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SPECIAL FEATURE: ORIGINAL ARTICLE

Development and function of roots of forest trees in Japan

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Individual-based measurement and analysis of root system development: case studies for *Larix gmelinii* trees growing on the permafrost region in Siberia

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Abstract We present results of individual-based root system measurement and analysis applied for *Larix gmelinii* trees growing on the continuous permafrost region of central Siberia. The data of root excavation taken from the three stands were used for the analyses; young (26 years old), mature (105 years old), and uneven-aged over-mature stand (220 years old). In this article, we highlight two topics: (1) factors affecting spatio-temporal pattern of root system development, and (2) interactions between aboveground (i.e., crown) and belowground (i.e., root) competition. For the first topic, the detailed observation of lateral roots was applied to one sample tree of the overmature stand. The tree constructed a superficial (<30 cm in depth) and rather asymmetric root system, and each lateral root expanded mainly into elevated mounds rather than depressed troughs. This indicated that spatial development of an individual root system was largely affected by microtopography (i.e., earth hummocks). For these lateral roots, elongation growth curves were reconstructed using annual-ring data, and annual growth rates and patterns were compared among them. The comparison suggested that temporal root system development is associated with differences in carbon allocation among the lateral roots. For the second topic, we examined relationships between individual crown projection area (CA) and horizontal rooting area (RA) for the sample trees of each stand. RA was almost equal to CA in the young stand, while RA was much larger (three or four times) than CA in the mature and overmature stands. Two measures of stand-level space occupation, crown area index (aboveground: CAI; sum of CAs per unit land area) and rooting area index (belowground: RAI; sum of RAs), were estimated in each stand. The estimates of RAI (1.3–1.8 $m^2 m^{-2}$) exceeded unity in all stands. In contrast, CAI exceeded unity (1.3 $m^2 m^{-2}$) only in the young stand, and was much smaller (<0.3 $m^2 m^{-2}$) in the two older stands. These between-stand differences in RAI–CAI relationships suggest that intertree competition for both aboveground and belowground spaces occurred in the young stand, but only belowground competition still occurred in the two older stands. Based on this finding, we hypothesized that competition below the ground may become predominant as a stand ages in *L. gmelinii* forests. Methodological limitations of our analysis are also discussed, especially for the analysis using the two indices of space occupation (CAI, RAI).

Key words Crown projection area · *Larix gmelinii* · Permafrost · Rooting area index · Root system development

Introduction

Much attention has recently been paid to fine roots rather than coarse roots in the studies of tree roots (e.g., Vogt et al. 1996). This research trend is mainly supported by advancement of observation instruments such as the minirhi-

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zotron: it enables us to directly monitor seasonal dynamics of the fine roots (e.g., Hendrick and Pregitzer 1996; Majdi 1996; Johnson et al. 2001). Based on this nondestructive technique, fine root biomass and annual net production have been estimated in many forest ecosystems (e.g., Steel et al. 1997; Noguchi et al. 2005; Hendricks et al. 2006). However, the minirhizotron method suffers from the fact that root observation is restricted to a very small part of the soil. Thus, many sampling points and the assumption of a uniform distribution of fine roots are required for the estimation of stand-level fine root mass and production. Similar problems may also exist in the case of destructive methods of fine root observation (e.g., sequential core and in-growth methods) (Vogt and Persson 1991). To overcome the problem, it is important to know how individual root systems are actually distributed within a target forest, including both the fine and coarse roots.

Individual root systems have been investigated for various tree species (MacMinn 1963; Leaf et al. 1971; Eis 1974; Fayle 1975; Karizumi 1979; Coutts 1983; Kuiper and Coutts 1992; Pavlis and Jenik 2000). Excavation and weighing of a whole root system are often laborious and time consuming. However, the obtained data (i.e., individual root mass) are essential for estimation of belowground biomass and production, although its application is generally restricted to larger coarse roots (Karizumi 1974; Santantonio et al. 1977; Deans 1981; Vogt and Persson 1991; Kurz et al. 1996). Description of the spatial distribution of root systems (i.e., rooting map) is another major outcome from the laborious root excavation. Fayle (1975) discussed details of the interaction between the development of crown and root systems of red pine (*Pinus resinosa* Ait.) trees based on the rooting maps and the analysis of lateral root growth patterns. This pioneering work and subsequent similar studies explored the possibility of the individual-based root measurement for understanding spatio-temporal developmental patterns of tree root systems in relation to soil conditions or a process of internal carbon allocation, if we combine both descriptive (i.e., rooting map) and reconstructive (i.e., annual ring analysis) data (Reynolds 1983; Drexhage and Gruber 1998; Drexhage et al. 1999).

From the viewpoint of belowground competition, Brisson and Reynolds (1994) examined all root systems of one shrub species (creosote bush) within a certain area in a desert ecosystem. They defined the horizontal rooting area of individuals as a closed polygon, and suggested that the root systems were distributed almost exclusively. A similar analysis was also reported for the seedlings of Loblolly pine (Mou et al. 1995). Such an arbitrarily defined rooting area may not exactly reflect the area that is actually influenced by the roots (Casper et al. 2003) or the intensity of root competition in response to depleted soil resources (Schenk 2006). However, these previous studies suggest that the relationship of a root system with its neighbors (i.e., extent of segregation or overlap) is helpful for analyzing the nature of belowground competition (Casper and Jackson 1997; Schenk et al. 1999). If we consider a corresponding measure of space occupation above the ground (i.e., crown projection area), interaction between aboveground and belowground intertree competition may be further analyzed.

