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RESEARCH PAPER

Variation in carbon concentrations and allocations among *Larix olgensis* populations growing in three field environments

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Abstract

• ***Key message*** **Variation in carbon concentration among *Larix olgensis* A. Henry provenances and tree tissues was significant, suggesting importance of such variation to carbon stock calculation. Provenance variation in carbon allocation was only significant in allocations to some tissues, including stem wood, and was strongly site-specific. Some allocation patterns correlated significantly with provenance growth and were related to geographic/climatic variables at the provenance origins.**

• ***Context*** Understanding variation in carbon concentrations and allocations to tree tissues among genetic entries is important for assessing carbon sequestration and understanding differential growth rates among the entries. However, this topic is poorly understood, in particular for mature trees in field conditions.

• ***Aims*** The study aims to assess genetic variation in C concentrations and allocations to tree tissues and further to link the variation to tree growth and to assess their adaptive nature.

• ***Methods*** In 2011, carbon concentrations and allocations to tree tissues (stem wood, stem bark, branches, foliage, and root components) were measured on 31-year-old trees of ten *Larix olgensis* A. Henry provenances growing at three sites located in northeast China: CuoHai Forest Farm (CH), LiangShui Forest Farm (LS), and MaoErShān Forest Farm (MES). Variation in carbon allocation was analyzed using allometric methods.

• ***Results*** Variation in C concentration among tree tissues and among provenances was significant and site-specific. The cross-tissue variation in concentration was driven primarily by high concentration in branches and leaves and low concentration in stem wood and coarse roots. Differences between the minimum and maximum provenance means reached 1% at the tree level. Provenance variation was only significant in allocations to stem wood, branches, and fine roots and was strongly site-specific. Provenance variation in stem wood allocation was independent of provenance growth rate. Some allocation patterns correlated significantly with provenance growth; the faster-growing provenances allocated more to branches and less to fine roots at the LS site, but an opposite pattern was true at MES site. Most significant allocation traits were related to geographic/climatic variables at the provenance origins, but the driving factors varied with site.

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Contribution of the co-authors J.Y. contributed in designing the experiment, collecting the data, analyzing the data, and writing the manuscript. Y.H. contributed in data analysis and writing of the manuscript; B.O. contributed in writing the manuscript. H.Z. contributed in designing experiment, collecting the data, and provided financial support of the study.

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• ***Conclusion*** Provenance variation in C concentration and allocation existed for *L. olgensis* but was strongly site-specific. Similarly, relationships of provenance variation in C allocation with provenance growth and their adaptive nature varied greatly with site. Our results will be of interest to ecologists and tree breeders studying dynamics of plantations in terms of climate change.

Keywords *Larix olgensis* · Carbon concentration · Carbon allocation · Provenance variation

1 Introduction

As global climate and markets change, there is an increasing interest in utilizing forest plantations for carbon (C) sequestration. Planting growth-improved stock when reforesting can be effective in sequestering C in general since it enhances plantation productivity substantially (Jayawickrama 2001; Aspinwall et al. 2012; Zhu et al. 2013; Wang et al. 2015). However, the fate of absorbed C in forest plantations depends on whether it ends up sequestered in biomass of ephemeral or perennial structures (Hyvönen et al. 2007). Therefore, it is increasingly important to understand patterns of C allocation into tree tissues of various longevities. Many factors contribute to variation in C allocation in trees: tree age (Bartelink 1998), environment (light, nutrient or water availability) under which the tree develops (Poorter and Nagel 2000; Iivonen et al. 2006; Norby et al. 2006; Poorter et al. 2012), and silvicultural treatments (Lopez et al. 2003; Litton et al. 2007). As more plantations are being established using genetically selected seedlots, the fundamental information regarding genetic variation in C allocation and its relationship with growth rate is needed for estimating the C stock in forest plantations and for incorporating genetic selection into C sequestration.

The mechanisms behind genetic variation in C allocations to tree tissues have received attention (Ericsson et al. 1996), but available information on this topic is still limited and often inconsistent, in particular for mature trees, mainly due to the difficulty in sample collection and measurement (Wang et al. 2015). Slow-growing provenances allocate proportionally more biomass/C to the roots than fast-growing ones (Bongarten and Teskey 1987; Li et al. 1991; Johnsen and Seiler 1996; Oleksyn et al. 1992; Stovall et al. 2012), but these studies are almost exclusively based on data from seedlings grown in controlled environments. Conversely, in field conditions (Oleksyn et al. 1999; Retzlaff et al. 2001; Aspinwall et al. 2013; Stovall et al. 2013; Zhu et al. 2013; Wang et al. 2015), tree biomass and C allocation are often independent of the growth rate. These studies either targeted young trees (Oleksyn et al. 1999; Retzlaff et al. 2001; Aspinwall et al. 2013; Stovall et al. 2013;), limiting their application to mature trees, and/or were based on single-site data (Oleksyn et al. 1999; Retzlaff et al. 2001; Aspinwall et al. 2013; Stovall et al. 2013; Zhu et al. 2013), without sufficient reference to specific site conditions. Furthermore, other than Zhu et al. (2013) and Wang et al. (2015), studies have used biomass allocation as a surrogate for C allocation by assuming a constant C concentration of 50%, without accounting for differences in C concentration among tree tissues and intraspecific variation. Carbon concentration varies with tree tissue (Bert and Danjon 2006; Fu et al. 2013; Martin et al. 2015) and tree genetic identity (Zhu et al. 2013; Martin et al. 2015; Wang et al. 2015). Biomass-based C allocation (assuming a 50% C concentration) to each tree part could differ substantially from actual C concentration-based allocation (Wang et al. 2015), suggesting that it is important to measure and incorporate actual C concentrations into C allocation estimates. We believe that if there is high variation in C concentration among tree tissues or among provenances, this trait deserves increased attention in estimates of C allocation and sequestration of forests or plantations. Furthermore, if enhancing productivity of merchantable aboveground tree components includes reallocation of available photosynthate from unharvestable belowground sinks, then the study of C allocation in the whole forest stand, both above- and belowground, is necessary. Few studies have compared variation in belowground C allocation among genetic entries (Oleksyn et al. 1999; Zhu et al. 2013; Wang et al. 2015).

Tree species are generally genetically diverse, and much of the variation in genetically controlled traits is associated with evolutionary adaptation of populations to their local growth conditions (White et al. 2007). Carbon allocation relates to physiological processes and environment (Pallardy 2008), and reflects the fitness of populations displayed in their growth performance. However, intraspecific variation in C allocation responses to environmental influences has rarely been documented. The few available studies have shown that C allocation to some tree tissues displays clinal patterns following climate variables at the provenance origin (Oleksyn et al. 1999; Wang et al. 2015). Understanding of environment-driven variation in C dynamics should be valuable in modeling C budget, improving accuracy of such estimates, and for deploying seedlots in reforestation.

