Plant Soil (2019) 442:355–367
https://doi.org/10.1007/s11104-019-04206-7

REGULAR ARTICLE

# Effects of morphology and stand structure on root biomass and length differed between absorptive and transport roots in temperate trees

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Received: 16 March 2019 / Accepted: 3 July 2019 / Published online: 11 July 2019

**Abstract**
*Aims* Absorptive and transport roots (diameter ≤ 2 mm) are closely related to soil resource uptake for plant growth, carbon budget and nutrient cycling in forest ecosystems, but how and why the relative share of root biomass or root length for both root functional types changes with tree species is not well understood. Our aims were to examine the inter-specific variations of root biomass and length per unit area of absorptive and transport roots, and their relationships with stand structure and soil characteristics, root morphological and architectural traits.

*Methods* We measured root biomass and length per unit area, diameter, specific root length (SRL), root tissue density (RTD), and branching ratio of the first five order roots, stand and soil characteristics in seven forests consisting of different tree species at a common site. The first order roots were classified as absorptive roots and the other orders as transport roots based on our earlier work.

*Results* Biomass ratios of absorptive to transport roots varied from 1:5.56 to 1:1.12 among species, and length ratios ranged from 1:1.56 to 1:0.29. Root biomass was not influenced by root morphology or architecture, nor by stand or soil characteristics. Absorptive root length was significantly correlated with SRL, RTD, and branching ratio of the first to second order roots among species, whereas transport root length was significantly correlated with stem density.

*Conclusions* The relative share of biomass and length for absorptive and transport roots differed among tree species, which may influence belowground carbon allocation and resource competition.

**Keywords** Absorptive roots · Fine root · Nutrient forage strategy · Root biomass · Root order

**Abbreviations**

| | |
|---|---|
| SRL | Specific root length |
| RTD | Root tissue density |
| N | Nitrogen |
| C | Carbon |

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Responsible Editor: Amandine Erktan.

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s11104-019-04206-7) contains supplementary material, which is available to authorized users.

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## Introduction

Fine root turnover plays an important role in carbon (C) and nutrient fluxes at the individual tree level and the ecosystem scale. Modeling simulation suggested that about one-third of photosynthates of terrestrial ecosystems was consumed by fine root turnover given the assumption of root turning over once a year (Jackson et al. 1997). However, accumulating evidence indicated that there was considerable uncertainty in estimating root biomass turnover using a single diameter size threshold (e.g., ≤2 mm) to define the fine root pool (Joslin et al. 2006; McCormack et al. 2015). Basically, fine roots are composed of individual roots differing in anatomy, morphology, longevity and physiological functions (Wells and Eissenstat 2001; Pregitzer et al. 2002; Hishi 2007; Guo et al. 2008b). Based on their main functions, fine roots can be categorized into two components, that is, absorptive roots and transport roots (McCormack et al. 2015). To minimize the heterogeneity of turnover rate and biomass within the fine root pools, it is more reliable to calculate these values on the basis of functional groups (Guo et al. 2008a; Gaudinski et al. 2010; McCormack et al. 2015). In this manner, McCormack et al. (2015) classified the traditional fine roots (diameter ≤ 2 mm) into two pools, absorptive and transport roots, and estimated the corresponding biomass and turnover rate, indicating that 22% of global net primary productivity was accounted for by fine root turnover, in contrast to the previous value (33%) estimated on a single pool (Jackson et al. 1997). However, only a few studies empirically determine the biomass of absorptive and transport roots separately (McCormack et al. 2015). Therefore, it is necessary to determine how and why absorptive and transport roots vary among tree species and forest ecosystems, when we seek to accurately estimate belowground C and nutrient fluxes via root turnover at the regional and global levels.

The biomass proportions of absorptive and transport roots within a fine root branch are inherently related to the deployment of root biomass among root branch orders (Wang et al. 2006; Zadworny et al. 2016). However, only a few studies have quantified fine root biomass per unit area on the basis of branch order (Table 1). Previous studies have shown that the amount and proportion of each root order within the branching fine root system varies largely among species and forest types (McCormack et al. 2015). First, in our synthesis, root biomass per unit area, for a given root order, varied over 20-fold among species (Table 1). Second, the first order roots, that is, the typical absorptive roots (Guo et al. 2008b; Zadworny et al. 2016), can account for up to 30% of the total biomass of the first five orders in temperate species of *Fraxinus mandshurica* (Wang et al. 2006) and sub-tropical species of *Mytilaria laosensis* (Liu et al. 2016), but less than 10% in other tree species (Liu et al. 2012; Wang et al. 2013b; Chen et al. 2017). The large discrepancy mentioned above reflects the difference between tree species, however, it is worth noting that the diverse climate and site conditions might also contribute to such variability (e.g., Vogt et al. 1996; Yuan and Chen 2010). Thus, the first objective of this study was to reveal how the biomass of absorptive and transport roots vary among seven temperate tree species growing under the same site conditions using the root-order-based method, which should enrich the root parameter dataset for estimating fine root turnover in temperate forests.

Root length density (root length per unit volume) is generally considered as an important indicator for the absorptive capacity (Jackson et al. 1997; Taylor et al. 2014; McCormack et al. 2017). In studies of mixed forests, root length density was used to evaluate the belowground interactions between the target and mixed tree species (Bauhus and Messier 1999; Richards et al. 2010). For example, in mixed boreal forests, root length of *Populus tremuloides* was high, ranging from 4.33 to 5.25 cm cm$^{-3}$, in comparison with the low values of 0.66 to 0.67 cm cm$^{-3}$ of other coniferous species, reflecting their different soil exploitation strategies (Bauhus and Messier 1999). On a global scale, Jackson et al. (1997) showed that live root length and root surface area varied significantly among different forest ecosystems, with the maximum in the systems with sclerophyllous shrubs and trees and the minimum in boreal forest, respectively. However, most of the previous studies sorted roots by diameter size classification (e.g., ≤2 mm), including both absorptive roots and transport roots, which might lead to some uncertainty in estimating root absorptive capacity of specific tree species or ecosystems (Liu et al. 2019). On the root order basis approach, Pregitzer et al. (2002) suggested that the first order roots generally have the largest proportion of length within the first three order roots in nine North American tree species. However, very few studies have determined the root length per unit area (or volume) within the context of root order, partly because of labor or time limitations (but see Wang et al. 2006).

