Differences in fine root traits between early and late-successional tree species in a Chinese subtropical forest

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The aim of this study was to compare fine root (≤2 mm diameter) traits (i.e. biomass distribution and architecture) of three tree species (Alniphyllum fortunei, Liquidambar formosana and Cyclobalanopsis glauca) growing in a mixed-species stand in a subtropical forest. Fine root samples were collected using soil cores. The collected samples were scanned with the Win-RHIZO system to analyse architectural parameters and were then oven-dried to determine dry mass. Fine roots of the three species were mainly distributed in the top 15 cm of soil and decreased with soil depth across all horizontal distances. C. glauca had the highest fine root biomass at 15–30 cm depth at 1.0 m from the tree trunk. The specific fine root area (SRA) and the length (SRL) were the highest for C. glauca, followed by L. formosana and A. fortunei. These species use different soil exploitation strategies. The early-successional species (A. fortunei and L. formosana) increase their fine root biomass and length through high carbon investment, whereas late-successional species (C. glauca) increase nutrient uptake efficiency via changes in fine root morphology and higher SRA and SRL values. In secondary broadleaf forest management and mixed plantation establishment, root trait differences among tree species and their effects on belowground competition and species coexistence should be considered.

Introduction

The relationship between biodiversity and ecosystem functions has attracted immense interest in ecological and environmental studies over the last two decades (Loreau et al., 2001; Scherer-Lorenzen et al., 2005). Having multiple tree species growing together in a forest is generally believed to increase overall biodiversity and consequently enhance ecosystem function (Loreau et al., 2001; Leuschner et al., 2009). However, tree species composition, their niche differentiation (competition or facilitation) and resource (nutrient, water and light) availability affect interactions among tree species and ecosystem functions in forests. For example, combining high productivity species and complementary species are the main reasons for higher productivity in polycultural forests than monocultures (Loreau et al., 2001; Brassard et al., 2011). Fine roots (≤2 mm diameter) play important roles in nutrient and water acquisition from soil to support their growth and survival (Pregitzer et al., 2002; de Kroon, 2007) and contribute a great deal to forest ecosystem carbon and nutrient cycling. As is the case for aboveground competition for light, the spatial patterning of belowground root interactions in forest communities profoundly affects tree growth, species coexistence and forest community dynamics (de Kroon, 2007).