This study aimed at investigating C concentrations of tree tissues and allocation differences of mature *Larix olgensis* A. Henry trees of various origins growing in three sites with various environments and management practices. *L. olgensis* represents a key component of temperate forests in northeastern China and is one of the most important reforestation species. Thirty years of provenance testing has demonstrated strong and commercially important population differentiation with respect to growth rate in this species (Yang and Liu

2001). With increasing deployment of planting stock selected for superior growth, results of this study provide information useful for incorporating C budgeting and tree improvement into on-going forest management activities to mitigate rising atmospheric CO_2.

2 Materials and methods

Data were collected from a 31-year-old provenance trial of three sites (all planted in 1982) located within Heilongjiang Province: at the CuoHai Forest Farm (47°16′12″ N, 122°30′36″ E; referred to as CH thereafter), at LiangShui Forest Farm (47°6′ N, 128°31′ 48″ E; LS), and at MaoErShān Forest Farm (45°19′48″ N, 127°34′12″ E; MES). Ten provenances were planted at each site. For CH and LS sites, the tests were established using a randomized complete block design of 5 blocks and 100 trees per plots, planted with a 2-row layout with 50 trees per row. The same design was used for the MES site, but only 60 trees (2-row) were planted per plot. The planting density varied with site, being 1 × 2 m for CH, 1.5 × 2.5 m for LS, and 1.5 × 2 m for MES, respectively. The MES site was thinned twice by removing one row per plot in 1995 and then removing every other tree of each remaining row in 2001. Details about the test establishment are described in Yang and Liu (2001). Figure 1 shows the original geographic locations of the sampled populations and of the testing sites, and Table 1 lists their geographic coordinates and climate variables.

Sampling from all sites took place in August 2011 as follows: (1) two trees per provenance were selected from the blocks 1 to 3 per site (averaging six trees per provenance per site). Therefore, at each site, in total, 60 trees (6 trees/provenance × 10 provenances) were sampled across three blocks. In order to improve representativeness, trees closest to the provenance mean diameter at breast height (DBH) of a block were selected as the sampling trees for each provenance of that block; (2) trees were cut just above the root-butt swell and DBH and tree height (HT) were recorded; (3) the aboveground portion of each tree was separated into the stem and branches, and subsamples were collected to calculate ratio estimators between stem wood and bark and between branch and needle; and (4) the belowground portion was excavated manually with shovels, lifted with a pulley, and sorted into coarse roots (> 5 cm in diameter), medium roots (2–5 cm), and fine roots (< 2 cm). Sub-samples were collected from tree tissues for biomass and C concentration measurements, as described below.

We followed Zhu et al. (2013) for biomass and C concentration measurements. The fresh weights of each tree tissue (stem wood, stem bark, branches, needles, fine roots, medium roots, and coarse roots) were measured, respectively, and subsamples of each tree part (for each tree, provenance and site) were selected and weighed in the field. In the laboratory, all subsamples were oven-dried at 70 °C until constant weights were reached. The ratios of dry weight to fresh weight of subsamples were computed and then used to calculate dry biomass of each tree part by multiplying its respective fresh weight.

We measured C concentrations using the oven-dried tissue sub-samples. The dried samples were ground in a Retsch Mixer Mill MM 400 (Retsch Lab Equipment, Germany) until particle size was reduced to 10–20 μm. Approximately 20 mg of each ground sample was used for measuring C concentration. The samples were burned completely at 1200 °C in a vial containing pure oxygen, and emitted C in the form of CO_2 was measured with a non-dispersion infrared ray (NDIR) analyzer (Multi N/C 2100 analyzer with HT1300 Solids Module, Analytik Jena AG, Germany). Volatile C was not measured with this method, possibly consistently underestimating C concentrations (Thomas and Malczewski 2007). The analyzer was stabilized and calibrated daily using a $CaCO_3$ standard (standard curve, $r^2 > 99.99\%$) with a concentration of 12%. The C concentration of each sample was calculated from the standard curve.

Amounts of C sequestered by tree tissues were calculated from their biomass and C concentrations, and whole-tree C values were summed from all its tissues. Fractional C allocation to each tree tissue was calculated by dividing each tissue C amount by total tree C amount.

Analysis of the data focused on four questions: (1) Were the C concentrations the same between tree tissues, between provenances, and how much variation is due to provenance variation? (2) Was C allocated in the same manner for trees of different provenances or different sites? (3) Was the provenance variation in C concentration and allocation related to provenance growth rate or consistent between sites? And, (4) was there any significant provenance variation in C allocation associated with geographic/climate variables of the provenance origins?

Since the experimental designs and cultural activities were not consistent among sites, the variation was dominated (over 75%) by site and its interaction with tissue, which overshadowed effects of tissue and provenance. Therefore, the effects of the tree tissue and provenance on C concentration and stock were analyzed by individual site using a mixed model including the fixed factor of tissue and the random factors of block, provenance, and the interaction between provenance and tissue. Most earlier studies have utilized analysis of variance to answer the second question (Zhu et al. 2013), which may result in biased conclusions due to the strong correlations between the relative weights of tree tissues and the total tree weight (Bongarten and Teskey 1987; Poorter and Nagel 2000; Wang et al. 2015). Also, the method of analysis of variance on C partitioning ratios calculates provenance variation without accounting for differences in growth rate of provenances (Poorter and Nagel 2000).

Ledig and Perry (1966) showed that the growth of one tissue (O_1) relative to another (O_2) of trees may be expressed as:

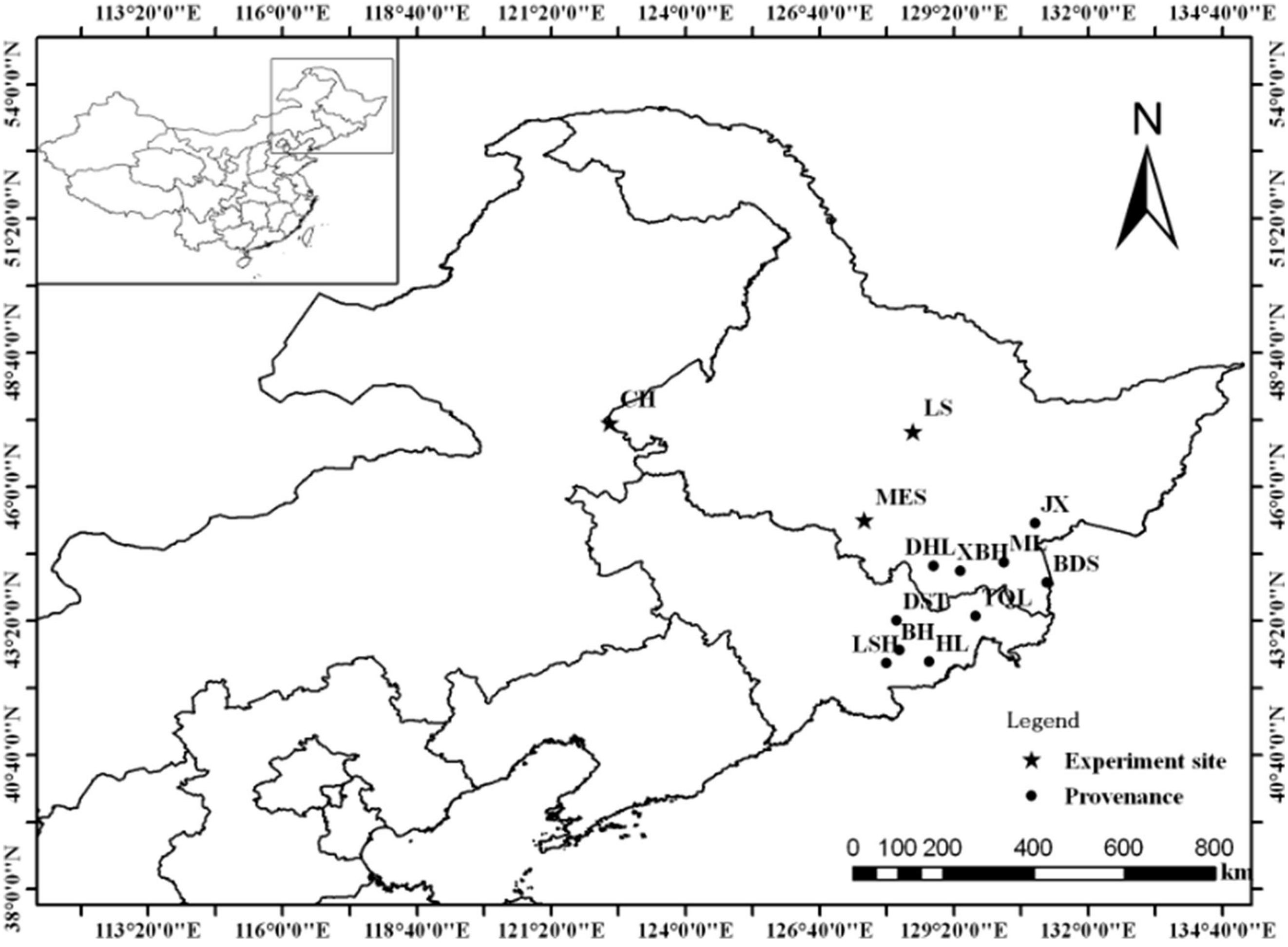

Fig. 1 Geographic locations of 10 *Larix olgensis* provenance origins and three testing sites

Table 1 Geographic coordinates, mean temperatures: annual (AnnT), January (JanT), July (JulyT), and accumulated (AccuT), absolute and relative humidity, mean annual precipitation (AnnP) and mean June–August precipitation (SumP), and growing degree days (GDD; heat sum>5 °C) for 10 *Larix olgensis* provenances (Prov) and 3 testing sites

		Coordinates			Temperature (°C)				Humidity		Precipitation (mm)		GDD
		Latitude	Longitude	Elevation	AnnT	JanT	JulyT	AccuT	Absolute (mg/L)	Relative (%)	AnnP	SumP	
Prov	BDS	44.10	131.18	116.9	5.3	− 14.2	21.6	1769.7	8.0	61.6	423.7	235.6	150
	BH	42.75	128.25	730.0	3.4	− 17.2	21.8	2631.0	8.3	66.2	743.3	349.8	130
	DHL	44.43	128.93	345.0	1.9	− 20.3	20.1	2120.4	7.7	72.0	590.6	528.2	117
	DST	43.35	128.20	523.7	2.7	− 17.5	19.7	2248.9	7.5	70.0	607.1	286.8	120
	HL	42.52	128.85	442.9	4.8	− 14.0	20.7	2582.9	8.0	65.0	535.6	249.7	137
	JX	45.28	130.95	232.3	4.0	− 16.9	21.6	2653.1	7.7	64.0	592.0	344.1	146
	LSH	42.50	128.00	730.0	3.0	− 17.2	21.8	2631.0	8.4	66.2	743.3	349.8	129
	ML	44.50	130.33	266.1	1.6	− 21.0	19.1	2084.3	8.0	77.3	471.3	253.5	124
	TQL	43.43	129.77	241.7	3.8	− 16.3	20.5	2471.7	8.0	68.0	610.1	263.7	133
	XBH	44.33	129.47	267.9	4.0	− 18.5	21.7	2689.4	7.9	66.4	513.9	271.0	134
Site	CH	47.27	122.51	340.0	3.4	− 16.7	22.7	2648.0	8.2	62.0	422.0	261.0	124
	LS	47.10	128.53	390.0	− 0.3	− 23.9	20.5	1690.0	6.7	73.0	638.0	410.0	115
	MES	45.33	127.57	320.0	2.8	− 19.7	21.0	2496.0	7.9	70.0	737.0	374.0	130

CH CuoHai, *LS* LiangShui, *MES* MaoErShān

$$O_1 = a(O_2)^b \tag{1}$$

which can be further transformed to:

$$\log(O_1) = \beta_0 + \beta_1 \log(O_2) \tag{2}$$

where, statistically, the β_0 values represent initial investment and the β_1 values represent relative tissue growth rates. Biologically, β_0 is related to the maximum tissue weight that governs the level of the fitted curve and β_1 is the shape parameter of the fitted relationship when transformed to the tissue-tissue scale. Logarithmic transformation eliminates the impact of heteroscedasticity on parameter estimation. We adopt this allometric (Eq. 2) to investigate provenance effects on C allocations at each individual site by employing the following model:

$$y_{\mathrm{ijk}} = \left(\beta_0 + P_{\mathrm{j}}\right) + \left(\beta_1 + P_{\mathrm{j}}\right)x_{\mathrm{ijk}} + B_{\mathrm{i}} + \varepsilon_{\mathrm{ijk}} \tag{3}$$

where y_{ijk} was the natural log-transformed dependent trait (C amount of a tree tissue, see Table 3) of the *k*th tree of the *j*th provenance growing in the *i*th block. x_{ijk} is the natural log-transformed independent variable (C amount of a whole tree, see Table 3), and β_0 and β_1 the global coefficients of the intercept and slope. P_{j} is the fixed effect of the *j*th provenance on β_0 and β_1, B_{i} the random *i*th block effect, and $\varepsilon_{\mathrm{ijk}}$ the random error. Preliminary analyses suggested that interaction effects between provenance and block were negligible and therefore not included in the model. Examination of residual plots showed that model assumptions such as normality, independence, and equal variances were generally met. A similar analysis was performed to test site effects using the same model (Eq. 3) by replacing provenance with site. A combined allometric analysis using all site data was tried to jointly test effects of site, provenance, and their interaction but failed, mainly due to the fact that provenances responded differently in different sites (see "Results"), which overshadowed the effects of the main factors. An analysis by individual site minimizes the risk of allocation being confounded with environmentally induced variation. Except where otherwise indicated, the term significant refers to $Pr < 0.10$ in the C allocation analysis due to the small sample size.