We have studied root systems of *Larix gmelinii* (Rupr.) Rupr. trees growing on the continuous permafrost in central Siberia. The previous studies showed that *L. gmelinii* trees in two mature stands (>100 years old) expanded lateral roots horizontally, and that the area occupied by an individual root system was much larger than the crown projection area (Kajimoto et al. 1999, 2003). Kajimoto et al. (2003) also estimated the rooting area index as a measure of stand-level space occupation by root systems, and indicated that these two mature stands were likely to be fully closed below the ground by a root network. Development of such superficial root systems of *L. gmelinii* is linked with rather root-oriented carbon allocation (Kajimoto et al. 2006). In contrast, mature *L. gmelinii* forests established in the Siberian permafrost region are generally characterized by sparse stand structure: individual crowns rarely overlap (Bondarev 1997). These features suggest that intertree competition below the ground for soil resources or nutrients (e.g., nitrogen) becomes predominant over the competition for light above the ground following stand development. In other words, tree mortality may be governed mainly by belowground competition as the stand attains a certain age or size. To confirm such a hypothesis regarding intertree competition in *L. gmelinii* forests, however, we need further data of individual root systems from younger stands (<100 years old), because our previous findings were restricted to the mature larch stands.

In this article, we present results of individual-based root system measurement and analysis applied for *L. gmelinii* trees of three stands with different ages; young (26 years old), mature (100 years old) and overmature (>200 years old) stands. Two topics are highlighted: (1) spatio-temporal development pattern of root system, and (2) interactions between aboveground and belowground competition. For the first topic, detailed observation and annual-ring analysis of roots were applied for one excavated tree from the overmature stand, and factors affecting root system development are discussed. For the second topic, relationships between individual crown area and rooting area were examined for the sample trees of each stand; data for the overmature stand were published previously (Kajimoto et al. 1999, 2003). We estimated stand-level measures of aboveground and belowground space occupation (i.e., crown area and rooting area index), and use this to discuss how intertree competition differed among the stands. We also discuss the limitations of our analysis using these two indices of space occupation.

Materials and methods

Study site

The study site was located near the town of Tura in central Siberia (64° N, 100° E; 160 m asl), where *Larix gmelinii* was distributed predominantly. Preliminary reconnaissance for information such as stand age, structure, and floor vegetation, which was conducted along the two rivers, Nizhnyaya Tunguska (a branch of Yenisey River) and Kochechum, indicated that a major stand-replacing fire occurred extensively in late 1890s, and near even-aged *L. gmelinii* stands (ca. 105 years old) were widely distributed in the area (Abaimov et al. 2000; personal observations). Small-scale fire disturbances also occurred relatively frequently (e.g., 1978, 1990, 1994), resulting in the establishment of younger larch stands (<30 years old). According to the regional fire history, some larch forests were selected for studies of biomass, net primary production, and nutrient cycling in relation to stand age.

For the present analysis, we used the data of a tree census and root excavation taken from three *L. gmelinii* stands of different ages: young (called CR1978, 26 years old), mature (CF, 105 years old), and overmature stands (C1, ca. 220 years old; some individuals aged >260 years) (Table 1). The young stand (CR1978) was located on the east-facing slope along the Kochechum River, where a stand-replacing fire occurred in 1978. The mature stand (CF) was located on the almost flat terrace near the Nizhnyaya Tunguska River (25 km east from Tura), which regenerated after the fire of the late 1890s. The overmature stand (C1) was located on the east-facing gentle slope of the Kochechum River, and was an uneven-aged forest, because the fire disturbances (mostly ground surface fires) had occurred several times in the past (Kajimoto et al. 1999). Other characteristics of each study site are described elsewhere, such as ground-floor vegetation and topography (Abaimov et al. 1997, 2000; Zyryanova and Shitova 1999; Sofronov et al. 2000) and soil conditions (Matsuura and Abaimov 1999, 2000).

Tree census and sampling

Four permanent research plots were established in both CR1978 (5 × 5 m in each plot area) and CF (20 × 20 m), while only one large plot was established in C1 (50 × 20 m). Stem diameter at breast height (D) and tree height (H) were measured for all living *L. gmelinii* trees ($H > 1.3$ m) within each plot. Crown diameters were also measured along two perpendicular directions and individual crown projection area (CA) was calculated as a circle using the average crown diameter.

Root excavation was conducted for some *L. gmelinii* trees of different sizes that were selected around the permanent plots of each stand ($n = 10$ in CR1978, $n = 10$ in CF, and $n = 7$ in C1). We selected these trees by covering the whole range of D in each stand in order to estimate biomass with site-specific D-base allometry. After harvesting the aboveground parts, roots were excavated manually, except for the largest tree of each of two stands (CF and C1). All coarse roots (≧5 mm in diameter) were excavated, and fine roots (<5 mm) were traced carefully to harvest most of the roots with diameters larger than 0.5–1 mm. For the majority of these excavated trees, we sketched a projection of each root system (i.e., structural lateral root system) on a horizontal plane by separating the parts of coarse and fine roots, and then the root map was used for calculation of individual rooting area (see explanations later). In this article, the term lateral root is used in the sense of morphologically defined roots (i.e., first-order lateral root that originated from tap root or stem), and thus one lateral root consisted of both size-class roots (i.e., coarse and fine roots).

