Research paper

Estimate of Coarse Root Biomass and Nutrient Contents of Trees in a Subtropical Broadleaf Forest in Taiwan

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【Summary】

In this paper, we studied the biomass and estimated the nutrient content of coarse roots (≥ 5 mm) of trees (dbh ≥ 10 cm) in a subtropical broadleaf forest at Fushan, northeastern Taiwan. The results from excavating 8 trees of 7 species indicated that the biomass of coarse roots accounted for 13.4~30.2% of the total tree biomass. This percentage was not correlated to the diameter at breast height (dbh). Based on the natural logarithmic regression established by sample trees, the biomass of each category and the total biomass of coarse roots were highly significantly related to dbh. In the coarse roots, the stump and ≥ 100-mm roots had the highest percentage of biomass, each accounting for approximately 30.0% of the coarse root biomass. Comparatively, the biomass of coarse roots accounted for 21.9% of the total tree biomass and 28.0% of aboveground biomass. The biomass of coarse roots of trees was 65.1 Mg ha^{-1}, which is higher than the average root biomass of tropical evergreen forests reported in the literature. The root/shoot ratio calculated from coarse roots was 0.28, higher than those for both tropical forests and the global average. The higher root/shoot ratio of the Fushan forest is likely a result of severe branch and leaf damage caused by frequent typhoons, leaving the forest with lower aboveground biomass. The nutrient allocation of coarse roots in trees of the Fushan forest is similar to that of temperate broadleaf forests.

Key words: subtropical broadleaf forest, regression model, root/shoot ratio, carbon storage, nutrient content.

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研究報告

亞熱帶闊葉林林木粗根生物量和養分含量之估算

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摘要

本研究調查位於台灣東北部福山亞熱帶天然闊葉林林木(胸徑≥10 cm)粗根(根徑≥5 mm)的生物量，並估算其養分含量。由8株樣木(7種樹)伐倒挖根調查結果顯示：樣木粗根生物量佔全株生物量的百分比為13.4~30.2%；此一比例與胸徑不具相關性。各根徑級及總粗根生物量，以胸徑建立之自然對數迴歸式皆呈顯著差異。林分林木粗根中以根頭及≥100 mm根徑級其生物量佔比例最高，各約佔粗根生物量的30.0%。粗根生物量佔全株生物量的21.9%，佔地上部生物量的28.0%。福山林木粗根生物量為65.1 Mg ha^{-1}，高於熱帶常綠林的根平均生物量，且粗根根莖比為0.28，高於熱帶地區及全球的平均值。其根莖比較高的原因之一為枝條和葉受颱風干擾，地上部生物量偏低之故。至於，福山闊葉林林木其養分分佈的比例則與溫帶闊葉林者相近。

關鍵詞：亞熱帶闊葉林、迴歸模式、根莖比、碳貯存、養分含量。

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INTRODUCTION

Estimating biomass is fundamental to understanding the dynamics of ecosystems and nutrient cycles. Traditionally, ecological research has been focused on natural forests, with a particular emphasis on tropical forests, which are unique and have complex structures (Lugo 1992). In ecosystem studies, roots have often been neglected as they are mostly hidden underground, and the measurement of their biomass is tremendously laborious and time-consuming. However, recent studies indicate that root biomass accounts for approximately half of the annual carbon cycle in many forests (Vogt et al. 1996), thus, it is very important to have accurate measurements. Currently, there are already data regarding root biomass from various forest ecosystems around the world (Jackson et al. 1996, Vogt et al. 1996, Cairns et al. 1997). Statistics shows that the underground biomass of subtropical evergreen broadleaf forest ecosystem ranges widely from 10.9 to 73.5 Mg ha^{-1} (Vogt et al. 1996). Comparatively, in wet subtropical forests that have over 2,000 mm of annual rainfall, the root biomass ranges from 65 to 115 Mg ha^{-1} (Brown and Lugo 1982). The information was mostly gathered from Central America, and few data have been gathered from the natural subtropical evergreen wet forests of Asia. Although some aboveground biomass data for natural subtropical forests of Taiwan, located in the subtropical region, have been measured (Horn et al. 1986, Lin et al. 1994, Hsiue and Sheu 2003), there has been no research on root biomass. The Fushan Experimental Forest is located in a humid subtropical climate zone in northeastern Taiwan (Hsia and Hwong 1999). It is one of the few subtropical broadleaf forests in Taiwan that is subject to little human interference and hence a long-term ecological research site for the Taiwan Ecological Research Network (TERN). Through comprehensive and integrated studies on this forest, we hope to gain a greater understanding of the structures and functions of subtropical natural broadleaf ecosystems and moreover, analyze the process of nutrient cycling. This research focused on trees (diameter at breast height, dbh ≥ 10 cm) because the aboveground biomass of the tree stratum accounts for 75~94% of the aboveground biomass in the Fushan forest (Lin et al. 1994). This research estimated the coarse root biomass of trees and analyzed their nutrient contents to be used as basic information for estimating nutrient cycles.

