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Original Research Paper

Biomass Allocation in Relation to Stand Age and Density in Natural *Larix gmelinii* Forests in Cold Temperate China

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ABSTRACT

Knowledge of belowground biomass allocation is largely hampered by the fact that root biomass is difficult to measure. In this study, allometric equations relating the specific components of root and aboveground biomass to diameter at breast height were developed for *Larix gmelinii* using the nested regression method. Patterns in above and belowground biomass allocation in relation to stand age and density were examined. Both root-shoot ratio and fine root-foliage ratio were smaller in older stands with lower density. Additionally, with increasing stand age and decreasing stand density, the proportion of foraging components (fine root and foliage) to total tree biomass decreased, whereas, that of the structural components (stem, branch and coarse root) increased. Differences in biomass allocation patterns between foraging and structural components of trees are considered as a driving force behind the variation in a tree structure along gradients in stand age and density. Application of these allometric equations and improved understanding of biomass partitioning patterns are expected to improve the accuracy of ecosystem carbon accounting as well as the reliability of modelling approaches.

INTRODUCTION

Forests make up the majority of the terrestrial carbon (C) pool, accounting for nearly 80% of all aboveground terrestrial C and 40% of belowground C (Dixon et al. 1994, Goodale et al. 2002, Peichl & Arain 2007). Above and belowground biomass allocation and transfer of photosynthates among organs, reflect a trade-off strategy of plant growth (Shipley & Meziane 2002). Optimal partitioning theory suggests that plants should allocate biomass to the organ responsible for acquisition of the most limiting resources (McCarthy & Enquist 2007). Previous researches have shown biomass allocation to be influenced by both endogenous (e.g., tree age and life form) and exogenous factors (e.g., nutrient and light availability) (Kobe et al. 2010, McConnaughay & Coleman 1999, Poorter et al. 2012). In-depth knowledge of biomass allocation patterns is critical for understanding individual growth processes and modelling terrestrial ecosystem carbon cycles in the context of global climate change (Landsberg 2003, Lin et al. 2014, Litton et al. 2007, Niklas 2006).

Boreal forests are important sinks for atmospheric CO_2. *Larix gmelinii* forests make up about 70% of the total forest land in the Daxing'anling region and are the typical natural vegetation type in the boreal zone of Northeast China (Xu 1998, Feng et al. 1999, Pan et al. 2011). Previous studies have shown that the contribution of roots, in particular fine roots (diameter ≤ 2 mm), to total net primary production of evergreen taiga trees, is significant in comparison with root contributions to primary production in other forest ecosystems (Ruess et al. 1996, Steele et al. 1997). This implies that precise estimation of belowground biomass and allocation patterns of boreal forest ecosystems are key issues for understanding global C budgets (Kajimoto et al. 2006, Li et al. 2003). However root biomass estimates are scarce, especially estimates of fine root biomass, which limits our current understanding of biomass allocation patterns (Sloan et al. 2013, Wang et al. 2013). Additionally, the information gap arising with unreliable root biomass estimates, hampers the efforts to estimate belowground C pools and flux (Litton et al. 2004, Reich et al. 2014).

In order to address this major information gap, more reliable and effective methods of root biomass estimation are required. Biomass regression function, which relates an easy-to-quantify metric (i.e., tree diameter at breast height, DBH) to tree biomass, is a common method for estimating forest biomass (Chojnacky et al. 2014, Wang 2006). However, the general method for acquiring root biomass data, for modelling its relationship with DBH, is to harvest the entire root system by excavation. This approach can be extremely time consuming and destructive of habitat, especially when dig-

ging out large trees with a huge and complex root system (Návar 2009, Niiyama et al. 2010, Xiao & Ceulemans 2004). To date, consequently, belowground biomass equations have been poorly developed (Bolte et al. 2004, Niiyama et al. 2010). Recently a new approach (the nested regression method) for estimating biomass was proposed, which is efficient and accurate for measuring root biomass, in particular fine root biomass, at individual tree level (Liu 2009). It provides a unique way to examine the allocation of biomass to belowground components.

In the present study, we measured above and belowground biomass in natural pure *L. gmelinii* forests in Daxing'anling, the north end of Northeast China, to examine biomass allocation patterns in relation with stand age and density. The objectives of our study were to: (1) develop regression relationships between above- and belowground biomass and DBH, (2) examine the relationships between component biomass and stand factors, i.e. age and density, and (3) clarify the changes in above-and belowground biomass allocation ratios relevant to stand age and density.