Detailed measurement of spatial distribution and elongation of lateral roots

Among the five excavated trees of the overmature stand (C1), we selected one relatively large tree (no. 3, 207 years old, D = 7.7 cm, H = 8.3 m) for detailed measurement of spatial distribution and elongation growth pattern analysis of the lateral roots. The root system of tree no. 3 consisted of nine first-order lateral roots (R1–R9) (Fig. 1); only a main axis of each lateral root, which was defined as the longest root among some proliferated roots, was used for these measurements and analysis. During excavation, vertical positions of these lateral roots (i.e., depth in soils from the ground surface) were measured along each main root at 10-cm intervals from the tree stump toward the end portion (i.e., the border of coarse and fine roots; diameter = 5 mm). Root disks (1–3 cm in thickness) were also sampled from these lateral roots at their basal portions (i.e., near a

Table 1. Stand characteristics of the three study stands of *Larix gmelinii* in Tura

Stand	Stand age[a] (years)	Tree density[b] (ha^{-1})	Mean diameter[b] D (cm)	Mean height[b] H (m)	Active layer depth[c] (cm)
Young CR1978	26	13 700	2.73	4.80	53
Mature CF	105	5475	3.15	3.41	64
Overmature C1	220	1910	6.83	5.50	25

[a] Stand ages of CR1978 and CF are expressed as the years (at 2004) after each stand-replacing fire, 1978 and late 1890s, respectively. For the uneven-aged, overmature stand (C1), average age of the seven excavated trees and other sampled trees is shown; minimum and maximum ages of the excavated trees are 147 years (no. 2) and 266 years (no. 6), respectively (Kajimoto et al. 1999, 2003)

[b] Tree density, and mean stem diameter at breast height (D) and tree height (H) of CR1978 and CF are the averages of four research plots

[c] Active layer depth was determined in mid-July or late July, but the measurement in each stand was conducted in different years; in 2000 (CR1978), 2004 (CF) and 1995 (C1). Original data for C1 are from Sofronov et al. (2000); those of the other two stands are from Matsuura et al. (unpublished)

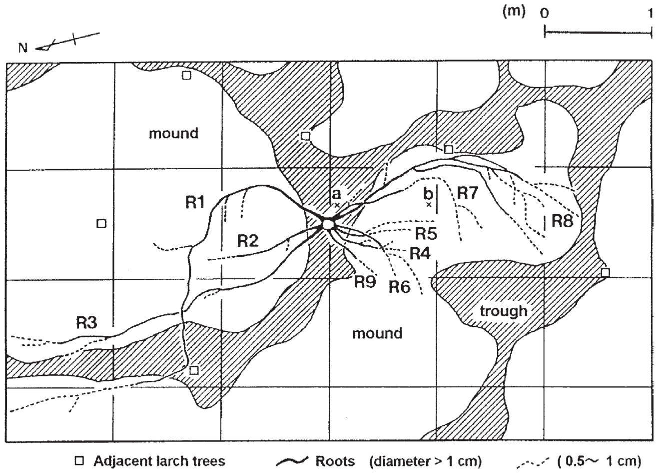

Fig. 1. Horizontal projection map of root system of *Larix gmelinii* tree (207 years-old) sampled in the overmature stand (no. 3, C1). Size dimensions and rooting area (RA) are $D = 7.7\,\mathrm{cm}$, $H = 8.3\,\mathrm{m}$, and RA = $5.3\,\mathrm{m}^2$. Each of nine first-order lateral roots is shown by the number from *R1* to *R9*. *Shaded area*, trough; *open area*, mound. Height difference between bottom of trough (*a*) and top of mound (*b*) is about 60 cm

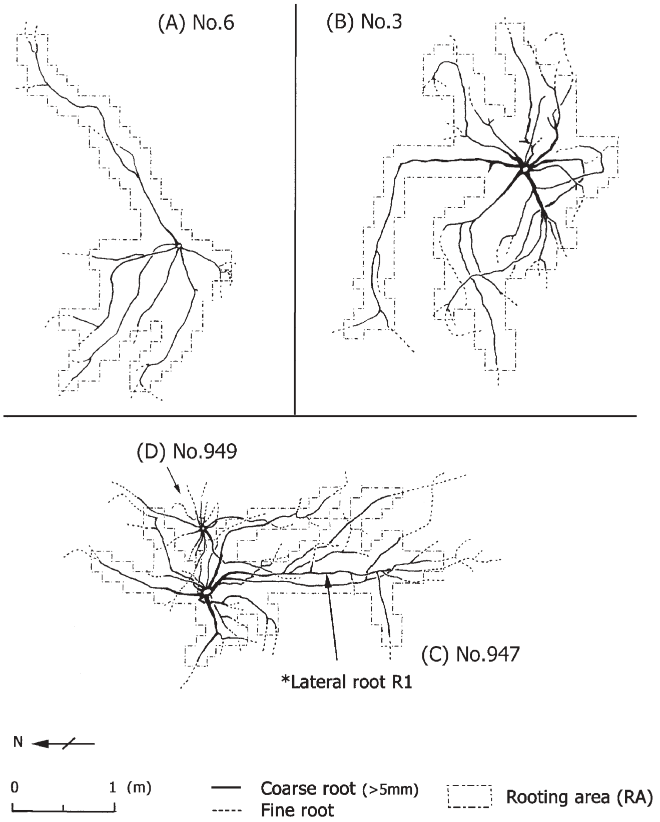

Fig. 2A–D. Examples of horizontal rooting maps of *L. gmelinii* trees sampled from the mature stand (tree nos. 6 and 3, CF, 105 years old) and young stand (tree nos. 947 and 949, CR1978, 26 years old) Rooting area (RA) of each tree is calculated as the area inside each closed polygon shown by the *dot-dashed line*. Stem diameter, tree height, and RA are as follows: **A** no. 6: $D = 2.3\,\mathrm{cm}$, $H = 2.5\,\mathrm{m}$, RA = $2.3\,\mathrm{m}^2$; **B** no. 3: $D = 5.9\,\mathrm{cm}$, $H = 6.4\,\mathrm{m}$, RA = $3.8\,\mathrm{m}^2$; **C** no. 947: $D = 4.4\,\mathrm{cm}$, $H = 6.7\,\mathrm{m}$, RA = $2.3\,\mathrm{m}^2$; **D** no. 949: $D = 2.1\,\mathrm{cm}$, $H = 4.5\,\mathrm{m}$, RA = $0.7\,\mathrm{m}^2$

junction with tap root; <5–7 cm from the center of the tap root) and at more distant positions with 10-cm intervals. The numbers of annual rings of these root disk samples were counted using a dissecting microscope. Continuity of circumference was examined to match the rings correctly that were measured along the four radii (see also Kajimoto et al. 1999). From these annual ring data, the past elongation curve of each lateral root was reconstructed.

