Research paper

Distribution and Nutrient Contents of Fine Roots in the Fushan Subtropical Broadleaf Forest in Taiwan

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[Summary]

The biomass and nutrient contents of fine roots were investigated and estimated in the Fushan subtropical broadleaf forest in northeastern Taiwan. The result indicated that the fine root density decreased with increasing soil depth. In $0\sim30$ cm of soil, the biomass of fine roots was approximately 677 g m⁻² for a size of < 2 mm, 335 g m⁻² for $2\sim5$ -mm fine roots, and 61 g m⁻² for the necromass. The total length of fine roots of < 2 mm was approximately 3,860 m m⁻², but only 120 m m⁻² for $2\sim5$ -mm roots. The fine root biomass in Fushan is higher than that in temperate forests and similar to that in tropical rain forests. This may mainly be due to the lower available P as a result of torrential rains, which promotes the accumulation of fine roots. At the same time, as fine roots accumulate a large amount of N and P, they play an important role in the storage of nutrients in the ecosystem.

- Key words: fine roots, nutrient content, subtropical broadleaf forest, excavation method, specific root length.
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研究報告

福山亞熱帶闊葉林細根的分布和養分含量

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摘要

本研究調查台灣東北部福山亞熱帶濶葉林細根的生物量和長度,並分析其養分的濃度及在土壤內 累積量。結果發現:細根密度隨深度增加而下降。在0~30 cm土壤中,<2 mm細根生物量約677 g m⁻²;

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2~5 mm細根約335 g m⁻²;死根約61 g m⁻²。至於< 2 mm細根總長約為3,860 m m⁻²,2~5 mm細根僅為 120 m m⁻²。福山細根生物量高於溫帶林者,與熱帶雨林者相近。主要可能是暴雨造成土壤的P有效量 較低,促進細根累積。同時,細根累積大量的N和P,使細根在生態系養分儲存中占重要地位。 關鍵詞:細根、養分含量、亞熱帶濶葉林、挖掘法、根長比。

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INTRODUCTION

Fine roots play an important role in forest ecosystems. Fine roots account for only a small percentage of the belowground biomass, but they grow rapidly and may constitute a large percentage of the net primary production (Santantonio et al. 1977, Keyes and Grier 1981). Fine roots also show great turnover and decomposition rates, which affect nutrient availability in soils (Arunachalam et al. 1996, West et al. 2004). In addition, fine roots have a high level of nutrient concentration. The nutrient concentration of fine roots in temperate coniferous forests is similar to that of needles (Kimmins and Hawkes 1978), indicating their importance in the storage of nutrients. Therefore, data regarding fine roots are critical to the understanding of nutrient cycles of forest ecosystems. However, fine root biomass differs greatly in different climatic zones. The accumulation of fine roots in tropical evergreen broadleaf forests is substantial, reaching 4,070 g m⁻², compared with 140 g m⁻² in cold temperate deciduous coniferous forests (Vogt et al. 1985). However, there are also stands in wet lowland tropical forests that have extremely low live fine root accumulation of merely 125 g m⁻² (Gower 1987). Currently, there are abundant data on fine roots in different climate zones and forest stands with the exception of the subtropical zone. The broadleaf forest in Fushan, Taiwan is located in a subtropical zone and is subject to frequent typhoons, which cause defoliation and large amounts of litterfall (Lin 1997, Mabry et al. 1998), and which result in an aboveground biomass that is significantly lower than that of the tropical rain forests but higher than that of temperate broadleaf forests (Lin et al. 1994). Typhoons and the concomitant large accumulations of rainfall also contribute to the lower total amounts of P and Ca in the soil (Horng and Chang 1996). However, it is still unclear whether the fine roots in this environment have similar characteristics to the aboveground biomass or if the soil nutrient contents influence the large accumulation of fine roots. Therefore, the purposes of this research were to investigate the distribution of biomass and length of fine roots in the broadleaf forest of Fushan, to explore differences in fine roots between Fushan and other climatic zones, and to analyze fine root nutrient accumulation in the soil.