**Table 1** Summary of root biomass (g m$^{-2}$) in each root order and their proportions (%, values in parenthesis) to all orders in previous studies

| Tree species | Location | Life form | Stand age (yr) | Sampling Depth (cm) | Root diameter [a] (mm) | First order | Second order | Third order | Fourth order | Fifth order | All orders | Source [h] |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Pinus palustris* | USA (31°22'N, 84°48'W) | Evergreen conifer | 22 | 0–10 | 1.56 | 13.3 (17.0) | 9.3 (11.9) | 15.1 (19.3) | 14.3 (18.2) | 26.4 (33.7) | 78.4 | 1 |
| *Larix gmelinii* | China (45°21–45°25'N, 127°30′-127°34′E) | Deciduous conifer | 17 | 0–10 | 1.70 | 19.7 (19) | 13.5 (13) | 15.5 (15) | 20.7 (20) | 35.2 (34) | 103.5 | 2 |
| *Fraxinus mandshurica* | | Deciduous broadleaf | 17 | 0–10 | 1.54 | 42.0 (30) | 18.2 (13) | 15.4 (11) | 18.2 (13) | 44.8 (32) | 139.9 | 3 |
| *Picea asperata* | China (31°43'N, 102°48'E) | Evergreen conifer | 50 | 0–40 | —[b] | 28.5 (8.2) | 30.7 (8.9) | 60.9 (17.6) | 76.6 (22.1) | 150.0 (43.3) | 346.7 | 3 |
| *Pinus tabuliformis* | China (35°39'N, 110°06′E) | Evergreen conifer | 51 | 0–20 | 1.26 | 8.8 (11.4) | 9.1 (11.8) | 12 (15.6) | 17.4 (22.6) | 29.8 (38.7) | 77.1 | 4 |
| *Cunninghamia lanceolata* | China (31°36'N, 119°01′E) | Evergreen conifer | 25 | 0–20 | 1.21 | 1.4 (6.5) | 1.7 (7.7) | 2.7 (12.1) | 4.7 (21.1) | 11.8 (52.7) | 22.3 | 5 |
| *Cupressus funebris* | China (31°5–31°20'N, 104°15′-104°33′E) | Evergreen conifer | 34 | 0–15 | 1.50 | 14.6 (13.0) | 18.1 (16.1) | 20.7 (18.3) | 26.7 (23.6) | 32.8 (29.1) | 112.9 | 6 |
| *Pinus elliottii* | China (26°44′29.1″N, 115°03′29.2″E) | Evergreen conifer | 30 | 0–10 | 1.26 | 2.2 (21.8) | 1.3 (12.9) | 1.8 (17.8) | 1.4 (13.9) | 3.4 (33.7) | 10.1 | 7 |
| *Quercus robur* | Poland (52°14′87″N, 18°06′35″E) | Deciduous broadleaf | 42 | 0–10 | 0.70 | 30 (15.4) | 22.2 (11.4) | 24.2 (12.4) | 29.4 (15.1) | 40.5 (20.8) | 194.9 [d] | 8 |
| | | Deciduous broadleaf | 42 | 0–10 | 0.80 | 41.8 (12.4) | 24.6 (7.3) | 46.2 (13.7) | 42.5 (12.6) | 78.6 (23.3) | 337.3 [e] | 8 |
| *Mytilaria laosensis* | China (26°48'N, 117°58′E) | Evergreen broadleaf | 22 | 0–10 | – | 47.8 (30.4) | 44.5 (28.3) | 45.4 (28.9) | 4.9 [c] (3.1) | | 157.2 | 9 |
| *Populus euramericana* | China (35°53'N, 116°50′E) | Deciduous broadleaf | 5 | 0–20 | – | 0.10 (7.0) | 0.18 (12.0) | 0.28 (19.2) | 0.28 (18.5) | 0.64 (43.7) | 1.48 [f] | 10 |
| | | Deciduous broadleaf | 5 | 0–20 | – | 0.28 (16.6) | 0.28 (16.7) | 0.30 (17.3) | 0.26 (15.5) | 0.58 (33.8) | 1.7 [g] | 10 |

[a] The mean diameter of the highest root order examined

[b] Not reported

[c] Fine roots were not separated into specific orders

[d] Trees grow in Brunic Luvisol soil

[e] Trees grow in Brunic Arenosol soil

[f] Stand of the first rotation

[g] Stand of the second rotation

[h] 1, Guo et al. (2004); 2, Wang et al. (2006); 3, Liu et al. (2012); 4, Wang et al. (2013a); 5, Wang et al. (2013b); 6, Su et al. (2015); 7, Kou et al. (2015);8, Zadworny et al. (2015); 9, Liu et al. (2016); 10, Chen et al. (2017)

Therefore, the second goal of this study was to determine how root length of absorptive and transport roots varies among tree species at a common site, which would deepen our understanding of the inter-specific variation in resource acquisition strategy at the ecosystem level.