The pattern of lateral root elongation was also examined for the other two excavated trees of C1; no. 2 (266 years old, $D = 7.9\,\mathrm{cm}$, $H = 6.9\,\mathrm{m}$) and no. 6 (147 years old, $D = 2.5\,\mathrm{cm}$, $H = 2.9\,\mathrm{m}$). We sampled root disks at different positions from three lateral roots ($n = 3$; R1–R3) selected from each tree, and reconstructed their elongation growth curves in the same manner as for the case of tree no. 3. As for these sample trees, the dimensions and some root parameters were previously reported, such as the numbers of lateral roots, maximum lateral root length, and tap root length (see Table 2 in Kajimoto et al. 2003).

Calculation of horizontal rooting area

As a parameter of belowground space occupied by the root system, horizontal rooting area (RA) was calculated for the root-mapped individuals ($n = 10$ for CR1978, $n = 7$ for CF, and $n = 5$ for C1). A circle or polygon has often been used for defining such horizontal area of plant root systems (see review by Schenk et al. 1999). For *L. gmelinii*, however, the horizontal distribution of the root system was rather asymmetric (see Results), and thus we calculated RA by imposing a closed polygon with combined squares on each rooting map (one square = $0.1 \times 0.1\,\mathrm{m}$) (Fig. 2). The area of RA was defined as the area within approximately 30 cm of the parts of coarse root along lateral roots. The definition was based on the previous observations for five sample trees of C1 and those of another mature stand: most of the fine roots that occurred along lateral roots were less than 30 cm in length (Kajimoto et al. 2003). However, at the time, it was uncertain whether such a definition of RA (i.e., <30 cm) was also applicable to younger *L. gmelinii* trees such as the sample trees of CR1978. To confirm this point, we examined spatial distribution and sizes of fine roots for one medium-sized sample tree (No. 947, 25 years old, $D = 4.4\,\mathrm{cm}$, $H = 6.7\,\mathrm{m}$) of CR1978. Among the eleven first-order lateral roots of this sample tree (Fig. 2C), the longest lateral root (R1) was selected; R1 was 300 cm in total length, of which the parts of coarse and fine roots were 200 cm and 100 cm in length, respectively. All living fine roots (<5 mm in basal diameter) occurring from R1 were measured for their horizontal positions (i.e., distance from the tree stump), basal diameters, and lengths.

Data analysis

First, we examined relationships between RA and CA for the sample trees of each study stand. As for the five sample trees of overmature stand (C1), it was previously found that

RA was linearly correlated with CA (Kajimoto et al. 2003). Thus, we applied a linear equation ($y = Ax + B$; A and B are regression slope and intercept, respectively) for fitting a model to data of the other two stands (CR1978, CF). Second, we examined relationships between RA and stem diameter (D). They were approximated by applying a power equation ($y = Ax^B$) (i.e., log–log linear model; $\ln y = B \ln x + \ln A$). Coefficients of each regression model were calculated using the ordinary least-squares method; the coefficients of power-form RA–D regression were determined after log transformation (natural base) of the data. A correction factor was applied to the regression intercept (A) (Sprugel 1983). Fit of each regression type was tested by coefficient of determination (r^2). Comparisons of the coefficients among the three stands were made by the analysis of covariance (ANCOVA) (Zar 1999), and post-hoc multiple comparison test (Tukey's HSD) was conducted if necessary.

We defined the rooting area index (RAI; $m^2 m^{-2}$) as the sum of individual RA per unit land area, which was considered a stand-level measure of belowground space occupation by the root network. Among the three stands, RAI of the overmature stand (C1) was previously estimated using a simple linear RA–D regression, which was determined by pooling the sample data of C1 and another mature stand (ca. 105 years old) (this mature stand was called W1 in Kajimoto et al. 2003). In the present article, RAI of each stand was estimated by applying the newly proposed site-specific RA–D allometric equation (as mentioned above) to the census data, because the regression intercepts differed among the three stands (see Results). We examined how RAI was related to crown area index (CAI; $m^2 m^{-2}$), which is a corresponding index of space occupation above the ground (sum of individual CA per unit land area). We discuss the interaction between aboveground and belowground competition using these two indices.

Results

Spatial distribution of root system

All the *Larix gmelinii* trees ($n = 27$ in total) excavated in the young (CR1978) and two old stands (CF, C1) developed shallow and rather asymmetric root systems (see examples in Figs. 1 and 2). For example, the sample tree of the overmature stand (no. 3, C1), which was employed for the detailed observation, had nine first-order lateral roots (R1–R9), and lengths of some longer lateral roots reached 4–5 m (e.g., R1, R3) (Fig. 1). In this overmature stand, earth hummock microtopography was typically developed: regularly spaced mounds (50–80 cm elevated) surrounded by narrow troughs (Kajimoto et al. 1999). All the lateral roots of the sample tree (no. 3) expanded into the nearby mounds rather than into the troughs (Fig. 1). Vertically, each lateral root was distributed only within the upper soils (<10 cm depth), except around the tree stump (<50 cm in distance) (Fig. 3). The tap root of the tree was aborted at a depth of 36 cm (Kajimoto et al. 2003).

