Chapter 16
Root System Development of Larch Trees Growing on Siberian Permafrost

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16.1 Introduction

Below-ground processes have been highlighted in the studies of carbon flux, nutrient cycling, and biodiversity in many terrestrial ecosystems under changing climates (e.g., Chapin and Ruess 2001; Schulze 2006). So far, as tree roots are concerned, much attention has recently been paid to the study of fine roots rather than coarse roots (Brunner and Godbold 2007), since fine roots are more important biologically, such as in resource uptake and mycorrhizal association (Vogt et al. 1996; Read and Perez-Moreno 2003). This trend is aided by improvements in observation techniques and/or devices (i.e., minirhizotron, digital image analyzer) that enable us to monitor fine root dynamics (e.g., Vogt and Persson 1991; Hendrick and Pregitzer 1996; Majdi 1996; Vogt et al. 1998; Johnson et al. 2001). In contrast, individual-based root observation (i.e., root system excavation), which requires laborious and time consuming work, seems outdated today, although many classical studies indicated advantages of this approach. For example, measurement of coarse root mass is essential in the estimation of stand-level below-ground biomass and production (e.g., Karizumi 1974; Santantonio et al. 1977; Deans 1981). Also, quantitative description of the spatial patterns of root systems (e.g., rooting map) tell us characteristics of species-specific strategies under local or microscale soil conditions in natural habitats (e.g., McMinn 1963; Eis 1974; Fayle 1975a, b; Karizumi 1979; Coutts 1983; Reynolds 1983; Kuiper and Coutts 1992; Drexhage and Gruber 1998).

Among these classical studies, some attempted to analyze root growth patterns using information of growth rings and discuss temporal patterns of root system development in monospecific conifer stands (Fayle 1975a, b; Coutts 1983; Kuiper and Coutts 1992). They also focused on the examination on below-ground space that was occupied by root systems (i.e., projection area, or width in horizontal spread), and its relationship to above-ground space that was occupied by tree crowns. These case studies demonstrated that analysis of temporal patterns in both root systems and crowns is a useful approach for understanding processes of above-/below-ground carbon partitioning. Furthermore, if corresponding stand-level indices of above- and below-ground space occupation are considered and

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if age-related change in their relationship is examined, we may evaluate the mode of intertree competition against major target resources (i.e., light vs. soil nutrients) in a given forest ecosystem (Kajimoto et al. 2007).

From these viewpoints, field observations and analyses of individual root systems have been recently conducted for *Larix gmelinii* (Rupr.) Rupr. (Gmelin larch) trees growing on permafrost in Central Siberia (Kajimoto et al. 1999, 2003, 2006, 2007). Before these studies, it was known that larch trees often developed shallow root systems (e.g., see literature in Abaimov and Sofronov 1996). However, available information had been mostly qualitative, and processes of root system development had not been discussed in relation to soil environments. As was reported earlier (see Chaps. 6 and 7), tree growth, productivity, and development of *Larix* taiga are likely to be influenced largely by constraints of peculiar soil environments in the permafrost region (i.e., low soil temperature and nutrient limitation). Thus, in this chapter, a linkage between the development pattern of *L. gmelinii* root systems and permafrost soil environments in the region was discussed by synthesizing results of previous papers and other unpublished data. Topics focused for discussion are the following:

- How is spatial development of the root system affected by microscale conditions of soil temperature and water created by typical topography (i.e., hummock) in the study area?
- How is temporal development of the root system characterized?
- Is the extent of below-ground space occupation by root systems balanced or not with that of above-ground space occupation by crowns?
- How does the mode of intertree competition change following stand development?

16.2 Data Source

16.2.1 Study Site

Root systems of *L. gmelinii* were sampled in several stands located in Tura, Central Siberia (64°N 100°E; 160 m a.s.l.) (see Fig. 1.1). The root sampling was mainly aimed at estimating coarse root biomass (see Chap. 6), but the data were further employed for the analysis of individual root systems. In this chapter, the data on root systems obtained from the following four larch stands with different ages were used; one young stand (26-year old; abbreviated as CR1978), two old stands (ca. 105-year old; CF and W1), and one old multiaged stand (averaged ca. 220-year old; C1) (Fig. 1.2). Three stands (CR1978, CF, and W1) were almost even-aged due to rapid tree establishment after a stand-replacing fire at each site (details see Table 6.1). Common procedures used in root sampling and measurement, and definitions of some key parameters that were used for data analysis will be explained later in the text. Further details of the procedures were described elsewhere;

CR1978 and CF (Kajimoto et al. 2007), W1 (Kajimoto et al. 2003), and C1 (Kajimoto et al. 1999, 2003).

16.2.2 Methods of Root System Excavation and Measurements

Root sampling was conducted for selected trees with different sizes in each stand (n = 5–10 per stand) (Table 16.1; see examples in Fig. 16.1). Roots were excavated manually, including both coarse (≧ 5 mm in diameter) and fine roots (< 5 mm). Fine roots were traced carefully as far as practical, so that roots with diameters larger than 0.5–1 mm were mostly uncovered. For each root system, its horizontal projection was sketched as a map, and all living lateral roots (≧ 5 mm in basal diameter) occurring from the tap root (or lower part of the stem) were labeled (e.g., R1 and R2). Basal diameter and length of each lateral root were measured. Lateral root length was defined as the length from the basal portion to the boundary between coarse and fine roots (i.e., diameter = 5 mm) along the longest main axis. In this article, the term "lateral root" was used as a morphologically defined unit synonymous to a first-order root (e.g., Drexhage et al. 1999). Lateral root contains both parts of coarse and fine roots in terms of root diameter size (Kajimoto et al. 2007).

Table 16.1 Size dimensions of *L. gmelinii* root systems excavated in the four stands at Tura in Central Siberia. Stand age indicates the years (at 2004) that passed after each stand-replacing fire, except for old multiaged stand (C1), and tree age shows the range of trees sampled in each stand (details see Table 6.1)

	Young	Old		Old multiaged
	26-year old	105-year old	105year old	>220-year old
Stand age name	CR1978	W1	CF	C1
Number of sample trees	10	7	9	5
Tree age (year)	24–26	92–100	104–105	147–266
Tap root length (cm)	12.4 (8–19)	17.4 (13–22)	19.4 (13–29)	28.6 (19–40)
Number of lateral roots	9.3 (4–15)	8.6 (6–13)	9.0 (5–14)	7.0 (4–9)
Maximum root diameter (cm)	2.2 (0.8–5.9)	3.3 (1.8–5.6)	2.3 (1.0–4.4)	5.6 (3.0–8.1)
Maximum root length (cm)	128 (25–320)	170 (80–350)	206 (75–320)	218 (100–460)

Lateral root diameter is the value measured at basal portion for a longest lateral root. Lateral root length is the distance between basal and end portion of a part of coarse root (i.e., diameter > 5 mm, excluding fine roots). Value of each size parameter is mean of sample trees (range is shown in parenthesis). Data source: W1 and C1 (Kajimoto et al. 2003); CR1978 and CF (Kajimoto et al. unpublished data)

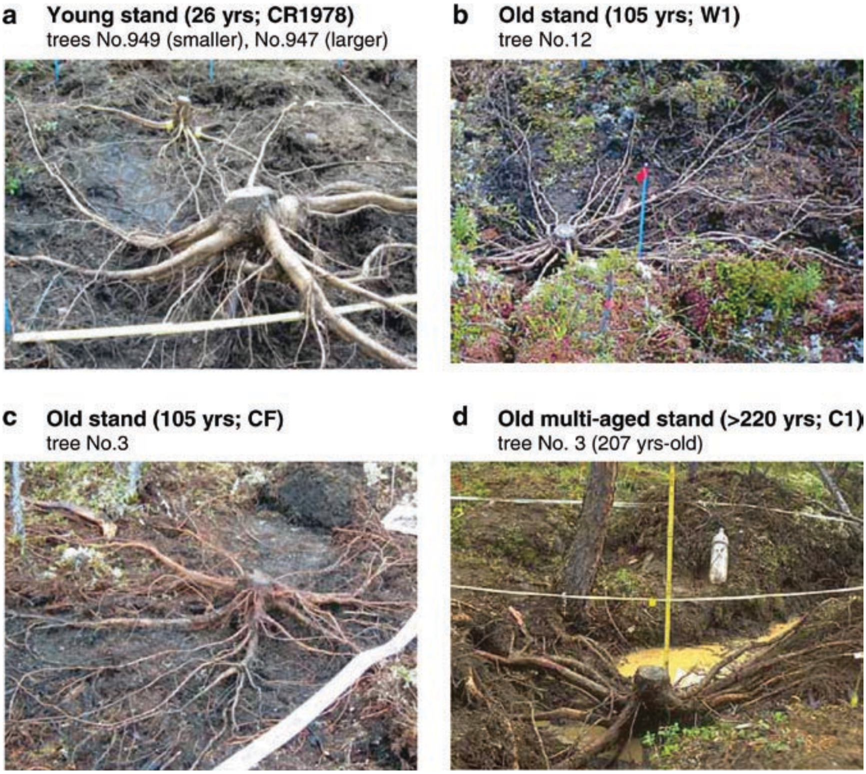

Fig. 16.1 Examples of *L. gmelinii* root systems excavated in four stands at Tura, Central Siberia. (**a**) Trees No. 947 (larger one; 25 years-old at sampling year, breast height diameter $D=4.4$ cm) and No. 949 (smaller one; 24 years-old, $D=2.1$ cm) in young stand (CR1978). (**b**) Tree No. 12 (99 years-old, $D=3.2$ cm) of old stand (W1). (**c**) Tree No. 3 (105 years-old, $D=5.9$ cm) of old stand (CF). (**d**) Tree No. 3 (207 years-old, $D=7.7$ cm) of old multiaged stand (C1). Tap root length (i.e., depth of aborted tip portion) is 14 and 12 cm (No. 947 and No. 949 of CR1978, respectively), 19 cm (No. 12 of W1), 23 cm (No. 3 of CF), and 36 cm (No. 3 of C1) (photos: T. Kajimoto) (*see* Color Plates)