MATERIALS AND METHODS

Study area: This study was conducted in Daxing'anling, Inner Mongolia, Northeast China (7°40'-53°20' N, 119°36' -125°19' E), from June to July of 2013. The region is dominated by continental monsoon climate of cold temperate with a mean annual temperature of -5.8°C and mean annual precipitation of 450-550 mm. Most rainfall comes in July to August. Mean annual snowfall is 300 mm from October to May. The frost-free and snow cover periods are 80 and 160 days, respectively.

Field measurement and sampling: In the natural pure *L. gmelinii* forests, 774 plots with various ages (from 19 to 132 a) and densities (from 151 to 4088 trees·ha^{-1}) were established and DBH was measured for all living trees larger than 5 cm DBH in each plot (Table 1). Aboveground biomass was estimated for 25 harvested trees, 17 of which were selected for belowground biomass measurements. DBH ranged from 5 to 41 cm spanning the entire range of DBH within all plots.

The stem volume of every felled sample tree was determined following the sectional method with 1 m intervals, and calculated with the formula below:

$$V = \left[\frac{1}{2}\left(r_0^2+r_n^2\right)+\sum_{i=1}^{n-1} r_i^2\right]\pi l+\frac{1}{3}\pi r_n^2 l$$

where r_0 is radii of the stem base, r_i and r_n are radii at the top and bottom of the i^{th} section, respectively, l and l' are section length and the length of the top section, respectively.

Table 1: Basic information of *Larix gmelinii* stands surveyed (n = 774).

	Max	Min	Mean
Mean DBH (cm)	19.8	5.1	9.3
Mean tree height (m)	18	7	11
Stand age (years)	132	19	49
Stand density (trees·ha^{-1})	4088	151	1385
Stem biomass (t·ha^{-1})	120.83	2.18	42.44
Branch biomass (t·ha^{-1})	13.92	0.17	3.26
Foliage biomass (t·ha^{-1})	16.01	0.43	4.98
Total root biomass (t·ha^{-1})	45.43	0.96	12.94
Fine root biomass (t·ha^{-1})	4.85	0.17	1.70
The root-shoot ratio	0.36	0.27	0.32
The fine root-foliage biomass ratio	0.47	0.24	0.35

Branch, root and fine root volume as well as needle counts were calculated using the nested regression method. Root measurements were performed by partly excavating the root system to acquire the lengths and diameters. The diameters and lengths of sample roots were measured with a digital calliper (± 0.01 mm) and branching hierarchy of measured roots were recorded *in situ*. Fine roots of the samples were taken to laboratory in sealable plastic bags, which were measured by a 40x stereomicroscope with an ocular micrometer (± 0.025 mm). The measurement procedure for branches was similar to that of roots. Meanwhile the number of needles were counted to develop foliage models. Detailed description of sampling and measurements for the nested regression method (Liu 2009).

To determine the tissue density for converting to biomass from volume, about 10 sections of stem, branch, and root were collected, respectively. Sample volume was determined by water displacement, after which samples were oven-dried at 65 °C to constant weight (48 h). Tissue density was the ratio of oven-dried mass to fresh volume, i.e. basic density. One hundred needles were also oven-dried before being weighed for calculations of mean single needle mass, a parameter for calculating needle biomass for individual trees.

Data analysis: For determining an appropriate model of each component biomass, linear, power, logarithmic and polynomial models were considered. The equation with significant parameters ($P < 0.05$) and the highest adjusted R square (R^2) was selected as the final model for estimating biomass. Partial correlation analysis between each component biomass and stand age or density was examined, respectively. All statistical analyses were performed on SPSS 20.0.

RESULTS

Above and below-ground biomass models: Total and fine

Table 2: Regression parameters for predicting biomass as a function of DBH for *Larix gmelinii.*

Dependent variable	*n*	*a*	*b*	R^2	*P* value
Total root	17	0.045	2.308	0.971	<0.001
Fine root	17	0.037	1.574	0.917	<0.001
Foliage	25	0.038	2.000	0.949	<0.001
Branch	25	0.002	3.025	0.968	<0.001
Stem	25	0.065	2.520	0.985	<0.001

Table 3: Partial correlation coefficients between tree component biomasses and stand age or density for *Larix gmelinii* (n = 774).