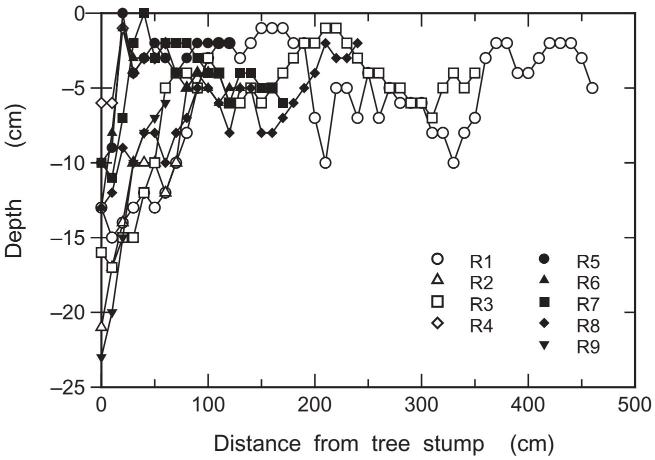

Fig. 3. Vertical distribution of the nine lateral roots (*R1–R9*) of *L. gmelinii* trees sampled from the overmature stand (no. 3 of C1; see Fig. 1). Depth of each lateral root (i.e., vertical distance from ground surface) at 10-cm intervals is plotted against horizontal distance from the tree stump

For the root systems of sample trees in CR1978 and CF, the numbers of first-order lateral roots ranged from 5 to 15, and their lengths varied between 0.5 and 4 m. Vertical distributions of the lateral roots of these two stands were not measured in detail. However, dieback of each tap root occurred at its tip portion (<10–30 cm in depth), and lateral roots were mostly found within the upper soils (<10–15 cm depth) (personal observations), as seen for the case of the sample tree of the overmature stand (no. 3, C1) (Fig. 3).

Expansion of lateral roots

For the sample tree of the overmature stand (no. 3, C1), the numbers of annual rings of the nine lateral roots at each basal portion ranged from 17 to 95. This indicated that the lateral roots had originated adventitiously and started expansion during a period of at least >100 years after the tree establishment (207 years ago). These nine lateral roots were roughly classified into three age groups according to the difference in the year of initial expansion; relatively old (R1, R2, R3: 82–95 years), intermediate (R8, R9: 57–72 years), and younger (R4–R7: 17–33 years) roots.

Reconstructed growth curves of these lateral roots (Fig. 4A) showed that average annual elongation rate (i.e., averaged throughout each observation period) reached 10–17 cm year^{-1} for the four younger roots (R4–R7). The average elongation rates of roots in the other age groups, 6–7 cm year^{-1} (R1, R3, R8) and less than 2 cm year^{-1} (R2, R9), were relatively small in comparison with the younger roots. At a shorter time scale, annual root elongation rates changed frequently for each lateral root. For example, the two old roots (R1, R3) that expanded into the same mound (i.e., left side mound in Fig. 1) changed elongation rates temporally, and the patterns were not coincident with each other in some cases: R1 grew faster in 1930–1940 and 1950–1965, while R3 grew slowly in these periods (Fig. 4A).

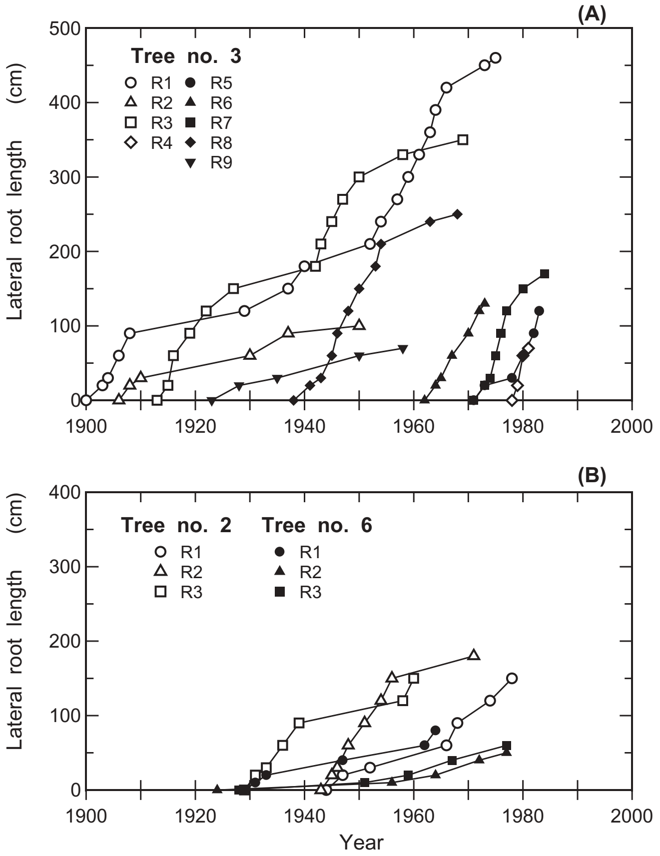

Fig. 4A, B. Reconstructed elongation growth curves of lateral roots for three *L. gmelinii* trees sampled in the overmature stand (C1). **A** Nine lateral roots (*R1–R9*) of tree no. 3 (see Figs. 1, 3); **B** three lateral roots (*R1–R3*) of each of trees no. 2 and no. 6. Dimensions of tree no. 3 are shown in Fig. 1. For the other two trees, age and dimensions are; no. 2: 266 years old, D = 8.9 cm, and H = 6.9 m; no. 6: 147 years old, D = 2.5 cm, and H = 2.9 m. Each rooting map was previously described (Kajimoto et al. 1999)