Fine root biomass and its spatial distribution (Schmid, 2002), morphology and architecture (Bauhus and Messier, 1999) and physiology (Comas and Eissenstat, 2009) are the key determinants of soil exploitation strategies of a tree species. In terms of fine root traits, recognizing that there are two strategies of soil exploitation provides insights into the mechanistic basis behind interspecific belowground interactions. One strategy is to expand the soil space accessed and filled by fine roots as they forage for soil nutrients and water resources (Brassard et al., 2011). This strategy is reflected in the vertical and horizontal fine root biomass distributions (Li et al., 2006). The second strategy is to improve the exploitation efficiency by deploying the fine roots in a root branch system. This strategy is reflected in the fine root morphology and architecture. The improvement in exploitation efficiency in the second strategy is achieved through enlarging the surface area of fine roots with the same carbon investment (Bauhus and Messier, 1999) and developing mycorrhizal associations (Sohn, 1981) to capture more soil water and nutrients. Several variables have been used to describe the fine root morphology and architecture, including the specific fine root area (SRA), specific root length (SRL) and branching patterns. Since the root morphology and architecture reflect the efficiency of root structural carbon investment in the root area to maximize nutrient and water uptake (Persson et al., 1995; Persson and Ahlström, 2002), high SRA and SRL values imply the large surface area per unit of root biomass allowing for more rapid nutrient uptake per unit root mass (Eissenstat et al., 2000).
Tree species with contrasting fine root traits can lead to belowground niche segregation and facilitate interspecific species coexistence (Rewald and Leuschner, 2009). To compete for soil resources with other species and to accommodate different environmental conditions, tree species may adjust considerably the way they invest carbon in fine root systems (Lambers, 1987; Bauhus and Messier, 1999; Fujii and Kasuya, 2008). This adjustment in fine root traits (Nielsen et al., 1994) results in belowground competition or niche separation. Belowground niche separation occurs when different tree species change the vertical distribution patterns of fine roots at the soil profile to reduce belowground competition (Casper and Jackson, 1997) and to promote coexistence. For example, Schmid and Kazda (2002) found that a higher fine root biomass in mixed stands was associated with a vertical fine root segregation of the tree species. Bolte and Villanueva (2006) indicated that beech fine roots shifted into deeper soil layers in a beech–spruce stand. However, belowground niche segregation in response to increasing tree species richness did not occur in four temperate broad-leaved forests (Meinen et al., 2009a, b). The horizontal extent of a plant root system also determines the dimensions of belowground interactions with neighboring plants (Casper and Jackson, 1997). A strong horizontal overlap in 75 per cent of the soil samples has been found for fine roots in forests that contained more than two tree species (Rewald and Leuschner, 2009). Hence, both vertical and horizontal distributions of fine root density are related to belowground niche segregation in mature forest stands. Modification of the morphology and architecture to improve soil exploitation efficiency is another response. Studies have shown that the fine root morphology can be highly plastic in response to different nutrient availabilities (Löhmus et al., 1989; Ostonen et al., 2007). Increasing soil exploitation efficiency (via higher SRA and SRL) can occur under intense competition (Persson and Ahlström, 2002; Fujii and Kasuya, 2008). However, Lei et al. (2012) found that the fine root morphology of a specific tree species did not significantly change with tree species richness of neighbours and nutrient enrichment.

The subtropical area of southern China is ~2.5 million km$^2$ and ranges from 20 to 34° latitude. With the characteristics of a monsoon climate, this area contains extensive and diverse forests. However, the climax subtropical evergreen broadleaved forests have largely been destroyed or replaced by tree plantations (Qi, 1990). Secondary broadleaved forests are, therefore, precious remnants for biodiversity maintenance and ecological function. These secondary forests contain diverse tree species that have grown and competed with each other during forest stand development. Knowledge of how they coexist, and in particular, the belowground interactions, is very limited. In this study, we used the fine root distribution and architecture to investigate the differences in soil exploitation strategies of two deciduous tree species (early-successional species) and one evergreen broadleaved tree species (late-successional species) in a secondary broadleaved forest. We hypothesized that: (1) the fine root distribution varies among the three tree species; (2) the three tree species exhibit different soil exploitation strategies for coexistence through changes in the fine root architecture.

### Materials and methods

#### Site description and target tree selection

This study was conducted in the Huitong Yingzuije Natural Reserve (26°50′N, 109°54′E) in the southwest of Hunan Province, China. The site belongs to the central subtropical region with a humid mid-subtropical monsoon climate. The annual mean temperature ranges from 15 to 17°C, with an average of 4.3°C in the coolest month (January) and 29.4°C in the warmest month (July). The mean annual precipitation ranges from 1270 to 1650 mm, mostly occurring between April and August.

The topography is characterized by low hills with altitude ranging from 330 to 370 m above the sea level. The soil type is mountainous yellow soil derived from metamorphic slate and shale parent rocks, classified as Alliti-Udic Ferralsols corresponding to Acrisol in the World Reference Base for Soil Resources (Institute of Soil Science, Chinese Academy of Science, 2001). The pH value of the soil samples at 0–10 cm depth, determined by 1:5 soil distillation in H$_2$O, was 4.3. The bulk density was 1.53 g cm$^{-3}$. Concentrations of soil organic carbon, total N, P and K were 31.38 g kg$^{-1}$, 2.20 g kg$^{-1}$, 0.79 g kg$^{-1}$ and 3.43 g kg$^{-1}$, respectively. The soil texture comprised of 9.17 per cent sand, 46.75 per cent silt and 44.08 per cent clay.

