

Size–mass allometry and biomass allocation of two larch species growing on the continuous permafrost region in Siberia

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Abstract

We examined size–mass allometry and biomass allocation of two larch species (*Larix gmelinii* (Rupr.) Rupr. and *Larix cajanderi* Mayer) that grow on the continuous permafrost regions in Siberia. Sample tree data (total $n = 27$) gathered from four mature stands (>100 years old) were employed for analysis. First, to determine good size predictor of biomass, site-specific allometric relationships (log-linear equation form) were derived between dry mass of four components (stem, branch, needle and coarse root; ≥ 5 mm in diameter) and seven size variables; stem diameters (breast height, 30 cm height and crown base), sapwood areas (breast height and 30 cm height), and two combined-variables (tree height \times diameter). For all components, site-specific allometric equations based on breast-height diameter (D) always gave high correlations as those using other size variables. However, between-stand comparisons of the D -base site-specific allometry indicated that size dependency (i.e., regression slope) differed for stem mass. Besides, needle and coarse root mass for a given size (i.e., regression intercept) differed significantly among the four stands. These facts implied that D -base regression model was reliable for biomass estimation by site-specific allometry, but was not suitable for developing general (i.e., site-common) allometry. Second, to examine carbon allocation pattern, we estimated each stand biomass by applying corresponding site-specific D -base allometry. Stand total biomass ranged from 8.6 to 33.1 Mg ha⁻¹, and aboveground-total/coarse root biomass ratio (i.e., T/R) ranged from 1.5 to 2.6. The variation was mainly due to trade-offs between stem and root biomass. Average T/R was about 2.3 that was calculated for some reported *L. gmelinii* and *L. cajanderi* stands ($n = 16$), including our four stands. This average T/R was extremely small in comparison to that (5.1) of Scots pine (*Pinus sylvestris* L.) stands on the non- or discontinuous permafrost regions in Siberia. This finding strongly suggested that the two *Larix* species invested annual carbon gains largely into root growth. We discussed its ecological implications in relation to stand structure and permafrost soil-N conditions in the larch taiga ecosystem.

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1. Introduction

Boreal forests are expected to affect significantly global carbon balance, although it is still uncertain whether they will function as net carbon sink or source under global warming

(Oechel et al., 1993; Goulden et al., 1998; Schulze et al., 1999; Chapin et al., 2000; Jarvis et al., 2001). Carbon stocks and net primary production of boreal forests have been well studied in the non- and/or discontinuous permafrost regions of Alaska (Van Cleve et al., 1983, 1986; Vogt et al., 1996), northern Canada (Gower et al., 2001; Bhatti et al., 2002), and Europe (Schulze, 2000), where evergreen conifers predominate. Many studies in the evergreen taiga emphasized that contribution of roots, especially fine roots, to total net primary production was

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relatively large in comparison with other forest ecosystems (e.g., Ruess et al., 1996; Steele et al., 1997). This suggests that precise estimation of belowground biomass and production is a key issue for understanding carbon flux in boreal forest ecosystems (Li et al., 2003).

Boreal forests of central and eastern Siberia are dominated by two larch species (*Larix gmelinii* (Rupr.) Rupr. and *Larix cajanderi* Mayer), respectively, where ground surfaces are continuously underlain by permafrost (Abaimov, 1995). These larch species are essentially similar, although there are some different characteristics concerning reproduction, e.g., morphology of cone and frequency of seed production (Abaimov, 1995). Because of their huge occupation areas and potentially large carbon pools (Alexeyev and Birdsey, 1998), the Siberian larch taiga might contribute considerably to global-scale carbon flux. However, most of previous studies have dealt only with aboveground components (Pozdynakov et al., 1969; Usoltsev, 2001), and we have as yet insufficient knowledge on its belowground carbon stocks and cycling.

Some previous studies reported that biomass allocation into coarse roots was considerably large (30–40% of total biomass) in the mature *L. gmelinii* stands (e.g., Khlynovskaya et al., 1988; Kanazawa et al., 1994). Kajimoto et al. (1999, 2003) also showed that mature *L. gmelinii* trees developed horizontally well-expanded, superficial root systems, and eventually the forests (>100 years old) were likely to be closed fully below the ground by dense root network. Rather root-oriented carbon investment, resulting in development of such an exploitative root network, may be primarily explained by positive growth response of the larch individuals against constraint of soil nutrients uptake (Kajimoto et al., 1999). Particularly, soil-N is indicated as a major factor limiting tree growth in this larch ecosystem, e.g., aboveground biomass accumulation in *L. gmelinii* stands decreased sharply due to lack of soil-N availability after attaining a certain age (about 100 years old) (Schulze et al., 1995). To understand the ecosystem carbon flux in relation to the permafrost soil conditions, we require more data on root biomass and production based on a reliable estimation method.

Size–mass allometric equation is the most standard way for forest biomass estimation, and breast-height stem diameter is known as a simple and good predictor for biomass of both aboveground components and root (e.g., Karizumi, 1974; Santantonio et al., 1977; Ter-Mikaelian and Korzukhin, 1997). However, several other variables are suggested as better predictors: crown-base stem diameter or sapwood area for needle and branch mass (Shinozaki et al., 1964; Pearson et al., 1984; Comeau and Kimmins, 1989; Bormann, 1990; Osawa, 1990) and stem diameters at lower positions for coarse root mass (Haynes and Gower, 1995; Bond-Lamberty et al., 2002; Guan and Cheng, 2003). It is necessary to determine such good size parameters for developing a reliable allometric equation for a target species. In addition, we should further examine applicability of so-called generic (or site-common) allometry that can be derived by pooling sample data from various sites if we apply it to assessing carbon stocks for a given stand of target

species (e.g., Jokela et al., 1986; Bond-Lamberty et al., 2002).

In this paper, we examined size–mass allometry and biomass allocation of *L. gmelinii* and *L. cajanderi* based on the sample tree data gathered from four different mature (>100 years old) stands. First, we tested the assumption that site-specific allometry using breast-height diameter as a independent size variable is reliable for biomass estimation, including coarse root. Second, we compared such site-specific allometry among the four study stands, and discussed applicability of site-common allometry that was derived by pooling all sample data. Finally, we discussed biomass allocation pattern of the two *Larix* species focusing on the hypothesis that was previously suggested: annual carbon gains are allocated largely into root at the expense of aboveground woody growth (Kajimoto et al., 1999). For this purpose, we reviewed available biomass data for the *Larix* stands, and compared its aboveground-total/root biomass ratio with those of other forest types, especially for Scots pine (*Pinus sylvestris* L.) forests on the non- or discontinuous permafrost regions in Siberia.