Controlling variable	Stand density	Stand age
Variable	Stand age	Stand density
Stem	0.48	0.27
Branch	0.53	0.17
Foliage	0.43	0.43
Coarse root	0.47	0.29
Fine root	0.38	0.56

All partial correlation coefficients are highly significant (P< 0.01).

root biomass of 17 trees and component biomass for stem, branch and foliage of 25 trees were calculated using the nested regression method. Biomass of all components significantly and positively correlated with DBH. Among all candidate models, the power equation provided the best fit for the biomass-DBH relationship for all tree components. For all of the final power relationships, the R^2s were more than 0.9 and P values less than 0.001 (Table 2).

Equations for all dependent variables are in the form of $y=ax^b$, where y is dependent variable (e.g., total root biomass, kg dry mass), x is DBH (cm), and a and b are constants. R^2 is coefficient of determination.

Stand biomass estimates: Stand biomass was estimated using the derived allometric equations (Table 2). All components varied across all plots, with total biomass ranging from 3.74 to 196.19 t·ha^{-1}. Total root biomass ranged from 0.96 to 45.43 t·ha^{-1}, whereas fine root biomass ranged from 0.17 to 4.85 t·ha^{-1} (Table 1); fine root biomass accounted for 6.59-23.34% of total root biomass. Aboveground biomass ranged from 2.78 to 150.76 t·ha^{-1}, with foliage biomass ranging from 0.43 to 16.01 t·ha^{-1}, branch biomass from 0.17 to 13.92 t·ha^{-1}, and stem biomass from 2.18 to 120.83 t·ha^{-1} (Table 1). Means of belowground, above ground and total biomass were 12.94 t·ha^{-1}, 50.68 t·ha^{-1}, 63.62 t·ha^{-1}, respectively.

Biomass allocation patterns: Biomass of all tree components positively correlated with stand age when stand density was controlled for (Table 3). The partial correlation coefficient between fine root and stand age was 0.38, which was the lowest among all tested components. The next lowest partial correlation coefficient was for foliage (0.43). A significant positive correlation was also found between biomass of all the tree components and stand density, when stand age was controlled for (Table 3). Among the dependent variables correlated with stand density, fine root biomass achieved the highest partial correlation coefficient of 0.56 followed by a value of 0.43 for foliage biomass.

For all investigated plots, stem biomass accounted for the greatest proportion to total biomass, followed by coarse root, foliage, branch and fine root biomass. The ratio of stem to total biomass ranged from 0.56 to 0.63 with a mean value of 0.60, and stem biomass significantly increased with stand age and decreased with stand density (Figs. 1, 2). The branch to total biomass ratio ranged from 0.04 to 0.09 with a mean value of 0.06. Branch biomass increased with stand age and decreased with stand density (Figs. 1, 2). The ratio of foliage to total biomass ranged from 0.06 to 0.13 with a mean value of 0.10, and foliage biomass decreased with stand age and increased with stand density (Figs. 1, 2). For belowground components, the ratio of coarse root to total biomass appeared to be no more than 0.21, statistically less significant. The ratio of fine root to total biomass ranged from 0.02 to 0.06 with a mean value of 0.03. Fine root biomass significantly decreased with stand age and increased with stand density (Figs. 1, 2).

The ratio of above to belowground biomass (R/S) ranged from 0.27 to 0.36 with a mean of 0.32, and decreased with stand age and increased with stand density (Figs. 3a, c). The ratios of fine root to foliage biomass (FR/N) ranged from 0.24 to 0.47 with a mean of 0.35, and also decreased with stand age and increased with stand density (Figs. 3b, d).

DISCUSSION

The above and belowground biomass for various stand ages or densities for *L. gmelinii* were estimated in the present study. The average belowground biomass reported here was similar to a *L. gmelinii* stand near Tura, central Siberia (16.70 t·ha^{-1}), however aboveground biomass reported here was about twice that of the previous report (Kajimoto et al. 1999). This is partly because our research area was far south of Kajimoto et al.'s research site, and the climatic conditions are more favourable for primary production (Wang et al. 2005). The average aboveground biomass in our plots was comparable with that reported in boreal coniferous forests, which ranged 10-90 t.ha^{-1} , while the average belowground biomass was well under previously reported means (29.00 t·ha^{-1}) for global boreal forests (IPCC 2006, Jackson et al. 1997).

