Climatic and permafrost dynamics of the Alaskan boreal forest. In: Chapin, F.S., Oswood, M.W., Cleve, K., Viereck, L.A., Verbyla, D.L. (Eds.), Alaska’s Changing Boreal Forest. Oxford University Press Inc., pp. 39–61.

Kajimoto, T., Matsuura, Y., Sofronov, M.A., Volokitina, A.V., Mori, S., Osawa, A., Abaimov, A.P., 1999. Above- and belowground biomass and net primary productivity of a *Larix gmelinii* stand near Tura, central Siberia. Tree Physiol. 19, 815–822.

Kajimoto, T., Matsuura, Y., Osawa, A., Abaimov, A.P., Zyryanova, O.A., Isaev, A.P., Yefremov, D.P., Mori, S., Koike, T., 2006. Size-mass allometry and biomass allocation of two larch species growing on the continuous permafrost region in Siberia. For. Ecol. Manage. 222, 314–325.

Mack, M.C., Treseder, K.K., Manies, K.L., Harden, J.W., Schuur, E.A.G., Vogel, J.G., Randerson, J.T., Chapin, F.S., 2008. Recovery of aboveground plant biomass and productivity after fire in mesic and dry black spruce forests of interior Alaska. Ecosystems 11, 209–225.

Makita, N., Hirano, Y., Dannoura, M., Kominami, Y., Mizoguchi, T., Ishii, H., Kanazawa, Y., 2009. Fine root morphological traits determine variation in root respiration of *Quercus serrata*. Tree Physiol. 29, 579–585.

Makita, N., Hirano, Y., Mizoguchi, T., Kominami, Y., Dannoura, M., Ishii, H., Finér, L., Kanazawa, Y., 2011. Very fine roots respond to soil depth: biomass allocation, morphology, and physiology in a broad-leaved temperate forest. Ecol. Res. 26, 95–104.

Noguchi, K., Konôpka, B., Satomura, T., Kaneko, S., Takahashi, M., 2007. Biomass and production of fine roots in Japanese forests. J. For. Res. 12, 83–95.

O’Connell, K.E.B., Gower, S.T., Norman, J.M., 2003. Net ecosystem production of two contrasting boreal black spruce forest communities. Ecosystems 6, 248–260.

Osawa, A., Zyryanova, O.A., 2010. Introduction. In: Osawa, A., Zyryanova, O.A., Matsuura, Y., Kajimoto, T., Wein, R.W. (Eds.), Permafrost Ecosystems: Siberian Larch Forests. Springer, pp. 3–15.

Osawa, A., Matsuura, Y., Kajimoto, T., 2010. Characteristics of Permafrost Forests in Siberia and potential responses to warming climate. In: Osawa, A., Zyryanova, O.A., Matsuura, Y., Kajimoto, T., Wein, R.W. (Eds.), Permafrost Ecosystems: Siberian Larch Forests. Springer, pp. 459–481.

Ostonen, I., Püttsepp, Ü, Biel, C., Alberton, O., Bakker, M.R., Lõhmus, K., Majdi, H., Metcalfe, D., Olsthoorn, A.F.M., Pronk, A., Vanguelova, E., Weih, M., Brunner, I., 2007. Specific root length as an indicator of environmental change. Plant Biosyst. 141, 426–442.

Ouimet, R., Camire, C., Brazeau, M., Moore, J.-D., 2008. Estimation of coarse root biomass and nutrient content for sugar maple, jack pine, and black spruce using stem diameter at breast height. Can. J. For. Res. 38, 92–100.

Petrone, K.C., Jones, J.B., Hinzman, L.D., Boone, R.D., 2006. Seasonal export of carbon, nitrogen, and major solutes from Alaskan catchments with discontinuous permafrost. J. Geophys. Res. 111, G02020.

Pregitzer, K.S., 2002. Fine roots of trees – a new perspective. New Phytol. 154, 267–273.

Rencz, A.N., Auclair, A.N., 1978. Biomass distribution in a subarctic *Picea mariana – Cladonia alpestris* woodland. Can. J. For. Res. 8, 168–176.

Rencz, A.N., Auclair, A.N., 1980. Dimension analysis of various components of black spruce in subarctic lichen woodland. Can. J. For. Res. 10, 491–497.

Ruess, R.W., VanCleve, K.J., Yarie, J., Viereck, L.A., 1996. Contributions of fine root production and turnover to the carbon and nitrogen cycling in Taiga forests of the Alaskan interior. Can. J. For. Res. 26, 1326–1336.

Ruess, R.W., Hendrick, R.L., Burton, A.J., Pregitzer, K.S., Sveinbjornsson, B., Allen, M.F., Maurer, G.E., 2003. Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecol. Monogr. 73, 643–662.

Soil Survey Staff, 1998. Keys to Soil Taxonomy, eighth ed.). USDA NRC.

Sprugel, D., 1983. Correcting for bias in log-transformed allometric equations. Ecology 64, 209–210.

Steele, S.J., Gower, S.T., Vogel, J.G., Norman, J.M., 1997. Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol. 17, 577–587.

Tarnocai, C., Canadell, J.G., Schuur, E.A.G., Kuhry, P., Mazhitova, G., Zimov, S., 2009. Soil organic carbon pools in the northern circumpolar permafrost region. Glob. Biogeochem. Cycles 23, GB2023. art. no. GB2023.

Tateno, R., Hishi, T., Takeda, H., 2004. Above- and belowground biomass and net primary production in a cool-temperate deciduous forest in relation to topographic changes in soil nitrogen. For. Ecol. Manage. 193, 297–306.

Ter-Mikaelian, M.T., Korzukhin, M.D., 1997. Biomass equations for sixty-five North American tree species. For. Ecol. Manage. 97, 1–24.

Ugawa, S., Miura, S., Iwamoto, K., Kaneko, S., Fukuda, K., 2010. Vertical patterns of fine root biomass, morphology and nitrogen concentration in a subalpine fir-wave forest. Plant Soil 335, 469–478.

Van Cleve, K., Barney, R., Schlentner, R., 1981. Evidence of temperature control of production and nutrient cycling in two interior Alaska black spruce ecosystems. Can. J. For. Res. 11, 258–273.

Viereck, L.A., Dyrness, C.T., Van Cleve, K., Foote, M.J., 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Can. J. For. Res. 13, 703–720.

Vogt, K.A., Vogt, D.J., Palmiotto, P.A., Boon, P., O'Hara, J., Asbjornsen, H., 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187, 159–219.

Wang, C., Bond-Lamberty, B., Gower, S., 2003. Carbon distribution of a well- and poorly-drained black spruce fire chronosequence. Glob. Change Biol. 9, 1066–1079.