2. Materials and methods

2.1. Study sites

Field measurements and tree sampling were conducted in three different locations within the continuous permafrost region of Siberia. Two sites were located in eastern Siberia; one was on the lower delta of Kolyma River (about 70 km west to Chersky; 69°N160°E, 100 m a.s.l.) and the other was on the upper stream of Indigirka River (about 100 km west to Oymyakon; 63°N145°E, 1160 m), where sparse *L. cajanderi* forest was predominant. The Oymyakon site was near altitudinal treeline of *L. cajanderi* in this region. Another site was located in central Siberia, along Kochechum River (a branch of Nizhnyaya Tunguska River) near the town of Tura (64°N100°E; 160 m), where *L. gmelinii* was distributed dominantly.

In all study sites, floor vegetation is represented by Ericaceae dwarf woody shrubs (e.g., *Ledum palustre* L., *Vaccinium vitis-idaea* L., and *V. uliginosum* L.), and some lichens (e.g., *Cladina*, *Cetraria* spp.) and mosses; they are major component species of mature *Larix* forests in the permafrost region (Abaimov et al., 2000). Climate is extremely continental, although local climate may be somewhat different, e.g., summer temperature (July mean) is 9.6 °C in Chokurdah (nearest meteorological station of Chersky), which is lower than 15.3 °C in Verhojansk (near Oymyakon) or 16.3 °C in Tura (Reference Book on the Climate of the USSR, 1969; other unpublished sources). Soil types are generally classified into Cryosols according to the WRB (FAO, 1998), or Gelisols in US Soil Taxonomy (Soil Survey Staff, 1998), and more detail soil types are as follows; Turbic Cryosol in the study site of Chersky, Leptic Cryosol in Oymyakon, and Haplic or Oxyaquic Cryosol in Tura (Matsuura and Abaimov, 1999, 2000; other unpublished data).

2.2. Field measurements and sampling

We established one research plot in each of the two study sites in eastern Siberia; Chersky (abbreviated plot CK, 0.06 ha in plot area) and Oymyakon (plot OM, 0.1 ha). Both plots were nearly even-aged *L. cajanderi* stands (ca. 155 and 140 years old, respectively) (Table 1). The plot CK was located on a flat plain apart from the nearest stream (ca. 500 m), and plot OM was on the middle part of a north-facing slope. Each place was selected as a representative of surrounding forests (e.g., topography, tree density and size); plot size was determined by considering difference in tree density. For the site Tura in central Siberia, we selected two *L. gmelinii* stands with different ages; almost even-aged young (plot W1, ca. 100 years old, 0.015 ha) and uneven-aged mature stands (plot C1, 100–280 years old, 0.1 ha). They were located on the opposite slopes across Kochechum River (ca. 300 m away each other). Three even-aged stands (CK, OM, W1) have regenerated after intensive fires, and the uneven-aged stand (C1) was likely to have experienced ground fires several times until early 1900s (Kajimoto et al., 1999, 2003, and other unpublished data).

Tree census and sampling were conducted in mid-summers from 1995 to 1998. In each plot, stem diameters at breast height (1.3 m) (D) and crown base (D_B), tree height (H), crown projection area (i.e., crown diameter along two directions), and other size dimensions were measured for all living larch trees taller than 1.3 m. We selected sample trees of different sizes so that its size range (minimum and maximum individuals) could cover almost a whole D -range in each stand. Apparently damaged or unhealthy trees (e.g., dieback of crowns) were excluded from the selection. In total, 27 trees were harvested ($n = 7$ in CK, C1, W1; $n = 6$ in OM). In the even-aged three stands, ages of the sample trees were 138–178 (CK), 135–147 (OM), and 95–100 years old (W1), except for the smallest individual in CK (86 years old) and the largest one in OM (253 years old) (Table 1). In the uneven-aged oldest stand (C1), ages

of sample trees ranged from 99 to 281 years old, but mostly exceeded 200 years ($n = 5$).

For each sample tree, fresh mass of aboveground three components were measured separately, and then determined dry mass (oven-dried at 85 °C) of stem with bark (w_S), branches (w_B) and needles (w_L) using corresponding dry/fresh ratio. Dry/fresh ratio was obtained by subsamples taken from each component. The amount of such subsample differed by tree size, e.g., for needle and branch, 30–40% of its total fresh mass was employed for smaller trees, and 5–10% for larger trees. Here, needle mass was defined as sum of both short-shoot and long-shoot needles, and branch mass was the total of old short- and long-shoots, and current long-shoots. Roots were harvested manually for 23 individuals, because root systems of the other four larger trees ($n = 2$ in CK; $n = 1$ in OM; $n = 1$ in C1) were still fixed partially in frozen soils during each sampling period. Dry mass of coarse roots (w_R) (≥ 5 mm in diameter) was determined after excluding dead roots carefully by visual inspection. Details of the definitions and sampling procedures were described by Kajimoto et al. (1999).

2.3. Data analysis and biomass estimation

For determining a good size parameter of site-specific allometry for each component mass, we considered D as a representative of independent size variables and selected other six variables as a candidate of better predictors; stem diameters at 30 cm height (D_{30}) and crown base (D_B), sapwood areas at breast height (SA) and at 30 cm height (SA_{30}), and two combined-variables (D^2H , D_{30}^2H). Site-specific allometry was approximated by power-form equation ($y = Ax^B$; x is size variable, y is dry mass). Two coefficients of regression (A and B) were determined after log-transformation (natural-base) of the data (i.e., linear equation; $\ln y = B \ln x + \ln A$) using the ordinary least square method. Significance of each regression was tested by coefficient of determination (r^2). A correction

Table 1
Outlines of the research plots of *Larix* forests. Dominant species is *L. cajanderi* in CK and OM, and *L. gmelinii* in C1 and W1. Tree density and size dimensions were the values only for living larch individuals (height > 1.3 m)

	Eastern Siberia		Central Siberia	
	CK	OM	C1	W1
Site location	Chersky	Oymyakon	Tura	Tura
Elevation (m)	100	1160	250	250
Tree density (ha ⁻¹)	1930	850	1910	5700
Canopy closure (ha ha ⁻¹)	0.37	0.09	0.34	0.12
Age (years old) range (mean)	86–178 (155)	135–253 (140)	99–281 (220)	95–100 (ca. 95)
Stem diameter (cm) mean (max.)	5.93 (18.60)	6.57 (16.10)	6.83 (18.50)	2.24 (5.40)
Tree height (m) mean (max.)	4.31 (8.50)	4.46 (9.10)	5.50 (10.29)	2.66 (7.00)
Soil properties				
Active layer depth (cm)	24–40	50–60	40–80	10–20
Total organic C (kg m ⁻³)	15.3	21.6	14.0	23.5
Total N (kg m ⁻³)	1.21	1.15	6.86	1.26
C/N ratio	12.6	18.8	20.4	18.7