MATERIALS AND METHODS

Site

A natural broadleaf forest with little human interference located in northeastern Taiwan was selected. This forest is part of the experimental forest of Fushan Research Center under the Taiwan Forestry Research Institute. It is located at 24°45'N and 120°35'E, on the border between Taipei County and Ilan County, at elevations of 400 to 1,400 m. The annual average temperature is 18.2 °C and the annual rainfall between 1993 and 2002 ranged from 2,800 to 7,300 mm (data source: Fushan Meteorological Station). This is a subtropical rain forest; its floristic composition is dominated by Fagaceae and Lauraceae, and the dominant tree species are *Castanopsis carlesii* (Hemsl.) Hayata, *Machilus thunbergii* Sieb. & Zucc., *Quercus longinux* Hayata, *Engelhardia roxburghiana* Wall., *Litsea acuminata* (Bl.) Kurata, and *Meliosma squamulata* Hance. The forest terrain is hilly, with interlacing streams. On gradual ridges, the terrain is dominated by yellowish soil composed of inceptisols and ultisols as classified by soil taxonomy.

In 2001, a representative stand in a 20 by 50-m plot was randomly selected as the sample area on the ridge of a hill. The mean diameter at breast height (dbh) and tree height (\pm standard error) of the trees (dbh \geq 10 cm) were 18.9 \pm 1.1 cm and 9.6 \pm 0.5 m, respectively, and number of trees was 1,150 ha⁻¹ in the plot. The sample plot was at an elevation of 690 m and had a slope of 10°. The soil in the sample plot is shallow yellowish-brown soil, derived from colluvial slate. It is 30~50 cm deep with a texture from silt loam to loam, and the gravel content is greater than 30%. The soil is weakly developed. It is well drained to over-drained, which may induce strong leaching and result in a low pH and nutrient status of the soil.

METHODS

1. Sampling and fine root processing

An excavation method was used to obtain soil samples. In order to gain an understanding of the distribution of fine roots in the forest, 3 distances, 15, 100, and 200 cm, from the base of the trunks of the closest trees (dbh ≥ 10 cm) were selected. The criterion for spot selection was that no trees or bushes (dbh ≥ 1

cm) could be between the spot and the trunk. Eight spots were selected at 100 cm from 8 different trunks. Another 3 spots were selected 200 cm from the trunk due to the difficulties selecting spots at this distance. A 30 by 30-cm square sample hole was excavated at each spot at these 2 distances. The litter layer was carefully removed before excavation in order to accurately measure the soil volume. Preliminary observations indicated that soil deeper than 30 cm contained a fairly small amount of fine roots and an extremely large amount of gravel, making it difficult to excavate. Therefore, the excavation process was stopped at 30 cm in depth. The excavated soil was divided into 4 layers, namely 0~5, 5~10, 10~15, and 15~30 cm. Soil excavated from these layers was carefully stored in sealed plastic bags which were brought back to the laboratory for further categorization. At 15 cm from the trees, due to the difficulty presented by excessive amount of roots, samples were collected using steel tubes of 10 cm in inner diameter and 15 cm in length. The steel tube was inserted into the soil and then carefully removed, and the different layers of the sample inside the steel tube were delicately extracted. For each sample spot, 5 sample points were selected in different directions from the trunks, and for each point 2 tubes were collected to 30 cm in depth. Soils from these 5 sample points were lumped into 1, based on the 4 layers of different depths described above. Totally, 7 spots at 15 cm from 7 trees were sampled, and these had evenly distributed dbh values, of between 10.7 and 40.0 cm. In the laboratory these samples were placed in 50-µm sieves and washed with water. Fine roots thinner than or equal to 5 mm were selected and divided into 3 categories of $< 2, 2 \sim 5$ mm, and necromass. Aside from the few randomly selected to be used in root length measurements, fine roots were dried at 45°C and weighed. The few fine roots that were randomly selected were pressed and photocopied onto B4-sized (257 by 364 mm) paper. Using a PC Arc/Info digitizer, these photocopies were digitized into computer coverage. The length of the fine lines in the computer coverage represents the length of these fine roots. Each B4 paper was digitized twice and the average total length of the small sample of fine roots was calculated. Dividing the total length by the oven-dry weight of the sample resulted in the specific root length (SRL), which was used to estimate fine root length.