Which factors affect the variation in root biomass and length have been extensively studied in the past 30 years. Some studies have confirmed that climatic conditions, vegetation types, stand characteristics and soil properties are important factors in determining fine root biomass on a global scale (Vogt et al. 1986, 1996; Yuan and Chen 2010; Finér et al. 2011). However, these previous studies have at least two limitations. Firstly, most studies used fine root data based on the root diameter threshold (e.g., ≤2 mm), in which different order roots were included. Roots of different orders performing absorption or transportation have been shown to respond diversely to shifts in environmental conditions, such as soil nitrogen (N) availability (Wang et al. 2013a; Wang et al. 2017a). Thus, it remains unclear whether absorptive and transport roots respond differently to stand or soil characteristics. Secondly, how root morphology contributes to the inter-specific variations in root biomass is not well assessed, despite being important information to help understanding the soil exploitation strategies of tree species at the individual root and the stand levels. Theoretically, the biomass of the root population is a function of the number and the mass of individual roots. The number of roots is related to the branching ratio (i.e., the ratio of abundance of daughter roots to mother roots), and root mass is related to the diameter, length and tissue density of individual roots (Wang et al. 2006). Helmisaari et al. (2009) found that the increase in ectomycorrhizal root tip biomass production was the result of high root numbers in both *Picea abies* and *Pinus sylvestris* stands. In a synthesis of global field trails, Zhou et al. (2018) showed that the drought-induced decrease in root biomass was mainly caused by changes in individual root diameter and length. However, at the local scale, how root morphology contributes to the variations in root biomass among tree species remains ambiguous. Thus, the third objective of this study was to investigate the effects of stand and soil characteristics, as well as the morphological (e.g., SRL) and architectural traits (e.g., branching ratio) of individual roots, on the inter-specific variation in absorptive and transport roots biomass and length per unit area.

In this study, we quantified root biomass and length per unit area of the first five order roots at 0–10 cm soil depth in seven temperate tree species (stands) at a common site in northeastern China, and concurrently measured the stand characteristics and soil conditions, as well as the morphological and architectural traits of each order roots. In our study site, an anatomical study (Guo et al. 2008b) covering six out of the seven species examined in this study, suggested that first-order roots exhibited primary development with intact cortex and high mycorrhizal colonization, mainly providing absorptive functions. Additionally, first-order roots showed strong differences with other order roots in morphological and chemical traits (Freschet and Roumet 2017; Liu et al. 2019). Thus, for all fine roots with diameter ≤ 2 mm, we categorized first-order roots as absorptive roots, and second- to fifth-order roots as transport roots. The overall objective of this study was to examine the variation patterns of the biomass and length of absorptive and transport roots among seven tree species (stands) on the basis of root order, and to reveal their relationships with stand and soil characteristics, and root morphological and architectural traits. We proposed the following hypotheses: (1) the ratio of biomass (g $m^{-2}$) of absorptive to transport roots varies significantly among tree species (ref. Table 1); (2) within each species, the length (m $m^{-2}$) of absorptive roots accounts for the largest proportion among the first five order roots; (3) the biomass and length of absorptive and transport roots exhibit different relationships with stand and soil characteristics, and root morphological and architectural traits.

## Materials and methods

### Study site and plot establishment

This study was conducted at the Maoershan Forest Research Station (45°21′–45°25’ N, 127°30′–127°34′ E) of Northeast Forestry University, Heilongjiang, China. The study area has a continental temperate monsoon climate with mean January, July and annual temperatures of −19.6 °C, 20.9 °C and 2.8 °C, respectively, and a growing season length ranging from 120 to 140 d. The mean annual precipitation is 723 mm with 477 mm distributed in June, July and August. During winter (December–April), the soil is usually frozen to a maximum depth of 1 m (Gu et al. 2017). Soils are welldrained, Haplic Luvisols that exceed 50 cm in depth, with high organic matter content and well-developed horizons (Gong et al. 1999).

A total of seven tree species (stands) were selected for this study; six of them were monospecific plantations, and the other one was a secondary forest. In the 1980s, the secondary forests at the study site were harvested by clear-cutting. In 1986, a series of monospecific plantations was established on a relatively uniform slope (450–500 m a.s.l.) to compare forest dynamics among common tree species, and to compare them with the natural regeneration of the secondary forest. Bare-root 2-year-old seedlings were planted using a 1.5 × 2.0 m planting grid, and the area of each plantation was over 5 ha. Six plantations were chosen for the present study: two deciduous broadleaf species, *Fraxinus mandshurica* and *Juglans mandshurica*; and three evergreen coniferous species, *Pinus koraiensis*, *Pinus sylvestris* var. *mongolica* and *Picea koraiensis*; and one deciduous coniferous species *Larix gmelinii*. Near to the plantation sites, a secondary forest dominated by white birch (*Betula platyphylla*) was chosen. In 2011, other accompanying tree species in this stand were thoroughly thinned, resulting in a natural white birch monospecific secondary forest. Three 20 × 30 m plots were placed randomly in each stand with a surrounding buffer zone in late April 2017, and stand characteristics were quantified concurrently (Table 2).

## Root excavation and preliminary processing

Fine root samples were collected by using the soil cores method to assess root morphological traits, root biomass and length per unit area. A relatively large diameter soil core (inner diameter = 100 mm) was used to sample roots, as this might be better than small diameter cores to capture intact root branches (McCormack et al. 2015). Ten soil cores in each stand (species) were randomly taken at 0–10 cm soil depth in July 2017, regardless of the boundary of plots. Thus, a total of 70 soil cores were excavated for seven tree species stands. Once excavated, the samples were spread on a white plastic sheet to enable easy recognition and separation of fine roots from the soil. According to root color, architecture, elasticity and resilience, we could discern roots of the target tree species from those of other shrubs or herbs. Roots were carefully removed by hand, and about 100 g fresh soil of each core was also sampled, both of which were stored in Ziploc® bags separately in a cooler with ice (0–4 °C), and then transported to the laboratory within 0.5 h for subsequent root and soil processing.