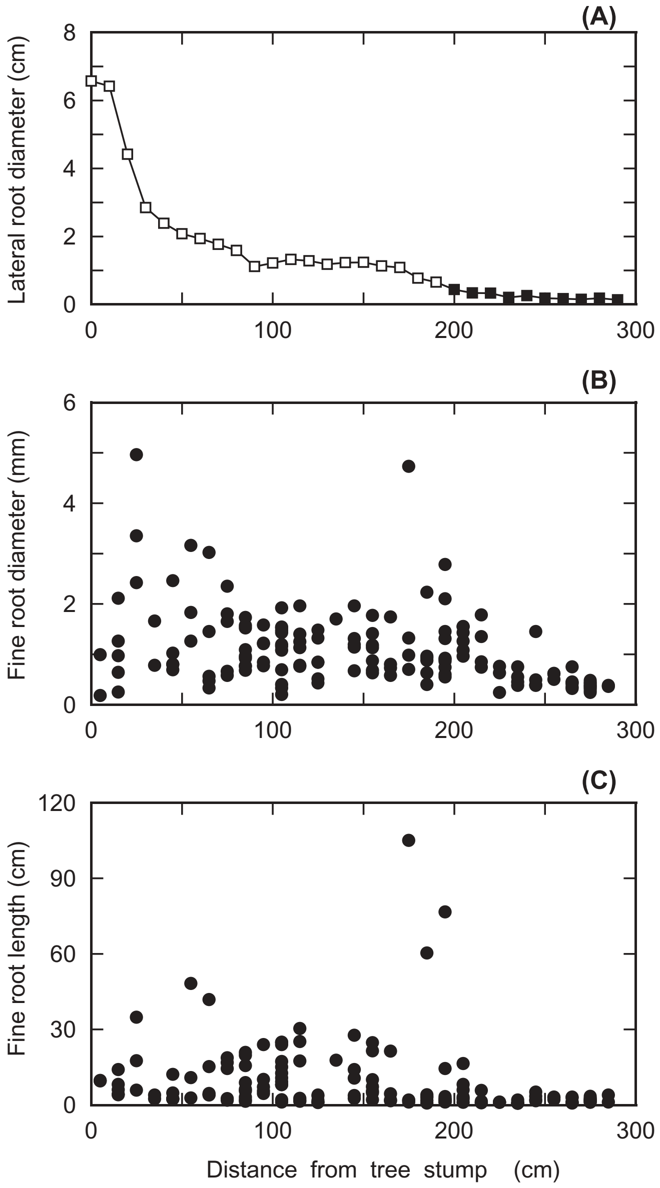

Fig. 5A–C. Diameter change of the lateral root (R1) of *L. gmelinii* tree sampled from the young stand (no. 947, CR1978) (**A**), and basal diameters (**B**) and lengths (**C**) of all fine roots (total $n = 146$) occurring from R1 (see root system map in Fig. 2C). Basal position of each fine root along R1 is expressed as a distance from the tree stump. **A** *Open squares*, parts of coarse root (0–200 cm); *filled squares*, fine roots (>200 cm)

As for the other two sample trees of C1, the average elongation rates of the three lateral roots were 5–6 cm year^{-1} (R1–R3 of no. 2) and 1–2 cm year^{-1} (R1–R3 of no. 6)(Fig. 4B). These values fell in the range of average elongation rates observed for the nine lateral roots of tree no. 3 (Fig. 4A). For these two trees, elongation growth pattern did not always synchronize among the lateral roots with similar ages, for example, R1 versus R3 of tree no. 2, and R1 versus R2 and R3 of tree no. 6.

Fine root distribution around lateral root

During the root excavation, we observed that fine roots were mostly distributed in the upper soils (<5–10 cm) for all the sample trees. For the sample trees of the two old stands (CF, C1), many fine roots expanded into litter layers (e.g., 6–12 cm in thickness in CF, and 4–8 cm in C1) and moss or lichen mats just near the ground surface (personal observations).

As shown in the case of one young sample tree (no. 947, CR1978) (Fig. 2C), fine roots occurred nearly continuously along the examined lateral root (R1). Diameter of R1 declined sharply near the tree stump (0–30 cm in distance), and then decreased gradually until the transition (i.e., 200 cm in distance) between the coarse and fine roots (each part was shown by white and black squares, respectively in Fig. 5A). In total, 146 fine roots occurred along this lateral root. These fine roots were mostly less than 2 mm in basal diameter (Fig. 5B), and were shorter than 30 cm, except for a few larger roots (>2 mm in diameter) (Fig. 5C). However, if we consider separately the parts of coarse and fine roots for this examined lateral root, lengths of all fine roots that occurred from the part of fine root of R1 (i.e., >200 cm in distance) were less than 10 cm. These results suggested that

