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PRODUCTION, DISTRIBUTION AND NUTRIENT RETURN OF FINE ROOTS IN A MIXED AND A PURE FOREST IN SUBTROPICAL CHINA *

YANG Yusheng[1 * *], CHEN Guangshui, He Zongming, CHEN Yinxiu & GUO Jianfen
(*Forestry College, Fujian Agriculture and Forestry University*, Nanping 353001, China)
([1]*Post-doctoral Station of Biology, Xiamen University*, Xiamen 360005, China)

Abstract The studies on production, distribution and nutrient return of fine roots (d < 2 mm) in a mixed Chinese fir (*Cunninghamia lanceolata*)-Tsoong' tree (*Tsoongiodendron odorum*) forest and a pure Chinese fir forest at age 27 were carried out in Sanming of Fujian, China. The standing crops of dry matter, N and P in fine roots of the mixed stand were 5.381 t hm^{-2}, 48.085 kg hm^{-2} and 4.174 kg hm^{-2}, 17.4%, 27.2% and 20.0% higher than those of the pure stand, respectively. The fine root production in the mixed forest was up to 4.124 t hm^{-2} a^{-1}, 16.9% higher than that in the pure stand. Fine roots of Chinese fir and Tsoong' tree in the mixed forest both concentrated in the surface soil, and showed a vertical stratification in the subsoil. Compared with those in the mixed forest, fine roots of Chinese fir in the pure forest had a deeper rooting zone, with a lower root density in the superficial soil. The turnover rates of fine roots for Tsoong' tree and Chinese fir in the mixed stand, and Chinese fir in the pure stand, were 1.16, 0.96 and 0.95, respectively. The undergrowth species had higher root turnover rates than their respective tree layers (1.46 in the mixed forest and 1.52 in the pure stand). The annual mortality, annual return of N and P of fine roots in the mixed forest amounted to 2.119 t hm^{-2}, 18.559 kg hm^{-2} and 1.565 kg hm^{-2}, 1.21, 1.23 and 1.14 times as much as that in the pure forest respectively. Bulk density, moisture content, total N and humic C were strongly correlated with fine root density along the soil profile in the two forests, with total N giving the highest coefficients of determination. Fig 1, Tab 4, Ref 32

Keywords fine root; net production; vertical distribution; nutrient return; soil factor
CLC S718

杉木观光木混交林和杉木纯林群落细根生产力、分布及养分归还 *

杨玉盛[1 * *] 陈光水 何宗明 陈银秀 郭剑芬
(福建农林大学林学院 南平 353001)
([1] 厦门大学生物学博士后流动站 厦门 360005)

摘 要 研究了福建三明27 a生杉木观光木混交林和杉木纯林群落细根(d< 2 mm)的生产力、分布和养分归还.结果表明,混交林细根生物量、N、P养分现存量分别为5.381 t hm^{-2}、48.085 kg hm^{-2}和4.174 kg hm^{-2},分别比杉木纯林增加17.4%、27.2%和20.0%.混交林细根的年净生产力达4.124 t hm^{-2} a^{-1},比纯林高出16.9%.混交林杉木和观光木细根均在表层土壤富集,而在较深层土壤两者分布具镶嵌性;与混交林杉木相比,纯林杉木土壤表层细根量较少,最大分布层次下移.混交林中观光木细根的周转速率为1.16,杉木为0.96和0.95;而林下植被层细根周转速率(1.46～1.52)均高于相应的乔木层.混交林细根的年死亡量、N和P养分年归还量分别达2.119 t hm^{-2}、18.559 kg hm^{-2}和1.565 kg

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* *通讯作者 Corresponding author (Tel: 0599-8504071; E-mail: ffcyys@public.npptt.fj.cn)

hm^{-2}, 分别是纯林的1.21倍、1.23倍和1.14倍, 其中林下植被细根占有较为重要位置. 对细根分布与土壤性质的相关分析表明, 细根的垂直分布与土壤全N的相关性最强(0.87~0.89). 图1表4参32

关键词 细根; 净生产力; 垂直分布; 养分归还; 土壤因子
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Due to the lack of knowledge on their ecological roles and many difficulties, study on fine roots has been one of the weak fields in forest ecology for a long time. Fine roots represent a functionally important portion of the biomass of forests and are constant in flux, with death and replacement taking place simultaneously. Even though fine roots contribute only a small part of the total stand biomass in forests, their growth and maintenance use a major part of total net primary production[1]. In the last two decades, a large amount of documents on fine root productivities have been accumulated world-widely. However, study on fine roots in relation to production and mortality has seldom been listed on the timetable of Chinese forest ecologists since it is a very laborious task.