Relationships between provenance C concentration or allocation and provenance growth rate were investigated using Pearson's correlation coefficients. For allocations, only those varying significantly with provenance were further investigated. Multiple regression analysis was used to describe the relationships of C allocation with climate and geographic variables unique to each provenance origin. Models were developed using the "forward" selection procedure, and the best models were selected based on Akaike Information Criterion (AIC) value (the lower the better). When the AICs were comparable, then models with higher r^2 were selected. The climate/geographic variables were confounded (i.e., latitude, longitude, and elevation were correlated with $|r| > 0.75$, while annual mean temperature, mean January temperature, relative humidity, and growing degree days correlated strongly with each other $|r| > 0.85$), resulting in a potential problem of multicollinearity. The assumptions of normality, equal variance, and independence of all the selected models were met, and multicollinearity was not serious with the variance inflation factor for each predictor ≤ 5. All analyses were done using the SAS statistical package (SAS Institute, 2008).

3 Results

Tree size varied substantially ($Pr < 0.001$) with site (Table 1). Trees at CH were the smallest (HT = 13.8 m; DBH = 14.1 cm), while trees at MES had the largest DBH (HT = 17.9 m; DBH = 22.8 cm) and those at LS were the tallest (HT = 19.1 m; DBH = 20.0 cm).

Across sites, tree tissues, and provenances, the average C concentration was 45.2%. Carbon concentration varied greatly with site. Compared to CH, the LS and MES were 3.6% and 5.0% higher on the whole-tree scale, respectively (Table 2). Results of analyses of variance on C concentration and stock by individual site are presented in Table 3. It is clear from the table that C concentration varied significantly among tree tissues, with branches and leaves being always ranked top and stem wood and coarse and medium roots ranked bottom (Table 2). The differences between the minimum and maximum tree tissue means were 3.2%, 2.3%, and 1.8% at the CH, LS, and MES sites, respectively. At each site, the variance of provenance was significantly different from zero and accounted for 3.3%, 2.8%, and 2.2% of the total variation at the CH, LS, and MES sites, respectively. At the tree level, provenances JX and XBH had the highest concentration values at sites CH and MES, while provenances BDS and DST were ranked top at the LS site. The differences between the minimum and maximum provenance means at the tree level were similar between sites, at around 1.0%, which may expand to a 2% error in calculating carbon stocks (Bert and Danjon 2006). The provenance and tissue interactions were negligible at all sites.

The C content varied substantially with site; the whole trees at the MES and LS sites contained 235% and 152% more C than those at the CH site, respectively. Tree tissue and provenance affected C stock significantly. The average tree stored 75.5 kg C, and on average, 58.7% of the C stock was partitioned to stem wood, followed by roots (20.7%), branches (11.1%), bark (6.4%), and needles (3.1%). For roots, the proportion allocated to coarse roots (74.0%) was the highest, while those to fine (10.2%) and medium (15.8%) roots were similarly low. The variance of provenance accounted for 6.8%, 9.3%, and 2.3% of the total variation at sites CH, LS, and MES, respectively. At the tree level, the differences between the minimum and maximum provenance means were 9.5 kg, 32.6 kg, and 35.8 kg, respectively, at the CH, LS, and MES sites (Table 2). Overall, provenances JX and XBH had the highest C content, while TQL had the lowest value. The interaction between provenance and tissue was non-significant at sites CH and MES, but was important at the LS site, where 13.3% of the total variation was due to this interaction.

Averages of carbon content and concentrations by site, provenance, and tree tissues can be found in annexed Tables 8 and 9.

Site showed a negligible effect on the allometric parameters of Eq. 3 other than those for stem wood, needles, and coarse roots (Table 4). Site variation was significant in β_0 and β_1 for stem wood but only in β_1 for needles and coarse roots. As suggested by values of β_1, trees at the MES site allocated more C to stem wood but less to needles, while trees at the CH site allocated relatively more to needles but less to coarse roots than trees growing at the other two sites.

Mixed results in provenance effects on allometric intercepts and slopes were observed (Table 5). For β_0, provenance effects were virtually negligible at each site and for all tree tissues except stem wood at LS and MES. For β_1, although the linearized allometric growth curves for most tissues were more or less parallel, site-specific exceptions existed. Provenances had significantly different slopes for medium roots at CH, stem wood, branches, and fine roots at LS, and stem wood, fine roots, and coarse roots at MES.

Pearson's correlation analyses failed to uncover a significant correlation between tree growth and C concentration of tree tissues (Table 6) across provenances other than for needles and stem wood. Needle C concentration correlated significantly with height, a trend that depended strongly on site, being negative at CH but positive at the other two sites. Stem wood C concentration was significantly and positively correlated with HT at LS and with DBH at MES. The significant provenance variation in C allocation was weakly correlated with provenance growth (data not shown), and this was particularly true at the LS and MES sites. Exceptions were allocations to branches and fine roots: The faster-growing provenances allocated more to branches and less to fine roots at the LS site but more to fine and coarse roots at the MES site (Fig. 2).

The final models describing relationships between C allocation with provenance variation and the geographic/climatic variables of provenance origins can be found in Table 7. The independent variables retained in the models varied with site and tree tissue. At the CH site, provenances from regions of lower latitude with lower January temperature and higher longitude allocated more C to medium roots. At the LS site, the accumulated temperature and precipitation-related variables were the important predictors; provenances from areas with lower accumulated temperature together with lower summer precipitation allocated significantly more C to stem wood, while those from lower elevation with higher accumulated temperature allocated more to fine roots. At MES, all models explained 70% or more of the respective phenotypic variation. Provenances from warmer areas allocated more to coarse and fine roots, at least to some level, but less to stem wood.

4 Discussion

Carbon concentrations and C allocations to tree tissues vary in response to the environment and genetic selection, resulting in significant interactions between site and tree tissue or provenance, a fact often suspected, but rarely verified in mature trees under natural conditions. Unfortunately, while we were unable to distinguish the effects of environmental factors (e.g., climatic conditions, thinning, or other factors), it appears that either one or all together did in some manner affect C concentration and allocation. Therefore, we concentrate discussion on C traits by individual site.