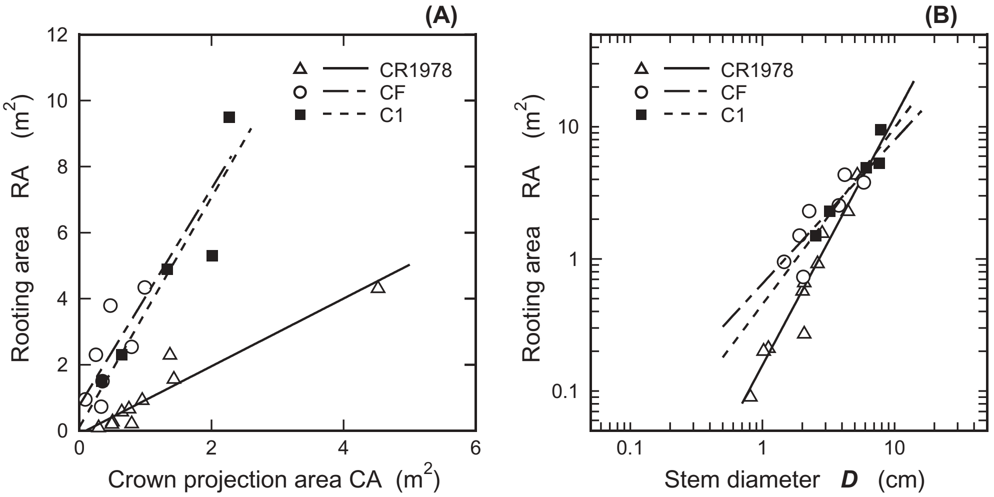

Fig. 6A, B. Relationships between rooting area (*RA*) and **A** crown projection area (*CA*) and **B** stem diameter (*D*) for the sample trees of three *L. gmelinii* stands. Regression lines are approximated by linear ($y = A\,x + B$) (**A**) and log–log linear ($y = A\,x^B$) (**B**) models. The regressions are **A** CR1978: RA = 1.02 CA − 0.10, $r^2 = 0.912$; CF: RA = 3.30 CA + 0.07, $r^2 = 0.571$; C1: RA = 3.48 CA + 0.12, $r^2 = 0.859$. **B** CR1978: RA = 0.16 $D^{1.93}$, $r^2 = 0.931$; CF: RA = 0.65 $D^{1.15}$, $r^2 = 0.730$; C1: RA = 0.45 $D^{1.35}$, $r^2 = 0.927$

Table 2. The estimates of crown area index (CAI) and rooting area index (RAI) in the three study stands of *L. gmelinii* in Tura

Stand	CAI[a] (m^2 m^{-2})	Mean CA (m^2)	RAI[b] (m^2 m^{-2})	Mean RA (m^2)
Young CR1978	1.33	0.97	1.80	1.31
Mature CF	0.18	0.33	1.35	2.47
Overmature C1	0.34	1.78	1.25	6.55

For CR1978 and CF, CAI and RAI are the average values of four research plots. Mean values of CA and RA were calculated by dividing CAI and RAI by tree density of each stand, respectively (Table 1)

[a] Sum of crown projection areas (CA) per unit land area; CA was directly measured for all living *L. gmelinii* trees in each stand

[b] Sum of individual horizontal rooting areas (RA) per unit land area; each RA was estimated by applying site-specific *D*–RA regression (Fig. 6B) to the census data

our definition of RA (i.e., area <30 cm around coarse root parts of lateral root) was applicable to the individuals of *L. gmelinii* in the young stand (CR1978).

Relationships between rooting area and crown area

Horizontal rooting area (RA) ranged from 0.09 to 4.31 m^2 for the sample trees of CR1978, and from 0.73 to 4.34 m^2 for those of CF (see some examples in Fig. 2). RA of the five sample trees of C1 ranged from 1.50 to 9.50 m^2 (original data were described in Kajimoto et al. 2003). In each stand, RA was positively correlated with the crown projection area (CA) ($P < 0.01$ for C1 and CR1978, $P < 0.05$ for CF) (Fig. 6A). The regression slopes differed significantly among the stands ($F_{[2,\ 16]} = 10.8$, $P < 0.01$; ANCOVA); the slope was smaller for the sample trees of CR1978 (1.02) than that of CF (3.30) and C1 (3.48) (Tukey's HSD test).

RA was significantly correlated with the stem diameter (*D*) for the sample trees of each stand ($P < 0.01$) (Fig. 6B). Slopes of the allometric relationships did not differ among the stands ($F_{[2,\ 16]} = 3.22$, $P = 0.07$; ANCOVA). However, the regression intercepts differed significantly ($F_{[2,\ 16]} = 7.05$, $P < 0.01$; ANCOVA). Based on the result, rooting area index (RAI) of each stand was estimated by applying site-specific *D*–RA allometry to the census data. The estimate of RAI was largest in CR1978 (1.80 m^2 m^{-2}), followed by CF (1.35 m^2 m^{-2}) and C1 (1.25 m^2 m^{-2}) (Table 2). The average value of RA (i.e., RAI/tree density) increased with stand age; 1.31 m^2 (CR1978), 2.47 m^2 (CF), and 6.55 m^2 (C1) (Table 2).

Discussion

Factors affecting spatio-temporal root system development of *Larix gmelinii*

Our previous studies reported that soil temperature and water conditions varied conspicuously along the well-developed earth-hummock topography in the overmature *Larix gmelinii* stand (C1). For example, in mid-summer, soils at 10-cm depth are much warmer (3°–5°C) and drier on elevated mounds than in surrounding depressed troughs (Kajimoto et al. 2003). Seasonally, the upper soils on the mounds start to melt earlier (1 month and more) than nearby troughs, and hence the annual heat sum (i.e., cumulative daily mean soil temperatures above 0°C) was two to three times larger on the mounds (1200°–1300°C days) than inside the troughs (400°–500°C days) (Kajimoto et al. 1998). As indicated by our sample tree of the overmature stand (no. 3, C1), all the lateral roots expanded within the upper soils (<10 cm), and their horizontal directions were restricted to the mounds rather than the nearby troughs (Figs. 1, 3). Thus, the configuration of spatial root system development is primarily related to such a gradient of soil temperature along the earth hummock topography. Tryon and Chapin (1983) reported that soil temperature largely controlled seasonal root growth for some subarctic tree species such as *Larix laricina* Du Roi.

The earth-hummock topography is not so typical in the young (CR1978) and mature (CF) stands. Active layer thickness (i.e., depths of thawed soils in summer) of the young and mature stands (53 and 64 cm) are larger than that of the overmature stand (25 cm) (Table 1), indicating that a space for vertical root growth is potentially large in these two stands. However, all the trees excavated from these two stands also constructed a similar root system as seen for the trees from the overmature stand: superficial root system (<30 cm in depth) and rather asymmetric expansion of lateral roots (Fig. 2). Thus, vertical development of the *L. gmelinii* root system in our study site may be essentially limited by cold soils due to the existence of permafrost, even for the individuals of the young stand (CR1978).