It is well known that, on a similar substrate, different tree species may differ markedly with respect to not only the extension of their coarse root system, but also the abundance and the productivity of their fine roots. Also, to reduce exploitation competition, spatial or temporal separation of the fine root systems and their activities is likely to occur in multi-species communities. However, most of the studies were conducted in monospecific tree stands where intra- but not interspecific competition could be expected[2]. Much less is known about the spatial separation of root systems in mixed forest stands[3].

Fine roots are important sources and sinks for nutrients in terrestrial ecosystems. In view of the higher nutrient concentrations than those in foliage and the relatively shorter life spans across the range of forests, the production, death and decomposition of roots are major processes in the carbon and nutrient dynamics of forest ecosystems[4,5]. In forests, for example, the amounts of carbon and nutrients returned to the soil from fine root turnover may be equal to or exceed those from leaf litter. Thus, soil fertility can benefit very much from the significant amounts of nutrient and organic matter transfers from fine root mortality. However, studies on organic matter and nutrient dynamics in forest ecosystems have been focused mainly on aboveground production, and the role of fine roots in nutrients and organic matter return and soil amelioration is poorly understood.

The purposes of this paper are: (1) to determine fine root biomass, production, mortality and turnover rate, (2) to characterize possible species differences in the vertical distribution of fine roots, (3) to quantify the annual transfers of organic matter and nutrients by fine root mortality, and (4) to estimate the potential effects of soil factors on fine root distribution in a mixed Chinese fir (*Cunninghamia lanceolata*)-Tsoong' tree (*Tsoongiodendron odorum*) forest and an adjacent Chinese fir plantation in Sanming, Fujian, P.R. China.

1 SITE DESCRIPTION

The sites are located at Xiaohu work area of Xinkou Experimental Forestry Farm of Fujian Agriculture and Forestry University, Sanming, Fujian (φ(*N*) 26°11′30″, λ(*E*) 117°26′00″). This area has a subtropical monsoonal climate with an mean annual temperature of 19.1 ℃, an annual precipitation of 1 749 mm, an annual evaporation of 1 585.0 mm, a mean annual relative humidity of 81%, and an frost-free period of around 300 d[6]. The soil is red earth derived from shale. The mixed stand of Chinese fir and Tsoong' tree, and the pure stand of Chinese fir, were both established with seedlings in 1973, with a planting density of 3 000 stems per hm^2. The mixed pattern is strip spacing, with three rows of Chinese fir spaced by one row of Tsoong' tree. At time of survey (at age 27), the pure stand had a density of 1 100 stems per hm^2, with a crown density of 0.80 and a coverage of 95% for undergrowth. The mean tree height and diameter at breast height (DBH) were 19.61 m and 23.6 cm for Chinese fir respectively. The mixed stand had a density of 907 stems per hm^2 for Chinese fir and 450 stems per hm^2 for Tsoong' tree. The mean tree height and DBH were 20.88 m and 25.1 cm for

Chinese fir, and 17.81 m and 17.0 cm for Tsoong' tree, respectively. The crown density was 0.95 and the undergrowth coverage was 80%.

2 METHODS

2.1 Extraction of roots

Three 20 m × 20 m marked plots were established within each of mixed and pure stands. On the 26th day of every other month during January to November in 1999, 10 soil cores per plot, totaled 30 per stand, were collected from surface to a depth of 100 cm at random across each plot using a steel core (6.8 cm diameter). The soil cores then were divided into the soil depths of 0~10, 10~20, 20~30, 30~40, 40~60, 60~80 and 80~100 cm. Soil samples were washed with tap water to remove adhering soil and accompanying organic debris, then the roots of object trees and undergrowth (shrubs and herbages) were detached with magnifying glass, scissors and tweezers etc. At the same time, fine roots (d < 2 mm) were picked up, and separated into live and dead categories according to their respective appearance, color, flexibility and the cohesion between cortex and periderm [7]. The fine roots of object trees were further sorted into three diameter classes (1~2, 0.5~1 and < 0.5 mm). All the roots were oven-dried (80 ℃) to constant weight and weighed. The standing crop of fine roots was calculated using the following formula: the standing crop of fine roots (ρ_A/t hm^{-2}) = dry weight of fine roots per core (m/g) × 10^{-6}/[π(6.8(d/cm)/2]^2 × 10^8.