Table 2 Average carbon concentration (%) and content (kg) and range (form the minimum to maximum provenance means) of 10 provenances by tree tissue and individual site

Tissue	Concentration (%)						Content (kg)					
	CuoHai		LiangShui		MaoErShān		CuoHai		LiangShui		MaoErShān	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Bole wood	42.8	42.4–43.8	44.2	44.0–44.5	45.4	43.6–47.3	20.1	16.5–21.6	49.3	38.3–54.3	60.6	51.8–70.8
Bole bark	44.8	44.2–45.5	46.1	45.5–47.1	46.7	46.1–47.4	2.1	1.9–2.7	5.3	4.2–6.5	6.7	5.6–8.2
Branch	46.0	44.9–47.1	47.0	46.6–47.5	47.2	46.5–47.6	3.4	2.4–4.2	8.6	5.7–11.7	14.9	11.2–21.4
Leaf	45.3	44.4–46.3	46.5	46.2–46.9	46.2	45.3–47.0	1.3	1.1–2.0	2.9	2.3–3.5	2.2	1.3–3.2
Fine root	43.9	42.8–45.8	45.6	44.6–46.3	46.8	45.3–48.2	0.7	0.5–0.9	1.5	1.2–2.1	2.4	1.8–3.1
Medium root	42.4	41.4–43.1	44.9	43.9–45.0	46.1	45.3–46.0	0.9	0.6–1.5	2.7	2.0–3.9	4.2	3.0–5.4
Coarse root	44.0	41.9–43.3	44.6	43.7–45.1	45.4	44.7–46.1	4.4	3.5–5.6	12.9	9.3–16.4	19.3	15.0–23.2
Tree[a]	44.0	43.4-44.5	45.6	44.9–45.9	46.2	45.1–46.1	33.0	27.1–36.6	83.1	63.7–96.2	110.4	97.7–133.5

[a] Carbon concentration of a tree was calculated as the biomass-weighted mean concentration

Table 3 Results (*F* and Pr values) of analysis of variance on carbon concentration (Con) and content by individual sites (*CH* CuoHai, *LS* LiangShui, *MES* MaoErShān)

Trait	Source	CH		LS		MES	
		F value	Pr	*F* value	Pr	*F* value	Pr
Con	Tissue	76.12	< 0.001	64.25	< 0.001	6.41	< 0.001
	Block	2.97	0.053	5.10	0.007	0.12	0.883
	Provenance	2.50	0.018	3.29	0.003	2.05	0.045
	Provenance × tissue	0.98	0.509	0.64	0.976	0.97	0.543
Content	Tissue	1339.73	< 0.001	720.35	< 0.001	648.80	< 0.001
	Block	1.75	0.174	6.36	0.002	9.85	< 0.001
	Provenance	3.43	0.002	3.50	0.001	2.61	0.014
	Provenance × tissue	1.32	0.074	2.03	0.001	0.73	0.917

The degrees of freedom of numerator and denominator for the appropriate *F* tests were 6 and 54 for tree tissue, 9 and 54 for provenance, and 54 and 348 for the interaction, respectively

Carbon concentration varies greatly with tree species (Lamlom and Savidge 2003; Thomas and Martin 2012). Conifers tend to have higher concentration values (50.8 ± 0.1%) than hardwoods (48.8 ± 0.2%) (Thomas and Malczewski 2007). Zhang et al. (2009) measured 10 Chinese temperate trees species and found that C concentration ranged from 43.7% for aspen (*Populous davidiana* Dode) to 55.1% for Amur cork-tree (*Phellodendron amurense* Rupr.). Two papers reported C concentrations for *L. olgensis* with both based on samples collected from natural stands in NE China: Thomas and Malczewski (2007) reported a concentration value of 49.1% (excluding volatile C), and Fu et al. (2013) reported a value of 48.1%. Lamlom and Savidge (2003) reported a concentration of 47% for two *Larix* species in Canada. Our estimates of C concentration (Table 2) are lower, which may be partly explained by a few factors. Our estimates were based on the oven-dry method, without including violate C, which could be substantial for *L. olgensis*, about 3.7% (Thomas and Malczewski 2007). Second, our estimates were based on samples collected from artificial plantations, which typically have lower concentration values than those for wild stands (Elias and Potvin 2003). The carbon concentration of *L. olgensis* in natural stands varies with age, being lowest at around age 30, at 46% (Fu et al. 2013), very similar to our values for 31-year old trees. This study focused on comparing provenances and tree tissues, and these inconsistencies are shared by all provenances and tissues and will unlikely significantly bias the main findings of our study.

Some studies have compared intraspecific (i.e., between trees and within a tree) variation in C concentration. Variation among tree tissues is significant, but this variation within a species is less important than interspecific differences (Zhang et al. 2009; Thomas and Martin 2012; Martin et al. 2015). Thomas and Martin (2012) reviewed the C concentrations of tree tissues and found substantial tissue-related variation, but most of the variation was driven by tree bark variation in concentration. This study showed substantial differences in C concentration existing between tree tissues for *L. olgensis* (Table 3), although the actual differences were site-dependent, ranging from 1.8% for the MES site to 3.2% for the CH site (Table 2). These differences were larger than

Table 4 Tests for site effects (shown by Pr) on parameter estimates for allometric equations of using *log*(total carbon of a tree in kg) to predict *log*(tissue carbon of the tree in kg). The actual parameter estimates were also included for each site (*CH* CuoHai, *LS* LiangShui, *MES* MaoErShān)

	Intercept (β_0)				Slope (β_1)			
	CH	LS	MES	Pr	CH	LS	MES	Pr
Stem wood	− 0.004	0.210	− 0.489	*0.070*	0.859	0.834	0.976	*0.024*
Branches	− 5.432	− 4.449	− 4.305	0.488	1.889	1.483	1.476	0.215
Needles	− 5.497	− 4.823	− 2.789	0.174	1.631	1.322	0.729	*0.021*
Stem bark	− 2.250	− 2.566	− 2.152	0.789	0.858	0.955	0.861	0.761
Fine roots	− 3.641	− 2.331	− 2.623	0.693	0.929	0.589	0.733	0.710
Medium roots	− 3.617	− 3.624	− 1.439	0.195	0.976	1.025	0.603	0.260
Coarse roots	− 1.382	− 3.033	− 1.828	0.183	0.812	1.257	1.014	*0.096*

The degrees of freedom were 2, 6, and 168 respectively for intercept (site), slope (site × *log*(total carbon of a tree)), and residual

Note that those Pr values <0.10 were initicized to show significant site effects

Table 5 Pr values for provenance effects on allometric parameters of using *log*(total carbon of a tree in kg) to predict *log*(tissue carbon of the tree in kg) at each site (*CH* CuoHai, *LS* LiangShui, *MES* MaoErShān)

	CH		LS		MES	
	Intercept (β_0)	Slope (β_1)	Intercept (β_0)	Slope (β_1)	Intercept (β_0)	Slope (β_1)
Stem wood	0.690	0.684	*0.062*	*0.053*	*0.061*	*0.058*
Stem bark	0.911	0.890	0.334	0.320	0.370	0.351
Branches	0.718	0.710	0.132	*0.084*	0.254	0.263
Needles	0.633	0.631	0.475	0.488	0.512	0.471
Fine roots	0.924	0.952	0.124	*0.087*	0.112	*0.068*
Medium roots	0.213	*0.011*	0.478	0.444	0.318	0.299
Coarse roots	0.204	0.192	0.376	0.362	0.113	*0.031*

At each site, the degrees of freedom were 9, 9, and 38, respectively, for intercept (provenance), slope (provenance × *log*(total carbon of a tree)), and residual

Note that those Pr <0.10 were initicized to show significant provenance effects

most between-tissue differences reported by Thomas and Martin (2012) and Martin et al. (2015) but were comparable to those for Chinese temperate tree species (Zhang et al. 2009; Zhu et al. 2013; Wang et al. 2015), including *L. olgensis* (Fu et al. 2013), and other tree species (Bert and Danjon 2006). In spite of the significant interaction between site and tree tissue, the pattern that branches and leaves had the highest, while stem wood and coarse roots had the lowest C concentration observed in this study, is in parallel to that reported by Fu et al. (2013), a study based on samples collected from *L. olgensis* natural stands in NE China. It is interesting to note the biases in C partitioning between using C concentration-specific and using a 50% concentration (conventional method) assumption. We found that using the 50% concentration method led to a systematic overestimated allocation to bole wood of 14.4%, 11.6%, and 9.2% at CH, LS, and MES, respectively, compared to those based on the actual bole wood concentrations. Therefore, even differences between the tree tissues may not be comparable to those between species (Zhang et al. 2009), and cross-tree tissue variation in C concentration should be considered in C allocation and stock evaluations (Bert and Danjon 2006).