16.2.3 Parameters of Above- and Below-Ground Space Occupation

Horizontal rooting area (RA) was considered as the measure of below-ground space occupied by an individual root system. For each excavated tree, RA was defined as the area within approximately 30 cm along both sides of all lateral roots (i.e., parts of coarse root) and was calculated by imposing a square-combined closed polygon on each rooting map (minimum square $=0.1\times0.1$ m^2) (see examples in Fig. 16.2). The definition was based on the observations that many fine roots occurred more or less continuously along the coarse lateral roots, and their lengths were mostly shorter than 30 cm for both young and mature trees (Kajimoto et al. 2003, 2007). Thus, RA covers the area where most of the active roots (i.e., living fine roots) are distributed; although, it ignores the space explored by a few extremely long fine roots (>30 cm).

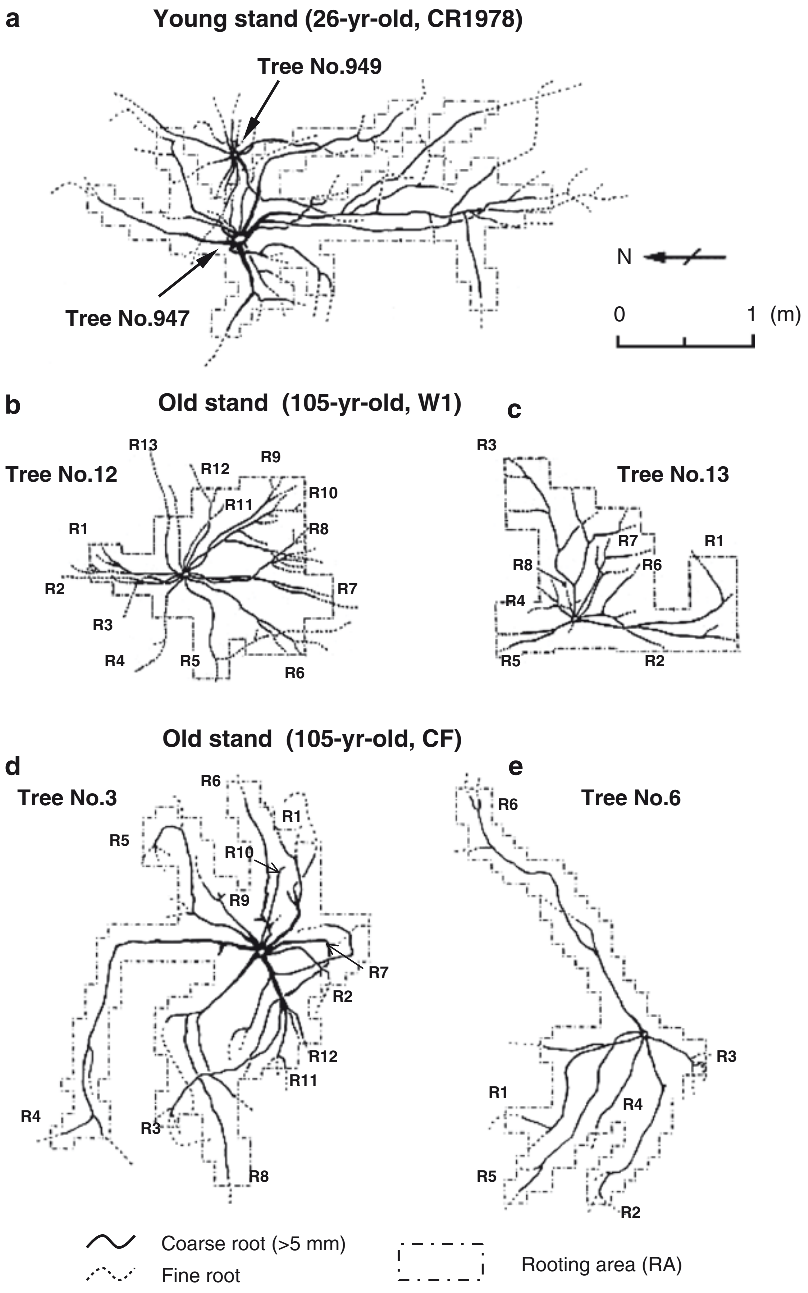

Fig. 16.2 Examples of horizontal projection maps of *L. gmelinii* root systems excavated in a young and two old stands. (**a**) Trees No. 947 and No. 949 of 26-year-old stand (CR1978). (**b**) Trees No. 12 and (**c**) No. 13 of 105-year-old stand (W1). (**d**) Trees No. 3 and (**e**) No. 6 of 105-year-old stand (CF). Ages and stem diameters of some trees are described in Fig. 16.1a–c. For some trees, labeled numbers (e.g., R1 and R2) of lateral roots within each root system are shown. Horizontal rooting area (RA) determined for each root system is shown by *dotted line* (from Kajimoto et al. 2003, 2007)

Rooting area index (RAI) was proposed as a stand-level measure of below-ground space occupied by root systems, and was expressed by the sum of RA per unit land area (i.e., $m^2 m^{-2}$). If RAI is equal to unity, the below-ground space is assumed to be occupied completely by the root systems, or root network is closed at the stand level. Note that RAI can exceed unity if there is substantial overlap of RA among adjacent trees. The RAI was estimated by applying the site-specific regression between stem diameter and RA that was derived from the data of excavated trees in each stand (see Sect. 16.6.2).

As for the corresponding parameters above ground, individual crown projection area (CA) and stand-level crown area index (CAI; $m^2 m^{-2}$) were determined. The CA was calculated as a circle using the average crown width along two radii. The CAI of each stand was estimated as the sum of CA values for all living trees in the permanent plots (the estimates of CAI are listed in Table 6.1).

16.2.4 Growth Pattern Analysis

Temporal development patterns of the root system were examined by applying growth ring analysis (i.e., in the same manner as for "stem growth analysis") to the lateral coarse roots. For each sample tree, root disks were taken from all lateral roots at their basal portions (i.e., just near tree stump). The numbers of annual rings were counted and then determined a period when each lateral root started to expand horizontally (i.e., root ages). Additionally, root disks were also sampled at further positions (20–30 cm intervals) along some lateral roots, and their elongation and diameter growth curves were reconstructed; this analysis was conducted only for a few selected trees in one 105-year-old stand (W1) and old multiaged stand (C1).

For each root disk sample, annual rings and their widths were measured along four radii using a dissecting microscope to 0.01 mm accuracy. However, reading annual rings of *L. gmelinii* roots was difficult in some cases. For example, very narrow rings were often found on smaller root disks (<ca. 1 cm in diameter). Missing rings also occurred especially for large roots (>ca. 3 cm diameter) that were taken near the basal portions; cross-sections were rather oval, and annual rings were compressed at right angle to ground surface. Similar features were examined for the roots of other conifer species (e.g., Fayle 1975b; Krause and Eckstein 1993; Richardson 2000). Thus, by applying cross-dating and other dendrochronogical techniques that were suggested in other reports, continuity of circumference on such root disk samples was carefully checked by referring to the ring count along the longest radius, and then, the number of rings was determined (Kajimoto et al. 1999).

16.3 Spatial Pattern of Individual Root System

All *L. gmelinii* trees excavated in both young and old stands developed superficial root systems (see examples in Fig. 16.1). Basically, the root system was composed of a short tap root and some horizontally spread lateral roots (average number is

7–9 per tree) (Table 16.1). Each tap root was already aborted at the tip portion (8–40 cm deep). Tap root length (average of sample trees) was longer in two 105-year-old stands (17 cm in W1, 19 cm in CF) or old multiaged stand (29 cm in C1) than that in the young stand (12 cm in CR1978).

For all root systems, lateral roots (both coarse and fines roots) were mostly distributed in upper soils (<10–15 cm deep) (also see Sect. 16.4.1). In two 105-year-old (W1, CF) and old multiaged stands (C1), lateral roots often grew in the litter layers or moss-lichen mats that covered the ground surface densely (e.g., Fig. 16.1b, c; see also Kajimoto et al. 1999, 2003). Vertically, root distribution of *L. gmelinii* was confined only in the upper parts of possible soil space that was expected from the soil depth of summer thawing (i.e., soil active layer) in each stand. For example, thickness of soil active layer was 53 cm (CR1978) and 64 cm (C1), and its range (measured at a number of points) was 20–50 cm (W1), and 30–80 cm (C1); although, these data were recorded in different seasons (from late July to late August) and/or years (Kajimoto et al. 2003, 2007; also see Chap. 8).