2. Chemical analyses

Each fine root sample was ground into powder (< 0.5 mm). Then, using a dry combustion method, 4.00 mg of each root sample was analyzed using an elemental analyzer (NA1500, Fisons Instruments, Paris, France) to measure their C and N concentrations (Sollins et al. 1999). In addition, using a wet digestion method, another 0.50 g of sample was analyzed with inductively coupled plasma atomic emission spectrometry (ICP-AES, JY2000, Johin Yvon Emission, Milan, Italy) for P, K, Ca, and Mg concentrations (Harmon and Lajtha 1999).

3. Statistical analysis

Using the oven-dry weight of fine roots, the average fine root density and fine root biomass per unit area were estimated based on distances to the base of the tree, soil depths, and root categories. Furthermore, the average length, length density, and total length of the fine roots for the 2 categories were estimated using SRL. After calculating the average nutrient concentration for the fine roots based on distances to the tree, soil depths, and fine root categories, the root biomass was used to estimate the nutrient accumulation per unit area. All statistical tests were performed with the GLM procedure of SAS (SAS 1988).

RESULTS

1. Fine root biomass

Differences in the fine root density and biomass did not reach statistical significance $(p \ge 0.05)$ among distances from the tree and were not related to the dbh of trees in the Fushan broadleaf forest. This indicates that fine roots are evenly distributed in the forest. However, there were statistical differences found in fine root densities and biomass among different soil depths and root categories (p < 0.01). Both fine root density and necromass density decreased with increasing depth. The density for fine roots of < 2 mm in diameter was the highest, followed by those 2~5 mm in diameter and then necromass (Table 1). Therefore, 43% of the biomass of fine roots was concentrated in soil of $0\sim5$ cm in depth. For fine roots of < 2 mm in diameter, the percentage of biomass at this depth was as high as 48% (Table 2). In soil depths of 0~30 cm, the biomass of fine roots of < 2 mm in diameter was approximately 677 g m^{-2} , accounting for 63% of the total; the biomass for 2~5-mm-diameter fine roots was approximately 335 g m⁻², accounting for 31% of the total; for necromass, the value was approximately 61 g m⁻², representing only 6%of the total.

2. Root length

There were no statistical differences ($p \ge 0.05$) in the SRL among distances to the tree or among soil depths. Differences were only present between fine root diameters. For fine roots of < 2 mm in diameter, the average SRL was 5.97 m g⁻¹ (standard error, 0.18 m g⁻¹), and for fine roots of 2~5 mm in diameter, the SRL was 0.35 m g⁻¹ (standard error, 0.01 m g⁻¹).

Distance from tree	Soil depth	Root di	Neeromoog	
(cm)	(cm)	0~2 mm	2~5 mm	- Inectomass
$\overline{15 (n=7)}$				
	0~5	6.37 ± 0.87	2.08 ± 0.23	0.45 ± 0.10
	5~10	2.49 ± 0.23	1.94 ± 0.38	0.17 ± 0.04
	10~15	2.00 ± 0.20	1.33 ± 0.07	0.26 ± 0.06
	15~30	0.99 ± 0.11	0.63 ± 0.09	0.15 ± 0.10
100 (<i>n</i> = 8)				
	0~5	6.71 ± 0.75	2.19 ± 0.24	0.42 ± 0.16
	5~10	2.35 ± 0.26	1.39 ± 0.15	0.26 ± 0.17
	10~15	1.85 ± 0.30	1.30 ± 0.23	0.24 ± 0.13
	15~30	0.88 ± 0.12	0.56 ± 0.08	0.14 ± 0.09
200 (<i>n</i> = 3)				
	0~5	6.41 ± 0.10	2.43 ± 0.28	0.39 ± 0.03
	5~10	2.10 ± 0.38	1.26 ± 0.33	0.08 ± 0.01
	10~15	1.55 ± 0.19	0.77 ± 0.09	0.08 ± 0.04
	15~30	0.91 ± 0.15	0.49 ± 0.13	0.04 ± 0.02