## Root morphology, biomass and length per unit area

In the laboratory, soil attached to intact root branches was brushed away carefully, and some small root segments were washed with deionized water (1 °C) to remove soil

**Table 2** Stand and soil characteristics (0–10 cm depth) of the seven tree species in northeastern China. Values are mean ± 1 SE. Significant differences ($P < 0.05$) among tree species are indicated by different lower-case letters

| Species | Life form | Stem density (No. ha$^{-1}$) | Stand age (Yr) | Height (m) | Diameter at breast height (cm) | Stand basal area (m$^2$ ha$^{-1}$) | Total soil carbon (g kg$^{-1}$) | Total soil nitrogen (g kg$^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| Frax | Deciduous broadleaf | $1452 \pm 157^{bc}$ | 31 | $18.9 \pm 1.2^{bc}$ | $9.7 \pm 1.9^{d}$ | $13.6 \pm 5.7^{b}$ | $78.9 \pm 7.3^{bc}$ | $8.8 \pm 0.7^{b}$ |
| Jugl | Deciduous broadleaf | $2356 \pm 210^{a}$ | 31 | $13.2 \pm 0.9^{d}$ | $10.5 \pm 0.5^{cd}$ | $24.1 \pm 2.0^{ab}$ | $110.9 \pm 6.2^{a}$ | $11.1 \pm 0.4^{a}$ |
| Betu | Deciduous broadleaf | $844 \pm 89^{c}$ | 34 ± 6 | $25.3 \pm 1.2^{a}$ | $16.1 \pm 0.7^{a}$ | $17.4 \pm 0.6^{b}$ | $62.2 \pm 4.8^{d}$ | $6.9 \pm 0.3^{c}$ |
| Lari | Deciduous conifers | $1244 \pm 133^{c}$ | 31 | $20.7 \pm 1.2^{b}$ | $17.2 \pm 0.9^{a}$ | $30.9 \pm 4.0^{a}$ | $79.9 \pm 4.8^{b}$ | $8.3 \pm 0.4^{b}$ |
| Pice | Evergreen conifers | $2222 \pm 567^{ab}$ | 31 | $8.9 \pm 0.8^{e}$ | $9.6 \pm 0.1^{d}$ | $19.0 \pm 5.0^{b}$ | $65.8 \pm 3.8^{cd}$ | $7.0 \pm 0.3^{c}$ |
| Pinu | Evergreen conifers | $1378 \pm 222^{bc}$ | 31 | $9.5 \pm 0.5^{e}$ | $13.0 \pm 1.1^{bc}$ | $19.4 \pm 0.9^{b}$ | $75.8 \pm 2.0^{bc}$ | $8.1 \pm 0.2^{b}$ |
| Pisy | Evergreen conifers | $770 \pm 283^{c}$ | 31 | $16.0 \pm 1.3^{cd}$ | $14.2 \pm 0.7^{ab}$ | $13.6 \pm 4.7^{b}$ | $44.6 \pm 1.0^{e}$ | $5.7 \pm 0.1^{d}$ |

Species abbreviation: Frax: *Fraxinus mandshurica*; Jugl: *Juglans mandshurica*; Betu: *Betula platyphylla*; Lari: *Larix gmelinii*; Pice: *Picea koraiensis*; Pinu: *Pinus koraiensis*; Pisy: *Pinus sylvestris* var. *mongolica* particles. Cleaned intact root branches and root segments were then sorted by the following process. Although a maximum of sixth order roots were found in some species, only the first five branch order roots were used for subsequent morphology and biomass analysis. Root samples were dissected into different branch orders by forceps under a 10× stereomicroscope (Motic SMZ-140, China), following the procedure described in Pregitzer et al. (2002) and Wang et al. (2006), that is, the distal non-woody roots were numbered as first-order roots. During the processing, the pioneer root tips and fibrous roots tips (Zadworny and Eissenstat 2011) were not distinguished in our analysis, because of the limited number of the former root type. For each soil core, at least one intact root branch (including five order roots) was randomly selected, the number of first-order roots (daughter roots) borne by second-order roots (mother roots) was recorded manually. The branching ratio was calculated as the total number of first-order roots divided by the total number of second-order roots within a root branch (Wang et al. 2006). Branching ratios from the fifth to the second order roots were not assessed because of labor limitations.

After dissection, root samples of each order per soil core were separated into two subsamples: one subsample was directly oven dried to constant weight (65 °C), then weighed (nearest = 0.00001 g); another subsample with 0.1–0.5 g fresh weight was scanned with an EPSON EXPRESSION 10000XL color scanner (DPI = 400). Mean diameter, total length and volume of each subsample were analyzed with the root system analyzer software (WinRhizo 2004b, Regent instruments Inc., Canada). Then the root subsamples were oven dried and weighed as mentioned above. The SRL (m $g^{-1}$) was calculated as total root length divided by dry mass. Root tissue density (RTD, g $cm^{-3}$) was calculated as dry mass divided by root volume. If possible, the SRL and RTD of each order were determined for each soil core, however, when the root biomass was limited, they were calculated from composited samples pooled from several cores. Based on the total root biomass of each order per soil core and the corresponding SRL, the root biomass and root length per unit area (g $m^{-2}$ and m $m^{-2}$, respectively) at 0–10 cm soil depth was calculated for the first to fifth order roots.

## Total soil C, N, and total available N concentrations

Soils separated from the root samples in each soil core (70 samples) were used to determine total soil C, N and total available N concentrations. Fresh soil samples were passed through a 2 mm sieve, and separated into two subsamples at the core level. One subsample of fresh soil was extracted with 2 M KCL, and soil ammonium ($NH_4^+$-N) and nitrate ($NO_3^-$-N) concentrations were determined with a flow-injection autoanalyzer (Auto Analyzer 3, SEAL Analytical GmbH, Norderstedt, Germany). Total available soil N concentration (mg $kg^{-1}$) was calculated as the sum of the $NH_4^+$-N and $NO_3^-$-N concentrations. Another subsample was air-dried, and passed through a 0.15 mm sieve; total soil C and N concentrations were determined by an elemental analyzer (vario MACRO cube, Elementar Analysensysteme GmbH, Langenselbold, Germany).