The sizes of lateral roots (e.g., diameter at basal portion, length) differed largely within each excavated root system, and their average values were also different among the sample trees in each stand (Table 16.1). In the case of 10 trees excavated in the 26-year-old stand (CR1978), the maximum root diameter and length (i.e., longest lateral root for each tree) ranged from 0.8 to 5.9 cm, and from 25 to 320 cm, respectively (Table 16.1). If the stand-average values were compared, the maximum root length was shorter in this young stand (128 cm) than in two 105-year-old stands (170 in W1, 206 cm in CF) or old multiaged stand (218 cm in C1).

Horizontally, lateral roots tended to expand into some specific directions for each examined tree. For example, two measured individuals of 26-year-old stand that were adjacent to each other expanded their lateral roots into either northern or southern directions (see tree No. 947 and 949 in Fig. 16.2a), suggesting that neighboring trees develop root systems that avoid one another in the dense young stand (i.e., tree density of plot CR1978 is 13,700 ha^{-1}; Table 6.1). However, such asymmetric pattern of lateral root expansion was also observed for some sample trees of two 105-year-old stands (Fig. 16.2b–e) or >220-year-old stand (Fig. 16.3; see Kajimoto et al. 1999) where trees grew much sparsely (density < ca. 5,000 ha^{-1}).

16.4 Effects of Microscale Soil Condition on Root Distribution

16.4.1 Topography and Soil Temperature

In arctic tundra, annual thaw–freeze cycle of soils (or cryoturbation) creates peculiar patterns on ground surface at variable scales, such as pingos, stony polygons, and soil hummocks (Williams and Smith 1989). Soil hummocks (also referred to as earth hummocks) often develop in the study sites at Tura in Central Siberia. Particularly, earth hummock was developed typically in old multiaged stand (C1):

mounds (each 1–2 m wide) were 50–70 cm higher than surrounding troughs. Spatial root distributions of the *L. gmelinii* trees sampled in the stand depended largely on such microtopography (Kajimoto et al. 1999, 2007).

For example, one medium-size tree (No. 3, 207-year old) expanded nine lateral roots (R1-R9) mostly into nearby elevated mounds other than troughs (Fig. 16.3). These lateral roots were distributed in the uppermost soils of the mounds (<10 cm in depth), except for places near the tree stump (<100 cm in distance) (Fig. 16.4). In the stand, microscale variation of soil temperature (at 10 cm depth) was examined along a line transect (5 m in length) across hummock topography (Fig. 16.5); the transect was located about 5 m apart from the place where root system of Tree No. 3 was excavated. The data indicate that monthly mean soil-temperatures were 7–8°C higher on the top of mounds (positions no. 8 or 9) than those at the bottom of trough (no. 6) during the summer 3 months (June–August) (Fig. 16.6a). Annual soil heat sum, which was defined as the sum of daily mean soil-temperature above 0°C (e.g., Van Cleve et al. 1981), also increased linearly with the relative height of observation positions: the values at the top of the mounds (1,000–1,200°C days) were about three or four times as those inside troughs (300–400°C days) (Fig. 16.6b). These observations suggest that larch trees expand lateral roots preferentially into warmer soils of mounds than into the colder troughs.

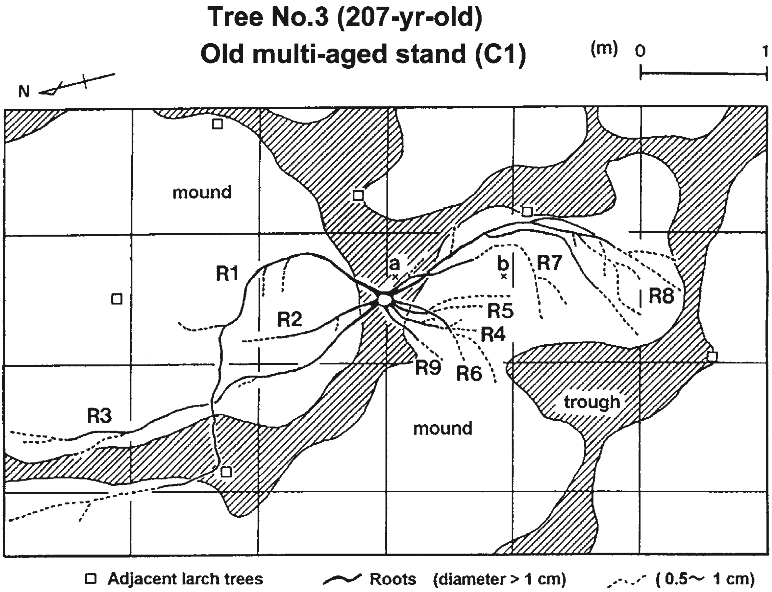

Fig. 16.3 Horizontal projection of root system of 207-year-old *L. gmelinii* tree excavated in the old multiaged stand (Tree No. 3, C1). Nine lateral roots are shown by the labeled numbers (R1–R9) (also see photo of the root system; Fig. 16.1d). *Shaded* and *white* areas show depressed troughs and elevated mounds; relative difference in elevation is about 60 cm between the bottom of trough ((**a**); just below tap root) and the top of nearby mound (**b**) (Kajimoto et al. 2007)

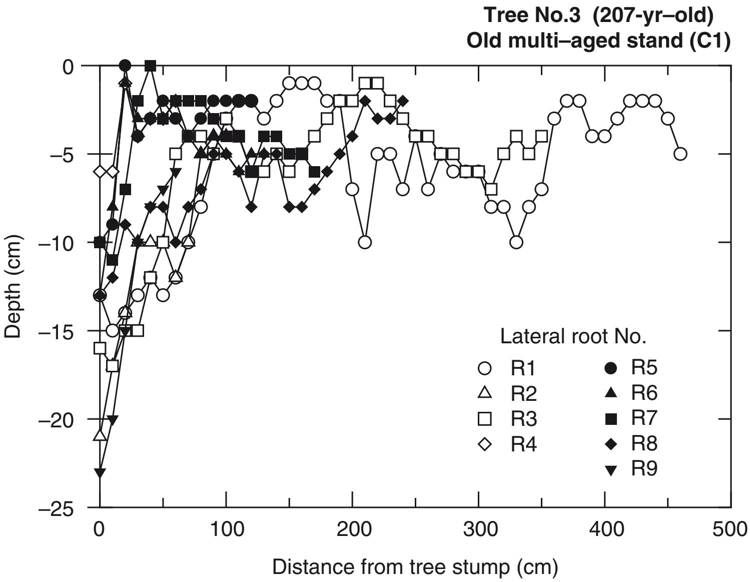

Fig. 16.4 Vertical distribution of nine lateral roots (R1–R9) of one *L. gmelinii* sample tree of the old multiaged stand (Tree No. 3, C1). Depth of each lateral root (vertical distance from ground surface) is plotted against horizontal distance at 10-cm intervals from the tree stump. Horizontal position of each lateral root is shown in Fig. 16.3 (Kajimoto et al. 2007)

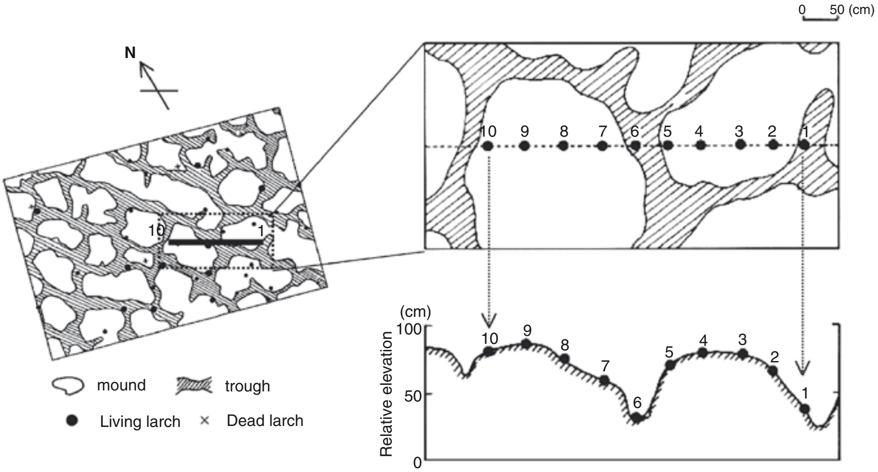

Fig. 16.5 Ground surface pattern and location of a line transect used for the measurement of soil-temperatures (10 cm deep) across hummocks in the old multiaged *L. gmelinii* stand (C1). Ten thermorecorders (Ondotori JR, T&D Ltd.) were installed at 50 cm intervals (positions no. 1–10) along the line (4.5 m in length), and soil-temperature was measured every hour from early September 1997 to late August 1998. The line was set about 5 m apart from the place where root system of tree No. 3 was excavated (the root system is shown in Figs. 16.1d and 16.3) (Kajimoto et al. unpublished data)