In the forest in this study is a secondary subtropical forest that has developed since the late 1950s on an abandoned clearcut formerly occupied by a Cunninghamia lanceolata plantation. In order to investigate the floristic composition and spatial pattern of the secondary forest, a 0.96 ha plot was defined in November, 2006. All trees ≥4 cm in diameter at breast height (dbh) within the plot were mapped and species, dbh, height and canopy width was recorded. The dominant canopy tree species in the forest consisted of three deciduous broadleaves (Alniphyllum fortunei, Choerophydon axillaris and Liquidambar formosana), an evergreen broadleaf (Cyclobalanopsis glauca) and one conifer (Pinus massoniana) species. The forest was at a mid-successional stage shifting from early-successional deciduous to late-successional evergreen forest. The high stand density and fully closed overstorey canopy indicated that interactions between tree species were intense. A detailed description of the forest is provided by Xiang et al. (2013).

Three dominant tree species, i.e. two deciduous (A. fortunei and L. formosana) and an evergreen species (C. glauca), were chosen to investigate the exploitation strategies of fine roots. We selected sample trees for each tree species from within the 0.96 ha plot based on the following four criteria: (1) tree size (diameter at breast height, dbh) range of each species, (2) no bifurcated stems originated on the same base, (3) few neighbour trees growing within the maximum area for fine root sampling and (4) exclusion of very steep slopes and rock outcrop sites. Four sample trees for each of A. fortunei and L. formosana and three sample trees for C. glauca were identified in the field. A 6 m radius plot was centred on each sample (‘target’) tree. The characteristics of the sample trees are presented in Table 1. We used the dbh and location of all trees within the plot to calculate the competition index (CI) according to the formula suggested by von Oheimb et al. (2011):

$$CI = \sum_{j=1}^{n} \frac{(dbh_i/dbh_j)^2}{\text{dist}_{ij} + 1},$$

where $n$ is the total number of neighbour trees within the 6 m radius of the target tree, dbh, and dbh$_j$ are the diameters at breast (cm) of a target tree (i) and its neighbour trees (j), dist$_{ij}$ is the horizontal distance (m) between the target tree (i) and the neighbour tree (j).
Species Tree selected for fine root (<2 mm diameter) measurement

<table>
<thead>
<tr>
<th>Species</th>
<th>Tree no.</th>
<th>dbh (cm)</th>
<th>H (m)</th>
<th>H_L (m)</th>
<th>H/DBH (m m⁻¹)</th>
<th>C_W (m)</th>
<th>Cl</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. fortunei</td>
<td>866</td>
<td>10.5</td>
<td>17</td>
<td>8.5</td>
<td>161.9</td>
<td>3.8</td>
<td>22.67</td>
</tr>
<tr>
<td>(Hemsl.)</td>
<td>760</td>
<td>14.0</td>
<td>12</td>
<td>6.8</td>
<td>85.7</td>
<td>3.8</td>
<td>21.11</td>
</tr>
<tr>
<td></td>
<td>911</td>
<td>18.5</td>
<td>23</td>
<td>7.1</td>
<td>124.3</td>
<td>11.8</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>970</td>
<td>22.1</td>
<td>18</td>
<td>16.0</td>
<td>81.4</td>
<td>7.2</td>
<td>0.95</td>
</tr>
<tr>
<td>L. formosana</td>
<td>278</td>
<td>10.8</td>
<td>9</td>
<td>4.6</td>
<td>83.3</td>
<td>2.9</td>
<td>7.45</td>
</tr>
<tr>
<td>Chang</td>
<td>315</td>
<td>17.2</td>
<td>16</td>
<td>8.0</td>
<td>93.0</td>
<td>4.2</td>
<td>4.69</td>
</tr>
<tr>
<td></td>
<td>885</td>
<td>33.1</td>
<td>25</td>
<td>14.0</td>
<td>75.5</td>
<td>13.2</td>
<td>0.11</td>
</tr>
<tr>
<td></td>
<td>891</td>
<td>33.9</td>
<td>22</td>
<td>11.0</td>
<td>64.9</td>
<td>15.3</td>
<td>0.23</td>
</tr>
<tr>
<td>C. glauca</td>
<td>883</td>
<td>8.9</td>
<td>8</td>
<td>1.8</td>
<td>89.9</td>
<td>7.0</td>
<td>7.71</td>
</tr>
<tr>
<td>(Thunb.)</td>
<td>968</td>
<td>10.5</td>
<td>8.7</td>
<td>3.7</td>
<td>82.9</td>
<td>4.3</td>
<td>4.27</td>
</tr>
<tr>
<td></td>
<td>960</td>
<td>31.8</td>
<td>20</td>
<td>5.1</td>
<td>62.5</td>
<td>11.4</td>
<td>0.45</td>
</tr>
</tbody>
</table>

