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Fine root architecture, morphology, and biomass response to cutting in a Chinese cork oak (*Quercus variabilis* Blume) forest

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Abstract: This study aims to detect the variety of fine root growth with branch orders in response to forest cutting. The branching ratio (R_b) , root morphological indices, and biomass of up to 3 branch orders of fine roots were investigated from 2 soil depths (0 cm to 10 cm and 10 cm to 20 cm) in Chinese cork oak (*Quercus variabilis* Blume) plots 1 and 3 years after forest cutting, compared with those of intact trees as the control. The number of fine roots was lower in the managed plots than in the control, particularly in the first-order roots. After 1 year of cutting, the proportion of the first-order roots decreased significantly, whereas the proportion of the second-order and third-order roots increased. R_b decreased significantly after forest management in the 0–10 cm soil depth of plots after 1 year of cutting. The fine roots in the plots after cutting exhibited less root length density, lower specific root length, less surface area, and higher tissue density compared with those in control plots. The mean root diameter showed no significant change. The average biomass of the first 3 orders of roots in the plots 1 and 3 years after cutting was 72% and 83% of that of the control plot, respectively. The reduction of fine root growth was influenced mainly by the lack of photosynthesis in the managed forest.

Key words: Root branch orders, specific root length, root biomass, root length density, root tissue density

1. Introduction

Fine roots have gained much attention because of their function in water and nutrient uptake (Hendrick and Pregitzer, 1993; Bassirirad, 2000). Various forest stand conditions, i.e. soil properties, air temperature, the amount of precipitation, geographical location, and elevation, are shown to affect fine root growth (Pregitzer et al., 2000; Borja et al., 2008; Helmisaari et al., 2009). However, little information exists on the growth pattern of fine roots in response to stem cutting in coppice forests (Montagnoli et al., 2012; Ma et al., 2013)

Forest management acts on the stability and activity of fine roots (Ronnberg, 2000; Leuschner et al., 2006; Noguchi et al., 2007). Alteration in carbohydrates and respiration of fine roots after canopy pruning has been reported in previous studies (Eissenstat and Duncan, 1992; Comas et al., 2000; Terzaghi et al., 2013). In oak forests, fine root biomass was reduced by clear cutting or thinning and then recovered after approximately 1 year or 3 years (Schilling et al., 1999; López et al., 2003). These studies considered the effect of above-structure removal on the metabolic activity and biomass of fine roots. consist of individual roots with heterogeneous anatomical, physiological, and morphological characteristics in different branch orders (Wang et al., 2006; Hishi, 2007; Guo et al., 2008). A large number of apical roots with high absorption ability have greater surface area with higher specific root length and lower carbon storage than basal roots (Pregitzer et al., 1997; Wells et al., 2002; Guo et al., 2004). A hypothesis states that fine roots in different branch orders respond in various ways to above-structure removal. To understand the heterogeneity of fine roots, the architecture and morphology of fine roots in forests after stem cutting should be studied.

Recently, fine root architecture has been suggested to

The Chinese cork oak (*Quercus variabilis* Blume) is an important deciduous broadleaf tree in East Asia (24°N to 42°N, 96°E to 140°E) (Zhang and Lu, 2002; Zhou et al., 2010). More trees have been cut for the increasing market share for utilizable cork and timber, thereby affecting the root storage in Chinese cork oak forests. The root architecture, morphological indices, and biomass of first-to third-order roots from 3 treatments of Chinese cork oak forest stands (control plots without cutting and plots

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1 year and 3 years after clear cutting) at 2 soil depths (0 cm to 10 cm and 10 cm to 20 cm) were examined in this study. We focused on the root length density, diameter, specific root length, root surface area, and tissue density to evaluate the morphological traits and biomass of fine roots. Specifically, this study aims to achieve the following goals: 1) verify if the forest management affects variously the architecture, morphology, and biomass of fine roots with increasing orders; and 2) determine the main factor affecting growth of fine roots in the managed forest.