## Data analysis

The experimental unit is soil core ($n = 10$) for all root indices, and total soil C, N, and total soil available N concentrations. Therefore, for each tree species, means and standard errors for root biomass and root length per unit area of each order, and for soil variables were calculated by averaging core-level measurements. Ratios of root biomass and length between absorptive and transport roots were also calculated at the species level. Multiple mean comparisons were made by Fisher's LSD test to identify the differences in root traits among tree species, including root diameter, SRL, and RTD of each order, the branching ratio of first-order to second-order, the total root biomass and root length of all five orders, and the ratios of root biomass and length between absorptive and transport roots. The differences in root biomass and length among root orders within each tree species were also tested by Fisher's LSD test. Pearson's correlations ($n = 7$) were used to determine the potential relationships between root biomass and length per unit area of each root order or all five orders, and corresponding root morphological and architectural traits (root diameter, SRL, RTD, branching ratio), stand characteristics (stem density, stand basal area), and soil conditions (total C, N, and total available N concentrations). All statistical analysis was performed using SPSS software (2010, V. 19.0, SPSS Inc., Cary, NC).

## Results

### Root biomass

The total root biomass of the first five orders varied by ~13-fold among the seven tree species, ranging from 11.9 g m$^{-2}$ (*P. sylvestris*) to 153.1 g m$^{-2}$ (*Picea koraiensis*, Fig. 1). With increasing root order, root biomass of *Picea koraiensis* first increased and then leveled off, while those of the other six species first decreased and then increased (Fig. 1). The biomass ratio of absorptive roots to transport roots varied significantly from 1:5.56 (*Picea koraiensis*) to 1:1.12 (*F. mandshurica*).

### Root length

The total root length of the first five orders varied by 13-fold among tree species, ranging from 349.8 m m$^{-2}$ (*P. sylvestris*) to 4552.1 m m$^{-2}$ (*F. mandshurica*, Fig. 2). With increasing root order, root length declined significantly across all seven species (Fig. 2). The proportion of length of absorptive roots to the first five orders increased from 39.0% (*Pinus koraiensis*) to 77.1% (*F. mandshurica*), leading to the corresponding ratio of absorptive roots to transport roots ranging from 1:1.56 to 1:0.29.

### Root morphology

Across all seven tree species, the mean root diameters of the fifth orders were < 2 mm (Fig. S1), indicating that most roots sampled here could be classified as fine roots from a traditional perspective. Within each order, root diameter, SRL and RTD generally varied significantly among tree species, but the rank of a specific trait among species depended on the order examined (Fig. S1). The branching ratio of first-order to second-order roots was the highest in *F. mandshurica* (6.7) and the lowest in

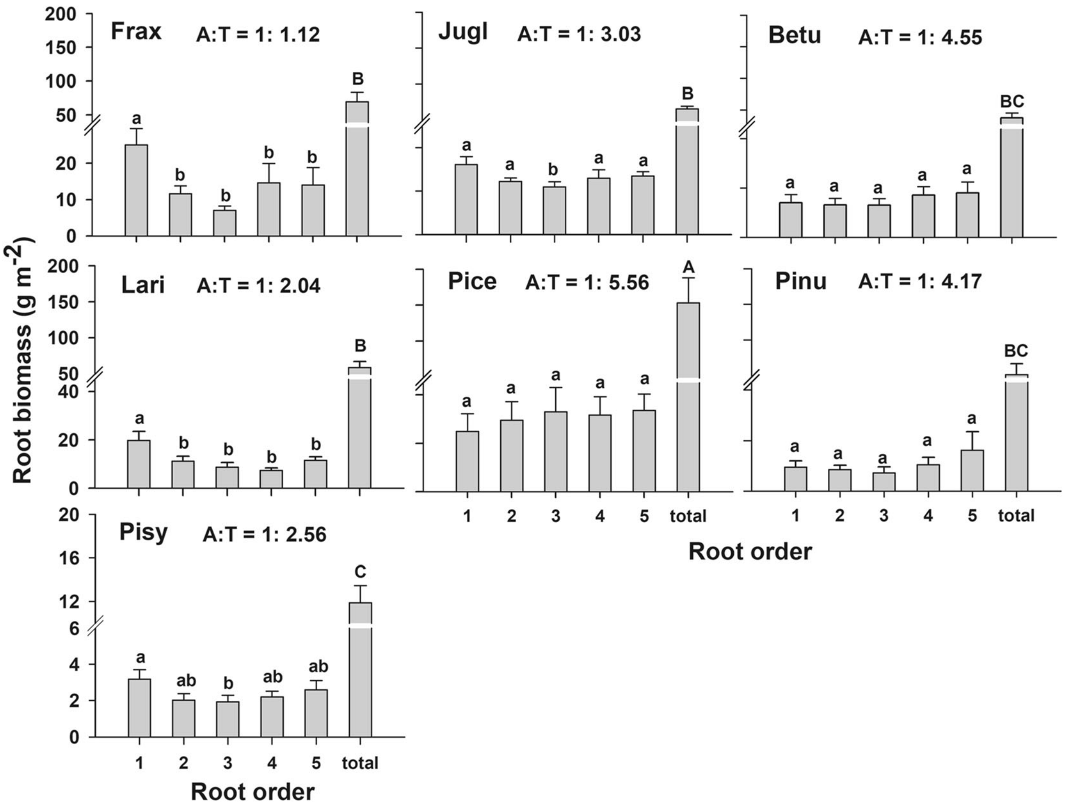

**Fig. 1** Root biomass per unit area (mean ± 1 SE) of the first to fifth orders of the seven tree species. The biomass ratio of absorptive roots to transport roots (A:T) of each species is shown in each panel. Abbreviations of species are provided in Table 2. Significant differences ($P < 0.05$) among branch orders within each species are indicated by different lower-case letters