dbh: diameter at breast height; H: total tree height, H_L: height under the lowest live branch; C_W: tree canopy width. Cl: competition index calculated by the formula suggested by (von Oheimb et al., 2011).

Sampling and sorting of fine roots
In May and August 2008, fine roots (<2 mm diameter) were collected using a soil corer (7.3 cm inside diameter and 15 cm length) driven by a motorized drill. Since trees grew at random distances from each other with overlapping root systems, soil cores were taken at 0.5 m intervals from the stem of each target tree in four radial directions. Each target tree thus had 12 coring locations (at 0.5, 1.0 and 1.5 m distance from the target tree stem in north, south, east and west directions; see Figure 1). At each location, the litter and humus layer of the forest floor remained and soil cores were separately taken from 0–15 (including the organic forest floor layer), 15–30 and 30–45 cm soil depth. Thus, there were 36 soil core samples per target tree. The soil cores were placed in plastic bags and labeled, and then transported to a laboratory to be cold stored until washing. The soil in this study site is clay (≏0.3–0.4 mm diameter) measurement from the target tree stem against the CI. The low correlation characteristics. Fine roots of L. formosana are yellow-red with wrinkled bark and few nodules, while A. fortunei have black, smooth bark fine roots without nodules. Fine roots of C. glauca are brown and show obvious wrinkled bark with a lot of nodules.

Determination of fine root attributes
Fine root attributes were assessed using the digital image analysis system Win-Rhizo 2005C (Regent Instruments Inc., Quebec, Canada). Fine root samples were placed in a water-filled transparent tray on a scanner to facilitate root spreading. The system scanned all fine roots and root architectural parameters including the surface area, length, number of forks and tips were recorded. After scanning, all fine root samples were oven-dried for 48 h at 75 °C and then weighed. Biomass, surface area, length, number of forks and tips of fine roots were summed for each soil core. While the fine root biomass density was calculated on a soil volume basis (e.g. kg m⁻³), other traits were calculated on a ground surface area (cm²) basis. The SRA and SRL reflect the surface and length per carbon investment unit for a given fine root and are the important indicators for soil exploitation strategies (Bauhus and Messier, 1999). Their values were determined by dividing the fine root surface area, and the fine root length, respectively, by the dry weight of the corresponding fine root biomass (Bolte and Villanueva, 2006).

Data analysis
In order to reduce the effects of the target tree size on fine root traits, the values of fine root biomass, surface area and length were adjusted by dividing with the stem basal area of the target tree according to the method reported by Bolte and Villanueva (2006). This adjustment did not affect the results of the comparison between tree species, so we used the original data for the statistical analysis. The mean value and standard deviation of the fine root biomass, length, number of forks, number of tips, SRA and SRL were calculated for each soil depth at the different distances from the target tree stem. To analyse the relationships between aboveground abundances and belowground root traits, least squares regressions were conducted for the fine root biomass density and SRA within 45 cm soil depth at three distances from the target tree stem against the CI. The low correlation coefficients (r) (for fine root biomass r² = 0.19–0.31, P = 0.07–0.21; for
Results