MATERIALS AND METHODS

Site

The natural broadleaf forest at Fushan is part of the Fushan Research Center administered by the Taiwan Forestry Research Institute. It is located at 24º45'N and 120º35'E, on the border between Taipei and Ilan Counties at elevations of 400 to 1,400 m. The annual average temperature is 18.2℃ and the annual rainfall between 1993 and 2000 ranged from 2,800 to 6,100 mm (data source: Fushan Meteorological Station). The dominant tree species in the Fushan forest belong to the Lauraceae and Fagaceae. The dominant trees are *Castanopsis carlesii* (Hemsl.) Hayata, *Machilus thunbergii* Sieb. & Zucc., *Quercus longinux* Hayata, *Engelhardia roxburghiana* Wall., *Litsea acuminata* (Bl.) Kurata, and *Meliosma squomulata* Hance. The research site is located on gradual slopes and is dominated by yellow soil (Lin et al. 1996a).

Plots and Sampling

In 2000, four 20×20-m plots were randomly selected as sampling sites on the ridges of a hill. Dominant trees included *M. thunbergii*, *C. carlesii*, *Diospyros morrisiana* Hance, *L. acuminata*, and *E. roxburghiana*. The average dbh of the trees was 20.6±0.4 cm (mean±standard error, hereafter), average tree height was 11.0±0.1 m, and the number of trees was 1110±80 tree ha^{-1} with a basal area at breast height of 44.6±4.3 m^2 ha^{-1}. The site was at an elevation of approximately 730~750 m and had a slope of 6~15º.

Trees were divided into 6 classes according to the dbh at intervals of 5 cm from 10 to 35 cm and upward. For each dbh class, 1 to 2 sample trees were selected. The selection criterion was that there was no other tree within 1-m diameter from the base of the sample tree. In total, 8 sample trees were selected: *C. carlesii* (2 samples), *M. squomulata*, *Q. longinux*, *E. roxburghiana*, *Machilus zuihoensis* Hayata, *Cryptacarya chinensis* (Hance) Hemsl., and *Gordonia axillaris* (Roxb.) Dietr.

After cutting down a tree at approximately 10 cm from the base, the aboveground section was divided into 3 components of the bole, branches (branches without leaves), and twigs and leaves. The fresh weight of each component was recorded. Two discs of approximately 5 cm were taken from the bole at 1.3 m in height and at the height of the under canopy, at approximately 6 m. The fresh weight of each disc was measured. The canopy of each sample tree was divided into a bottom and top layer. From each layer, 2 sub-samples of approximately 400 g of branches and twigs/leaves were collected. The fresh weight of the branches was determined. Twigs and leaves were further divided and weighed separately. Using the proportions of twigs and leaves, the fresh weights of twigs and leaves of the entire tree were estimated. The discs and sub-samples were taken back to the lab and baked at 50℃ to a constant weight, and this was recorded as the oven-dry weight. Using the ratio of oven-dry weight to fresh weight of each sample, the biomass of each component and total biomass of the sample trees were estimated.

After carefully removing the litter layer, roots within 1 m radius of the bole of the sample trees were excavated. All coarse roots ≥ 5 mm (including necromass) below the forest floor were collected and washed with stream water. The coarse roots were divided into 7 categories of necromass, 5~10, 10~20, 20~50, 50~100, and ≥ 100 mm, and the stump. For each category, the fresh weight was measured, and a sub-sample of approximately 400 g was also weighed and brought back to the lab. The sub-samples were dried at 50℃ until reaching a constant weight. The ratio of oven-dry weight to fresh weight was calculated, and the biomass of coarse roots for each sample tree was estimated.