In addition to variation among tree tissues, C concentration varied significantly with provenances of *L. olgensis* (Table 3), with the difference between the provenance means of the highest and lowest C concentrations ranging from 1.7 to 3.7%, depending on site and tree tissue, and around 1% on the whole tree scale at each site (Table 2). The contribution of provenance variation to total variation was similar across sites, accounting for ~2.2–3.3%. The interaction between provenance and tissue was weak (Table 3), suggesting that the rankings of provenances were similar for all tissues. Provenance variation in C concentration has only recently been investigated. In support of our results, substantial population differences in C concentration were reported in other tree species (Elias and Potvin 2003; Zhu et al. 2013; Wang et al. 2015). Incorporating provenance variation of key C traits into C-budget calculations has been recommended by the Intergovernmental Panel on Climate Change (IPCC 2006). A 1% difference in C concentration conceivably could have a significant impact on wood and pulp industries in relation to allocation of carbon credits within the Kyoto Protocol. The provenance differences detected in this study confirmed the importance in incorporating provenance variation in C concentration in increasing the precision of C stock calculations.

Faster-growing provenances often have a high proportion of earlywood with a higher lignin/cellulose ratio than that of the latewood (Lamlom and Savidge 2003). It is reasonable to assume that higher C concentrations exist in faster-growing provenances. This generalization was confirmed at the LS and MES sites, where the faster-growing provenances had

Table 6 Correlation coefficients (Pr values) between provenance carbon concentrations of tree tissues and growth in tree diameter at breast height (DBH) and height (HT) of 10 provenances by site. Note that only those with statistically significant relationships ($Pr < 0.10$) are presented

Tissue	CuoHai		LiangShui		MaoErShān	
	DBH	HT	DBH	HT	DBH	HT
Coarse roots	0.60 (0.07)	–	–	–	–	–
Needles	–	− 0.72 (0.02)	–	0.63 (0.05)	–	0.62 (0.06)
Bark	–	− 0.60 (0.07)	–	–	–	–
Stem wood	–	–	–	0.79 (0.01)	0.76 (0.01)	–

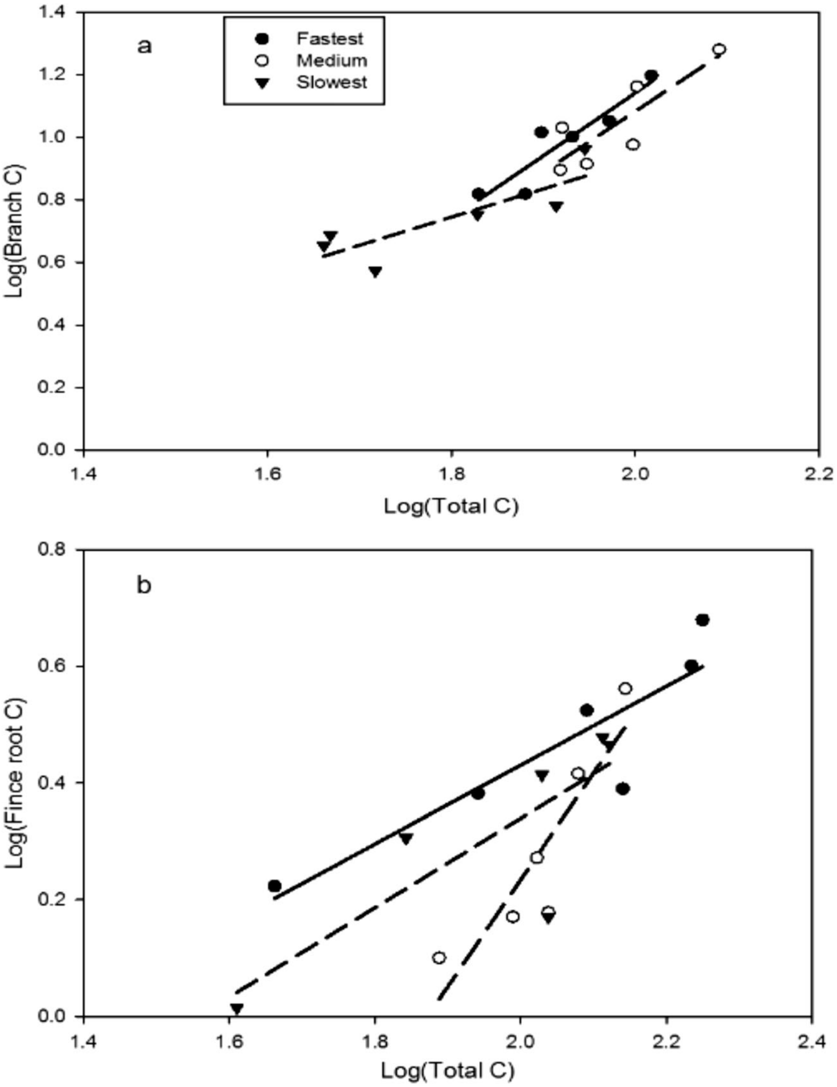

Fig. 2 Comparing three provenances (fastest-, medium-, and slowest-growing) in allometric relationships. **a** Between *log*(branches C) and *log*(tree total C) in kilograms at the LiangShui site. **b** Between *log*(fine roots C) and *log*(tree total C) in kilograms at MES site. Note that the fastest, medium, and the slowest growing provenances were JX, DST, and TQL at LS, and were HL, XBH, and TQL at the MaoErShān site, respectively

Table 7 Selected geographic/climatic variables for predicting C allocations and their model significance level (Pr) and coefficients of determination (r^2) by individual site. The analysis was based on the averages of 10 provenances

Site	Dependent variable	Independent variables[a]	Pr	r^2
CH	Medium roots	Lat (−), Long, JanT (−)	0.021	0.78
LS	Stem wood	ACCUT (−), AnnP, SumP(−)	0.034	0.74
	Branches	AbHum, Lat	0.122	0.45
	Fine roots	Elevation(−), ACCUT, RelHum (−)	0.007	0.85
MES	Stem wood	AnnT (−)	0.001	0.78
	Fine roots	AnnT, RelHum, SumP	0.044	0.72
	Coarse roots	Lat, AnnT, ACCUT	0.013	0.81