2. Materials and methods

2.1. Study site and plot establishment

This study was carried out in a 60-year-old Chinese cork oak forest in Foping National Reserve in the southern part of the Qinling Mountains (33°33'N to 33°46'N, 107°40'E to 107°55'E). This region belongs to the warm temperate zone, with an annual mean temperature of 14 °C and an annual precipitation of 750 mm during the entire research period. More than 50% of the annual rainfall occurs in July, August, and September. There is haplic luvisol soil (FAO classification) with depths of between 25 cm and 35 cm in the study plots. This region belongs to the central distribution area of the Chinese cork oak. Numerous shrubs are distributed in the area, including *Cephaltaxus sinensis* Li, *Cotinus coggygria* var. *cinerea* Engl., and *Grewia biloba* G.Don, as well as herbages including *Carex tristachya* Thunb. and *Ophiopogon japonicus* Ker Gawl..

One permanent square stand of Chinese cork oak was established in this region. The Chinese cork oak trees in the stand have regenerated since the 1950s without any management during the subsequent 60 years. This stand was divided equally into 3 plots with 3 treatments ($20 \text{ m} \times 60 \text{ m}$). One of the treatments included intact trees as the control plot (CP). The other 2 treatments were designed as cutting plots, in which Chinese cork oak trees were cut in December 2009 (1 year after cutting: C1) and in November 2007 (3 years after cutting: C3) for timber production, respectively. After cutting, fallen stems and leaves were removed from the plots. Each treatment plot was divided into 3 subplots as replications. The average diameter at breast height and average height of intact trees were measured, and the basal diameter and height of sprouts in the cutting subplots were recorded (Table 1). The crown radius was defined as the average horizontal distance from the trunk of a tree (or stump) to the edge of the crown (drip-line).

2.2. Analysis of soil properties

Six sites in each subplot were selected to detect the soil properties at a depth of 10 cm below the soil's surface in September 2007 and October 2010, including soil bulk density, soil pH, organic matter content, and total available N, P, and K (Institute of Soil Science, 1978) (Table 2). The monthly soil moisture was recorded with a Theta KIT TK3-BASIC meter (DELTA-T Inc., UK) with the soil temperature detected by HI8751 probe type thermometer (Hanna Inc., Italy) from January to December in 2010.

2.3. Root excavation

Root samples were collected in October 2010. Ten trees (or stumps) with the same basal diameter of stems (or stumps) were chosen along the 2 diagonal paths of each subplot. Soil blocks $(0.2 \text{ m} \times 0.2 \text{ m} \times 0.1 \text{ m})$ were excavated perpendicularly to the slope at 2 soil depths (0 cm to 10 cm and 10 cm to 20 cm) in 4 cross directions at a distance of 0.5 m from each selected tree (or stump) to avoid roots of neighbor trees or shrubs. Roots with soil were placed in a plastic bag, labeled, and then transported to the laboratory in a 4 °C icebox. A total of 80 samples from each subplot were used in both soil depths; 720 samples were collected in 9 subplots.

Roots were carefully collected from the soil and placed in water at 4 °C in the laboratory. Large root branches were carefully removed from the soil with forceps, and the remaining soil on roots was brushed away. Roots of herbs were separated out based on their light color, and live oak roots were easily distinguished by their dark red color, great elasticity, and more intensive cohesion of stele and cortex or periderm than roots of shrubs. All root

	Mean height (m)	Mean diameter (cm)	Basal area (m ² ha ⁻¹)	Crown radius (cm)	Canopy cover (%)	Number of sprouts per stump
СР	11.4 ± 1.2 a	11.3 ± 1.4 a	15.6 ± 2.7 a	320.5 ± 61.2 a	90 ± 3.6 a	_
C1	1.2 ± 0.3 c	1.5 ± 0.4 c	$0.3 \pm 0.1 \text{ c}$	76.1 ± 13.4 c	55 ± 3.2 c	11.9 ± 1.2 a
С3	$2.2\pm0.6~\text{b}$	$4.1\pm0.9~b$	$2.3\pm0.6~\text{b}$	187.6 ± 51.7 b	70 ± 2.8 b	9.6 ± 0.9 b

Table 1. Stand characteristics of study plots.