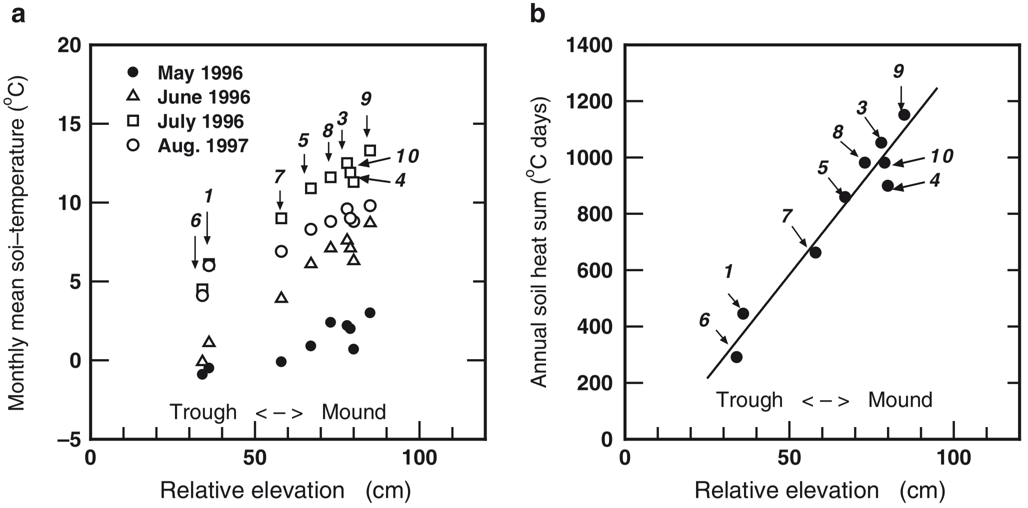

Fig. 16.6 Comparisons of (**a**) monthly mean soil-temperature and (**b**) annual soil heat sum among different positions across the hummock topography in the old multiaged *L. gmelinii* stand (C1). The data are plotted against relative elevations; small numbers indicate parts at the bottom of trough (e.g., position no. 1, 6), at the intermediate position between mound and trough (no. 5, 7), and on the tops of two mounds (no. 3, 8, 9) (see each position in Fig. 16.5). Annual soil heat sum (i.e., degree days) was defined as cumulative daily mean temperatures (above 0°C) during 1 year. Positive correlation was observed between relative elevation and soil heat sum ($n=9$, $r^2=0.95$, $p<0.01$); for calculation, position no. 2 was excluded due to lack of data in some periods. The regression slope was about 14.7°C days cm^{-1} (Kajimoto et al. unpublished data)

Unlike the old multiaged stand, hummocks are not developed conspicuously in the other old larch stands (W1, CF). However, similar microscale variations of soil temperature were observed. In the 105-year-old stand (W1), for example, daily mean soil-temperatures (at 10 cm depth) were 2–6°C higher on mounds than those inside troughs during the summer, where the mounds (only 10–30 cm higher than troughs) were covered with peat moss (*Sphagnum* sp.) or lichens (*Cladina* and *Cetraria* spp.), while the troughs were mainly covered with other moss (*Dicranum* spp.) (Kajimoto et al. 2003). Microscale variations of soil thermal regime were also reported for another 105-year-old stand (CF), which may be associated with the hummock topography and/or its corresponding specific moss/lichen types (see Chap. 9).

Soil-temperature condition might fluctuate interannually. However, the topography-related spatial variation of soil thermal regime is evident every year. In the old multiaged stand (C1), soil-temperature (at 10 cm depth) was also monitored at another hummock for 5 years (2001–2006). The data indicate that daily mean soil-temperature at top of the mounds increased sharply from mid- or late-May to early July, and peaked (>15°C) in mid-July every summer (Fig. 16.7b). The seasonal pattern closely followed that of the air-temperature (Fig. 16.7a). In contrast, soil-temperature inside a nearby trough started to increase much later (between mid- and late-June), and reached a seasonal peak (<10°C) in late July. The difference might be associated with the pattern that snow accumulates deeper in troughs than on mounds, and hence soil-thawing begins later and ends much later inside the troughs. As a result, thickness of soil active layer differs largely across hummock topography within this old stand: active layer is much shallower (<20 cm) inside depressed troughs than on elevated mounds (70–80 cm) (Sofronov et al. 2000; see Chap. 4).

Tryon and Chapin (1983) reported that black spruce (*Picea mariana* Mill. B.S.P.) and tamarack larch (*Larix laricina* (Du Roi) K. Koch) that grew in interior Alaska expanded roots mostly in upper soils, and elongation rates of their roots varied with the seasonal pattern of soil-temperature. Seasonal root growth of *L. gmelinii* might also be regulated largely by the soil thermal condition. Van Cleve et al. (1981, 1983a, b) reported that annual soil heat sum (above 0°C, at 10 cm deep) ranged from 480 to 1,300°C days for various boreal forests in interior Alaska. They also indicated that the value was relatively low (< ca. 700°C days) for black spruce stands that were established on lowlands with permafrost as compared with those of other forest types (>800°C days), such as white spruce (*Picea glauca* (Moench) Voss) and broadleaved deciduous species (e.g., *Populus tremuloides* Michx., *Betula papyrifera* Marsh.), which were mainly distributed on permafrost-free uplands. The range of soil heat sum (300–1,200°C days) that was recorded in the old multiaged *L. gmelinii* stand (C1) encompasses the whole range reported for the evergreen taiga. However, as was discussed earlier, rooting zone of *L. gmelinii* is restricted to the warmer, upper soils even on elevated mounds (>1,000°C days; Fig. 16.6b). This suggests that a threshold of soil heat sum that is sufficient for seasonal root growth of *L. gmelinii* might be as high as those of white spruce and broadleaved deciduous species in the Alaskan taiga.

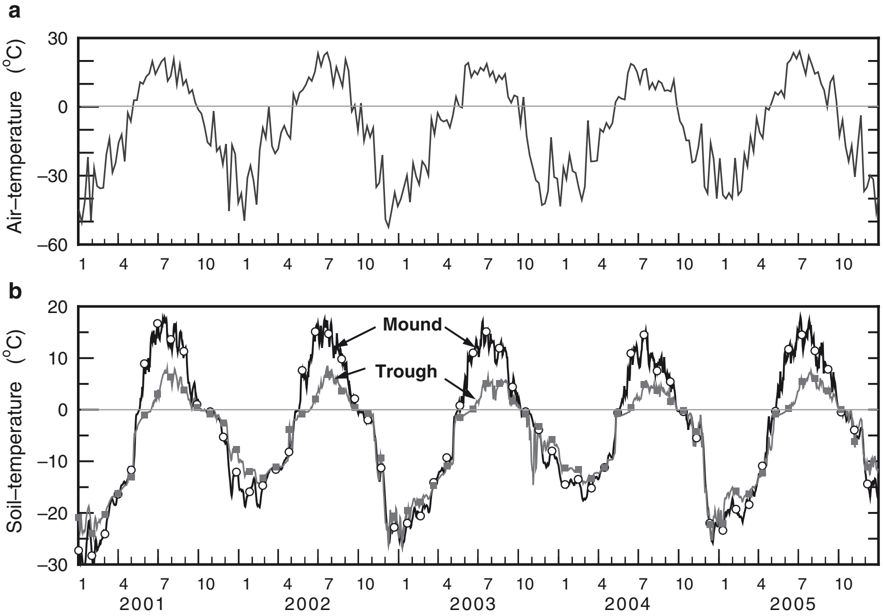

Fig. 16.7 Seasonal changes in (**a**) daily mean air-temperature and (**b**) soil-temperatures during recent 5 years (2001–2005) measured in the old multiaged *L. gmelinii* stand (C1). Soil temperatures (each 10 cm deep) were recorded using thermo-recorders (Ondotori JR, T&D Ltd.) at two positions across hummock topography; on the top of mound and inside nearby trough (relative elevation was about 50 cm). This measurement was conducted at about 15 m away from the line transect used for the measurement of soil-temperatures across hummock topography (see results in Figs. 16.5 and 16.6) (Kajimoto et al. unpublished data)

16.4.2 Topography and Soil Water

Soil water might be another external factor affecting spatial root development of *L. gmelinii*, since the hummocks create microscale variations of not only temperature but also water. Soils inside troughs are generally immersed with melting water from the thawing soils during summer: water begins to pool inside troughs even during root excavation (see Fig. 16.1d). In the old multiaged stand (C1), soil water suction (at 10 cm depth) was measured across a mound-trough topography using tensiometer with porous cups; the measurement was conducted in the same location where soil-temperature was monitored (Fig. 16.7b). According to the data on a mid-summer day (i.e., 5 days after last rainfall), soil water potential was almost stable inside trough, but it was reduced clearly at the top and/or middle parts of a nearby mound (Kajimoto et al. 2003). The difference indicates that soils inside troughs are immersed with water more than those on mounds. Thus, the fact that lateral roots of *L. gmelinii* rarely expanded into troughs (e.g., Fig. 16.3) might be associated with both conditions of low temperature and water logging (Kajimoto et al. 2007).

The superficial root systems of *L. gmelinii* are similar to those reported for two boreal conifer species, tamarack larch (*L. laricina*) and black spruce (*P. mariana*), which grow at poorly drained sites such as peatlands and lowlands in the evergreen taiga. In peatlands of Alberta in Canada, both species developed shallow root systems (< 30 cm deep), and their tap roots were aborted at the tip portions (Strong and La Roi 1983a, b; Lieffers and Rothwell 1987). These reports suggest that high water table mainly limits vertical root growth and may cause tap root abortion of these species. In Central Siberia, permafrost might play a role similar to water table as in sites of the evergreen taiga.