To gain an understanding of the distribution of coarse roots outside of 1 m from the bole, one 30×30-cm square hole was excavated outside of 1 m from each sample bole and 1 m away from other trees, for a total of 8 holes. In addition, another 3 sample holes were excavated 2 m away from all trees. The excavation and sampling method of the holes are described in a previous paper (Lin et al. 2005). In the lab, roots that were ≥ 5 mm in diameter were collected from the soil samples and categorized based on the method used in categorizing coarse roots. These roots were then washed, dried and weighed to estimate the amount per unit area.

Biomass Estimate

The most commonly used natural logarithm equation, $Y = a + b \ln(\text{dbh})$, was selected as the regression model (Dudley and Fownes 1992). In the equation, Y represents the root biomass of each category or total biomass (kg), dbh represents the dbh (cm), and a and b are constants. Also, a correction factor needs to be applied to the constant a ($cf = S_{y.x}^2/2$, where $S_{y.x}$ is the standard error of the estimate), and a is equal to c + cf, where c is the constant in the equation $Y = c\,(\text{dbh})^b$. After selecting the regression models, the root biomass values of the different categories of each tree in the plot were calculated. These values were then converted into biomass per unit area. For the aboveground biomass estimation of the stand using the regression model of each component published by Lin et al. (2001), the tree biomass of the plot for each component of each tree was calculated. These values were then used to calculate the aboveground biomass and the total biomass per unit area. All biomass values were represented by the ash-free oven-dry weight.

Chemical Analyses

Each coarse root sample and aboveground sample were finely ground up (< 0.5 mm) for chemical analysis. Using an elemental analyzer and a dry combustion method, approximately 4.00 mg of sample was analyzed for C and N concentrations (Sollins et al. 1999). Another 0.50 g of sample was heated for 4 h at 500℃ to measure its ash content. Using a wet digestion method, the ash was mixed with 2 N HC1 in a solution to analyze the concentrations of P, K, Ca, and Mg using inductively coupled plasma atomic emission spectrometry (ICP-AES, JY2000, Johin Yvon Emission) (Harmon and Lajtha 1999). Due to its small mass, necromass was not analyzed.

The average biomass for each root category and the aboveground components of all trees in each plot were multiplied by the average nutrient concentration to estimate the nutrient contents of the coarse roots and aboveground components. The total nutrient contents of the trees per unit area were then estimated.

RESULTS

Coarse Root Biomass of Trees

The highest biomass in the trees was in the boles, comprising over 50% of the total, followed by branches, with over 6% (Table 1). In the roots, the stump accounted for the largest biomass, with over 3.8% of the total biomass. Generally, roots that had smaller diameters also had smaller amounts of biomass, and their contributions to the biomass of the entire tree were also smaller. However, depending on the species and dbh, there were large differences among the percentages of root biomass for different root categories. For instance, the percentage of root biomass could be 9 times different for roots with diameters of 5~10 mm. Also, coarse roots of larger than 100 mm could not be found in samples with a dbh of < 15 cm. The contribution of coarse root biomass to the entire tree's biomass varied substantially, ranging from 13.4 to 30.2%, with an average of 20.8% for the 8 samples. After analyzing the relationship between root biomass and dbh, it was noted that the percentage of root biomass relative to the entire tree for each root category (except roots ≥ 100 mm) was not correlated to dbh ($p > 0.05$), indicating that when dbh increased, the percentage of biomass for roots with larger diameters might increase, decrease, or not change.

The roots/shoot ratio calculated for coarse roots from the sample trees was 0.15~0.43 (Table 1). Values of the mean root/shoot ratio from the harvested sample trees and all trees in the plots were 0.27 and 0.28, respectively.