Canopy closure is defined as sum of crown projection area of all living larches per unit land area. Age shows the range of sample trees used for the analysis ($n = 7$ in CK, C1, W1; $n = 6$ in OM), and mean value in parenthesis was determined with some additional sample tree data. For soil properties, active layer depth was the range of some examined soil pits, and carbon and nitrogen stocks were assessed on one soil pit in each plot (Matsuura and Abaimov, 1999, 2000; other unpublished data).

factor (CF) was applied for A -value of each regression, which is required for correcting systematic bias due to log-transformation (Sprugel, 1983).

In the following analysis and estimation of stand biomass, we considered only one regression model (i.e., D -base allometry). Slope and intercept of site-specific D -base regression (i.e., coefficient B and $\ln A$) determined for each component were compared among the four plots by analysis of covariance (ANCOVA). Irrespective of significant differences in each or both of these coefficients, site-common allometric equations were derived for each component and individual total mass (w) by pooling all sample tree data ($n = 27$ for w_S , w_B and w_L ; $n = 23$ for w_R and w). Significance of each site-common allometry was tested by r^2 or analysis of variance (ANOVA), and its linearity was examined by residual plotting (Zar, 1999).

Each stand biomass was estimated by applying site-specific allometry to the census data. Aboveground total biomass was defined as sum of stem, branches and needles, and stand total biomass was obtained by adding coarse roots. Also, to examine applicability of general (or site-common) allometry to biomass estimation for a given stand of the two *Larix* species, each component biomass by the site-specific allometry was compared with the corresponding estimate obtained by site-common D -base allometry.

Dry mass ratio of aboveground total to coarse root (T/R) was defined on a tree basis: $(w_S + w_B + w_L)/w_R$. To detect factors affecting individual T/R , correlations with tree age and total mass (w) were examined by study sites. By eliminating effect of difference in individual age, correlations of T/R with the following two parameters were also tested; mean annual growth rates of total mass (w/age) and tree height (H/age). When correlations were not significant, averages of sample tree's T/R were compared among the four plots by ANOVA, and post hoc multiple comparison test was conducted if necessary (Tukey's HSD).

2.4. Biomass data for comparisons

For comparisons of our biomass estimates with those of the other stands of *L. gmelinii* and *L. cajanderi*, we selected some published papers from the biomass dataset compiled by Usoltsev (2001). Definition of treated root size in each original paper was examined carefully. In most of these selected studies, root biomass was estimated including both coarse and fine roots, and only the two studies dealt with roots separately by diameter size: one *L. gmelinii* stand (definition of coarse roots is the same as ours; ≥ 5 mm) (Kanazawa et al., 1994) and four *L. cajanderi* stands (≥ 7 mm) (Moskalyuk, 1980, 1984) (see details Appendix A, Table A.1). Second, to compare aboveground-total/root biomass ratio (i.e., stand-level T/R) of these two *Larix* species with other boreal forest types, we selected available biomass data of Scots pine (*Pinus sylvestris*) stands in Siberia (Appendix A, Table A.1): the pine grows mostly on the non- or discontinuous permafrost regions. In these data, root biomass was also estimated including both coarse and fine roots. T/R s between the *Larix* and *Pinus* stands was compared

by applying a linear regression to the data, and significant difference in the two regression slopes was tested (ANCOVA).

All statistical tests in our analysis were made on the basis of individual data or its average value of each plot.

3. Results

3.1. Allometric relationships

All site-specific size–mass allometric equations were significant ($p < 0.01$), except for one case (D_B – w_R relationship in OM) (Table 2). For stem and coarse root mass, correlations (r^2) of the D -base allometry were somewhat improved when D_{30} was used as a size variable, especially for the sample trees of youngest stand (W1). However, two combined-parameters (D^2H , D_{30}^2H) did not always produce higher r^2 than the cases using each of single parameters (D , D_{30}). For branch and needle mass, correlations of site-specific allometric regressions with D_B , SA and SA_{30} were not necessarily higher than those using D .

Slopes (i.e., coefficient B) of D -base site-specific regressions did not differ among the four plots, except for stem mass ($F_{[3,19]} = 3.89$, $p = 0.025$; ANCOVA) (Table 3). Intercepts of site-specific regressions (i.e., $\ln A$) differed for needle mass (w_L) ($F_{[3,19]} = 4.59$, $p < 0.025$) and coarse root mass (w_R) ($F_{[3,15]} = 5.68$, $p < 0.01$). When all sample tree data were pooled, each component mass was highly correlated with D ($r^2 = 0.91$ – 0.94 ; $p < 0.01$) (Fig. 1). However, linearity of site-common allometry was doubted for stem mass: residual distribution tended to be relatively high at smaller or larger D classes (Fig. 1A), although its regression was significant ($F_{[3,19]} = 3.09$, $p = 0.091$; ANOVA) as those for other three components (Table 3).

Individual total mass (w) was also highly correlated with D for the sample trees of each site ($r^2 > 0.92$; $p < 0.01$). These four site-specific D – w regressions did not differ significantly in both slope and intercept ($F_{[3,15]} = 2.09$, 1.97 , $p > 0.05$; ANCOVA) (Table 3). When all sample tree data were pooled, correlation of site-common D – w allometry was as high ($r^2 > 0.95$; $p < 0.01$) as that of the site-common regression determined separately for each component (Table 3).

3.2. Stand biomass and biomass allocation

Stand total biomass estimated by applying each site-specific allometry (Table 3) ranged from 8.6 (W1) to 33.1 Mg ha^{−1} (C1) (Table 4). In all plots, relative biomass proportion was the largest for stems (ranged 45–61%; averaged 54%), followed by coarse roots (28–40%; 33%), branches (9–12%; 10%) and needles (2.0–3.5%; 3%). Trade-offs of biomass allocation between stems and roots were observed, e.g., proportions of stem (61%) and coarse root (28%) in OM were the highest and lowest, respectively, and vice versa (45%, 40%) in CK. Aboveground-total/coarse root biomass ratio ranged from 1.5 (CK) to 2.6 (OM) (Table 4).