Fine root biomass and morphology

Overall differences among *A. fortunei*, *L. formosana* and *C. glauca* were found in the fine root biomass density and fine root architecture traits (Table 2). The fine root biomass density was similar for *A. fortunei* and *L. formosana*, while the fine root biomass density for *A. fortunei* and *L. formosana* was 2.8 times and 3.2 times higher than for *C. glauca*, respectively. For the fine root architecture traits, *A. fortunei* and *L. formosana* had a similar surface area and length, and these values were approximately three times higher than for *C. glauca* (Table 2). In contrast, other fine root architecture traits (SRA, SRL, average diameter, tips and forks) were similar for all the three species, although the Kruskal–Wallis *H* test indicated that tree species had marginally significant effects on the average diameter, tips and forks (Table 3).

Fine root biomass and length distribution

The fine root biomass density and length significantly differed with depth in the soil profile, but did not differ significantly with the horizontal distance from the stem (Table 3, Figure 2). The vertical distribution of the fine root biomass density and length pooled for all of the horizontal gradient samples for each depth interval within each species, decreased with increasing soil depth (Figure 2). The maximum fine root biomass density and length were observed in the 0–15 cm soil depth interval for each horizontal distance from the stem of all species, whereas *C. glauca* fine root biomass values at 1.0 m horizontal distance was highest in the 15–30 cm soil layer (Figure 2). The fine root biomass density and length along a horizontal gradient had different distribution patterns among species and soil depth intervals. Generally, fine root biomass density and length values for all three species were higher towards the stem (Figure 2).

Fine root architecture

The SRA and SRL of fine roots were significantly affected by the soil depth and horizontal distance from the stem, but not by species (Table 3, Figure 3). Highest values for SRA and SRL of fine roots occurred at the 15–30 cm soil depth for *A. fortunei* and *C. glauca*, followed by 0–15 cm and 30–45 cm soil depth. However, the SRA and SRL of *L. formosana* decreased with increasing soil depth (Figure 3). Along the horizontal distance from the stem, the SRA and SRL of *A. fortunei* increased with increasing distance from the stem, whereas the SRA and SRL of *L. formosana* showed the opposite distribution pattern. For *C. glauca*, fine roots’ SRA and SRL for each soil layer were highest at 1.0 m from the stem (Figure 3).

Tip and fork densities differed significantly among species, soil depth and horizontal distance from the stem (Table 3, Figure 4). With increasing soil depth, the tip and fork density at each horizontal distance within each species generally decreased, while the vertical distribution patterns of the tip density for *C. glauca* at 1.0 m from the stem showed the opposite distribution pattern. In addition, the maximum tip density for *A. fortunei* at 1.5 m from the stem occurred in the 15–30 cm soil layer, whereas the maximum tip density for *L. formosana* at both 0.5 and 1.5 m distances from stem was observed in the 15–30 cm soil layer. Along the horizontal gradient, the tip and fork densities of the three species showed different distribution patterns. The fine roots of *A. fortunei* and *L. formosana* had higher tip and fork densities near the stem, while the highest total biomass was observed in the 0–15 cm soil depth interval for each horizontal distance from the stem of all species, whereas *C. glauca* fine root biomass values at 1.0 m horizontal distance was highest in the 15–30 cm soil layer (Figure 2). The fine root biomass density and length along a horizontal gradient had different distribution patterns among species and soil depth intervals. Generally, fine root biomass density and length values for all three species were higher towards the stem (Figure 2).