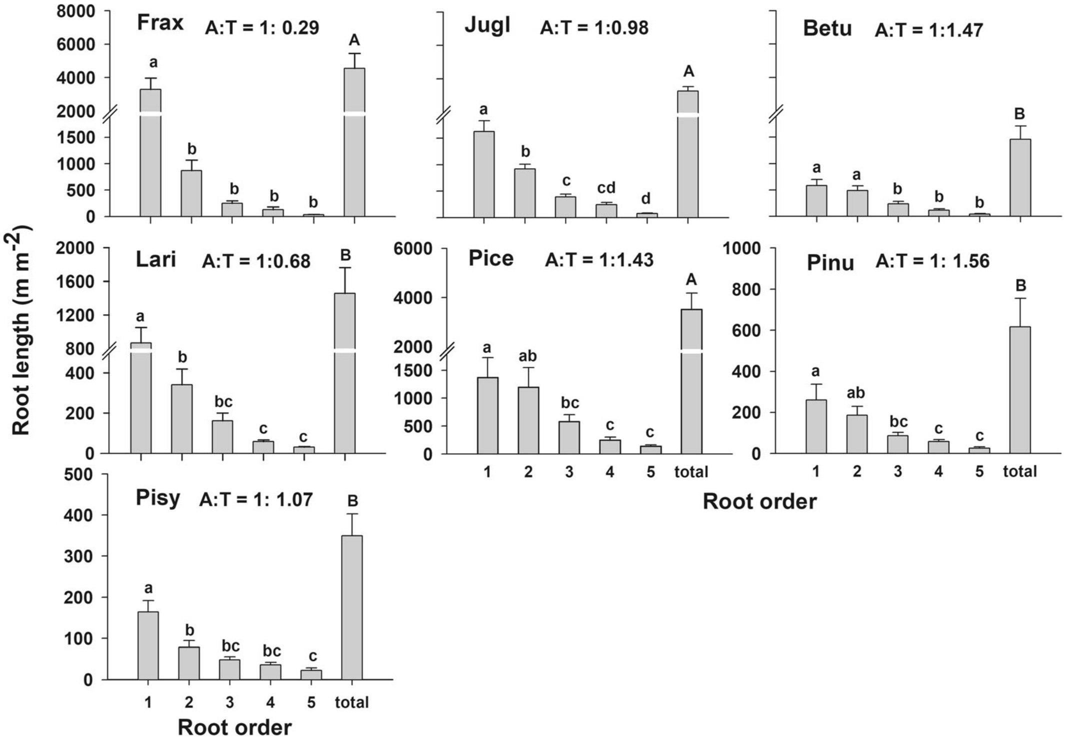

**Fig. 2** Root length per unit area (mean ± 1 SE) of the first to fifth orders of the seven tree species. The length ratio of absorptive roots to transport roots (A:T) of each species is shown in each panel. Abbreviations of species are provided in Table 2. Significant differences ($P < 0.05$) among branch orders within each species are indicated by different lower-case letters

*Pinus koraiensis* (3.1; Fig. S2). Across all seven species, root diameter and RTD generally increased but SRL decreased with ascending root order (Fig. S3).

### Relationships between root biomass, length and the characteristics of stand, soil and individual roots

Both absorptive and transport root biomasses were positively correlated with the stem density when all tree species were pooled together, but this relationship was only significant in second-order roots (Table 3). As with root length, a dichotomous pattern emerged between absorptive roots and transport roots. Specifically, the length of the absorptive roots was positively correlated with SRL and branching ratio, and negatively correlated with RTD ($P < 0.05$). In contrast, the length of transport roots was positively correlated with stem density ($P < 0.05$). The total root biomass of the first five orders was also significantly positively correlated with the stem density (Table 3). Nonetheless, no significant correlations were observed between root biomass or length of both absorptive and transport roots, and soil nutrients among tree species (Table 3). Also, the ratios of the biomass or length between absorptive roots and transport roots were not correlated with any stand or soil characteristics among tree species (data not shown).

## Discussion

### Root biomass of absorptive and transport roots varies with tree species at the stand level

In this study, the total root biomass of absorptive roots and transport roots, and their ratios, varied largely with tree species, consistent with our first hypothesis. To the best of our knowledge, this is the first study using the root order method to quantify the root biomass and length per unit area of multiple tree species at the same site, the variations in ratios of absorptive to transport root biomass were the result of different tree species occurring under the similar stand age, the same stand structure, climate and site conditions, and originated not from conditions related to a large scale of observation.

**Table 3** Pearson's correlations between root biomass (g m$^{-2}$), root length (m m$^{-2}$), morphology of the first to fifth orders and the stand and soil characteristics among tree species. Values in bold type indicate significant correlations ($P < 0.05$)

| Root order | Root biomass and length | Root diameter | Specific root length | Root tissue density | Branching ratio | Stem density | Stand basal area | Total soil carbon | Total soil nitrogen | Total available soil nitrogen |
|---|---|---|---|---|---|---|---|---|---|---|
| 1 | Root biomass | −0.270 | 0.377 | −0.570 | 0.546 | 0.648 | 0.259 | 0.438 | 0.417 | 0.077 |
| | Root length | −0.580 | **0.803** | **−0.892** | **0.797** | 0.433 | −0.168 | 0.442 | 0.500 | 0.402 |
| 2 | Root biomass | −0.095 | −0.017 | 0.094 | / | **0.757** | 0.180 | 0.198 | 0.120 | 0.078 |
| | Root length | −0.546 | 0.515 | −0.458 | / | **0.812** | 0.005 | 0.444 | 0.419 | 0.491 |
| 3 | Root biomass | −0.027 | −0.188 | 0.273 | / | 0.704 | 0.136 | 0.077 | −0.010 | 0.047 |
| | Root length | −0.408 | 0.248 | 0.267 | / | **0.815** | 0.109 | 0.342 | 0.281 | 0.392 |
| 4 | Root biomass | 0.186 | −0.327 | 0.089 | / | 0.746 | −0.024 | 0.163 | 0.100 | 0.208 |
| | Root length | −0.246 | 0.235 | 0.287 | / | **0.877** | 0.073 | 0.523 | 0.483 | 0.521 |
| 5 | Root biomass | 0.166 | −0.354 | 0.150 | / | 0.725 | 0.105 | 0.172 | 0.092 | 0.128 |
| | Root length | −0.303 | 0.071 | 0.448 | / | **0.784** | 0.101 | 0.190 | 0.112 | 0.214 |
| 1–5 | Root biomass | / | / | / | / | **0.761** | 0.148 | 0.214 | 0.141 | 0.114 |
| | Root length | / | / | / | / | 0.666 | −0.091 | 0.487 | 0.508 | 0.479 |

The results reported here thus will greatly advance our understanding of the inter-specific variations in belowground C allocation and resource acquisition strategy in woody plants.