Table 1. Fine root density (kg m⁻³) in the upper 30 cm of soil in the Fushan broadleaf forest with respect to distance from the tree, root category, and soil depth (mean \pm standard error)

Table 2. Fine root biomass (g m⁻²) in the upper 30 cm of soil in the Fushan broadleaf forest with respect to root category and soil depth (mean \pm standard error, n = 18)

Soil depth (cm) _	Root diameter		Necromass	Sum	
	0~2 mm	2~5 mm	rectomass	Sum	
0~5	$327\pm23~(48)^{11}$	109±7 (33)	21±4 (35)	457 (43)	
5~10	118±8 (17)	79±9 (23)	10±4 (16)	207 (19)	
10~15	93±8 (14)	61±6 (18)	11±3 (18)	165 (15)	
15~30	139 ± 10 (21)	86±8 (26)	19±8 (31)	244 (23)	
Total	677	335	61	1073	

¹⁾ Numbers in parentheses are percentages of the total.

The fine root length density calculated by the SRL and the fine root biomass are shown in Table 3; it is clear that fine root length density decreased as soil depth increased. In terms of total fine root length, about 42% was concentrated in 0~5 cm of soil depth. At soil depths of 0~30 cm, the total length of fine roots of < 2 mm in diameter was approximately 3,860 m m⁻², and the total length of 2~5-mm-diameter fine roots was merely 120 m m⁻² (Table 4).

Table 3. Fine root length density (km m⁻³) in the upper 30 cm of soil in the Fushan broadleaf forest with respect to root diameter and soil depth (mean \pm standard error, n = 18)

c1101, <i>n</i> 1	0)				
Soil depth	Root dia	Root diameter			
(cm)	0~2 mm	2~5 mm			
0~5	32.90 ± 2.41	0.82 ± 0.05			
5~10	14.40 ± 1.04	0.56 ± 0.06			
10~15	11.96 ± 1.05	0.41 ± 0.04			
15~30	5.94 ± 0.51	0.20 ± 0.02			

Soil depth	Root dia	Root diameter		
(cm)	0~2 mm	2~5 mm	Sum	
0~5	$1645 \pm 121^{(1)} (43)^{(2)}$	41±3 (34)	1686 (42)	
5~10	720 ± 52 (19)	28±3 (24)	748 (19)	
10~15	598 ± 52 (15)	21 ± 2 (17)	619 (16)	
15~30	892 ± 76 (23)	29 ± 3 (25)	921 (23)	
Total	3855	119	3974	

Table 4. Total length per unit area (m m⁻²) of fine roots with respect to root diameter and soil depth (n = 18)

¹⁾ Mean \pm standard error.

²⁾ Numbers in parentheses are percentages of the total.