Mean height refers to the height of intact trees or sprouts in the stumps. Mean diameter refers to the diameter at breast height of intact trees or the basal diameter of sprouts. Basal area refers to the basal area per ha of stems in the control or sprouts in the cutting plots. — represents no observational value. Different letters represent significant differences among the 3 treatments (Duncan's test, P < 0.05).

segments of the Chinese cork oak were dissected following the procedure described by Pregitzer et al. (2002). The most distal root tips were labeled as first-order; roots with 2 first-order roots were classified as second-order roots, and so on. Small root segments remaining in the soil were collected by floating in 4 °C water and sieving (0.25 mm mesh). These roots were assigned to different branch orders by comparing their diameter and length with the mean diameter and length ±1 standard deviation of the identified roots (Guo et al., 2004). Only the first 3 orders of live roots were included in this analysis because of their higher physiological activity as compared to posterior orders (Pregitzer et al., 2002; Guo et al., 2008). The number of each order of roots was calculated, and it was divided by the sum of the first 3 orders of roots as the proportion of each order. The branching ratio (R_1) in each soil block at different treatments was calculated with the following formula:

$$R_b^{i-j} = \frac{N_i}{N_j},$$

where R_b^{ij} is the ratio between the number of fine roots in the branch order (N_i) and the number of its parent root (N_i) (Fitter et al., 1991; Wang et al., 2006).

2.4. Morphology measurement

Fine roots of each order were scanned in gray scale at 400 dpi (TWAIN PRO, Epson). The root length and surface area were determined by using WinRHIZO Pro 2007a (Regent Instruments, Canada), an image analysis system specifically designed for root measurement. After scanning, segments were dried at 80 °C for 24 h and then

weighed as the root biomass. The specific root length (m g⁻¹) was calculated by dividing the root length with the root biomass of each soil depth (Wang et al., 2006; Ostonen et al., 2007). Root tissue density (g cm⁻³) was calculated by dividing the root dry biomass with the root fresh volume (given by WinRHIZO). The root length density (m m⁻²), root surface area (m² m⁻²), and root biomass (g m⁻²) were expressed in relation to the soil block area (0.2 m × 0.2 m).

2.5. Data analysis

A total of 720 samples were pooled across treatments, soil depths, and root orders. The normal distribution of the data was tested by Shapiro–Wilk test. Within each root order, ANOVA was used to identify differences in root length density, diameter, surface area, specific root length, tissue density, and biomass among treatments within the same soil depth. Duncan's test ($\alpha = 0.05$) was performed for comparisons of mean values with SPSS 18.0. The same method was employed to test the differences in the root branching ratios, the number of different order roots, and the proportion of roots. Graphs were constructed using Origin software (OriginLab Corporation Pro v.7.5).

3. Results

3.1. Dynamics of soil properties

No significant difference was recorded for soil properties between 2007 and 2010 (Table 2). In the control plot, the available K, total available N, and organic matter of the 0–10 cm depth soil increased slightly from 2007 to 2010, whereas a decreasing trend was observed in C1 and C3. In 2010, the patterns of seasonal variations of soil temperature and moisture in the 10 cm soil depth were similar among the 3 treatment plots (Figure 1). The average soil temperature

Table 2. Soil properties in the 10 cm soil depth in the 3 treatment plots.