Estimate of stand total biomass obtained by applying site-common allometry (Fig. 1, Table 1) ranged from 10.8 (W1) to

Table 2
Coefficients of determination (r^2) in site-specific allometric equations ($y = Ax^B$) for each component mass y (stem w_S , branch w_B , needle w_L , and coarse root w_R), with seven size parameters (x)

Parameter		Coefficient of determination r^2			
y	x	CK	OM	C1	W1
Stem w_S (kg)	$D_{30}(\text{cm})$	0.980***	0.993***	0.976***	0.908***
	D_{30} (cm)	0.995***	0.993***	0.993***	0.989***
	$D_B(\text{cm})$	0.944***	0.872**	0.939***	0.920***
	SA (cm ²)	0.910***	0.867**	0.970***	0.789**
	SA_{30} (cm ²)	0.918***	0.939**	0.942***	0.955***
	D^2H (cm ³)	0.980***	0.995***	0.984***	0.906***
	D_{30}^2H (cm ³)	0.996***	0.999***	0.992***	0.989***
Branch w_B (kg)	D (cm)	0.976***	0.950***	0.981***	0.841**
	D_{30} (cm)	0.924***	0.909**	0.988***	0.852**
	D_B (cm)	0.892**	0.877**	0.867**	0.936***
	SA (cm ²)	0.966***	0.911**	0.988***	0.863**
	SA_{30} (cm ²)	0.949***	0.924**	0.960***	0.920***
	D^2H (cm ³)	0.973***	0.939**	0.980***	0.834**
	D_{30}^2H (cm ³)	0.942***	0.912**	0.979***	0.861**
Needle w_L (kg)	D (cm)	0.973***	0.966***	0.981***	0.843**
	D_{30} (cm)	0.915***	0.939**	0.991***	0.875**
	D_B (cm)	0.888**	0.871**	0.900**	0.956***
	SA (cm ²)	0.975***	0.945**	0.982***	0.866**
	SA_{30} (cm ²)	0.915***	0.959***	0.944***	0.952***
	D^2H (cm ³)	0.972***	0.959***	0.982***	0.838**
	D_{30}^2H (cm ³)	0.937***	0.942**	0.982***	0.882**
Coarse root w_R (kg)	D (cm)	0.971**	0.993***	0.929**	0.933***
	D_{30} (cm)	0.986***	0.973**	0.940**	0.953***
	D_B (cm)	0.989***	0.707 ns	0.908**	0.895**
	SA (cm ²)	0.901*	0.860*	0.880**	0.807**
	SA_{30} (cm ²)	0.942**	0.975**	0.821*	0.912***
	D^2H (cm ³)	0.974**	0.978**	0.934**	0.930***
	D_{30}^2H (cm ³)	0.988***	0.968**	0.934**	0.967***

The numbers of sample trees in each plot are as follows: $n = 7$ in CK, C1 and W1 and $n = 6$ in OM for w_S , w_B and w_L ; $n = 5$ in CK and OM, $n = 6$ in C1, and $n = 7$ in W1 for w_R . ns: not significant.

* Significance level: $p < 0.05$

** Significance level: $p < 0.01$

*** Significance level: $p < 0.001$

26.3 Mg ha⁻¹ (Table 5). When compared with corresponding estimates by the site-specific allometry (Table 4), the site-common regression underestimated biomass of all components in the two plots (CK, C1), while it overestimated in the youngest stand (W1). Deviations of the estimate from that by site-specific allometry were relatively large for needle (from -22 to 78%) and coarse root (-27 to 44%) than those for stem (-23 to 14%) and branch (-20 to 41%). When aboveground total biomass was compared, such deviations were reduced to $< \pm 20\%$.

3.3. Allocation in individual trees

Individual T/R s ranged from 0.76 to 2.71. Average values of individual T/R differed significantly among the four plots ($F_{[3,15]} = 5.77$, $p = 0.006$; ANOVA); the sample trees of C1 had smaller average T/R (1.4) than those of OM (2.2) and W1 (2.1) ($p < 0.05$; Tukey's HSD). Within each plot, individual T/R did not correlate with either tree age or total mass (w) ($p > 0.05$) (Fig. 2A and B). There were also no correlations between T/R and mean annual growth rates of total mass (w/age) and tree height (H/age) ($p > 0.05$) (Fig. 2C and D) in each plot, except

for one case: T/R was related positively to H/age for the sample trees of OM ($r^2 = 0.79$; $p < 0.05$).

4. Discussion

4.1. Applicability of site-common allometry

For site-specific allometry, correlations of all D -base regressions were as high as corresponding regressions using other seven size variables (Table 2). Even for branch and needle mass, correlations were not always improved if using other variables, such as crown-base diameter (D_B) or sapwood area (SA), although these two parameters are known as better predictors for many conifer species (e.g., Waring et al., 1980; Pearson et al., 1984; O'Hara, 1988; Comeau and Kimmins, 1989; Osawa, 1990). For coarse roots, site-specific regressions using D showed similar correlations as those using stem diameter at lower position (D_{30}). Breast-height diameter was indicated as a good predictor for coarse root biomass in Norway spruce (*Picea abies* L. Karst.) stands (Drexhage and Gruber, 1999). These findings support our assumption that D -base site-

Table 3

Coefficients of site-specific and site-common allometric equations between stem diameter (D ; cm) and mass of stem (w_S), branch (w_B), needle (w_L), coarse root (w_R) and individual total (w)