Coarse Root Biomass of Trees in the Stand

The natural logarithmic regressions for each coarse root category and total coarse

Table 1. Dimensional characteristics of sample trees in the Fushan forest

Dimensions	Mean (range)	Range of percentages[1]
A. Tree		
Dbh (cm)	23.6 (10.7~40.0)	
Height (m)	14 (9~19)	
B. Biomass (kg tree^{-1})		
Aboveground		
Leaves	5.1 (0.1~16.7)	0.1~5.8
Branches[2]	84.1 (4.7~342.7)	6.1~29.9
Twigs[3]	1.8 (0.2~3.1)	0.2~1.8
Bole	219.8 (17.2~630.8)	52.3~66.9
Subtotal	310.8 (23.7~993.4)	69.8~86.6
Belowground (coarse roots)		
Necromass	0.2 (0~1.6)	0~0.2
5~10 mm	1.3 (0.3~3.7)	0.1~0.9
10~20 mm	4.7 (0.5~19.7)	0.4~2.7
20~50 mm	11.7 (0.9~30.4)	1.3~6.2
50~100 mm	11.2 (1.0~25.0)	1.8~8.0
> 100 mm	19.8 (0~52.4)	0~9.7
Stump	21.6 (2.1~45.8)	3.8~12.0
Subtotal	70.5 (9.1~156.5)	13.4~30.2
Total for tree	381.3 (31.1~1146.8)	
Root/shoot ratio	0.27 (0.15~0.43)	

[1] The percentage of the total biomass of each tree.

[2] Branches without leaf.

[3] Branches with leaf.

root biomass were all significant ($p < 0.05$) (Table 2). The only exception was necromass ($p > 0.05$).

For coarse roots, the stump and roots ≥ 100 mm still accounted for the highest percentage, approximately 30.0%, of coarse root biomass (Table 3). The amount of necromass was extremely low and was not included in the calculation. Coarse roots accounted for 21.9% of the total tree biomass and 28.0% of the aboveground biomass.

Sample holes were excavated to evaluate the coarse root biomass outside of 1 m from the bole. The biomass for each root category of the sample holes did not show significant differences ($p > 0.05$) between 1 and 2 m outside of the bole. Therefore, the averages of the 11 sample holes were used to estimate coarse root biomass (Table 3). Compared to the results of sample tree estimations, the only category that showed higher biomass in samples taken outside of 1 m of the boles

Table 2. Regression coefficients and statistics of the allometric equation (ln (Y) = a + b (ln dbh)) estimating total coarse root biomass and coarse root biomass by root diameter categories (kg tree^{-1})

Y	a	b	Adjusted R^2	*SEE*[1]
Necromass	-5.8919	2.6275	0.03[ns2)]	3.77
5~10 mm	-4.8863	1.6135	0.74*	0.45
10~20 mm	-5.1058	2.0383	0.74**	0.58
20~50 mm	-5.0823	2.3407	0.77**	0.61
50~100 mm	-4.6347	2.1795	0.86**	0.43
> 100 mm	-7.4445	3.1913	0.92**	0.46
Stump	-4.8421	2.4408	0.94**	0.29
Total	-4.2327	2.6087	0.96**	0.28

[1] Standard error of the estimate.

[2] ns, not significant; *, $p < 0.05$; **, $p < 0.01$.

Table 3. Estimated biomass (Mg ha^{-1}) among coarse root categories, total aboveground, and total trees in the Fushan forest

Item	Biomass[1]	Percentage of the total	Biomass[2]
5~10 mm	1.2±0.1	1.8	3.8±0.6
10~20 mm	3.9±0.4	6.0	6.0±2.0
20~50 mm	11.0±1.2	16.9	11.1±3.3
50~100 mm	10.0±1.0	15.4	0
> 100 mm	19.4±2.9	29.8	
Stump	19.6±2.2	30.1	
Total belowground (Coarse roots)	65.1±7.9	100 (21.9)[3]	
Total aboveground	232.9±24.9	(78.1)	
Total for tree	298.0±32.8		

[1] Mean±standard error of 4 plots.

[2] Mean±standard error of 11 sample holes.

[3] Numbers in parentheses are the percentage of the total for the entire tree.

than the tree estimation was the 5~10-mm root category ($p < 0.05$). Although other root category had higher values, they did not reach statistical significance.

While excavating sample trees in this research, roots from non-sample trees were separated and excluded from calculation. These were likely roots extending from nearby shrubs or other trees. The biomass (kg tree^{-1}) of non-sample-tree roots in each category (mean ± standard error) were 0.54 ± 0.12 for 5~10 mm, 0.88 ± 0.17 for 10~20 mm, 1.09 ± 0.32 for 20~50 mm, and 0.31 ± 0.29 for 50~100 mm.