		СР	C1	C3
Soil pH	2007	7.51 ± 0.34 a	7.48 ± 0.27 a	7.55 ± 0.26 a
	2010	$7.80\pm0.21~aA$	$7.45\pm0.25~\mathrm{aA}$	$7.53\pm0.23~\mathrm{aA}$
Available potassium (K, mg g ⁻¹)	2007	186.95 ± 37.63 a	225.46 ± 48.43 a	237.34 ± 35.09 a
	2010	220.60 ± 47.43 aA	$217.40 \pm 40.60 \text{ aA}$	204.01 ± 44.01 aA
Total available nitrogen (N, mg g ⁻¹)	2007	70.56 ± 21.62 a	75.41 ± 20.18 a	98.05 ± 24.15 a
	2010	87.75 ± 29.35 aA	74.95 ± 28.77 aA	96.35 ± 19.05 aA
Available phosphorus (P, mg g ⁻¹)	2007	22.36 ± 2.74 a	23.51 ± 3.37 a	25.69 ± 5.31 a
	2010	23.15 ± 3.55 aA	$24.80\pm9.54~aA$	23.98 ± 6.52 aA
Soil organic matter (OM, %)	2007	11.08 ± 2.39 a	11.73 ± 1.85 a	12.41 ± 2.04 a
	2010	12.31 ± 2.15 aA	10.62 ± 2.45 aA	11.63 ± 2.92 aA
Soil bulk density (BD, g cm ⁻³)	2007	1.03 ± 0.19 a	0.92 ± 0.14 a	0.97 ± 0.08 a
	2010	0.99 ± 0.21 aA	$0.92 \pm 0.03 \text{ aA}$	0.95 ± 0.11 aA

Mean data of each treatment are denoted as mean \pm standard error. Capital letter 'A' means no significant difference between 2007 and 2010 (paired t-test, P > 0.05). Lowercase letter 'a' means no significant differences among the 3 treatments in the same year (Duncan's test, P > 0.05).



Figure 1. Monthly average soil temperature (line) and moisture (bar) among 3 treatment plots at 10 cm soil depth in 2010.

from April to October (the growing season) was 14.8 °C in CP, which was lower than that in C1 (16.3 °C) and C3 (15.5 °C) after cutting. The average soil moisture from April to October was 16.2% in CP, which was greater than that in C1 (13.4%) and C3 (14.2%).

3.2. Root architecture

The number of the first 3 orders of roots presented a decreasing trend after cutting, whereas the proportion of first-order roots declined with the increasing proportion of the second- and third-order roots (Table 3). In the 0–10 cm soil depth, the number of the first 3 orders of roots in C1 decreased significantly (P < 0.05) by 38.9%, 19.2%, and 14.1% compared with CP, whereas the parameters in C3 decreased by 13.6%, 11.3%, and 10.3%, respectively (Table 3). The proportion of the first-order roots in C1 decreased by 8.3% compared with the control, whereas the proportion of the second- and third-order roots increased by 22.3% and 30.6%, respectively. In the 10–20 cm soil depth, no significant difference (P > 0.05) was observed in the number and the proportion of second- and third-order roots among the 3 treatments.

The R_b between a daughter root and its parent root directly represents the change in root architecture (Table 3). In the 0–10 cm soil depth, the R_b between the first- and second-order roots decreased significantly by 24.3% in C1 compared with CP. In the 10–20 cm soil depth, R_b decreased in both C1 and C3 with no significance (P > 0.05).

3.3. Specific root length, root surface area, and tissue density

The specific root length and surface area of fine roots were reduced by the forest cutting (Figures 2a and 2b). The specific root length of the first-order roots in C1 decreased by 13.2% in the 0–10 cm soil depth and 30.7% in the 10–20 cm soil depth compared with the control, whereas it decreased by 11.8% and 18.3% in C3, respectively. The decline of specific root length after cutting was not significant (P > 0.05) in the second- and third-order roots in the 10–20 cm soil depth. Compared with the control, the surface area of the first-order roots decreased by 51.2% in C1 and 25.5% in C3 in the 0–10 cm soil depth, whereas the decrease was 52.2% and 32.1% in the 10–20 cm soil depth, respectively.