Component y	Site-specific allometry						Site-common allometry
	Coefficients	CK	OM	C1	W1	F -value	
w_S (kg)	A	1.13×10^{-1}	1.40×10^{-1}	1.76×10^{-1}	2.64×10^{-1}	1.39 ns	1.90×10^{-1}
	B	2.04	1.96	1.96	1.39	3.89*	1.81 (3.09, $p = 0.09$)
	r^2	0.98	0.99	0.98	0.91	–	0.95
	CF	1.02	1.01	1.05	1.06	–	1.05
w_B (kg)	A	3.96×10^{-2}	5.96×10^{-2}	5.60×10^{-2}	3.99×10^{-2}	0.55 ns	4.28×10^{-2}
	B	1.91	1.48	1.69	1.70	2.33 ns	1.79(1.41, $p = 0.25$)
	r^2	0.98	0.95	0.98	0.84	–	0.94
	CF	1.02	1.03	1.03	1.19	–	1.07
w_L (kg)	A	1.06×10^{-2}	1.86×10^{-2}	2.27×10^{-2}	1.38×10^{-2}	4.59*	1.48×10^{-2}
	B	1.94	1.31	1.58	1.60	1.37 ns	1.68(0.48, $p = 0.50$)
	r^2	0.97	0.97	0.98	0.84	–	0.92
	CF	1.02	1.02	1.02	1.16	–	1.09
w_R (kg)	A	9.71×10^{-2}	1.28×10^{-1}	3.34×10^{-1}	1.55×10^{-1}	5.68**	1.71×10^{-1}
	B	2.07	1.63	1.46	1.42	2.02 ns	1.67(0.13, $p = 0.72$)
	r^2	0.97	0.99	0.93	0.93	–	0.91
	CF	1.04	1.00	1.08	1.05	–	1.09
w (kg)	A	2.57×10^{-1}	3.46×10^{-1}	5.91×10^{-1}	4.71×10^{-1}	2.09 ns	4.39×10^{-1}
	B	2.04	1.75	1.65	1.43	1.97 ns	1.70 (2.15, $p = 0.16$)
	r^2	0.98	0.99	0.97	0.92	–	0.95
	CF	1.02	1.00	1.05	1.06	–	1.05

Allometry is expressed as a power-form equation ($y = AD^B$). The number of sample trees used for each regression is listed in Table 2. Site-common allometry is derived by pooling all data ($n = 27$ for w_S , w_B and w_L ; $n = 23$ for w_R and w). Each A value is corrected by CF. All site-specific regressions are significant at $p = 0.01$, and differences of coefficients among four site-specific regressions are shown by F -values with significance levels, ns; not significant at $p = 0.05$; ANCOVA). Results of ANOVA for site-common allometry are shown in parenthesis (F -value, p -level).

* $p < 0.025$.

** $p < 0.01$.

specific allometry is a simple and reliable model for estimating all component biomass of mature stands of *L. gmelinii* and/or *L. cajanderi*.

However, such a simple regression model (i.e., D -base allometry) is insufficient for developing site-common allometry. At least for stem mass, slopes of four site-specific regressions differ (Table 3), and the site-common regression that derived by pooling all sample data tends to lose its linearity (Fig. 1A). This model failure is due to the fact that only the youngest stand (W1) ($B = 1.39$) has much smaller site-specific regression slope than those of the other older stands ($B = 1.96$ – 2.04). The sample trees selected from W1 were smaller ($H < 4$ m) than those of the other stands ($H < 7$ – 10 m); this reflects differences in tree sizes among the stands (Table 1). Thus, D is not necessarily a good predictor if we apply the site-common allometry to stem biomass estimation, especially for a stand consisting of relatively small trees. Such discrepancy of D -base allometry by tree sizes was also suggested for other conifer species, i.e., regression slopes differed between seedlings and adult trees, (Haynes and Gower, 1995; Bond-Lamberty et al., 2002).

Besides, intercepts of four site-specific regressions differed for needle and coarse root mass (Table 3). This indicates that needle and coarse root mass for a given size tree vary significantly by sites. However, relative proportion of needle biomass (3–6% of aboveground total biomass; Table 4) is much smaller than those of stems and branches. Similar values were

reported for other mature *L. gmelinii* stands (> 100 years old) in eastern Siberia; needles shared only 2–3% of aboveground total biomass (Kanazawa et al., 1994; Schulze et al., 1995; Tsuno et al., 2001). Thus, if we estimate only aboveground total biomass using D -base site-common allometry, estimation bias due to site-to-site variation of individual needle mass might be offset considerably (e.g., deviation $< \pm 20\%$ for above-total biomass; Table 5). In contrast, coarse roots are not negligibly small fraction as needles (i.e., 28–40% of stand total biomass) (Table 4), and thus its estimation bias by site-common allometry may still hold to a larger extent. In all, it is noted that site-common D -base allometry that was tested in our analysis might cause a certain bias in estimation of each component biomass for a given stands of the *Larix* stands. For precise estimation, more improved regression models should be further examined, e.g., including other size parameters (e.g., tree height), although such a model often loses simplicity.

4.2. Biomass allocation pattern

Relative proportion of coarse roots rarely exceeds about 30% of individual total mass (i.e., $T/R > 2.3$) for many conifer species (e.g., Karizumi, 1974; Santantonio et al., 1977; Cairns et al., 1997). Kurz et al. (1996) proposed that relationships between biomass of aboveground total and coarse roots (≥ 5 mm in diameter) were approximated by a linear equation with slope of 0.23 (i.e., an inverse of T/R) by reviewing many