CH CuoHai, *LS* LiangShui, *MES* MaoErShān, *Lat* latitude, *Long* longitude, *JanT* January mean temperature, *ACCUT* mean accumulated temperature, *AnnT* mean annual precipitation, *SumP* mean June–August precipitation, *AbHum* absolute humidity, *RelHum* relative humidity, *AnnT* mean annual temperature

[a] (−) represents a negative relationship

significantly higher stem wood C concentrations but was not true at the CH site, probably because the faster growing provenances did not grow much differently from slower growing provenances at this site. A significant positive relationship with growth was also confirmed for needle C concentration at the LS and MES sites, but this relationship was negative at the CH site (Table 6). This divergence almost certainly reflects various functional adaptations of needles for photosynthesis functions under various environmental conditions. However, for most tree tissues, our results do not support the inference and confirm that C concentrations are independent of provenance growth, a pattern also confirmed in *P. koraiensis* (Zhu et al. 2013) and *Betula platyphylla* (Wang et al. 2015). We conclude that using fast-growing provenances may mostly have a random impact on tissue C concentrations in plantations, and factors other than growth may be involved in controlling C concentration in populations of *L. olgensis*.

We tested the hypothesis that genetic differences in C allocation to tree tissues are contributing factors toward influencing differences in aboveground growth, and our data show that the answers are strongly tissue- or site-specific. All provenances at the CH site grew poorly, which might mask provenance differences in C allocation to all tree tissues (Table 5). At the other two sites, provenance effects were significant for some tree tissues only (Table 5). One tissue varying substantially with provenance was stem wood, but this variation was independent of provenance growth, which is confirmed by findings on other species (Aspinwall et al. 2013; Zhu et al. 2013). Other tissues varying substantially with provenance showed different patterns between the LS and MES sites (Fig. 2). A larger fraction of the carbohydrates was used for root growth, in particular for fine roots, at the expense of stems for the faster-growing provenances possibly to access more nutrition in order to maintain aboveground growth at the MES site, whereas the faster-growing provenances at the LS site allocated more to branches possibly to compete better for light. The apparent contradiction between sites suggests that the exact outcome in relationship between population variation in C allocation and growth rate may be difficult to predict without sufficient environmental information and may partly explain the inconsistent results in the literature. While some studies reported that the fast-growing conifer provenances allocate relatively less to fine than to coarse roots (Oleksyn et al. 1999; Zhu et al. 2013), others found that they allocate proportionally more photosynthate to leaf growth (Hari et al. 1982), compared to slow-growing provenances. More recently, Wang et al. (2015) compared the allocation of 16 *Betula platyphylla* populations sampled from two field environments in northeastern China. At one site, they found that the faster-growing provenances allocated significantly more C to fine roots. Results of all these studies suggest that the large aboveground gain in growth for provenances in field conditions is at least partly a result of a changed C allocation pattern with trees, but the actual changes are strongly environment-dependent or could even be overshadowed by poor site conditions. Studies have shown that assimilate allocation to tree tissues could be strongly controlled by mechanical and environmental cues (Nicoll et al. 2008; Niez et al. 2018). For example, conifer species have been observed to allocate a larger proportion of total biomass belowground when they experience increased wind loading, in particular for suppressed trees (Nicoll et al. 2008; Bonnesoeur et al. 2016). Overall, carbon allocation patterns are complex and other physiological and structural differences between provenances are sure to have major influences on growth and growth efficiency (McCrady and Jokela 1996, 1998).

Trees develop various physiological adaptions to maintain growth and survival in diversified stresses. C allocation relates to physiological processes, and therefore, its variation is expected to relate to environment factors at the provenance origin. However, our results suggest that this was not true for most tree tissues, in particular at the CH site, where C allocations varied non-significantly with provenance. Exceptions did stand out at the LS and MES sites, where C allocation to stem wood and roots, in particular fine roots, varied among provenances in accordance with environmental factors at the provenance origin (Table 7). The best predictors retained in the selected models varied with tissue and site, suggesting that site conditions strongly influence provenance responses to selection stresses. Nevertheless, the annual temperature was the common predictor for all the models for the MES site and the accumulated temperature was the common predictor for the LS site. Our results are in partial agreement with observations for other tree species. Wang et al. (2015) found that population differentiation in C allocation to leaves and fine roots of *Betula platyphylla* in NE china was determined by temperature in August and longitude of population origins, respectively. In a seedling study, Johnsen and Seiler (1996) found that northern provenances of *P. mariana* allocated more biomass to roots than southern sources. Understanding adaptive C allocation patterns in trees would provide the knowledge necessary to develop physiologically based management strategies and genetic improvement programs.

There are uncertainties in this study which need to be acknowledged. Other than genetics and environments, tree ontogeny and silvicultural treatments (Aspinwall et al. 2013) may contribute to C allocation patterns in trees. Since different plant tissues may be genetically determined to grow at different times or their growth response to temperature may vary, carbon allocation can change throughout the growing season. As trees grow, age- and size-related changes in tree shape and form alter the contribution of tree biomass compartments to whole-tree biomass increment (Bartelink 1998). This study measured C at a single time during the growing season at the pole-stage of plantation development and may only represent provenance differences at this particular stage. Our root C amount may also underestimate allocation to the roots due to the difficulty in extracting entire root systems of trees. This, however, would not change provenance comparisons of C traits greatly. The current study is one of the few that actually harvested all root-size classes, and this offers better-individual tree estimates than those from methods dependent upon soil coring. Furthermore, this study is one of the few which utilized mature trees of the same genetic entries from multiple locations and thus provided a comparison of provenances under various environmental stresses. Also, carbon allocations were calculated using the actual C concentrations of tree tissues, leading to more accurate C allocation calculation than based on biomass (Wang et al. 2015). Our data suggest that genetic differences in C allocation to tree tissues in *L. olgensis* are complex and can be a contributing factor toward differences in aboveground growth, which, however, is strongly dependent on site condition.

Data availability statement The datasets generated during and/or analyzed during the current study are not publicly available due to that the authors are working on another manuscript using the same dataset but are available from the corresponding author on reasonable request.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Annexes

Table 8 Average carbon content (kg) and sampled trees (# trees) by site, provenance (Prov), and tree tissue. Note that the sample size was six trees per site and provenance