The biomass ratio of absorptive roots to transport roots at the stand level is seldom measured but important to estimate fine root turnover in forest ecosystems (McCormack et al. 2015), and might have great potential to improve terrestrial biosphere models (Warren et al. 2015). Our results provide an opportunity to explore how the ratio varies among tree species at a common site. Given the assumption that only first-order roots are absorptive roots, the biomass ratio of absorptive roots to transport roots varied from 1:5.56 (*Picea koraiensis*) to 1:1.12 (*F. mandshurica*) in our study. Previous studies (Table 1) showed that such ratios changed from 1:14 (Wang et al. 2013b) to1:2.3 (Wang et al. 2006). When the first three order roots are assumed to be absorptive (e.g., McCormack et al. 2015), the ratio would range from 1:1.07 (*B. platyphylla*) to1:0.59 (*L. gmelinii*) in our study. With the same assumption, the ratio reported in the literature (Table 1) changed from 1:2.8 (Wang et al. 2013b) to 1:0.03 (Liu et al. 2016). Accordingly, the magnitude of the variation in the biomass ratio in our study is quite large, although it is still less than those values recorded in previous studies (Table 1). Obviously, the large variation is not only related to tree species, but also to site and stand characteristics (e.g., Ostonen et al. 2011). Considering that the ratio varies significantly among tree species even at the local scale (e.g., this study), if we attempt to use an invariable value to represent the ratio and then estimate fine root turnover, a large uncertainty would remain. Thus, it is necessary to quantify the standing biomass of absorptive and transport roots at the species level, when we seek to improve the accuracy of simulation models for belowground C allocation and nutrient cycling in forest ecosystems.

The total root biomass of the first five orders ranged from 12 g m$^{-2}$ to 153 g m$^{-2}$ among tree species, showing an almost 13-fold variation (Fig. 1). In comparison, previous studies reported that, the total root biomass of the first five orders varied over 220-fold, ranging from 1.48 g m$^{-2}$ to 337 g m$^{-2}$ (Table 1). However, such large variability was not only caused by tree species, but also by stand characteristics and climatic conditions (Vogt et al. 1996; Noguchi et al. 2007; Finér et al. 2007, 2011; Wang et al. 2017b). In this study, except *B. platyphylla*, the stands of the other six tree species had same initial planting density, and all the seven species stands grew up under similar site conditions. Therefore, as mentioned above, the differences in root biomass observed in our study are mainly due to the characteristics of tree species.

Why do some tree species have greater fine root biomass (or length) than others? Some large-scale studies have suggested that fine root biomass of deciduous species was larger than that of evergreen species (Leuschner and Hertel 2003; Finér et al. 2007; Lehtonen et al. 2016), but others did not (e.g., Vogt et al. 1996). For example, based on the data of 95 boreal forest stands in Finland, Lehtonen et al. (2016) found that the stands dominated by birch had higher fine root biomass than stands of Norway spruce and Scots pine with the same stand basal area. In contrast, Vogt et al. (1996) showed that there was no significant difference in fine root biomass between deciduous and evergreen forests grown in the same soil order in a cold temperate zone. Our study appears to support the study by Vogt et al. (1996), as both maximum and minimum root biomass of the total five orders were observed in the evergreen coniferous species (Fig. 1). Thus, our study and others confirmed the complex interactions of tree species, life form, and climate condition on fine root biomass. Recently, several studies have shown that some key functional traits of fine root anatomy, morphology, and chemistry are closely related with the species phylogeny (Chen et al. 2013; Gu et al. 2014; Liu et al. 2019), whereas how species phylogeny shapes root biomass and length is not clear. Overall, the seven tree species in this study must have different capacities for resource absorption, belowground competition, and root litter production, which might profoundly impact aboveground productivity and C allocation at the stand level (Leuschner and Hertel 2003).

## Absorptive roots predominate in root length compared with transport roots

The first order roots are nonwoody, highly colonized by mycorrhizae, and considered as the main body of absorptive roots (Guo et al. 2008b; McCormack et al. 2015), their relative proportion to the fine root population can therefore be used to evaluate the strategy of C repartition to absorptive and transport roots. The current study showed that, across all tree species, root length per unit area of the first order roots always accounted for the largest proportion of the first five orders, ranging from 39% (*Pinus koraiensis*) to 77% (*F. mandshurica*). Thus, absorptive roots dominate in root length distribution of those seven tree species, supporting the second hypothesis.

It seems a common phenomenon that the proportion of first-order roots is the highest within a fine root branch on a length basis in woody plants. For example, Pregitzer et al. (2002) suggested that first-order roots accounted for ~50% of the total length of the first three order roots in nine North American tree species. Xu et al. (2015) showed that root length of the first-order roots accounted for 67% of the total of the first five orders in a hybrid poplar plantation (*Populus×euramericana* 'Neva'), which was close to the value of *F. mandshurica* in this study. In our study, more than 39% of the total length of the first five order roots was invested in the formation of absorptive roots across all seven species. This means that absorptive roots provide a disproportionally important share to root length compared with their biomass portion, reflecting their inherent function for resource absorption. The greater proportion of first-order roots found here might be related to the higher branching ratio of first-order to second-order roots, and the larger SRL of first-order roots. For one thing, the branching ratio was the lowest in *Pinus koraiensis* (3.1) and the highest in *F. mandshurica* (6.7), correspondingly, the minimum and maximum of the length proportion occurred in those two species, respectively. For another, root length of first-order per unit area was significantly correlated with the branching ratio and SRL among tree species (Table 3), indicating the strong impacts of root morphological and architectural traits. Taken together with the root biomass data, we conclude that the dominant role of absorptive roots in length of fine root system is not only caused by the repartition of root biomass among root orders, but also by the changes in SRL and root branching ratio.