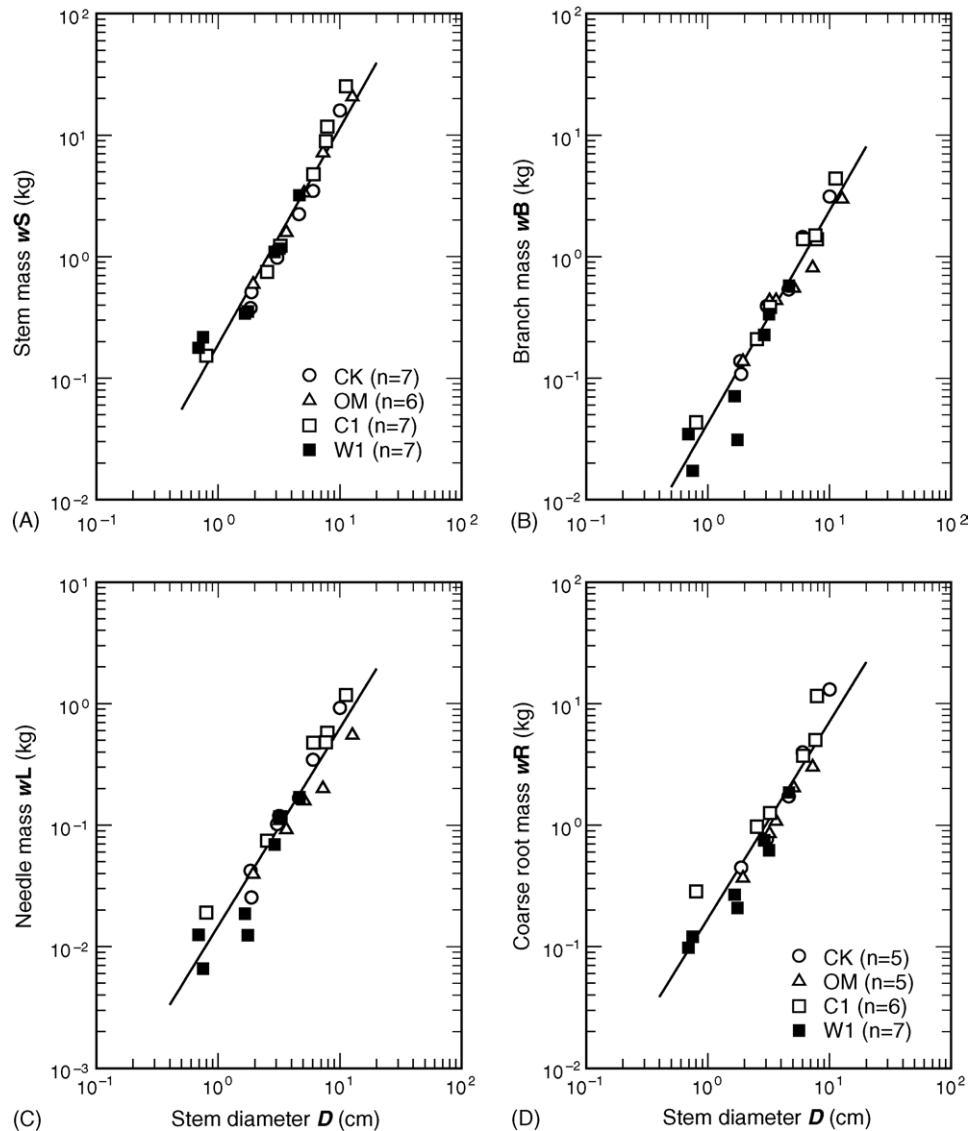


Fig. 1. Relationships between stem diameter at breast height (D) and (A) stem mass (w_S); (B) branch mass (w_B); (C) needle mass (w_L); and (D) coarse root mass (w_R) for the sample trees of *L. gmelinii* and *L. cajanderi*. Regression line of each component shows site-common allometry derived by pooling all sample tree data; values of regression slope and intercept are shown in Table 3. Symbols with abbreviated study plots are as follows; CK (Chersky), OM (Oymyakon), C1 (Tura) and W1 (Tura) (Table 1).

biomass data of temperate and boreal conifer forests ($n = 260$). This indicates that T/R is about 4.3 averaged for various forest types, including boreal conifer forests. In this review, however, available biomass data of boreal forests in Siberia, especially *L. gmelinii* and *L. cajanderi*, may not be included sufficiently. T/R s of our study stands (1.5–2.6; Table 4) are only one-third or half of such average value, suggesting a large discrepancy in above/root biomass partitioning from other boreal species.

To confirm this possibility, we re-examined relationships between aboveground total and root biomass for some stands of the two *Larix* species ($n = 19$), and compared with that of *P. sylvestris* stands ($n = 16$) growing on the non- or discontinuous permafrost regions in Siberia (Fig. 3). Here, aboveground total biomass is plotted against root biomass in order to read T/R immediately as a slope of linear regression. Linear relationship of

Larix stands has a slope of 2.3 ($r^2 = 0.90$, $p < 0.001$), irrespective of broad ranges of stand age (40–220 years old) and total biomass (5–260 Mg ha⁻¹). In contrast, the regression slope determined for *P. sylvestris* ($r^2 = 0.81$, $p < 0.001$) reaches about 5.0, which is about two times that of the *Larix* stands ($F_{[1,31]} = 22.7$, $p < 0.001$; ANCOVA) and is more closed to the average T/R (4.3) suggested by Kurz et al. (1996). There are still some uncertainty for this comparison, e.g., differences in definition of estimated root size among the data. However, quite a large discrepancy from the pine forests strongly suggests that mature *Larix* stands in Siberia have extremely smaller above-total/root ratio, or invest annual carbon gains largely into roots.

Rather root-oriented allocation pattern may be primarily explained as a result of growth response of the *Larix* individuals against constraints of soil nutrients in this larch taiga, especially nitrogen (Kajimoto et al., 1999). In fact, soil-N availability is