Nutrient Content of Trees

For coarse roots and the aboveground section, there were significant differences ($p < 0.01$) in the average nutrient concentration among species. Among tree components, leaves had the highest concentration and the boles had the lowest concentration (Table 4). In coarse roots, the larger the root diameter was the lower their nutrient concentration (except for C), but K concentration was the only nutrient that reached statistical significance ($p < 0.05$, Table 4).

In terms of the coarse root's nutrient storage, roots ≥ 100 mm and the stump comprised the largest percentages. However, because roots ≥ 100 mm and the stump had lower nutrient concentrations (Table 4), their contributions to nutrient storage of total coarse root nutrients were lower than that of biomass except for Ca (Table 3). The storage of all nutrients in coarse roots relative to the entire tree was lower than the contribution of root biomass to the entire tree's biomass, except for N. Among all nutrients, P was the lowest, at only 24.2 kg ha^{-1}, which equaled 10.5% of the total P value for the entire tree, and N was the highest, at 488 kg ha^{-1}, which was 23.9% of the total N value for the entire tree (Table 5).

DISCUSSION

Compared with the average biomass of the sample-tree roots, non-sample-tree roots of 5~10, 10~20, 20~50, and 50~100 mm each accounted for 41.3, 18.6, 9.4, and 2.8% of each size category's total, respectively. From these figures, it is evident that with an increase in root diameter, the percentage of

Table 4. Nutrient concentrations (mg g^{-1}) (mean ± standard error) among aboveground tree components and coarse root categories of the sample trees

Item	C	N	P	K	Ca	Mg
Aboveground						
Bole	457±2	4.0±0.2	0.26±0.04	1.4±0.2	2.9±0.6	0.5±0.1
Branches	471±4	7.9±0.4	0.96±0.11	3.5±0.3	4.2±0.6	0.9±0.1
Twigs	469±4	11.9±0.7	2.27±0.20	7.7±0.7	6.1±0.7	2.0±0.2
Leaves	499±8	19.5±1.5	2.57±0.13	7.5±0.6	5.1±0.3	2.5±0.2
Belowground (Coarse roots)						
5~10 mm	486±6	9.7±1.0	0.57±0.09	2.3±0.3	2.2±0.3	1.4±0.4
10~20 mm	488±4	9.2±0.1	0.53±0.09	2.3±0.3	2.1±0.3	1.2±0.3
20~50 mm	486±4	8.3±0.8	0.49±0.08	2.1±0.3	2.0±0.3	1.0±0.3
50~100 mm	491±3	8.5±0.1	0.40±0.06	1.7±0.2	1.8±0.3	0.8±0.3
> 100 mm	493±6	7.1±0.9	0.31±0.05	1.5±0.2	2.0±0.5	0.6±0.2
Stump	490±4	6.4±0.5	0.31±0.05	1.4±0.2	2.0±0.2	0.8±0.3

Table 5. Estimated nutrient storage (kg ha^{-1}) among coarse root categories, total aboveground portion, and entire tree in the Fushan forest

Item	C	N	P	K	Ca	Mg
5~10 mm	600 (1.8)[1]	12 (2.4)	0.7 (2.9)	2.8 (2.6)	2.7 (2.1)	1.7 (3.3)
10~20 mm	1900 (6.0)	36 (7.4)	2.1 (8.7)	8.9 (8.2)	8.4 (6.6)	4.8 (9.3)
20~50 mm	5300 (16.8)	91 (18.6)	5.3 (22.0)	23.0 (21.3)	22.0 (17.3)	11.0 (21.2)
50~100 mm	4900 (15.4)	85 (17.4)	4.0 (16.6)	16.9 (15.6)	17.7 (13.9)	8.1 (15.6)
> 100 mm	9600 (30.0)	138 (28.2)	6.0 (24.8)	29.3 (27.1)	38.3 (30.0)	11.2 (21.6)
Stump	9600 (30.0)	126 (25.8)	6.1 (25.0)	27.3 (25.2)	38.3 (30.1)	15.0 (29.0)
Total belowground (Coarse roots)	31,900 (<u>22.9</u>)[2]	488 (<u>23.9</u>)	24.2 (<u>10.5</u>)	108.2 (<u>12.2</u>)	127.3 (<u>12.4</u>)	51.8 (<u>18.8</u>)
Total aboveground	107,700 (<u>77.1</u>)	1552 (<u>76.1</u>)	206.7 (<u>89.5</u>)	779.3 (<u>87.8</u>)	896.6 (<u>87.6</u>)	223.9 (<u>87.2</u>)
Total for tree	139,600	2040	230.9	887.5	1023.9	275.7

[1] Numbers in parentheses are percentages of the total for coarse roots.