16.5 Temporal Pattern of Root System Development

16.5.1 Replacement of Root System

Formation of adventitious roots was reported for many *Larix* species (e.g., Cooper 1911; Islam and Macdonald 2004). In Central Siberia, *L. gmelinii* also produced roots adventitiously from tap root and/or lower part of stem, in both young and old stands (Figs. 16.8 and 16.9). Consequently, the root systems of all larch trees sampled in old stands (>100-year old) consisted of lateral roots of different ages (Kajimoto et al. 2003). As shown in Fig. 16.8, for example, the ages of five lateral roots (labeled No. R1–R5) of one 105-year-old tree (No. 1 of CF) ranged from 14 to 71 years; here, the root age means a time that passed after each lateral root started to expand. This example also indicates that the roots occurring at upper positions (No. R2 and R5) are relatively small and young (14 and 35 years) than those at lower positions (R1, R4, and R3; > 50 years), and that some dead roots remain near the bottom of the root system.

Similar relationship between lateral root age and its vertical position (i.e., depth in soil) was recognized for the other root-excavated larch trees (Fig. 16.10). For nine trees of two 105-year-old stands (W1, CF), the ages of lateral roots ranged between 10 and 80 years, and roots occurring at upper positions (>–5 cm in depth) were generally younger than those at lower positions (Fig. 16.10a, b). In the cases of two sample trees of old multiaged stand (No. 2, 3; C1), the ages of their lateral roots at lower positions were also older than those of the upper roots (Fig. 16.10c). These evidence indicate that *L. gmelinii* produces lateral roots successively from the lower to upper part of the tap root and/or stem.

The root age-depth diagram (Fig. 16.10) also shows that some older roots started to expand at similar periods within each root system. For example, at one 105-year-old stand (W1), four roots of tree No. 11 (shown by open circles) were initiated 64–65 years ago, and six roots of No. 13 (open triangles) and four roots of No. 14 (closed circles) did so 51–58 and 46–48 years ago, respectively (Fig. 16.10a). Likewise, such a tendency of simultaneous initiation of lateral roots can be observed for the sample trees of another 105-year-old stand (CF), e.g., for tree No. 1, the ages of five roots ranged 51–56 years among eleven lateral roots

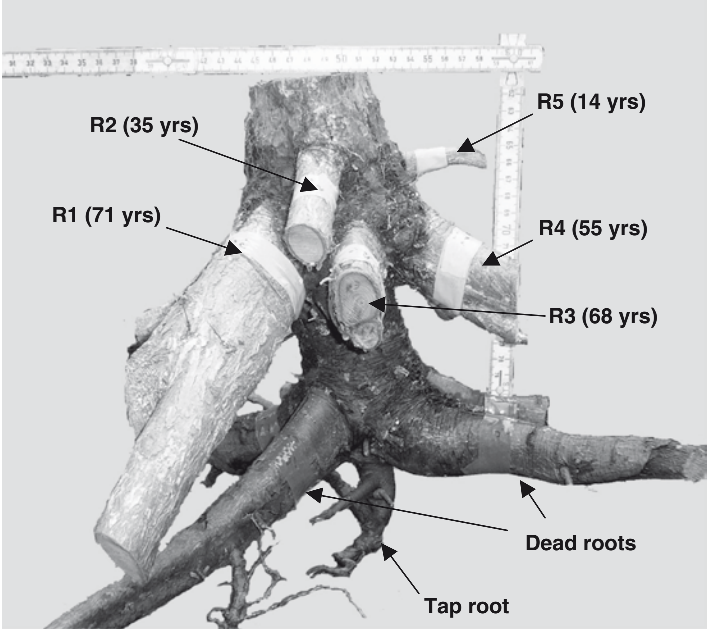

Fig. 16.8 Vertical profile of *L. gmelinii* root system excavated in the old stand (Tree No. 1, 105 years-old, CF). The root system consisted of 14 living lateral roots; here, ages of only five lateral roots (numbered R1–R5) are shown in parenthesis. Root age indicates the number of annual rings counted on the disk sample taken at basal portion (i.e., <5 cm in distance from tree stump; see Sect. 16.2.2). Tap root was aborted at its tip (29 cm deep), and some dead lateral roots were observed at the bottom part of root system

that occurred at the depth of 10–15 cm (Fig. 16.10b). In the stand, ages of all lateral roots that occurred at such relatively deeper portion (below 15 cm in depth) fell in the range of 40–80 years, indicating that lateral root expansion started intensively after the stand age of 25 years. Mund et al. (2002) reported that sinker roots of old *Picea abies* trees (112-year old) started to grow vertically after the stand aged about 20 years.

As was seen in Fig. 16.8, some dead lateral roots were found in each excavated root system of the two 105-year-old stands (W1, CF). These dead roots were mostly located at the bottom of the root system, suggesting that they were among the roots developed initially just after tree establishment (i.e., about 100 years ago). Three individuals of old multiaged stand (tree No. 2, 3, 4; C1) have regenerated at least 200 years ago, but lacked living lateral roots that aged 160 years or more (Fig. 16.10c). However, some dead lateral roots also remained at the bottom of each root system, suggesting that initially occurring older roots might have already been dead, probably due to stresses under cold and wet soil conditions (see Sect. 16.4). In contrast, all the excavated root systems in 26-year-old stand (CR1978) were composed of only living and young (20–24 years) lateral roots (Kajimoto et al. unpublished data). In the young stand, successive replacement of root system from

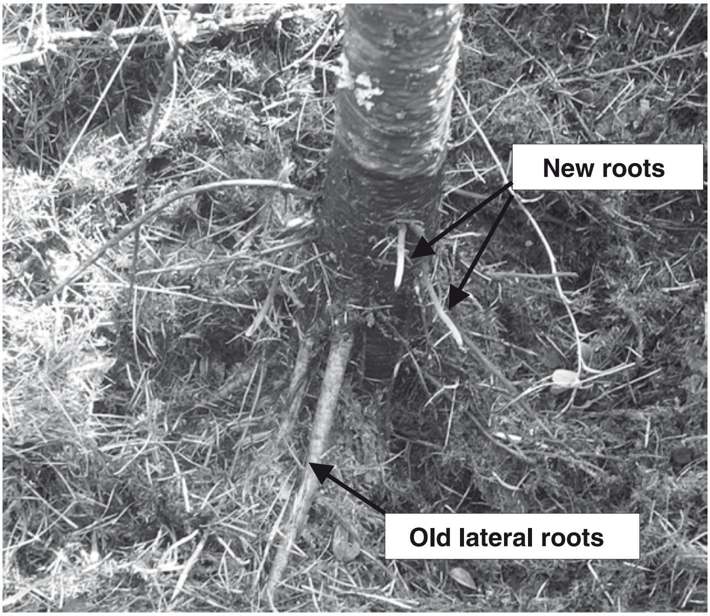

Fig. 16.9 Example of new lateral roots (i.e., adventitious roots) emerging from lower part of stem on young *L. gmelinii* tree (Tree No. 947, 25 years-old, CR1978). Root system of this young tree is shown in Fig. 16.1a (photo: mid-July in 2005, Kajimoto)

older roots to newly emerged roots, which were observed in the other old stands, may not have yet started.

16.5.2 Growth Rate and Pattern of Lateral Root

Elongation rates of lateral roots differed within a single root system of *L. gmelinii*. For example, mean annual rates of root elongation (i.e., root length/entire observation period) ranged from 1.0 to 11.4 cm year^{-1} (averaged 4.8 cm year^{-1}) for 13 lateral roots of 105-year-old tree (No. 12 of W1) (Fig. 16.11a). The elongation rates were smaller among roots of relatively older (>50 years) age-group (3–4 cm year^{-1}; R8, R9) than among younger (<50 years) roots (>7–8 cm year^{-1}; R5, R10). For one 207-year-old tree (No. 3, C1), the mean elongation rates were also relatively high in younger roots (10–23 cm year^{-1}; R4–R7) compared with those in older roots (2–8 cm year^{-1}; R1–R3, R8–R9) (Fig. 16.11b). Such smaller elongation rates were also observed in some older lateral roots (1–6 cm year^{-1}) of the other two old trees (No. 2, 6, C1) (Fig. 16.11c). The tendency suggests that elongation rates of lateral roots decline as they age.