## Factors affecting inter-specific variation of root biomass and length of absorptive and transport roots

We found that the biomass of absorptive and transport roots was generally not significantly influenced by stand and soil characteristics, as well as root morphological and architectural traits. In comparison, for root length, the controlling factors on absorptive roots (first-order roots) were obviously different from those of transport roots (second- to fifth-order roots). Specifically, the length of the absorptive roots was significantly correlated with SRL, RTD, and branching ratio, whereas the length of transport roots was significantly correlated with the stem density, thus the third hypothesis was partly supported.

Our results suggested that, to enhance the absorption capacity, tree species with a higher absorptive root length per unit area tended to produce much thinner (smaller diameter), lighter (lower RTD) individual roots with higher uptake efficiency (greater SRL), and to develop more distal root branches (higher branching ratio). Further analysis by linear regression suggested that tree species that possessed more absorptive roots per unit area also have larger root length and biomass per tree (Fig. S4). Therefore, species with a large number of absorptive roots at the stand or tree level, tend to produce cheaper and slender individual roots; in contrast, species with less absorptive roots at the stand or tree level, tend to produce more expensive and thicker individual roots. Our findings reflect that there possibly exists a balance of belowground C investment to absorptive roots between the individual root level and the stand level (i.e., per unit area). Recently, a series of studies have suggested that thin- and thick-root species have different nutrient forage strategies, such as the former had greater growth rate of length or biomass in response to nutrient-rich patches (Eissenstat et al. 2015; Liu et al. 2015; Cheng et al. 2016; Chen et al. 2018). Our study further demonstrated that those thin-root species generally have greater root length at the stand level, given similar stand and site conditions. To our knowledge, this is the first report relating absorptive root length at the stand level to root morphology at the individual level among species; further studies with more tree species under diverse site conditions are needed.

Differing from absorptive roots, the length and biomass of transport roots were generally correlated with stem density, and the former was significant (Table 3). This means that with more trees growing in each stand (species), there is more transport root length and biomass. There are two possible reasons. First, at the present stage, transport roots might not have fully occupied the soils. There is space for those transport roots to extend when the number of trees per unit area increases. Second, the branching ratio from the fifth to the second order might be stable and similar among tree species, although they were not measured here. Wang et al. (2006) reported that the branching ratios from the second to the fifth orders were all approximately three in broadleaved *F. mandshurica* and coniferous *L. gmelinii*, two species that were also studied here. Thus, stable correlations between root length and stem density generally occurred from second-order to fifth-order roots. In addition, we also noted that there was a significantly positive correlation between the total root biomass of the first five orders and stem density among tree species, confirmed by another study (Miyamoto et al. 2016).

Finally, several important stand and soil characteristics, such as stand basal area and soil N availability in this study, did not influence root length and biomass calculated either on root order basis or as totals of all the roots. Some studies have shown that the correlations between stand basal area and fine root biomass or length were positive (Finér et al. 2011; Lehtonen et al. 2016) or negative (Finér et al. 2007), but no significant correlation was found in our study, in accord with another study (Vanninen and Mäkelä 1999). The weak relationship might be because of the narrow range of stand basal area (13–30 $m^2$ $ha^{-1}$) in this study. The lower values of stand basal area indicate that the growth of individual trees is not constrained by space, including the belowground parts. Thus, this result partly confirms the greater impacts of stem density on transport root biomass and length per unit area (see the discussion above). In addition, differing from our results, some studies have shown that fine root biomass was negatively correlated with soil total N in boreal forests (Yuan and Chen 2010) and with total inorganic N in tropical heath forest (Miyamoto et al. 2016). The weak relationships found here likely results from the lower variability (<2 fold) of soil N availability, reflecting the uniform site conditions at the local scale. Overall, the types of forests examined (e.g., multiple tree species (this study) vs. a single species (Finér et al. 2007)), the spatial scale of the study (e.g., local scale (this study) vs. regional scale (Yuan and Chen 2010)), and the root sampling method (e.g., root order based (this study) vs. root diameter based (Finér et al. 2011)) could mask or alter the relationships between root biomass or length and climatic conditions, stand structure and soil characteristics (Miyamoto et al. 2016).

## Conclusions

Our results, through investigation of seven tree species (stands) grown at a common site, showed that the biomass and length per unit area of the typical absorptive roots (first-order roots) and transport roots (second- to fifth-order roots) varied largely among tree species, and so did the biomass and length ratios of absorptive roots to transport roots. The first order roots always accounted for the highest proportion of the length in the first five orders across tree species, reflecting the inherent function of tree fine roots for resource absorption. The species with higher absorptive root biomass and length at the stand or tree level, tends to produce cheaper and slender individual roots; in contrast, those species with less absorptive roots are likely to produce more expensive and thicker individual roots. Such results indicate the balance of belowground C investment to absorptive roots occurred between the individual root level and the stand level. In comparison, the biomass and length of transport roots were mainly influenced by stem density. It seems that there are different growth strategies of absorptive roots and transport roots in woody plants. Although limited by the number of tree species examined, our findings should shed light on the understanding of belowground resource uptake, C allocation, and inter-specific competition in temperate forests.

**Acknowledgements** We thank Lijuan Xiao, Zhendong Ma for assistance on field work. We also thank Catherine Dandie, PhD, for editing the English text of an earlier draft of this manuscript. We especially appreciate two anonymous reviewers and the editor for comments that improved this article. This research was jointly supported by the Fundamental Research Funds for the Central Universities (2572018BA11), National Natural Science Foundation of China (31870608 and 31100470), and the Natural Science Foundation of Heilongjiang Province (No. C2016004).

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