3. Fine root nutrient contents

Analysis of fine root nutrient concentrations indicated that there were no differences ($p \ge 0.05$) in terms of distances from the tree (except for C and Ca). However, the majority of the nutrient concentrations showed significant differences with soil depth (except for C and N) and root category (p < 0.01) (Table 5). Among these nutrients, concentrations of C, N, and P were higher in fine roots of < 2 mm in diameter than those in thicker fine roots. However, K and Ca showed contrary results, having lower concentrations in fine roots of < 2 mmin diameter. Concentrations of Mg were similar in these 2 groups. There were lower nutrient concentrations in the necromass. But for Ca concentration, the necromass and living roots showed similar results. Nitrogen concentration in the necromass was even higher than that in $2\sim5$ -mm-diameter living roots (Table 6). The estimated total amounts of different nutrients in fine roots are shown in Table 7. Nutrients of fine roots were concentrated in a soil depth of $0\sim5$ cm, accounting for over 43% of the total. For P and Ca, concentrations in this layer of soil were even higher (> 50%).

DISCUSSION

1. Fine root biomass

Fine root biomass in tropical forests generally ranges between 300 and 10,000 g m⁻² (Vogt et al. 1985). The biomass of fine roots of < 2 mm in diameter at Fushan (Table 2) was higher than that of the world average for tropical rain forests (570 g m⁻²) (Jackson et al. 1997). The biomass for these fine roots was slightly higher than that of a lowland

	Table 5. Analysis	of variance	for nutrients	of fine roots
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Nutrient	Distance from tree	Soil depth	Root diameter	N
С	* ¹⁾	n.s.	* *	147
Ν	n.s.	n.s.	* *	147
Р	n.s.	* *	* *	142
Κ	n.s.	* *	* *	142
Ca	*	* *	* *	142
Mg	n.s.	* *	* *	142

¹⁾ * p < 0.05; ** p < 0.01; n.s., $p \ge 0.05$.

to root unume				
Nutrient	$0 \sim 2 \text{ mm} (n = 63)$	$2 \sim 5 \text{ mm} (n = 63)$	Necromass $(n = 21)$	
С	505 ± 2 $a^{1)}$	491±2 b	476±10 c	
Ν	23.7±0.4 a	12.7±0.3 c	17.2±0.6 b	
Р	1.38 ± 0.05 a	0.77 ± 0.03 b	0.81 ± 0.08 b	
Κ	1.63 ± 0.06 b	1.91 ± 0.08 a	0.97 ± 0.09 c	
Ca	2.00±0.14 b	2.86±0.16 a	2.39 ± 0.29 ab	
Mg	1.21 ± 0.03 a	1.24 ± 0.06 a	0.78 ± 0.06 b	
C/N	21.8±0.4 c	39.9±0.9 a	28.6±1.3 b	

Table 6. Nutrient concentrations (mg g⁻¹) (mean \pm standard error) of fine roots with respect to root diameter

¹⁾ Values in a row with the same letter do not significantly differ at the 5% significant level by new Duncan's multiple range test.

category							
Soil depth (cm)	Roots	С	Ν	Р	Κ	Са	Mg
0~5	0~2 mm	1666	84.7	61.5	51.2	91.4	42.6
	2~5 mm	539	15.1	10.7	26.8	37.2	14.2
	Necromass	102	3.7	1.7	2.1	5.1	1.6
	Subtotal	2307	103.5	73.9	80.1	133.7	58.4
		$(43.0)^{1)}$	(47.8)	(55.1)	(44.2)	(51.4)	(44.5)
5~10	0~2 mm	595	27.7	16.1	19.2	20.3	14.3
	2~5 mm	388	10.6	6.3	15.5	23.3	9.8
	Necromass	46	1.7	0.8	1.0	2.3	0.8
	Subtotal	1029	40.0	23.2	35.7	45.9	24.9
		(19.2)	(18.5)	(17.3)	(19.7)	(17.6)	(19.0)
10~15	0~2 mm	467	21.3	11.3	15.5	15.0	11.6
	2~5 mm	297	7.6	4.2	11.3	17.6	8.1
	Necromass	53	1.9	0.9	1.1	2.7	0.9
	Subtotal	817	30.8	16.4	27.9	35.3	20.6
		(15.2)	(14.2)	(12.2)	(15.4)	(13.6)	(15.7)
15~30	0~2 mm	699	29.5	14.3	22.1	21.6	16.2
	2~5 mm	421	9.5	4.9	13.5	19.1	9.6
	Necromass	91	3.3	1.5	1.9	4.6	1.5
	Subtotal	1211	42.3	20.7	37.5	45.3	27.3
		(22.6)	(19.5)	(15.4)	(20.7)	(17.4)	(20.8)
	Total	5364	216.6	134.2	181.2	260.2	131.2