Soil depths	Treatments	First-order		Second-order		Third-order			
		Number (number m ⁻²)	Proportion (%)	Number (number m ⁻²)	Proportion (%)	Number (number m ⁻²)	Proportion (%)	R_b^{1-2}	R_{b}^{2-3}
10 cm									
	СР	13,162 ± 211 a	73.9 ± 1.9 a	3523 ± 217 a	19.7 ± 1.6 b	1119 ± 67 a	6.2 ± 0.5 b	3.7 ± 0.5 a	3.2 ± 0.6 a
	C1	$8050\pm164~c$	67.8 ± 1.7 b	2846 ± 202 b	24.1 ± 1.9 a	$961\pm44~\mathrm{b}$	8.1 ± 1.2 a	$2.8\pm0.2~b$	$2.9\pm0.6~\mathrm{a}$
	C3	11,375 ± 206 b	73.8 ± 3.1 a	3123 ± 226 ab	$20.2\pm1.7~\mathrm{b}$	1004 ± 46 ab	6.4 ± 1.4 ab	3.6 ± 0.2 a	3.1 ± 0.7 a
20 cm									
	СР	3571 ± 139 a	68.7 ± 1.2 a	1136 ± 166 a	21.8 ± 1.7 a	491 ± 53 a	$9.4\pm0.5~\mathrm{a}$	3.1 ± 0.2 a	$2.3\pm0.3~\mathrm{a}$
	C1	2158 ± 132 c	64.1 ± 2.1 b	833 ± 127 a	24.8 ± 2.3 a	374 ± 76 a	11.1 ± 1.9 a	2.6 ± 0.5 a	2.2 ± 0.4 a
	C3	2525 ± 161 b	65.8 ± 1.7 ab	890 ± 157 a	23.2 ± 1.8 a	422 ± 34 a	10.9 ± 0.5 a	2.8 ± 0.4 a	2.1 ± 0.2 a

Table 3. The number and the proportion of the first 3 orders of roots with the branching ratios (R_{k}) between 2 different orders.

Different letters represent significant differences among the 3 treatments (Duncan's test, P < 0.05). Mean data of each treatment are denoted as mean \pm standard error.



Figure 2. Specific root length, root surface area, and root tissue density of 3 orders of roots of Chinese cork oak under 3 treatments and 2 soil depths (0–10 and 10–20 cm). Error bars represent standard errors of the means. Different letters in the same root order represent significant differences among 3 treatments (Duncan's test, P < 0.05).

Root tissue density increased significantly after forest cutting in both soil depths (Figure 2c). Compared with CP, the root tissue density of first-order roots in the 0–10 cm soil depth increased by 40.1% in C1 and 23.2% in C3, whereas the increase was 9.9% and 1.2% in the 10–20 cm soil depth, respectively. An increasing trend was also observed in the second- and third-order roots.

3.4. Root length density, diameter, and biomass

Root length density was lower in C1 and C3 than in CP (Figure 3a). Compared with CP, the root length density of the first 3 orders of roots in C1 decreased by 46.3%, 58.2%, and 36.8% in the 0–10 cm soil depth, whereas the decrease in C3 was 22.4%, 41.7%, and 27.3%, respectively.

A reduction of root length density after forest clear cutting was also found in the 10–20 soil depth. A slight decline of mean root diameter was observed in C1 and C3 compared with CP, whereas the difference was not significant (Figure 3b).

The total biomass of the first 3 orders of roots in the 0-20 cm soil depth was 141.7 g m⁻² in CP, 102.9 g m⁻² in C1, and 118.2 g m⁻² in C3 (Figure 3c). In the 0–10 cm soil depth, the biomass of the first 3 orders of roots in C1 significantly decreased by 38.1%, 27.6%, and 19.7%, whereas the parameters in C3 were 11.9%, 19.3%, and 11.2%, respectively. The same pattern was observed in the 10–20 cm soil depth.



Figure 3. Root length density, mean diameter, and biomass of 3 orders roots of Chinese cork oak under 3 treatments and 2 soil depths (0–10 and 10–20 cm). Error bars represent standard errors of the means. Different letters in the same root order represent significant differences among the 3 treatments (Duncan's test, P < 0.05).