The R/S in our stands was comparable with the range of 0.11-0.43 for *Larix* forests (*L. gmelinii* and *L. olgensis*, etc.)

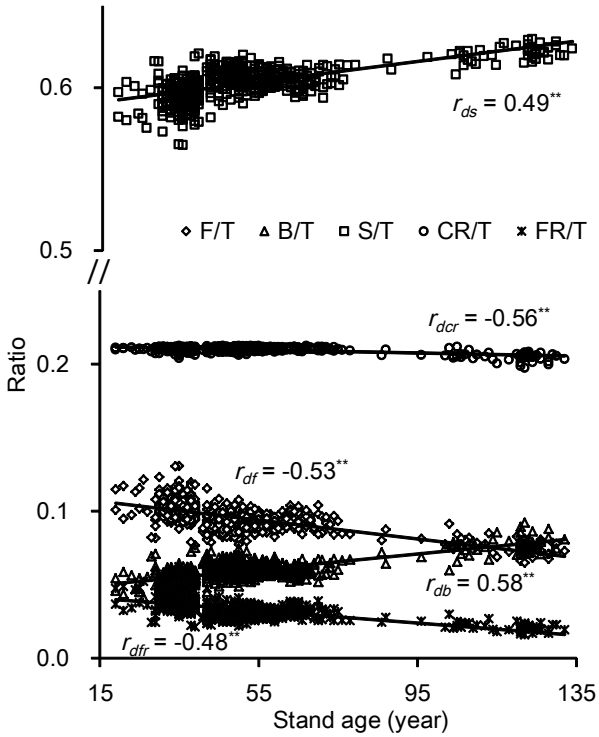

Fig. 1: Relationships between the ratios of tree component to total biomass and stand age for *Larix gmelinii*. F/T: foliage to total biomass ratio; B/T: branch to total biomass ratio; S/T: stem to total biomass ratio; CR/T: coarse root to total biomass ratio; FR/T: fine root to total biomass ratio. r_{ds}, r_{db}, r_{df}, r_{dcr} and r_{dfr} are partial correlation coefficients between stand age (controlling for stand density) and S/T, B/T, F/T, CR/T and FR/T, respectively. Significant correlations are indicated with ** (P< 0.01).

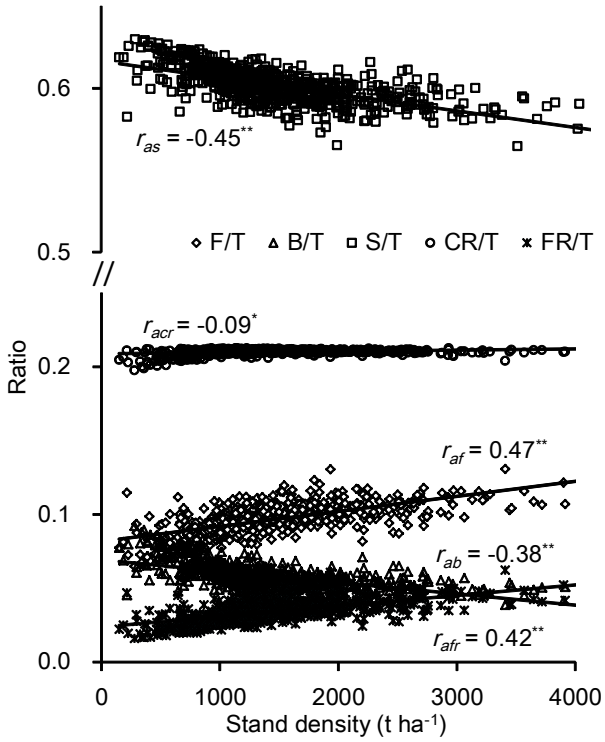

Fig. 2: Relationships between the ratios of tree component biomass and stand density for *Larix gmelinii*. r_{as}, r_{ab}, r_{af}, r_{acr} and r_{afr} are partial correlation coefficients between stand density (controlling for stand age) and S/T, B/T, F/T, CR/T and FR/T, respectively. Significant correlations are indicated with * (P< 0.05) and ** (P< 0.01).

reported in Northeast China (Wang et al. 2008). The R/S of boreal and temperate conifer forests were 0.39 and 0.40, respectively (Mokany et al. 2006), which were higher than our findings, suggesting that aboveground and root biomass partitioning varies among boreal and temperate conifer species.