2.2 Collection of soil samples

Soil samples were collected at each time of root coring at five sampling points following "sigmoid" route across each plot. Each time at each sampling site, six soil rings for determination of soil water-physical properties and three soil samples for analysis of soil chemical properties were collected at three depths: 0~20, 20~40 and 40~60 cm.

2.3 Decomposition experiment

Fine roots of Chinese fir, Tsoong's tree and undergrowth were obtained from the upper 0~20 cm soil layer in the mixed and pure forests by excavating. Root materials of Chinese fir and Tsoong's tree were sorted into three diameter classes: < 0.5 mm, 0.5~1 mm, and 1~2 mm. Thus, there were 7 categories of root samples for mixed forest and 4 for pure forest. 5 g air-dried root sample was confined into a nylon bag (18 cm × 18 cm, 0.25 mm mesh size), and there were 100 bags for each category. The bags were incubated in the soil at a depth of 10 cm in May 1999, and 5 to 6 bags for each category were retrieved after 30, 60, 90, 150, 210, 270, 360, 450 and 540 d at random.

2.4 Chemical analysis

For the determination of N, the root materials were digested in $K_2Cr_2O_7$-H_2SO_4 solution and then N was determined by micro-Kjeldahl technique. Samples for P analysis were wet digested in a mixture of HNO_3, H_2SO_4 and $HClO_4$ solution. Concentration of P was analyzed colorimetrically by a mixture of $(NH_4)_6Mo_7O_{24}$-$KSbOC_4H_4O_6$-$C_6H_8O_6$ [8]. Determination of soil physical and chemical properties used the same procedures previously described by Yang *et al*. (1994) [9].

2.5 Calculation

Fine root production was estimated by the Maximum-Minimum method using these following formulas: $M = M_{max} - M_{min} + D$, $P = P_{max} - P_{min} + M$, $T = P/Y$, Where M, P, D and T represent annual mortality, production, decomposition and turnover rate of fine roots, respectively. M_{max} and M_{min} represent the maximum and minimum of current biomass of dead roots in a year, while P_{max}, P_{min} and Y stand for the maximum, minimum and average of the standing crop of living root in a year, respectively [10].

The data on the standing crop of fine roots for each species at all sampling date in 1999 were pooled according to the same soil depth, then the vertical distribution of fine roots for each species was analyzed based on the mean value of each depth.

The standing crop of nutrient in fine roots was calculated as the product of the standing crop of dry mass and the nutrient concentration. Annual nutrient return from fine root turnover was estimated as the product of annual root mortality and the mean nutrient concentration in fine roots in a year.

For each sampling date, the data on fine root biomass and soil properties in each forest were pooled according to the same depth (0~20, 20~40 and 40~60 cm) and plot. Thus, we got a set of 54 data for root density and for each soil index in a forest in a year. A linear regression analysis was then made between root density and each soil index.

Tab 1 The standing crop of dry matter, N and P in fine roots ($\bar{x} \pm s$)