4. Discussion

The fine root system of trees could be affected by a series of change after forest management, i.e. shifting the soil thermal and moisture regimes, increasing or decreasing nutrient supply through added litter and microbial activities, and reducing photosynthesis supplied to the root system (Ma et al., 2013; Terzaghi et al., 2013). In this case, the K, N, and soil organic matter declined slightly after cutting because of the decrease in litterfall (Table 2). High soil temperature and low soil moisture were found in C1 and C3 after canopy opening (Figure 1). This finding is in agreement with an increase of 14.2% in soil temperature and a decrease of 18.3% in soil moisture in thinning forests of Pinus resinosa Aiton (Tian et al., 2010). However, the change of soil properties was not significant due to short-term forest management. Therefore, these soil factors affecting root growth in our study were negligible. The significant decline in the height and crown radius of the stump sprouts indicates that stump sprouts have lower photosynthetic ability compared with intact trees (Table 1). The photosynthetic ability of plants is the major factor influencing the growth of fine roots (Kosola et al., 2002; Guo et al., 2004).

The architecture of fine roots is composed of individual roots with sequence emergence and varying amounts, which reflect the root plasticity in response to environmental change (Fitter et al., 1991; Lynch, 1995). In this study, the number of the first 3 orders of roots declined after forest cutting (Table 3), indicating the death and decomposition of fine roots. It has been confirmed in previous studies that the trees did not maintain preexisting fine root systems after forest management (Spinelli et al., 2005; Borja et al., 2008). The first-order roots of large woody trees constitute approximately 75% of the total number of fine roots (Pregitzer et al., 2002). In our study, the proportion of the first-order roots decreased from 71.3% in CP to 65.9% in C1 and 69.8% in C3, whereas the proportion of the second- and third-order roots showed an increasing trend. A significant reduction of R_{h} between the first- and second-order roots was observed in the 0-10 cm soil depth of C1 (Table 3). These results suggest that the number of first-order roots had a sharper decline than that of second- and third-order roots. This is possibly explained by weak acquisition from the photosynthate source and low need for water uptake when the crown radius was reduced (Eissenstat and Yanai, 1997; Kosola et al., 2002; Pregitzer et al., 2002). Similar results were reported by Di Iorio et al. (2013), who pointed out that the number of small roots was significantly affected by forest practices. Borja et al. (2008) suggested that the finest fraction of fine roots is strongly dependent on the stand age of Norway spruce (Picea abies H.Karst.).

Specific root length and surface area are linked to the ability of water and nutrient uptake, and root tissue density is considered as a characteristic of root functional status. In plots after cutting, fine roots tend to have less surface area, lower specific root length, and higher tissue density compared with those in the control (Figure 2). Several studies have concluded that the traits of relatively low specific root length and high root tissue density indicate that fine roots adapt to resource-poor environments by reducing absorptive capacities (Eissenstat, 1992; Comas et al., 2000). Our study suggests that fine roots in the stump after above-structure removal possibly employ a strategy in which more carbon is invested in building a dense root system and less carbon is invested in absorption. Moreover, the root diameter tended to decline after forest cutting in C1 and C2. Roots might shrink in diameter because of cortical senescence (Liljeroth et al., 1996). The dynamic of root diameter with the ability of carbon assimilation capability has been reported in previous studies (Guo et al., 2004; Wang et al., 2006), whereas no change was marked in our case.

Root length density and biomass are key indices for root growth (Wang et al., 2006). Leuschner (2006) concluded that the fine root (<2 mm) biomass in heavily disturbed forests reached less than 60% that of undisturbed natural forests. Ahrens and Newton (2008) estimated that live root biomass with diameters ranging from 0.25 mm to 2.00 mm was 25% after trees were harvested in mature tanoak (Lithocarpus densiflorus Rehd.) forests. The same results were confirmed by our study. The average root length density and biomass of the first 3 orders of roots in C1 declined by 47% and 27% compared with the control. The root length density and biomass in C3 increased slightly to 71% and 83% of the control (Figure 3). These results reflect that fine roots were retrieved with sprout regeneration and acquired more photosynthesis from the leaves (Makkonen and Helmisaari, 1998). Eissenstat and Duncan (1992) confirmed that root length density in citrus recovers rapidly from partial canopy pruning with regrowth of leaves. Montagnoli et al. (2012) reported that root biomass increased by 24.8% and 76.4% after 4 and 14 years of forest conversion, respectively, compared with the coppice stand. The duration required for fine roots to recover depends on the severity of the above-structure damage.