Table 7. Estimated nutrient content (kg ha⁻¹) of fine roots with respect to soil depth and root category

¹⁾ Numbers in parentheses are percentages of the total.

tropical forest in central America (490~530 g m⁻²) (Klinge 1973), a tropical wet forest in Costa Rica (58~110 g m⁻²) (Gower 1987), and wet land forest in Panama (370~400 g

 m^{-2}) (Cavelier 1992, Yavitt and Wright 2001), but lower than that of largely accumulated fine roots in Venezuela (1380~3950 g m^{-2}) and a lowland rain forest in Ivory Coast (1100~1260 g m⁻²) (Cavelier 1992). The biomass of Fushan's fine roots that are 2~5 mm in diameter was similar to values of most above-mentioned forest stands. Compared to temperate broadleaf forests, the density for fine roots of < 2 mm in diameter at Fushan (Table 1) was far higher than that of an oak (Quercus douglasii Hook and Arn.) stand in northern and central California in the US (Callaway et al. 1991, Millikin and Bledsoe 1999). The biomass of fine roots of < 5 mm in diameter at Fushan was slightly higher than that of a mixed forest composed of pitch pine (Pinus rigida Mill.), and oaks in Pineland, NJ, US (Ehrenfeld et al. 1992) and higher than that of a mixed deciduous forest in the US (790 g m⁻²) and a *Liriodendron tulipifera* forest stand (760~900 g m⁻²) reported by Santantonio et al. (1977).

The accumulation of fine roots tends to stabilize when forest stands become mature (Santantonio et al. 1977). At that time, fine root biomass is influenced by the state of soil nutrition and characteristics. For instance, the fine root biomass of a tropical rain forest was inversely related to the concentration of available P and Ca (Gower 1987), or only inversely related to the available Ca concentration (Cavelier 1992). The available P in Fushan soils is comparatively low (0.81 kg ha⁻¹) (Horng and Chang 1996). This may be one of the reasons for the higher biomass for fine roots at Fushan. Although the amount of aboveground biomass at Fushan is lower than that of an average tropical rain forest (Lin et al. 1994), fine root biomass was actually comparable to that of a tropical rain forest. This indicates that although typhoons affect the aboveground biomass (Lin et al. 1994), the loss of nutrients due to torrential rains might actually promote the accumulation of fine roots. But some studies have shown that fine root biomass increases or shows no significant changes after fertilization (Brække 1992, Son and Hwang 2003). Clarifying the actual reason for the accumulation of fine roots at Fushan requires additional studies.

Fushan's fine root density and biomass both decreased with depth, conforming to the phenomenon of typical tropical and temperate forests. However, there was a large accumulation of fine roots in the litter laver and humus in the above-mentioned mixed forest of oak and pitch pine (Ehrenfeld et al. 1992). A similar phenomenon was also found in a lowland tropical forest in the central Amazon (Klinge 1973). There was also a tropical forest where fine roots in the organic layer accounted for over 50% of the total (Priess et al. 1999). At Fushan, the amount in the litter layer was very small, only 4.6~8.9 Mg ha⁻¹ (Lin 1997). Although no investigation of the fine root biomass in the litter layer was made in this research, it is expected that the amount is low. In this research, fine roots were only investigated at soil depths of between 0 and 30 cm. Therefore, it is possible that the total fine root biomass was underestimated.