Table 2  Fine root (≤2 mm diameter) biomass density and architecture traits of *A. fortunei*, *L. formosana* and *C. glauca* trees in a secondary subtropical broadleaved forest

<table>
<thead>
<tr>
<th>Parameter</th>
<th>A. fortunei (Hemsl.)</th>
<th>L. formosana (Chang)</th>
<th>C. glauca (Thunb.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Biomass (g m⁻³)</td>
<td>412.20 (52.33)</td>
<td>463.07 (72.60)</td>
<td>145.67 (19.87)</td>
</tr>
<tr>
<td>Surface area (cm² cm⁻²)</td>
<td>10.94 (1.35)</td>
<td>11.18 (1.63)</td>
<td>3.71 (0.46)</td>
</tr>
<tr>
<td>Length (cm cm⁻²)</td>
<td>0.104 (0.015)</td>
<td>0.109 (0.01)</td>
<td>0.031 (0.006)</td>
</tr>
<tr>
<td>SRA (cm² g⁻¹)</td>
<td>90.03 (13.58)</td>
<td>99.27 (20.67)</td>
<td>116.06 (27.76)</td>
</tr>
<tr>
<td>SRL (m g⁻¹)</td>
<td>5.73 (1.11)</td>
<td>7.22 (2.05)</td>
<td>7.99 (2.09)</td>
</tr>
<tr>
<td>Average diameter (mm)</td>
<td>0.61 (0.02)</td>
<td>0.61 (0.03)</td>
<td>0.56 (0.02)</td>
</tr>
<tr>
<td>Tips (number cm⁻³)</td>
<td>1.90 (0.12)</td>
<td>1.65 (0.12)</td>
<td>1.32 (0.15)</td>
</tr>
<tr>
<td>Forks (number cm⁻³)</td>
<td>1.70 (0.13)</td>
<td>1.40 (0.12)</td>
<td>0.89 (0.11)</td>
</tr>
</tbody>
</table>

Mean values and standard errors (in parentheses) of total cores with each species are displayed, *n* = 144 samples for *A. fortunei* and *L. formosana*, *n* = 108 samples for *C. glauca*.
Discussion

Fine root biomass and distribution

Analysis of the depth distribution patterns of the fine root biomass density revealed that there was no clear vertical separation of the fine root systems of the three species within the top 45 cm of the soil profile. With the exception of \textit{C. glauca} fine roots at 1.0 m from the stem, all species showed a strong exponential decrease in fine root biomass density with increasing soil depth. The majority of fine roots were distributed on the top 15 cm of the soil (72.4 per cent of total fine root biomass for \textit{A. fortunei}, 73.3 per cent of total fine root biomass for \textit{L. formosana} and 60.0 per cent of total fine root biomass for \textit{C. glauca}). Based on these results, there is no pronounced segregation of the fine root systems of the three coexisting tree species in this stand. Fine roots are often highly concentrated in the upper mineral soil layer (e.g. Finér et al., 1997; Steele et al., 1997) with the purpose of maximizing their potential for resource capture, as nutrient-enriched material is mainly concentrated near the surface and temperature decreases rapidly at increasing soil depth (e.g. Steele et al., 1997; Bennett et al., 2002).

Avoidance of belowground competition could be one reason for fine root system segregation in mixed forests. However, the similar fine root vertical distributions of \textit{A. fortunei}, \textit{L. formosana} and \textit{C. glauca} in our study indicate an overlap, and presumably competition, in resource use by these species.

The biomass density of fine root of \textit{A. fortunei}, \textit{L. formosana} and \textit{C. glauca} generally decreases in the horizontal direction with increasing distance from their respective stems. This may be a way for tree species to reduce competition among co-occurring species. However, other researchers have found that fine roots were distributed evenly within the soil profile in the horizontal direction (Puri et al., 1994), implying that fine roots forage extensively and suffer from intensely intraspecific and interspecific competition.

The high \textit{A. fortunei} and \textit{L. formosana} fine root biomass values indicate the ability of these tree species to form a dense fine root system, while the lower fine root biomass of \textit{C. glauca} indicates that \textit{C. glauca} had a lower ability to explore large soil volumes and developing mycorrhizal associations would help its root improve soil resource exploitation. These patterns may be related to the successional strategies of these species. As early-successional tree species, \textit{A. fortunei} and \textit{L. formosana} would be
expected to exploit the soil volume and resource rapidly and extensively after disturbance (Brian et al., 2009). As a late-successional tree species, *C. glauca* would be expected to share available nutrients and increase nutrient uptake efficiency in order to coexist successfully on a site with established pioneer species (Brian et al., 2009).