This research focused on the fine root architecture, morphology, and biomass of Chinese cork oak trees that responded differently to forest cutting. The number of fine roots was hindered by forest cutting, and the sharp decline of the number of the first-order roots led to the alteration of the proportion of the first 3 orders of roots. The root length density, surface area, and biomass of fine roots decreased after forest cutting. Low specific root length and great root tissue density were observed in the managed plots, with no significant change in root diameter. Our study showed that forest management considerably affects fine root growth in Chinese cork oak forest through less photosynthesis. Parallel studies should be conducted on the relationship between root morphology and forest management in other woody species.

References

- Ahrens GR, Newton M (2008). Root dynamics in sprouting tanoak forests of southwestern Oregon. Can J Forest Res 38: 1855– 1866.
- Bassirirad H (2000). Kinetics of nutrient uptake by roots: responses to global change. New Phytol 147: 155–169.
- Borja I, De Wit HA, Steffenrem A, Majdi H (2008). Stand age and fine root biomass, distribution and morphology in a Norway spruce chronosequence in Southeast Norway. Tree Physiol 28: 773–784.
- Comas LH, Eissenstat DM, Lakso AN (2000). Assessing root death and root system dynamics in a study of grape canopy pruning. New Phytol 147: 171–178.
- Di Iorio A, Montagnoli A, Terzaghi M, Scippa GS, Chiatante D (2013). Effect of tree density on root distribution in *Fagus sylvatica* stands: a semi-automatic digitising device approach to trench wall method. Trees-Struct Funct 27: 1503–1513.
- Eissenstat DM, Duncan LW (1992). Root growth and carbohydrate responses in bearing citrus trees following partial canopy removal. Tree Physiol 10: 245–257.
- Eissenstat DM, Yanai RD (1997). The ecology of root lifespan. Adv Ecol Res 27: 1–60.
- Fitter AH, Stickland TR, Harvey ML, Wilson GW (1991). Architectural analysis of plant-root systems. 1. Architectural correlates of exploitation efficiency. New Phytol 118: 375–382.
- Guo DL, Mitchell RJ, Hendricks JJ (2004). Fine root branch orders respond differentially to carbon source-sink manipulations in a longleaf pine forest. Oecologia 140: 450–457.
- Guo DL, Xia MX, Wei X, Chang WJ, Liu Y, Wang ZQ (2008). Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. New Phytol 180: 673–683.
- Helmisaari HS, Ostonen I, Lohmus K, Derome J, Lindroos AJ, Merila P, Nojd P (2009). Ectomycorrhizal root tips in relation to site and stand characteristics in Norway spruce and Scots pine stands in boreal forests. Tree Physiol 29: 445–456.
- Hendrick RL, Pregitzer KS (1993). The dynamics of fine-root length, biomass, and nitrogen-content in 2 northern hardwood ecosystems. Can J Forest Res 23: 2507–2520.
- Hishi T (2007). Heterogeneity of individual roots within the fine root architecture: causal links between physiological and ecosystem functions. J Forest Res-JPN 12: 126–133.
- Institute of Soil Science (1978). The Analysis of Soil Physical and Chemical Properties. Shanghai, China: Shanghai Science and Technology Press.