2. Fine root length

There were no differences in the SRL of fine roots in Fushan among distances to the tree or among soil depths. However, for some fine roots of Scots pine (*Pinus sylvestris* L.) in Norway, the SLR decreased with increasing soil depth (Brække 1992), indicating that the deeper the soil, the thicker and fewer were the fine roots. Fine roots in Fushan did not exhibit these characteristics; the distribution of fine roots in the same diameter class had similar tendencies. On a plantation in Victoria, Australia, fine roots of < 2 mm in diameter of *Eucalyptus globulus* Labill and *Acacia mearnsii* de Wild showed SRL values of 27.4 and 25.5 m g⁻¹, respectively (Bauhus et al. 2000). These values were 4.3- to 4.6-times that of Fushan's values, indicating the percentages of extremely small fine roots (more than 90%) for these 2 species were much higher than in the forest at Fushan. The total length of fine roots of < 2 mm in diameter at Fushan was 3,900 m m⁻², slightly shorter than the average for tropical evergreen forests of 4.100 m m^{-2} (Jackson et al. 1997). but far longer than the above-mentioned fine roots in a tropical rain forest in the central Amazon of 410 m m⁻² (Klinge 1973). In terms of fine roots of 2~5 mm in diameter, the total length at Fushan (Table 4) was in between that of *Eucalyptus nitens* (40 m m⁻²) and E. globules (140 m m⁻²) at Tasmania, Australia (Moroni et al. 2003). With regard to the distribution of fine roots at different depths, the density of fine roots of < 2 mm indiameter at 0~15-cm depth was 19.7 km m⁻³, far higher than that of the above-mentioned E. globules, which had a density of 12.6 km m^{-3} , but similar to that of *A. mearnsii*, which had a density of 19.9 km m⁻³. The situation was reversed for fine root density at depths of 15~30 cm. Fushan's fine roots at this depth had a density of 5.9 km m⁻³, lower than that of A. mearnsii at 7.1 km m⁻³ and slightly higher than that of *E*. globules at 5.1 km m⁻³ (Bauhus et al. 2000).

3. Fine root nutrient contents

Generally speaking, fine roots' nutrient concentrations decrease with increasing root diameter (Santantonio et al. 1977, Vogt et al. 1987). For instance, in a *Pinus radiata* D. Don plantation, concentrations of N, P, and Ca significantly decreased with increasing root diameter (Nambiar 1987). In the case of Scots pine, concentrations of N, P, K, and Mg significantly decreased with increasing root diameter (Helmisaari 1991). However, only N and P showed significant decreases in Fushan, while concentrations of K and Ca increased (Table 6). The reason for this increase is still unclear, and it is possibly a result of species-specific differences. When comparing nutrient concentrations for necromass and living roots, there were significant differences between results for N, K, and Mg. Concentrations of K and Mg in the necromass were significantly lower than those in living roots. This is possibly due to retranslocation and leaching. Retranslocation might not be a factor for other nutrients. The necromass had a higher N concentration than fine roots of 2~5 mm in diameter, and the reason may be biological immobilization.

The fine root biomass of the Fushan broadleaf forest accounted for 3.8 to 5.5% of the total aboveground biomass (197~290 Mg ha⁻¹) (Table 2) (Lin et al. 1994). This percentage was higher than that of some temperate coniferous forests (Fogel and Hunt 1983, Helmisaari et al. 2002). In addition, the fine root biomass in Fushan was higher than the foliar biomass $(481 \sim 738 \text{ g m}^{-2})$ (Lin et al. 1994). Comparing the nutrient accumulation of fine roots and the nutrient accumulation of the above-ground broadleaf forest of Fushan estimated by Lin et al. (1996), it was found that the amounts of N, P, K, Ca, and Mg as a percentage of above-ground nutrient were 22.8~38.4, 20.2~38.5, 2.9~4.9, 3.2~8.7, and 6.7~7.9% respectively. These figures indicate that fine roots not only have the function of absorbing nutrients, but their N and P accumulations also play important roles in the ecosystem.

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