[2] Underlined numbers in parentheses are percentages of the total for the entire tree.

non-sample-tree roots gradually decreased and the variation gradually increased. In a coniferous forest in Canada, the amount of coarse roots larger than 10 mm decreased as they extended further away from the bole; however, those roots were able to extend for 2.5 m (Wang et al. 2002). A root's ability to extend varies widely and is often determined by environmental factors. For example, roots are concentrated under the canopy where nutrients are more plentiful (Millikin and Bledsoe 1999). Since the canopy is closed at the sampled sites, a part of the non-sample roots are likely to have been extensions of other trees. Non-sample-tree roots with diameters of 5~10 mm accounted for over 40% of sample roots, which was twice the amount of all other categories. Therefore, it is assumed that these roots belonged to shrubs within 1 m radius of the sample trees. Roots from non-sample trees could be considered to have been underestimated by the regression method and by neglecting the roots of the shrubs. The results from root samples taken outside of 1 m from the bole indicated that the biomass of coarse roots < 50 mm was not related to the distance from bole. This finding differed from the above-mentioned Canadian coniferous forest where the biomass of coarse roots exceeding 10 mm decreased with increasing distance away from the bole (Wang et al. 2002). Furthermore, the results calculated from the soil samples were all higher than the results estimated from the regression method. Even after adding the non-sample-tree root biomass, the results from sample trees were still low in the 5~10-mm root category, and contributed only 45% of the total from the sample outside of 1 m from the bole. Further research is required to determine whether this difference was a result of either the different sampling methods or shrub roots. For the 10~20-mm root category, the difference between the 2 methods was less than 25%. For 20~50-mm roots, the difference was less than 10%. No ≥ 50-mm roots were found in the soil sample, and only limited ≥ 50-mm roots were found in the non-sample roots. This indicated that ≥ 50-mm roots rarely extended beyond 1 m from a tree.

Root biomasses of forest ecosystems vary drastically, from 1.2 to 206.3 Mg ha^{-1} (Cairns et al. 1997). An extreme case is a mountain evergreen tropical forest in Brazil where the root biomass reached 328 Mg ha^{-1} (Santantonio et al. 1977). A global analysis of root distribution indicated that root biomass for tropical evergreen forests is approximately 49 Mg ha^{-1} (Jackson et al. 1996). In Fushan subtropical broadleaf forests, the coarse root biomass reached 65.1 Mg ha^{-1}. Adding the biomass of fine roots (10.1 Mg ha^{-1}) and necromass (0.6 Mg ha^{-1}) (Lin et al. 2005), Fushan had a total root biomass of 75.8 Mg ha^{-1}, which is much higher than the average for tropical evergreen forests. Santantonio et al. (1977) calculated the root biomasses for tropical and subtropical forests. From their research, there were 2 ecosystems that have similar root biomass values to Fushan: a Cambodian evergreen seasonal forest which had a root biomass of 70 Mg ha^{-1} and a subtropical laurel forest which had a root biomass of 78 Mg ha^{-1}. However, the aboveground biomass of these ecosystems both exceeded 320 Mg ha^{-1}, much higher than Fushan's recorded value of 233 Mg ha^{-1}. The reason could be that the average tree heights of these forests are over 25 m (Santantonio et al. 1977), which is much higher than that of trees in the Fushan forest (11 m). Compared with temperate broadleaf forests, Fushan's root biomass is similar to that of the Hubbard Brook Experimental Forest in the US, which was 63.0~73.5 Mg ha^{-1} (Whittaker et al. 1979), and slightly lower than the 80-year-old oak-hornbeam forest ecosystem of Czechoslovakia, which was 78.9 Mg ha^{-1} (Šimonović 1991). A *Cryptomeria japonica* (L. f.) D. Don plantation, a major plantation species in Taiwan, also had a coarse root biomass of 63.4 Mg ha^{-1} at age 30 years, similar to that at Fushan. However, the aboveground biomass was 212.2 Mg ha^{-1} (Lee 1978), which is lower than that of Fushan.