Significantly positive relationships between stand age and component biomasses were recognized in this study, which were consistent with previous reports for other forest ecosystems (Luyssaert et al. 2008, Peet 1981). In addition, the partial correlation coefficients were lower between stand age and fine roots and foliage than for the other components (Table 3). The unexplained variance for these components may be due to turnover rates of organs, because fine roots and foliage have much higher turnover rates than stems or coarse roots (Reich et al. 2014). The fact that component biomasses significantly and positively correlated with stand density corresponds with a previous study on young lodge pole pine forests (Litton et al. 2003). Partial correlation coefficients of fine root and foliage biomasses regressed with stand density were higher than for the other component biomasses (Table 3). Fine roots and foliage, which make up foraging components of trees, are important for inter-individual competition, which may have a closer association with stand density than other organs. In addition, more than 70% of the sunlight is intercepted by the canopy layer (Brix 1981), which may limit the amount of foliage of sub-canopy individuals. This implies that stand density has a greater influence on foliage than other aboveground organs. In contrast, structural components (stem, branch and coarse roots) correlate less strongly with stand density than foraging components do (Table 3).

Biomass reflects the cumulative energy status of trees and biomass allocation patterns are commonly regulated by both endogenous and exogenous factors (Mokany et al. 2006, Schmid 2002). Biomass allocation among organs of *L. gmelinii* is greatly influenced by stand age and density (Fig. 1, 2). R/S and FR/N decreased with increasing stand age (Fig. 3a, b). In other words, we found reduced allocation of biomass to belowground organs in old relative to young stands, which corresponds with other studies (Grulke & Retzlaff 2001, Litton et al. 2003). The variation in biomass allocation between above- and belowground is primarily driven by fine root for belowground, whereas the propor-

tion of coarse root biomass was levelled off across all plots (Fig. 1). For many forest types, the ratio of fine root to total root biomass is generally less than 0.2 and decreases with stand age (Cairns et al. 1997, Li et al. 2003). In *L. gmelinii* forests the ratios also decreased with stand age, and was, on average, 0.13. In contrast, increased allocation of biomass to aboveground is caused by increases in the ratios of stem and branch biomasses to total biomass, associated with the accumulation of aboveground woody tissues as the stand develops (Reich et al. 2014, Wang et al. 2008). However, the decrease in foliage to total biomass with stand age may be due to decreased nutrient availability with lower soil temperatures after canopy closure in boreal forests (Gower et al. 1994).

When ratios of components to total biomass were related with stand density, the proportion of aboveground biomass decreased with density, mainly due to decrease in proportion of stem and branch biomasses (Fig. 2). Meanwhile the ratios of fine root and foliage biomasses to total biomass tended to increase with increasing stand density, i.e., allocation of biomass to structural and foraging components decreased and increased, respectively with stand density. As stand density increases, both aboveground and belowground intraspecific competition increases, potentially influences the most advantageous partitioning of biomass among the tree components. Higher density stands tend to allocate more organic matter to fine roots, which is favourable for water and nutrient acquisition, whereas increased partitioning to foliage is favourable for sunlight capture (Burkes et al. 2003, Oliver & Larson 1996). These conclusions are consistent with the optimal partitioning theory (McCarthy & Enquist 2007).

The *L. gmelinii* plots had a wide range of FR/N but relative conservative values of R/S (Fig. 3). According to the optimal partitioning theory, allocation of biomass among plant organs maximizes growth through acquisition of nutrients, water and light (McCarthy & Enquist 2007). Sensitivity of fine roots and foliage to stand age and density demonstrates a hierarchy in the priority of biomass partitioning with foliage and fine root growth higher in priority than other organs (Burkes et al. 2003, Oliver & Larson 1996).