The annual extension rates of *L. gmelinii* lateral roots were mostly less than 10 cm year^{-1}. The root extension rates are much lower than those (generally ranged

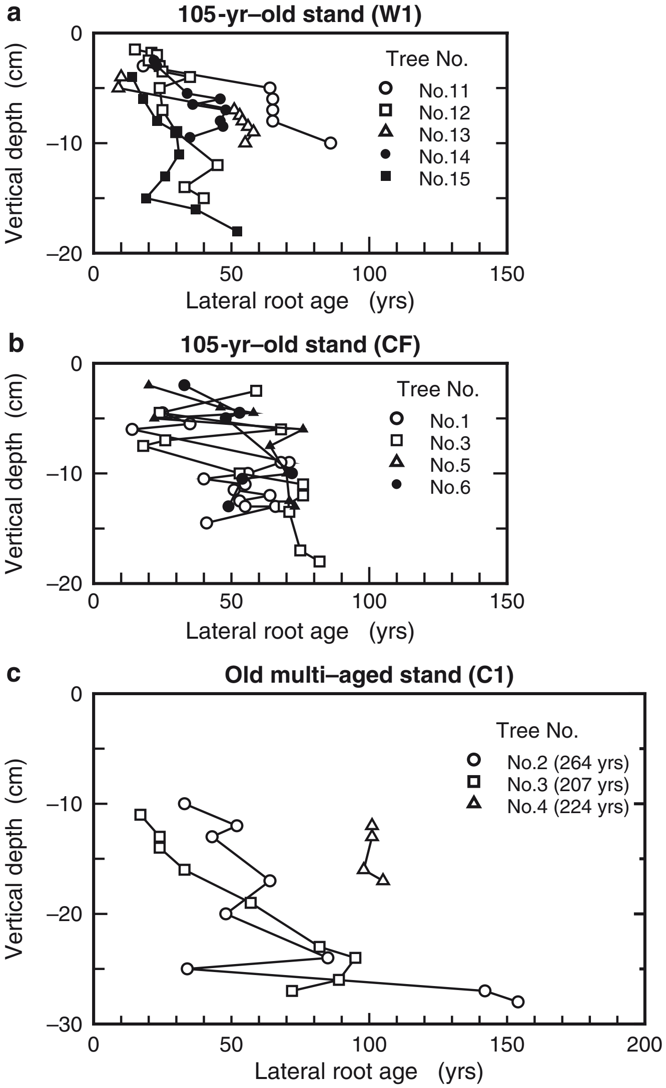

Fig. 16.10 Relationships between ages and vertical positions of lateral roots examined in some old *L. gmelinii* trees. (**a**) Five trees (No. 11–15) of old stand (105 years old, W1). (**b**) Four trees (No. 1, 3, 5, and 6) of old stand (105 years old, CF). (**c**) Three trees (No. 2, 3, and 4) of old multiaged stand (> 220 years old, C1). Vertical depth indicates the position where each lateral root occurs within each root system. The data are connected with line segments from the uppermost to the lowest root. Photos and/or rooting maps of these sample trees are shown elsewhere: Tree No. 12 of W1, No. 3 of CF, and No. 3 of C1 (see Fig. 16.1b–d), and No. 1 of CF (see Fig. 16.8) (original data of two stands, W1 and C1, are from Kajimoto et al. 2003; others are Kajimoto et al. unpublished data)

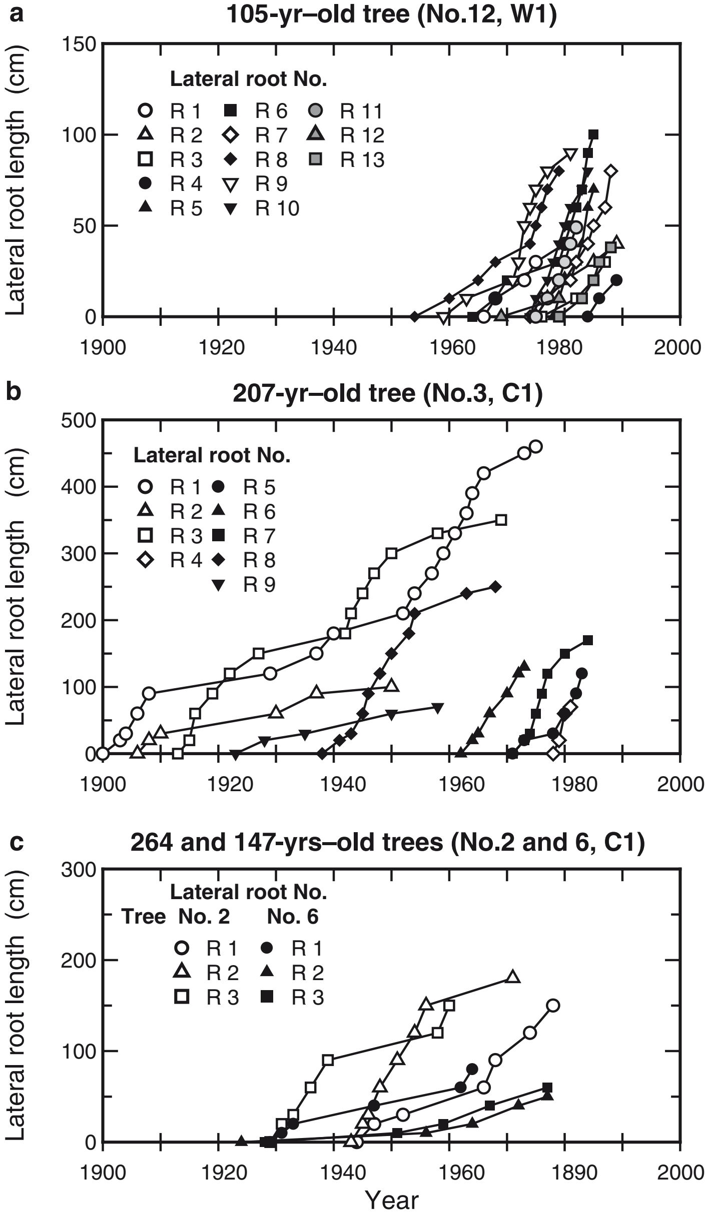

Fig. 16.11 Elongation growth curves of lateral roots reconstructed for some old *L. gmelinii* trees. (**a**) Thirteen lateral roots of Tree No. 12 (105 years old) of old stand (W1). (**b**) Nine lateral roots of Tree No. 3 (207 years old) of old multiaged stand (C1). (**c**) Three lateral roots of each of Tree No. 2 (264 years old) and No. 6 (147 years old) of old multiaged stand (C1) (original data of C1 from Kajimoto et al. 2007; others are Kajimoto et al. unpublished data)

10–80 cm year⁻¹) reported for other conifer species growing under climates milder than Siberia, such as *Pinus resinosa* Ait (Fayle 1975a), *Picea sitchensis* Bong. Carr. (Coutts 1983), and *Pseudotsuga menziesii* (Mirb.) Franco. (Kuiper and Coutts 1992) in North America, and *Picea abies* (Drexhage and Gruber 1998; Puhe 2003) in Eurasia.

Figure 16.12a shows diameter growth curves that were reconstructed for nine lateral roots (at basal portion) of one 207-year-old *L. gmelinii* tree (No. 3, C1). The pattern of root diameter growth varied largely within a root system, as was also seen

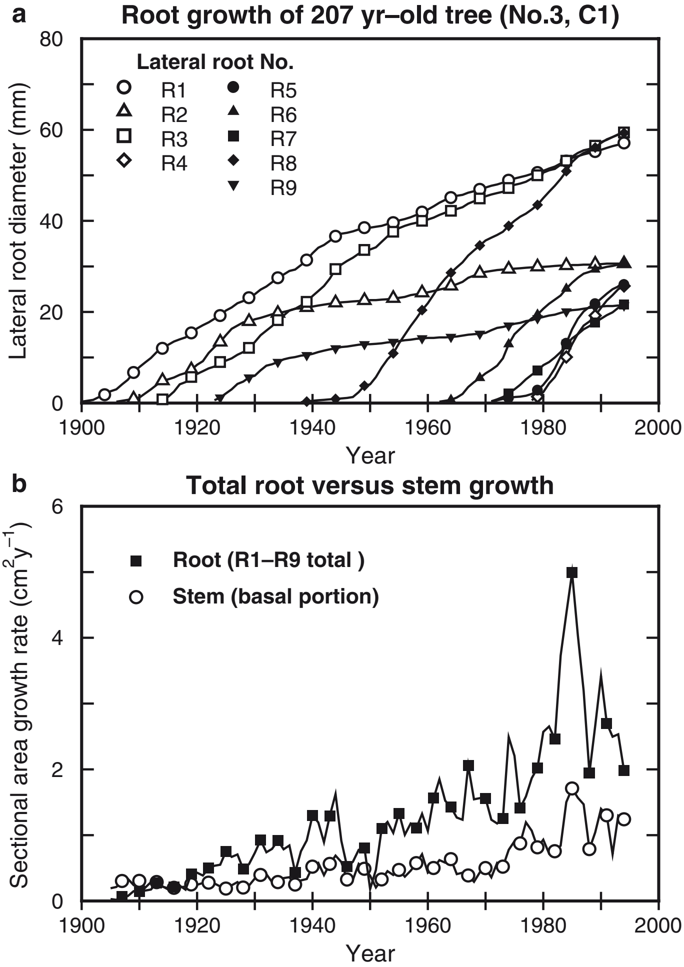

Fig. 16.12 (**a**) Diameter growth curves of nine lateral roots (R1–R9) at basal portions, and (**b**) changes in sectional area increments of total root (i.e., sum of these nine lateral roots) and stem (at basal portion) reconstructed for a 207-year-old *L. gmelinii* tree (No. 3) in the old multiaged stand (C1). Values of diameter and sectional area increments of both roots and stem were the averages; annual ring-widths were measured along four radii on each sample disk (Kajimoto unpublished data)

in their elongation growth patterns (Fig. 16.11b). Mean annual increments of root diameter, which was calculated by root diameter/entire observation period, ranged from 0.3 (R2) to 1.5 mm year^{-1} (R4). Four younger roots (No. R4–R7), which started to elongate after 1960, appears to keep higher diameter increments than the older roots (R1–R3, and R9) (Fig. 16.12a). However, these older lateral roots did not necessarily synchronize patterns in both elongation and diameter growth. Namely, two old roots, R1 (shown by open circle in Figs. 16.11b and 16.12a) and R3 (open square), grew much faster from early periods and maintained higher growth rates as compared to the other two roots, R2 (open triangle) and R9 (closed reverse triangle). A process of carbon allocation within the root system might cause such among-roots variation in growth rates or growth patterns (Kajimoto et al. 2007).