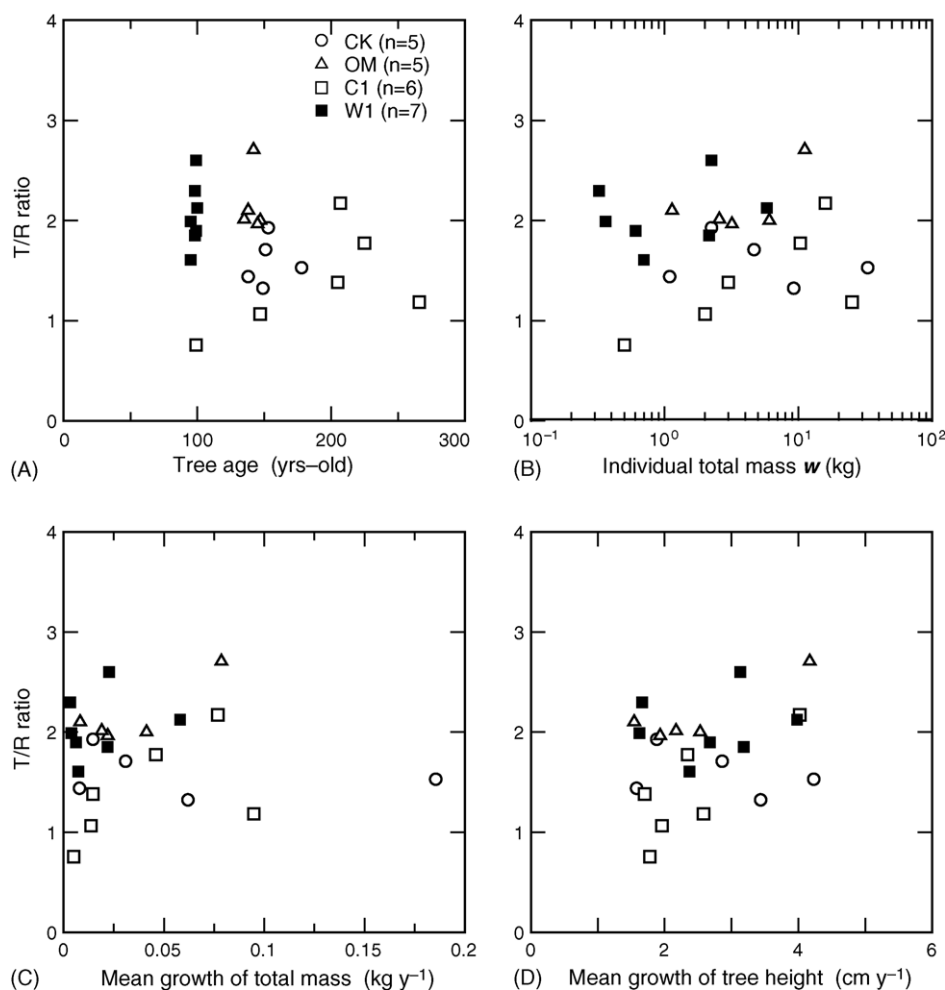


Fig. 2. Variations of individual T/R (aboveground total/coarse root mass ratio) in relation to two size parameters, (A) tree age and (B) individual total mass (w), and two growth potential parameters, mean annual growth rates of (C) total mass (i.e., w/age) and (D) tree height (i.e., H/age) for the sample trees of *L. gmelinii* and *L. cajanderi* (total $n = 23$). Correlation was significant only for one case: T/R vs. mean height growth rate for the sample trees ($n = 5$) of OM ($r^2 > 0.79$; $p < 0.05$). Symbols are the same as in Fig. 1.

limited on mature *Larix* stands (>100 years old) in terms of both inorganic N-pool (Schulze et al., 1995) and net N-mineralization rate (Matsuura and Abaimov, 2000; Tokuchi et al., 2003, 2004). Under such poor-N condition, larger biomass allocation to roots might be indispensable for individual growth by constructing exploitative root system (Kajimoto et al., 2003). In this viewpoint, however, we should further examine individual biomass allocation by including fine roots (<5 mm in diameter) that are really functioning for nutrient uptake.

For many forest types, fine root ratio (i.e., fine root/total root biomass) generally decreases with stand age or total biomass, and becomes stable around 0.1 after attaining a certain level of total biomass (Kurz et al., 1996; Li et al., 2003). In our study sites, fine root biomass was estimated only in the two *L. gmelinii* stands using the soil core sampling method; 4.1 and 5.9 Mg ha^{-1} in W1 and C1, respectively (Kajimoto et al., 1999, 2003). Fine root ratio is higher in the younger stand (0.58, W1) than in the older stand (0.34, C1). However, the relatively high fine root ratios in both stands suggest that the *Larix* trees still allocate annual carbon gains into secondary thickening of coarse root but also fine root production even at mature growth stage.

In our analysis, it remains uncertain why individual T/R varied largely in each stand. The inter-tree T/R variation did not correlate with tree size (Fig. 2B) even in the three even-aged stands (CK, OM, W1). Besides, there were no clear relationships between individual T/R and average growth rates of total mass or tree height (Fig. 2C and D). These facts indicate that the process of above/root carbon partitioning is not explained simply by difference in long-term growth potential. In other words, individuals with higher growth rates may have not been necessarily investing annual carbon gains into aboveground parts (mainly stems) more than roots in comparison with smaller individuals with lower growth potential, or vice versa.

L. gmelinii forests in the continuous permafrost region are generally characterized by sparse, open-growth stands, and canopies are rarely to be closed at mature stage (canopy closure index = 0.1–0.4) (Bondarev, 1997). The index of our each study site falls within this range (Table 1). This implies that difference in local light conditions between larger and smaller trees within each stand may be relatively small in comparison to other well-closed forest ecosystems, such as temperate and tropical

Table 4
Aboveground and coarse root biomass of the four larch stands estimated by site-specific allometric equations

Component	Biomass (Mg ha ⁻¹)			
	CK	OM	C1	W1
Stems	12.18 (44.7)	6.47 (61.4)	18.93 (54.2)	4.93(53.2)
Branches	3.24 (11.9)	0.96 (9.1)	3.29 (9.4)	1.04(11.2)
Needles	0.91 (3.3)	0.21 (2.0)	1.03 (2.9)	0.32(3.5)
Aboveground total	16.33 (59.9)	7.64 (72.5)	23.25 (66.5)	6.29(67.9)
Coarse roots	10.92 (40.1)	2.89 (27.5)	11.72 (33.5)	2.98(32.1)
Stand total	27.25	10.53	34.97	9.27
Above-total/root	1.49	2.64	1.98	2.11

Value in parenthesis is a relative proportion (%) of each component biomass.

Table 5
Biomass estimates of the four larch stands by applying site-common allometric equations

Component	Biomass (Mg ha ⁻¹) by site-common allometry				Deviation (± %)			
	CK	OM	C1	W1	CK	OM	C1	W1
Stems	12.12	6.30	14.60	5.60	−0.5	−2.5	−22.9	13.7
Branches	2.61	1.36	3.14	1.23	−19.4	40.7	−4.7	18.5
Needles	0.71	0.37	0.85	0.38	−21.7	78.1	−17.4	17.4
Above-ground total	15.44	8.03	18.59	7.21	−5.4	5.2	−20.1	14.7
Coarse roots	7.98	4.16	9.55	4.30	−26.9	43.8	−18.5	44.5
Stand total	23.42	12.19	28.14	11.52	−14.0	15.8	−16.9	24.8

Deviation shows relative difference from corresponding biomass estimated by site-specific allometry (Table 4).

forests. In contrast, spatial heterogeneity of soil conditions is conspicuous due to micro-topography (i.e., earth hummock) in this region, such as temperature, water (Kajimoto et al., 2003) and net N-mineralization rate (Tokuchi et al., 2003, 2004). Many experimental studies indicate that shoot/root ratio changes dramatically in response to N-addition (Linder and

Axelsson, 1982; Axelsson and Axelsson, 1986; Colbert et al., 1990; Haynes and Gower, 1995; Albaugh et al., 1998). For understanding more carbon allocation of the two *Larix* species, we may need to consider effects of such micro-scale variation of soil nutrients.

5. Conclusion

Our analysis suggests that coarse roots are relatively large carbon sink in mature stands of the two *Larix* species established on the continuous permafrost region of Siberia. This means that precise estimation of root biomass is particularly important for understanding carbon flux of the larch taiga ecosystem. From ecological viewpoint, however, questions still remain on factors causing larger inter-tree variation of above/root carbon partitioning. To address the question, we need information on biomass allocation at younger growth stage, such as seedlings or saplings (<10–20 years old) that occur just after fire disturbance. The *Larix* seedlings may have different carbon allocation pattern from that of mature trees, because soil environments change throughout stand development in the permafrost region: depth of active soil layer and soil-temperature decrease gradually due to recovery of floor vegetation (e.g., Abaimov and Sofronov, 1996), and then soil-N availability will be limited after a certain stand age (Schulze et al., 1995). These environmental changes might affect proportion of annual carbon investment required for root growth. Future analysis should focus on such linkage between individual carbon allocation and post-fire dynamics of permafrost soil environments.