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- Kosola KR, Dickmann DI, Parry D (2002). Carbohydrates in individual poplar fine roots: effects of root age and defoliation. Tree Physiol 22: 741–746.
- Leuschner C, Wiens M, Harteveld M, Hertel D, Tjitrosemito S (2006). Patterns of fine root mass and distribution along a disturbance gradient in a tropical montane forest, Central Sulawesi (Indonesia). Plant Soil 283: 163–174.
- Liljeroth E, Franzon-Almgren I, Gustafsson M (1996). Root colonization by *Bipolaris sorokiniana* in different cereals and relations to lesion development and natural root cortical cell death. J Phytopathol 144: 301–307.
- López BC, Sabate S, Gracia CA (2003). Thinning effects on carbon allocation to fine roots in a *Quercus ilex* forest. Tree Physiol 23: 1217–1224.
- Lynch J (1995). Root architecture and plant productivity. Plant Physiol 109: 7–13.
- Ma C, Zhang WH, Wu M, Xue YQ, Ma LW, Zhou JY (2013). Effect of aboveground intervention on fine root mass, production, and turnover rate in a Chinese cork oak (*Quercus variabilis* Blume) forest. Plant Soil, 368: 201–214.
- Makkonen K, Helmisaari HS (1998). Seasonal and yearly variations of fine-root biomass and necromass in a Scots pine (*Pinus sylvestris* L.) stand. Forest Ecol Manag 102: 283–290.
- Montagnoli A, Terzaghi M, Di Iorio A, Scippa GS, Chiatante D (2012). Fine-root seasonal pattern, production and turnover rate of European beech (*Fagus sylvatica* L.) stands in Italy Prealps: possible implications of coppice conversion to high forest. Plant Biosyst 146: 1012–1022.
- Noguchi K, Konopka B, Satomura T, Kaneko S, Takahashi M (2007). Biomass and production of fine roots in Japanese forests. J Forest Res-JPN 12: 83–95.
- Ostonen I, Puttsepp U, Biel C, Alberton O, Bakker MR, Lohmus K, Majdi H, Metcalfe D, Olsthoorn AFM, Pronk A et al. (2007). Specific root length as an indicator of environmental change. Plant Biosyst 141: 426–442.
- Pregitzer KS, DeForest JL, Burton AJ, Allen MF, Ruess RW, Hendrick RL (2002). Fine root architecture of nine North American trees. Ecol Monogr 72: 293–309.
- Pregitzer KS, King JA, Burton AJ, Brown SE (2000). Responses of tree fine roots to temperature. New Phytol 147: 105–115.
- Pregitzer KS, Kubiske ME, Yu CK, Hendrick RL (1997). Relationships among root branch order, carbon, and nitrogen in four temperate species. Oecologia 111: 302–308.

- Ronnberg J (2000). Logging operation damage to roots of clear-felled *Picea abies* and subsequent spore infection by *Heterobasidion annosum*. Silva Fenn 34: 29–36.
- Schilling EB, Lockaby BG, Rummer R (1999). Belowground nutrient dynamics following three harvest intensities on the Pearl River floodplain, Mississippi. Soil Sci Soc Am J 63: 1856–1868.
- Spinelli R, Nati C, Magagnotti N (2005). Harvesting and transport of root biomass from fast-growing poplar plantations. Silva Fenn 39: 539–548.
- Terzaghi M, Montagnoli A, Di Iorio A, Scippa GS, Chiatante D (2013). Fine-root carbon and nitrogen concentration of European beech (*Fagus sylvatica* L.) in Italy Prealps: possible implications of coppice conversion to high forest. Front Plant Sci 13: 1–8.
- Tian DL, Peng YY, Yan WD, Fang X, Kang WX, Wang GJ, Chen XY (2010). Effects of thinning and litter fall removal on fine root production and soil organic carbon content in Masson pine plantations. Pedosphere 20: 486–493.

- Wang ZQ, Guo DL, Wang XR, Gu JC, Mei L (2006). Fine root architecture, morphology, and biomass of different branch orders of two Chinese temperate tree species. Plant Soil 288: 155–171.
- Wells CE, Glenn DM, Eissenstat DM (2002). Changes in the risk of fine-root mortality with age: A case study in peach, *Prunus persica* (Rosaceae). Am J Bot 89: 79–87.
- Zhang WH, Lu ZJ (2002). A study on the biological and ecological property and geographical distribution of *Quercus variabilis* population. Acta Bot Boreali-Occidental Sinica 22: 1093–1101 (article in Chinese with an abstract in English).
- Zhou JY, Lin J, He JF, Zhang WH (2010). Review and perspective on *Quercus variabilis* research. J Northwest Forestry University 25: 43–49 (article in Chinese with an abstract in English).