Carbon allocation process within root system still remains unclear, and should be further examined. As shown in Fig. 16.12b, a time trend of lateral root growth (i.e., sectional area increment at basal portion) examined for the 207-year-old tree (No. 3, C1) was fairly synchronized with that of stem if all lateral roots (R1–R9) were combined. This indicates that carbon allocation within the root system is primarily regulated at a whole-tree level, as was suggested for root systems of other conifer species (e.g., Fayle 1975b; Krause and Eckstein 1993; Drexhage et al. 1999). In other words, the amount of carbon allocation into a whole root system might be regulated or limited to attain a balance with allocation into above-ground parts (i.e., stem), although *L. gmelinii* tends to allocate annual photosynthetic production largely into roots as it grows (Kajimoto et al. 2006). Thus, the among-roots variation in growth rate and pattern (Fig. 16.11) suggests that the larch may allocate annual carbon gain into growth of one or two specific roots among similar-aged roots (e.g., R1 and R3 in Fig. 16.12a), and then expand newly emerged lateral roots at the expense of other growth-declined, older roots during development of the root system.

16.6 Below-ground Space Occupation by Root System

16.6.1 Relationship Between Root System and Crown

Old forests of *L. gmelinii* (>100-years old) in Central Siberia are generally sparse with open canopy. Individual crowns are thin and rarely overlap with their neighbors. This is reflected in the fact that extent of canopy closure, or crown projection area index (CAI) defined in this chapter, is generally lower than 0.4–0.5 m^2 m^{-2} for old larch forests in the region (Abaimov and Sofronov 1996; Bondarev 1997). The values of CAI (0.1–0.3 m^2 m^{-2}) of three 105-year-old larch stands at Tura (W1, CF, C1) also fall in such range (see Table 6.1).

Figure 16.13 shows relationships between stem diameter at breast height (*D*) and crown projection area (CA) for sample trees of each of these study stands. The CA value for a given tree size is larger in 26-year-old stand (CR1978) than in two 105-year-old stands (W1 and CF), suggesting that *L. gmelinii* tends to hold a thin

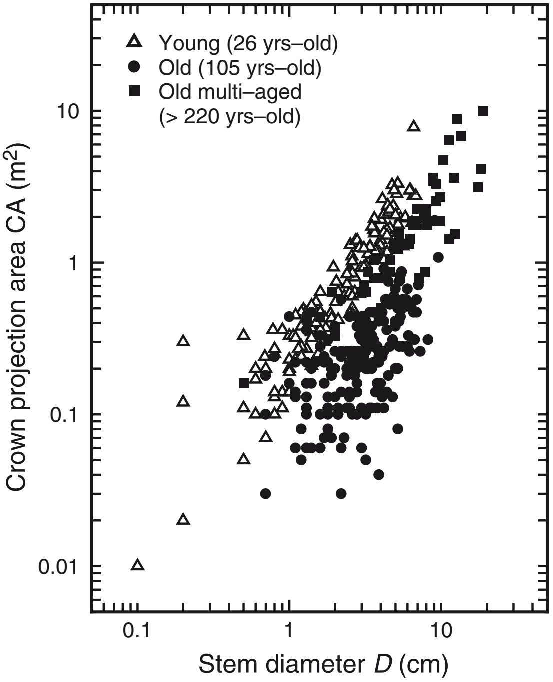

Fig. 16.13 Relationships between stem diameter at breast height (*D*) and crown projection area (CA) of living *L. gmelinii* trees in young (26 years-old, CR1978), old (105 years-old, CF) and old multiaged (>220 years-old, C1) stands. Here, tree census data for individuals taller than 1.3 m in permanent plots of each stand are used (Kajimoto et al. unpublished data)

crown even as it grows larger. In contrast, larch trees may continue to expand their root systems as they grow. Figure 16.14a shows that horizontal RA was about three or four times larger than the crown projection area (CA) for the sample trees of two old stands, while RA was nearly equivalent to CA (regression slope = 0.98) for those of young stand. A similar CA–RA relationship was also observed for the seven sample trees of another 105-year-old stand (W1) (Kajimoto et al. 2003). In addition, the size dependency of RA was similar between these two old stands (W1, CF), but was significantly different from that of young stand: RA of CR1978 was smaller than that of CF and C1 if similar-sized individuals ($D < 3–4$ cm) were compared (Fig. 16.14b). These discrepancies between young and old stands suggest that, after the stand age of about 30 years, the surviving trees mainly expand their root systems (Kajimoto et al. 2007). The CA–RA relationship that was found in the young *L. gmelinii* stand is similar to those reported for other monospecific conifer forests at relatively younger stages (10–60-year old), such as *Picea sitchensis* (Hinderson et al. 1983) and *Pseudotsuga menziesii* (McMinn 1963; Kuiper and Coutts 1992); in these conifer stands, individual RA (or width) rarely exceeded crown area.

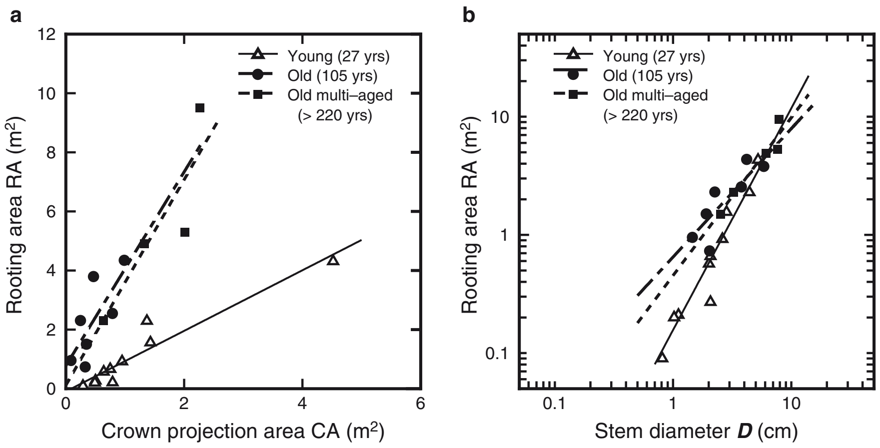

Fig. 16.14 Relationships between RA and (**a**) crown projection area (CA), and (**b**) breast height stem diameter (*D*), for *L. gmelinii* trees excavated in the young (26 years old, CR1978), old (105 years old, CF) and old multiaged (>220 years old, C1) stands. Regression lines are approximated by (**a**) linear and (**b**) log-log linear models, respectively. The coefficients of each regression are as follows: (**a**) $RA=1.02\ CA-0.10$, $r^2=0.912$ (CR1978); $RA=3.30\ CA+0.77$, $r^2=0.571$ (CF); $RA=3.48\ CA+0.12$, $r^2=0.859$ (C1). (**b**) $RA=0.16D^{1.93}$, $r^2=0.931$ (CR1978); $RA=0.65D^{1.15}$, $r^2=0.730$ (CF); $RA=0.45D^{1.35}$, $r^2=0.927$ (C1) (Kajimoto et al. 2007)

16.6.2 Stand-Level Root Network

RAI, which was estimated using site-specific *D*-RA regression (Fig. 16.14b), was the largest in the 26-year-old *L. gmelinii* stand (1.80 $m^2 m^{-2}$, CR1978), followed by 105-year-old stand (1.35 $m^2 m^{-2}$, CF) and >220-year-old stand (1.25 $m^2 m^{-2}$, C1) (Kajimoto et al. 2007). The RAI of another old stand (1.1 $m^2 m^{-2}$, W1; Kajimoto et al. 2003) was also as low as that of two old stands. All estimates of RAI exceed unity, indicating that stand-level root network is assumed to be closed in both young and old stands, although RAI of these old stands tends to be smaller than that of young stand. In contrast, the crown projection area index (CAI) exceeded unity only in the 26-year-old stand (1.33 $m^2 m^{-2}$), whereas those of the old stands were considerably less than unity (<0.3 $m^2 m^{-2}$) as was mentioned earlier (see Table 6.1). These comparisons suggest that canopy becomes open gradually due to tree mortality until the stand ages (>100-year old), but root network is kept fully closed. In other words, the stand at younger stage is over-crowded in both above- and below-ground spaces, but old stands are crowded only in below-ground space by surviving individuals.