**Fine root architecture**

Fine root biomass values may be insufficient to explain the capacity of roots for water and nutrient uptake (e.g. Lehmann, 2003). In comparison with biomass, SRA and SRL data are more important in explaining the resource exploitation of trees, and providing additional information on fine root morphology and exploration. Our study revealed some marked differences in fine root SRA and SRL values among the three tree species. Based on the Optimality theory (Bloom et al., 1985), the fine root system may increase the exploitation efficiency via changes in cost/gain ratios for carbon and nutrients for soil exploitation and resource uptake to increase in absorbing root surface area and root length per unit biomass. In this respect, the thinner fine roots and higher SRA and SRL values of *C. glauca* in this study indicate a better ability to uptake and use soil resources, than for *A. fortunei* and *L. formosana*. To some extent, this greater exploitation efficiency may compensate for the apparent lower exploitation capacity. Late- and early-successional tree species have many different morphological characteristics (Finegan, 1984), and greater exploitation efficiency may be an element of *C. glauca*’s late-successional colonization strategy.

In our study, the fine roots of *A. fortunei* exhibited dichotomous branching, strong lateral roots, and high tip and fork densities; *L. formosana* showed a herringbone system, long lateral roots, and high tip and fork densities; whereas *C. glauca* showed short lateral roots, and low tip and fork densities. These different characteristics indicate different soil exploitation strategies. *A. fortunei* and *L. formosana* had higher tip and fork densities, and this dense highly branched fine root system may create many overlaps between soil depletion zones around individual root systems, thus decreasing the efficiency of the C invested in fine roots with respect to nutrient and water capture (Caldwell and Richards, 1986). The average diameter of the fine roots of *C. glauca* (0.56 mm) is slightly lower than those of *A. fortunei* and *L. formosana* (0.61 and 0.61 mm, respectively) in this study, indicating that the fine roots of *C. glauca* are more involved in nutrient absorption. Previous studies have shown that roots of smaller diameter absorb more nutrients as they contain greater nutrient concentrations (Fahey et al., 1988; Burke and Raynal, 1994), although smaller-diameter roots have shorter lifespans than larger-diameter roots.
roots (Coleman et al., 2004; Kern et al., 2004; Baddeley and Waston, 2005) and are more metabolically active (Pregitzer et al., 1998; McDowell et al., 2001).

**Implications for forest management**

Recently, China has implemented ecological rehabilitation policies and promoted sustainable forest management (Zhou, 2004). Secondary broadleaved forests and mixture plantations have become the focus in subtropical areas to meet multi-purpose needs (including biodiversity conservation, soil and water protection and carbon sequestration). Management of the complex structure forest stands requires information on interactions between tree species (von Oheimb et al., 2011). Fine root traits reflect belowground interactions and are the important factor in determining appropriate silvicultural practices. For example, thinning and selection harvest are the common operations applied to regulate tree growth and facilitate regeneration in heterogeneous structure forests (von Oheimb et al., 2011). In addition to aboveground competition, the operations should consider differences in fine traits between different tree species to create complementary resource use and to facilitate coexistence. For tree species selection and space configuration, understanding belowground fine root competition is also important for plantation establishment (Lei et al., 2012).

Overall, the soil exploitation strategies vary for the three species selected in our study, with coexistence of these species promoted by differences in exploitation capacity and exploitation efficiency rather than belowground niche differentiation. It appears that the early-successional tree species used a larger belowground space than the late-successional species. Thinning and selected harvest would be practical management options to reduce belowground competition. However, these conclusions must be considered with caution and the soil exploitation strategies of these species should be examined on a greater range of soil types, depths and stand ages.

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**Conflict of interest statement**

None declared.
References