Annual ring data are useful for growth analysis of stems and also for the roots; however, as yet few attempts of such growth analysis have been reported for tree roots (e.g., Fayle 1975; Deans 1981; Reynolds 1983; Drexhage et al. 1999). The reconstruction of growth curves of the lateral roots, which was applied to some old sample trees of C1 (nos. 2, 3, and 6), showed that average annual elongation rates differed among the roots of each tree. Also, it was detected that elongation rates changed temporally for each lateral root, and such changes did not necessarily synchronize between roots of similar age groups (Fig. 4). These results suggest that the temporal pattern of the larch root system development reflects the difference in the amount of annual carbon allocation among lateral roots. Our present analysis is, however, restricted to only elongation growth of the first-order lateral roots. For discussion of a whole root system development in relation to such a carbon allocation process, we must also analyze diameter and/or volume growth patterns of the roots.

Interaction of aboveground and belowground space occupation in *Larix gmelinii* forest

The relationships between individual crown area (CA) and rooting area (RA) differed among the three stands: RA was almost proportional to CA in the young stand (CR1978), but RA was much larger than CA in the other two older stands (CF, C1) (Fig. 6A). The difference might reflect differences in size dependency of these two parameters on space occupation, although both CA and RA increased with stem diameter (*D*) within each stand. For example, RAs were generally larger in the two older stands than in the young stand if smaller sample trees (i.e., $D < 4$–5 cm) are compared (Fig. 6B). As for the case of crown area, however, there was no such clear difference between the young stand and the two older stands (data not presented).

Generally, individual crown architecture (e.g., CA) varies largely by stand age and tree density (O'Hara 1988; Smith and Long 1989, Seymour and Kenefic 2002), but might also be influenced by many other factors (e.g., site location, and soil water and nutrient conditions). In our three study stands, the average CA and some of tree size parameters (i.e., mean tree height) did not increase substantially following the increase of stand age (Tables 1, 2), indicating that any of such site-specific external factors affect individual crown development. In contrast, the average RA and other parameters changed regularly in the order of stand age (i.e., mean *D* increases, and tree density decreases). Thus, the clear discrepancy of CA–RA relationships between the young stand and the two older stands (Fig. 6A) shows that *L. gmelinii* certainly continues to expand the root system with aging, but may not enlarge the crown area correspondingly.

Larix gmelinii regenerates intensively after fire disturbance and generally forms dense stands at an early growth stage in central Siberia (Abaimov and Sofronov 1996). At the mature stage, however, the larch forests are characterized by sparse stand structure, as seen for our two older stands (CF, C1). Bondarev (1997) reported that the extent of canopy closure (CAI in our study) ranged between 0.2 and $0.4\,\mathrm{m^2\,m^{-2}}$ for many *L. gmelinii* stands (mostly mature stands, >100 years old) in this region. It is still uncertain why such a very sparse larch forest is eventually formed in the region of continuous permafrost. As suggested by Abaimov et al. (2000, 2002), we may need to consider how the intertree competition occurs below the ground following stand development.

At a stand level, we found that RAI exceeded unity ($>1.0\,\mathrm{m^2\,m^{-2}}$) in all study stands, although the estimate was slightly larger in the young stand than those in the two older stands (Table 2). This indicates that the root network is fully closed, or individual root systems are certainly overlapped in both young and old stands. In contrast, individual crowns were completely overlapped with one another only in the young stand ($\mathrm{CAI} = 1.3\,\mathrm{m^2\,m^{-2}}$), while there were much open space between the neighboring crowns in the two older stands ($\mathrm{CAI} < 0.3\,\mathrm{m^2\,m^{-2}}$) (Table 2). These CAI–RAI relationships suggest that intertree competition for both aboveground and belowground spaces occurs in the young stand, but only belowground competition still occurs in the two older stands. In other words, competition below the ground for the uptake of soil resources may become predominant over the competition that occurs above the ground for light as a stand reaches the mature stage (>100 years).

Advantages and limitations of individual-based root system measurement

Our case studies emphasized some advantages of individual-based measurement and analysis of root systems. In particular, we have proposed a method of analyzing the interaction between aboveground and belowground competition using the two indices of space occupation at individual (CA, RA) and stand levels (CAI, RAI). However, some limitations apply in this analysis. First, we defined RA by considering only two-dimensional space (i.e., horizontal area). The definition was based on a unique feature that occurs in the permafrost region: *L. gmelinii* develops a superficial root system exclusively within the upper soils. Two-dimensional analysis might not be applicable immediately to other forest ecosystems where the roots are able to penetrate more deeply.

Second, our rooting maps were obtained mostly for individuals that were located within a certain distance of each other, except for some cases of sample trees in the young stand (e.g., Fig. 2C, D). Thus, RAI implies the extent of root network closure, but does not provide any information on how much the root systems are segregated or overlapped (Casper and Jackson 1997), or where root competition occurs intensively in response to depleted soil resources (Schenk et al. 1999; Casper et al. 2003). To address this question, excavation of root systems for all trees within a certain area may be required (e.g., Brisson and Reynolds 1994), although it seems extremely laborious to have to apply to forest trees.

Although our method using the two indices (CAI, RAI) requires some improvement, the results suggest an interactive feature of aboveground and belowground space occupation in *L. gmelinii* forests: belowground intertree competition may become predominant as a stand ages. In the larch forest of Siberia, it is suggested that availability of soil nitrogen is essentially limited, and its reduction with stand age primarily controls individual growth and aboveground biomass accumulation (Schulze et al. 1995). Thus, for further discussion of our hypothesis, we should assess how the belowground space occupation (RAI) or biomass allocation into root systems are connected with such a major limiting soil resource. For this purpose, we also need to fill the lack of data along an age sequence, including intermediate (30–100 years) and very young stands (<30 years).

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