16.7 Linkage with Postfire Permafrost Soil Environment

Patterns of postfire changes in soil physical properties such as soil temperature and thickness of soil active layer were well documented in evergreen taiga established on the permafrost in interior Alaska (e.g., Viereck 1982; Dyrness et al. 1986) and northern

Canada (e.g., Wein and Bliss 1973; Rouse 1976; Landhäusser and Wein 1993; Mackay 1995). According to these reports, soil temperature and active layer thickness increase sharply at once just after stand-replacing fires, since ground floor vegetation such as woody shrubs, mosses and lichens, and accumulated litter, that function as thermal insulator are eliminated (e.g., Viereck 1982; Oechel and Van Cleve 1986; see also Chap. 4). However, both temperature and active layer thickness subsequently decrease with recovery of floor vegetation as the stand ages, then return to prefire level. A return time of active layer thickness varies from about 10 years to several decades, depending on local conditions such as topography, fire intensity, and recovery rate of the floor vegetation. Likewise, these postfire changes in the soil environment also occur in the permafrost region in Central Siberia (Abaimov and Sofronov 1996; Gorbachev and Popova 1996; Sofronov et al. 2000). For example, Kharuk et al. (2005) examined various-aged stands of *L. gmelinii* (from a few years to >150-years old) in Central Siberia, and indicated that thickness of active soil layer decreased gradually (about 0.3 cm year^{-1}) with increase in stand age.

Figure 16.15 illustrates a concept that explains how temporal development of *L. gmelinii* root systems is linked to such postfire changes in permafrost soil environment (Kajimoto et al. 2003). There are distinct phases of root system development. First, when a dense seedling population becomes established after a stand-replacing fire, larch individuals grow roots vertically to some extent, and also start to expand lateral roots from the deeper part of the tap roots. This reflects the conditions of high soil temperature and deep active layer thickness. As the stand

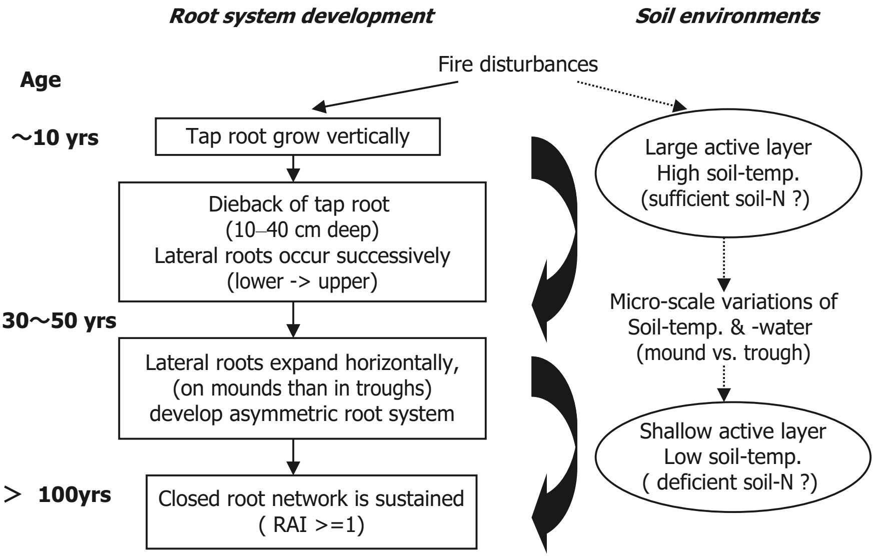

Fig. 16.15 Schematic diagram of a developmental process of individual root system of *L. gmelinii* in relation to postfire changes in soil environment in the permafrost larch taiga in Central Siberia (redrawn from Kajimoto et al. 2003)

develops, however, reduction in both temperature and active layer thickness limit vertical root growth, which results in death of the deeper portions of the tap root, or death of older and deeper lateral roots. Subsequently (after ca. 30 years), larch trees continue to expand lateral roots horizontally, especially into the warmer and drier soils on the elevated mounds. At this phase, they also replace lateral roots by growing new roots successively at upper positions of the tap root. Consequently, a fully closed root network would be maintained at the stand level due to horizontally spread individual root systems, at an old stand age (>100 years).

Associated with changes in these soil physical properties, nutrient conditions may also change with stand age. Generally, soil inorganic N-pool increases immediately after a stand-replacing fire (Grogan et al. 2000; Certini 2005), but declines to the prefire level within several years as a result of immobilization or uptake due to vegetation recovery (Wan et al. 2001; Smithwick et al. 2005). Soil nutrient, especially nitrogen, is essentially limited in the permafrost larch taiga in Siberia (e.g., Schulze et al. 1995; also see Chaps. 8 and 12). After the recovery of vegetation, constraint of available soil-N might become crucial and then limit individual growth. In the study site at Tura, height growth rates of *L. gmelinii* trees examined in two 105-year-old stands (W1 and CF) declined sharply at stand age of 30–50 years (see Figs. 6.5b, c and 7.5). The growth reduction occurred irrespective of difference in individual tree size, suggesting contributing effect of limitation in soil N. This period corresponds to the phase when larch trees start to replace the lateral roots successively (30–50 years; Fig. 16.15). The postfire change and limitation of available soil nutrients may trigger lateral root expansion, and hence affect temporal root system development of *L. gmelinii*.

16.8 Below-ground Competitive Interactions

As was mentioned earlier (Sect. 16.6.2), relationships between two indices of space occupation (CAI and RAI) change along stand age sequence, and old stands are suggested to be crowed only in the below-ground space. This implies shift in the mode of intertree competition following stand development in the permafrost *Larix* taiga. Namely, tree competition for available below-ground space or soil nutrients may become predominantly important more than above-ground competition for light after a stand age of about 30 years (Kajimoto et al. 2007). In other words, tree mortality may be caused not by shading among crowns but by competition among roots after this stand age.

Generally, root competition for soil resources (water, nutrients) is considered a size-symmetric (or two-sided) competition where two neighboring plants uptake resources evenly at the zone of influence (i.e., overlapped place of roots) even if they differ in size (e.g., Weiner 1990). There are still few evidence supporting this concept (Schwinning and Weiner 1998; Schenk 2006). However, the concept of size-symmetric competition means that larger individuals do not necessarily outcompete smaller ones when below-ground competition was dominant under nutrient-poor condition. Such a mode of competition is likely to be occurring in monospecific, even-aged *L. gmelinii* forests in the permafrost taiga, since soil nutrients (e.g., nitrogen) are essentially limited (Schulze et al. 1995), and even smaller individuals can survive longer than larger ones during stand development (Osawa et al. 2003; also see Chap. 7). If so, it may be advantageous for larch trees to develop root systems that could explore limited soil resources by avoiding overlap with neighboring root systems, or by reducing root interference with neighbors. In other words, larger root system may not be necessarily advantageous for survivorship.

For further discussion of intertree competitive interference below the ground, more quantitative analyses are required regarding spatial arrangement of individual root systems. RAI of the present analysis indicates extent of closure in the root network at the stand level. However, it does not tell us how the root systems are interacting with one another, or to what extent the root systems are segregated or overlapped (Casper and Jackson 1997), and whether root competition actually occurs in response to depleted soil resources (Schenk et al. 1999; Casper et al. 2003). There are two possible approaches to address these questions. One approach is to examine spatial patterns of fine roots which uptake soil resources (e.g., Schmid and Kazda 2005). Another approach is to apply an intensive method of root excavation at whole-tree level, then visualize all root systems within a certain target area. Application of such intensive method has been few in forest ecosystems. However, this approach might be useful for quantitatively analyzing among-root interactions at the stand level, as was demonstrated in a monospecific shrub population of desert ecosystem (Brisson and Reynolds 1994).

16.9 Conclusions

Some characteristic features of *L. gmelinii* root system were suggested from the individual-based measurements and analysis.

- *L. gmelinii* trees generally develop superficial, horizontally spread root systems. The rooting depths in the study area in Central Siberia (<30–40 cm) are much shallower than those reported for other tree species in forest ecosystems worldwide (Stone and Kalisz 1991; Canadell et al. 1996; Schenk and Jackson 2002); exceptions are two boreal species (black spruce and tamarack larch) growing on specific conditions (see Sect. 16.4.2). The shallow root system of *L. gmelinii* is primarily a result of low soil temperature and potentially limited growing space (i.e., soil active layer) due to permafrost, and is further affected by microscale soil conditions of both temperature and water that are created by the peculiar topography (i.e., hummock) in the region of study.
- The temporal pattern of development in *L. gmelinii* root systems is closely linked to postfire changes of soil environment in the permafrost region. Larch trees gradually replace lateral roots with new roots (i.e., adventitious roots). This seems reflect constraints of soil physical properties (i.e., reductions in temperature

and active layer thickness) that might become crucial as the stand ages (to 30–50-year-old). Consequently, the larch continue to expand root systems horizontally (but not their crowns) so that the presumably limited soil nutrients are better exploited. Such a priority of root system development is supported by a process of carbon allocation at a whole-tree level (i.e., root-oriented carbon allocation).

- The analyses using two indices of space occupation of above (CAI) and below (RAI) the ground provide some insights into the mode of intertree competition that occurs in the permafrost larch taiga. The root systems of *L. gmelinii* are likely to be closed fully at the stand level ("closed root network") throughout stand development, suggesting predominance in below-ground intertree competition. The achievement of a closed root network seems to be primarily due to the effect of external factors (i.e., microscale soil conditions) on individual root system development (i.e., horizontally asymmetric distribution). This may also be affected by root competition among neighboring trees. However, the nature of below-ground intertree competition still remains unclear. To clarify these possible contributing processes, it is important to examine further the mechanisms related to patterns of tree mortality and stand development in the larch taiga on Siberian permafrost.

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