The regression functions of *L. gmelinii* component biomasses with DBH developed in this study explained more than 90% of the observed variation (Table 2), supporting the application of these equations in estimating biomass of *L. gmelinii*, especially for root system biomass. Conse-

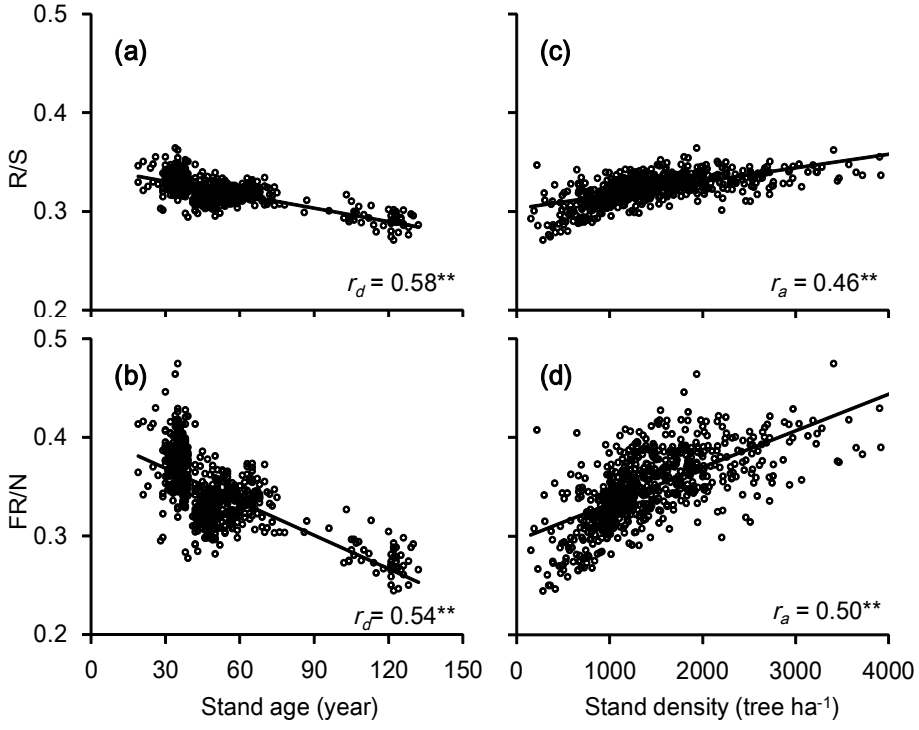

Fig. 3: Relationships of ratio of above- to belowground biomass (R/S; a, c) and ratio of fine root to leaf biomass (FR/N; b, d) with stand age or density for *Larix gmelinii*. r_d is the partial correlation coefficient of the relationship between stand age and R/S or FR/N controlling for stand density. r_a is the partial correlation coefficient of the relationship between stand density and R/S or FR/N, controlling for stand age. Significant correlations are indicated with ** (P< 0.01).

quently, the nested regression method provides an effective approach to estimate biomass with minimal excavation of root systems, and hence minimal workload and disturbance to trees and soil. A regression function can even be developed with measurements from only one complete root branch with the largest size that includes all suborder roots (Liu 2009). The root biomass, traditionally, is measured by excavating the entire root system, which is a very labour-intense and time-consuming task, including large errors associated with an extremely large number of hair-like fine roots to estimate. In most cases, fine root biomass is underestimated due to sample loss during excavation (Niiyama et al. 2010, Xiao & Ceulemans 2004).

Fine root biomass measurements are notoriously difficult due to the complex and unseen distribution of roots within soil (Koteen et al. 2014). In this study, it showed reliable estimates of fine root biomass using nested regression with DBH as the predictor variable. This once-for-all tool, the regression model, is convenient for evaluating fine root biomass at both individual and stand levels. Also, the contribution of plant populations to carbon and nutrient cycling can be correctly identified without confusion among species in multi-species stands.

Biomass density estimated by core sampling is highly sensitive to site properties, such as tree size and stand density (Das & Chaturvedi 2008, Hertel et al. 2013, Meinen et al. 2009, Ugawa et al. 2010). Application of these estimating methods to other stands with the same species, but different in structure would be risky. Compared with the soil core method, the nested regression approach tested in this study is more practical and universally applicable, i.e. an important contribution to root biomass research, particularly for fine root biomass.

In summary, we conclude that biomass allocation patterns between above and belowground components (or foraging and structural components) of *L. gmelinii* forests vary uniformly across gradients of stand age and density. These findings help to fill gaps in current knowledge about the effects of stand age and density on biomass allocation and C storage. The nested regression approach for biomass measurement, in particular for fine roots, outlined in this study can be used to enhance the scope and accuracy of terrestrial C models by identifying allocation patterns that allow for the estimation of belowground C with an efficient estimate of root biomass.

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