The root/shoot ratio often decreases with increases in age and dbh (Gholz and Fisher 1982, Helmisaari et al. 2002), however, this was not the case for the Fushan forest. This character is similar to *Quercus ilex* in a montane Mediterranean forest in Spain (Canadell and Rodà 1991). The compositions of tree species affect the root/shoot ratio of ecosystems (Cairns et al. 1997). As the sample trees from Fushan are comprised of many tree species, this may have been the main reason that the root/shoot ratio was not related to dbh. Most of the root/shoot ratios in the world's forest ecosystems ranged from 0.20 to 0.30. The world's average root/shoot ratio is 0.26 and the average for the tropical zone is 0.24 (Cairns et al. 1997). The average for Fushan forest was 0.28, higher than the averages of both the world and tropical zone. Generally speaking, sites with lower soil water levels have higher root/shoot ratios (Becker et al. 1999). Since the Fushan forest is humid with frequent rainfall, root growth is not stimulated by soil water. The reason that Fushan had a higher root/shoot ratio could have been a result of lower aboveground biomass. Forests stands mentioned above with similar root biomass values to Fushan, such as the evergreen seasonal forest of Cambodia, a subtropical laurel forest, and Hubbard Brook Forest, all have higher aboveground biomass than Fushan (Santantonio et al. 1977, Whittaker et al. 1979). The Fushan forest is subject to frequent typhoon disturbances, and the damage is most severe to branches and leaves resulting in a lower tree height and aboveground biomass (Lin et al. 1994, Mabry et al. 1998) and hence a higher root/shoot ratio. Furthermore, this root/shoot ratio did not take fine roots into account. If fine roots are included for a total biomass of 75.8 Mg ha^{-1}, the root/shoot ratio will be as high as 0.32. This ratio is still within the range for the *Q. douglasi* forest stand in California, in the US, at 0.23 to 0.69 (Millikin and Bledsoe 1999), but lower than the *Q. ilex* forest stand, at 0.37 (Canadell and Rodà 1991).

The C concentration of the various tree components ranged from 47 (small branches) to 50% (leaves) (Table 4). These values are slightly lower than the generally used default value of 50%. This information could be used in evaluating the C storage inventory of subtropical broadleaf forests in Taiwan to minimize uncertainty. Total C storage of the trees was 140 Mg ha^{-1}, which is at the upper level of the range of C storage for tropical forests (46~183 Mg ha^{-1}, Brown and Lugo 1982). If the C storage of fine roots was added (5.4 Mg ha^{-1}, Lin et al. 2005), Fushan trees had a belowground C stock of 37.3 Mg ha^{-1}, which accounted for 26% of the total tree C storage and 35% of the aboveground C storage. Therefore, C accumulation by roots also plays an important role in the subtropical forest ecosystem.

The ranking for accumulated nutrients in coarse roots was similar to that of the aboveground portions, where N was ranked the highest, followed by Ca and K, with Mg and P being the lowest (Lin et al. 1996b). This ranking was also similar to that of a temperate broadleaf forest (Whittaker et al. 1979). Generally, coarse roots for conifers have lower nutrient concentrations (Santantonio et al. 1977). However, the P, K, and Ca concentrations for Fushan coarse roots were similar to those of *Abies amabilis* in Washington State in the US (Vogt et al. 1987). The above-mentioned Hubbard Brook ecosystem ranks low in terms of coarse root nutrient concentrations among temperate broadleaf forests. Comparatively, Fushan only had higher concentrations of Mg. Fushan's N and K concentrations were similar to those of Hubbard Brook, and its P and Ca concentration were lower (Whittaker et al. 1979). The percentage of coarse root nutrients to total nutrients at Fushan was lower than the above-mentioned Hubbard Brook ecosystem (Whittaker et al. 1979); compared with an oak forest of Germany, Fushan had lower levels of N and P, similar levels of K and Mg, and a higher level of Ca in terms of the percentage of nutrient accumulation (Cole and Rapp 1981). In other words, the Fushan forest is similar to temperate broadleaf forests in its nutrient allocation by coarse roots.

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