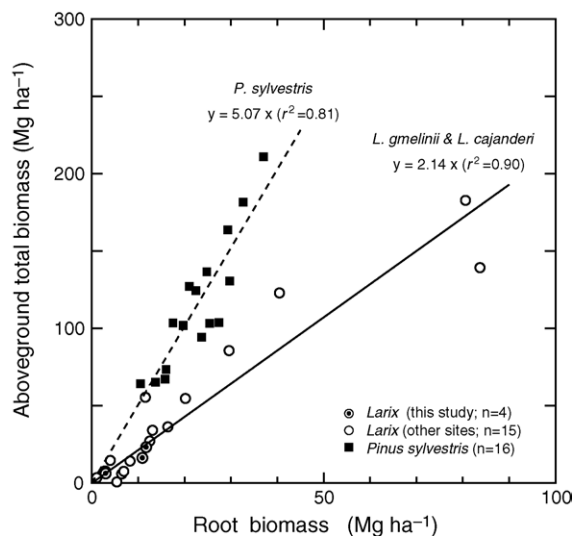


Fig. 3. Relationships between root and aboveground total biomass for the stands of two *Larix* species ($n = 12$ for *L. gmelinii*, $n = 7$ for *L. cajanderi*) and Scots pine (*Pinus sylvestris*) ($n = 16$) in Siberia. Details of data source are listed in Appendix A, Table A.1. Solid and dotted line shows linear regression determined for *Larix* ($r^2 = 0.90$, $p < 0.001$) and *P. sylvestris* ($r^2 = 0.81$, $p < 0.001$, respectively); slopes of the two regressions are different ($F_{[1,31]}$, $p < 0.001$; ANCOVA).

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Appendix A

See Table A.1.

Table A.1

Aboveground total and root biomass data reported for the stands of two larch species (*L. gmelinii*, *L. cajanderi*) and Scots pine (*Pinus sylvestris*) in Siberia

Species and site	Age (years)	Density (ha ⁻¹)	Diameter ^a (cm)	Height ^b (m)	Biomass (Mg ha ⁻¹)				Data source ^c
					Aboveground ^d	Root ^e	Total ^f	T/R ^g	
<i>Larix gmelinii</i> (n = 7)									
72°N101°E	142	430	8.3	4.6	5.97	6.46	12.43	0.92	1
	142	240	3.2	2.5	0.78	5.40	6.18	0.14	1
70°N90°E	155	490	19.5	15.3	55.49	11.56	67.05	4.80	2
	155	280	8.0	7.0	3.54	1.06	4.60	3.33	2
62°N129°E	169	900	18.0	16.9	123.01	40.47*	163.48	3.04	3
64°N100°E	220	1910	6.8	5.5	23.25	11.72*	34.97	1.98	This study (C1)
	100	5700	2.2	2.7	6.29	2.98*	9.27	2.11	This study (W1)
<i>Larix cajanderi</i> (n = 12)									
60°N148°E	146	500	27.5	24.6	182.82	80.60**	263.42	2.26	4
	181	630	22.6	22.2	139.35	83.72**	223.07	1.66	4
	193	860	14.3	13.3	54.75	20.20**	74.95	2.71	4
	208	390	12.3	8.0	14.66	4.00**	18.66	3.67	4
61°N152°E	35	550	11.1	12.4	36.40	16.40	52.80	2.22	5
	43	3870	8.1	7.8	34.20	13.10	47.30	2.61	5
	84	3050	11.6	10.0	85.70	29.60	115.30	2.90	5
	150	280	24.0	11.0	14.30	8.25	22.55	1.73	5
	150	200	9.5	5.5	7.60	6.90	14.50	1.10	5
	153	240	19.5	11.8	27.20	12.50	39.70	2.18	5
69°N160°E	155	1930	5.9	4.3	16.33	10.92*	27.25	1.49	This study (CK)
63°N145°E	140	850	6.6	4.5	7.64	2.89*	10.53	2.64	This study (OM)
<i>Pinus sylvestris</i> (n = 16)									
66°N87°E	100	390	22.0	15.0	65.40	13.70	79.10	4.77	6
	120	590	19.0	14.0	67.30	15.80	83.10	4.26	6
	140	510	23.0	16.0	94.30	23.70	118.00	3.98	6
	180	380	27.0	19.0	103.30	25.40	128.70	4.07	6
	180	570	23.0	17.0	103.80	27.40	131.20	3.79	6
62°N90°E	40	7930	7.0	9.0	73.50	16.00	89.50	4.59	6
	70	1850	15.0	18.0	136.60	24.80	161.40	5.51	6
	80	780	18.0	16.0	103.60	17.50	121.10	5.92	6
	160	940	23.0	23.0	211.00	37.00	248.00	5.70	6
	160	900	21.0	17.0	130.70	29.70	160.40	4.40	6
52°N94°E	30	6400	6.0	9.0	64.30	10.50	74.80	6.12	6
	50	1870	14.0	13.0	102.00	19.70	121.70	5.18	6
	70	580	22.0	17.0	127.20	21.00	148.20	6.06	6
	80	580	24.0	16.0	124.40	22.40	146.80	5.55	6
	100	650	24.0	18.0	163.70	29.30	193.00	5.59	6
	130	360	33.0	23.0	181.80	32.60	214.40	5.58	6

^a Mean stem diameter at breast height.

^b Mean tree height.

^c (1): Knorre (1977); (2): Yarmishko and Dem'yanov (1983); (3): Kanazawa et al. (1994); (4): Moskalyuk (1980, 1984); (5): Khlynovskaya et al. (1988); (6): Pozdynakov et al. (1969), Pozdynakov (1975) and other papers. Details of each original data are listed in the dataset compiled by Usoltsev (2001).

^d Total biomass of stems, branches and needles.

^e Most of studies included both coarse and fine root biomass, except for some sites: only coarse root (*: defined as roots > 5 mm in diameter) is estimated in our four sites and one *L. gmelinii* stand (data source 3), and coarse root (**: defined as roots > 7 mm) is estimated in four *L. cajanderi* stands (data source 4).

^f Sum of aboveground total and root biomass.

^g Aboveground total/root biomass ratio; as mentioned above, T/Rs of some sites are calculated as aboveground total/coarse root biomass ratio (this study, and data source 3, 4).

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