Site	Prov	Stem wood	Bark	Branches	Needles	Fine roots	Medium roots	Coarse roots	Total tree
Cuohai	BDS	19.1474	2.0456	2.3624	1.0508	0.6884	0.9664	4.5896	30.851
Cuohai	BH	18.6279	1.9903	3.0400	1.1290	0.6410	0.9097	3.7268	30.065
Cuohai	DHL	20.9610	2.0488	3.5441	1.0985	0.9052	0.7896	4.2314	33.579
Cuohai	DST	16.5126	1.8959	2.8643	1.1236	0.5393	0.6710	3.4969	27.104
Cuohai	HL	21.5897	2.6741	4.2100	1.5497	0.7373	1.1724	4.5456	36.479
Cuohai	JX	20.7770	2.0380	4.1242	1.2109	0.7674	0.6995	4.5357	34.153
Cuohai	LSH	20.7307	2.0033	3.6045	1.2758	0.8039	0.5814	4.3285	33.328
Cuohai	ML	20.7907	2.2342	3.9225	2.0060	0.6809	1.4486	5.5477	36.631
Cuohai	TQL	21.2387	2.2874	3.5952	1.5317	0.7943	1.0292	4.0633	34.540
Cuohai	XBH	20.9675	2.1119	2.8978	1.1117	0.7133	0.7323	4.6715	33.206
LiangShui	BDS	52.8881	6.5118	8.5242	3.1368	2.1013	3.6672	11.6230	88.453
LiangShui	BH	52.8617	5.2139	10.451	3.2755	1.3355	2.5188	16.4038	92.060
LiangShui	DHL	49.1565	6.1824	8.4509	2.8250	1.2313	2.1334	12.5871	82.567
LiangShui	DST	50.0202	5.3399	8.8014	2.9886	1.4752	2.3237	13.3165	84.266
LiangShui	HL	47.3318	4.7585	9.0127	2.6141	1.6905	2.9810	11.7339	80.123
LiangShui	JX	54.3163	6.1962	11.655	3.4687	1.4910	3.8669	15.2594	96.254
LiangShui	LSH	42.3949	4.1698	6.5023	2.3224	1.3406	2.2950	11.0841	70.109
LiangShui	ML	54.0637	5.7857	7.3044	2.4665	1.2909	2.0386	11.4994	84.449
LiangShui	TQL	38.3463	4.3088	5.6685	2.4256	1.2314	2.3433	9.3334	63.657
LiangShui	XBH	51.6366	4.8165	9.4656	3.1044	1.5756	2.5225	16.3436	89.465
MaoErShān	BDS	56.4444	6.6070	11.154	2.7998	2.1357	3.6792	21.5431	104.364
MaoErShān	BH	51.8202	5.6076	15.0613	3.2053	2.4440	4.5995	15.0104	97.748
MaoErShān	DHL	61.6543	7.3653	16.368	2.3775	2.5696	2.9889	19.7549	113.079
MaoErShān	DST	56.8295	6.3014	14.8809	2.5353	1.8125	4.0706	21.4959	107.926
MaoErShān	HL	62.5628	6.6875	14.5284	1.8779	1.9843	3.5165	16.8726	108.030
MaoErShān	JX	70.7505	7.6933	21.3897	2.2381	3.1126	5.4029	22.9425	133.530
MaoErShān	LSH	63.9483	6.2434	11.8757	1.6924	2.7921	4.7184	19.4000	110.671
MaoErShān	ML	62.0418	6.7687	12.8400	1.2810	2.0970	4.1020	17.4672	106.598
MaoErShān	TQL	52.4170	5.8613	15.3612	2.4236	2.1056	4.2393	15.6257	98.034
MaoErShān	XBH	67.9455	8.2471	15.3771	1.4608	3.0938	4.5494	23.2436	123.917

Table 9 Average carbon concentration (%) by site, provenance (Prov) and tree tissue. Note that the sample size was six trees per site and provenance

Site	Prov	Stem wood	Bark	Branches	Needles	Fine roots	Medium roots	Coarse roots	Total tree
CuoHai	BDS	42.8267	44.9200	45.9533	45.4817	43.2233	42.1283	43.0267	43.9367
CuoHai	BH	42.695	44.6300	46.1200	45.3100	43.9800	42.1933	41.8867	43.8300
CuoHai	DHL	42.4717	44.7967	44.9467	45.3500	43.2750	42.7417	42.5183	43.7300
CuoHai	DST	42.6467	45.0317	45.7900	45.5467	43.7633	42.8117	41.9200	43.9283
CuoHai	HL	42.5233	44.3767	46.2617	45.1483	44.3250	42.8283	42.4133	43.9833
CuoHai	JX	42.9183	45.1750	46.2517	45.5217	45.7600	41.4400	42.4133	44.2117
CuoHai	LSH	43.8383	45.4600	46.0617	46.2550	43.3167	42.3467	42.6450	44.2733
CuoHai	ML	42.3517	44.1767	45.1950	44.4250	42.7683	41.8550	43.3217	43.4383
CuoHai	TQL	42.8383	44.5100	45.8500	44.3500	44.0800	42.7983	42.3433	43.8233
CuoHai	XBH	43.2133	44.9150	47.0933	45.7117	44.6483	43.0883	43.0767	44.5350
LiangShui	BDS	44.2600	47.0883	47.2733	46.8517	45.9767	45.4267	44.4883	45.9083
LiangShui	BH	44.2483	45.4867	46.5950	46.2500	44.6450	43.4183	43.9417	44.9417
LiangShui	DHL	44.4517	45.8900	46.7767	46.7283	45.9233	44.2917	45.1017	45.5933
LiangShui	DST	44.4367	45.7617	47.4950	46.5783	46.3183	45.3983	44.8400	45.830
LiangShui	HL	44.3450	45.4633	47.0650	46.3067	45.7200	45.7933	44.9667	45.6667
LiangShui	JX	44.0567	46.2717	47.3617	46.5683	45.5517	45.4233	44.8850	45.7317
LiangShui	LSH	44.1583	46.4417	47.1817	46.4633	45.7450	44.2583	44.5017	45.5350
LiangShui	ML	44.0933	46.4383	46.6100	46.3550	45.6850	44.4917	44.7633	45.4933
LiangShui	TQL	44.0350	46.0333	46.6517	46.3617	45.1817	45.6350	43.7050	45.3717
LiangShui	XBH	44.2167	45.9583	46.6583	46.1783	45.1233	45.0517	45.0167	45.4600
MaoErShān	BDS	43.6250	47.2667	47.3500	46.3267	46.9333	43.5833	45.2750	45.7667
MaoErShān	BH	44.0267	46.2000	47.1217	46.0283	47.0500	47.0667	45.9750	46.2100
MaoErShān	DHL	45.3533	46.9500	46.9017	45.9550	46.7333	46.7333	45.6750	46.3283
MaoErShān	DST	43.7367	46.4167	47.4250	40.9683	47.1833	46.6000	45.0583	45.3400
MaoErShān	HL	45.6617	46.4000	47.2017	46.2283	45.8833	45.9667	44.6750	46.0000
MaoErShān	JX	46.5150	46.5833	47.5483	46.3033	46.7833	46.5167	46.0500	46.6150
MaoErShān	LSH	46.2567	46.9167	47.0317	46.5500	46.4500	46.4000	44.9083	46.3583
MaoErShān	ML	45.8133	46.6167	47.1083	45.9500	45.3333	46.0000	45.5250	46.0500
MaoErShān	TQL	45.3800	46.0500	47.0683	45.3517	47.0667	46.0167	44.9500	45.9833
MaoErShān	XBH	47.2550	47.4167	47.1867	46.9633	48.2167	46.1333	46.0833	47.0367

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