Forest type	Species	Root diameter	Live root			Dead root			Gross product		
			Dry weight (ρ_A/t hm^{-2})	N (ρ_A/kg hm^{-2})	P	Dry weight (ρ_A/t hm^{-2})	N (ρ_A/kg hm^{-2})	P	Dry weight (ρ_A/t hm^{-2})	N (ρ_A/kg hm^{-2})	P
Mixed stand	Chinese fir	1~2 mm	0.627±0.090	3.604±0.555	0.210±0.025	0.232±0.034	1.261±0.173	0.071±0.011	0.859±0.142	4.865±0.642	0.281±0.040
		0.5~1 mm	0.439±0.051	3.018±0.380	0.180±0.018	0.162±0.020	1.051±0.118	0.062±0.008	0.601±0.081	4.069±0.439	0.242±0.028
		<0.5 mm	1.623±0.188	14.913±1.858	0.890±0.087	0.728±0.087	6.625±0.737	0.391±0.049	2.351±0.314	21.538±2.300	1.281±0.148
		subtotal	2.689±0.371	21.535±3.196	1.281±0.149	1.122±0.161	8.937±1.184	0.524±0.078	3.811±0.606	30.472±3.876	1.805±0.249
	Tsoong' tree	1~2 mm	0.110±0.013	0.849±0.112	0.107±0.011	0.051±0.006	0.370±0.043	0.043±0.006	0.161±0.023	1.219±0.138	0.150±0.018
		0.5~1 mm	0.091±0.014	0.987±0.159	0.078±0.010	0.039±0.006	0.409±0.059	0.029±0.005	0.13±0.022	1.396±0.193	0.107±0.016
		<0.5 mm	0.389±0.053	6.056±0.890	0.527±0.061	0.133±0.019	1.836±0.241	0.152±0.022	0.522±0.082	7.892±0.994	0.679±0.093
		Subtotal	0.590±0.071	7.892±1.016	0.712±0.072	0.223±0.028	2.615±0.301	0.224±0.029	0.813±0.112	10.507±1.160	0.936±0.112
	Underground vegetation	<2 mm	0.593±0.080	5.593±0.814	1.149±0.131	0.164±0.023	1.513±0.197	0.284±0.041	0.757±0.118	7.106±0.887	1.433±0.194
	total								5.381±0.783	48.085±6.126	4.174±0.510
Pure stand	Chinese fir	1~2 mm	0.635±0.062	3.636±0.384	0.213±0.026	0.234±0.025	1.267±0.131	0.072±0.009	0.869±0.098	4.903±0.502	0.285±0.027
		0.5~1 mm	0.415±0.050	2.858±0.370	0.171±0.026	0.181±0.024	1.175±0.149	0.069±0.010	0.596±0.082	4.033±0.506	0.24±0.028
		<0.5 mm	1.590±0.177	14.603±1.752	0.875±0.123	0.656±0.080	5.654±0.664	0.336±0.045	2.246±0.286	20.257±2.355	1.211±0.132
		Subtotal	2.640±0.329	21.097±2.835	1.259±0.197	1.071±0.147	8.096±1.065	0.477±0.072	3.711±0.530	29.193±3.801	1.736±0.211
	Underground vegetation	<2 mm	0.675±0.090	6.707±0.966	1.374±0.231	0.198±0.029	1.907±0.269	0.368±0.060	0.873±0.134	8.614±1.202	1.742±0.227
	total								4.584±0.719	37.807±5.187	3.478±0.458

3 RESULTS

3.1 Biomass and nutrient content in fine roots

The mixed forest had a higher fine root biomass than the pure forest (5.381 t hm^{-2} vs. 4.584 t hm^{-2}, $P<0.01$). The fine root biomass/necromass ratios for various diameter classes of both Chinese fir and Tsoong' tree were about 7/3. The N and P contents in fine roots in the mixed stand were 48.085 kg hm^{-2} and 4.174 kg hm^{-2} respectively, 27.2% and 20.0% higher than that in the pure stand (Tab 1). The undergrowth vegetations accounted for 14.1% of dry matter, 14.6% of N amount and 34.3% of P amount in fine roots in the mixed forest, respectively, compared with the corresponding values of 19.0%, 22.8% and 50.1% in the pure stand (Tab 1). For fine roots of both Chinese fir and Tsoong' tree, above 60% of the biomass, N and P contents were contributed by the roots of less than 0.5 mm in diameter.

3.2 The vertical distribution of fine roots

Fine root density of Chinese fir in the mixed stand decreased with the increase of soil depth, and 59.7% of the fine roots were concentrated in the upper 0 ~ 20 cm layer but only 5.4% occurred in soil deeper than 80 cm. Fine roots of Tsoong' tree were highly concentrated in the upper 0 ~ 10 cm layer with a proportion of 56.0%, then decreased with the increase of soil depth to the minimum in the depth of 30 ~ 40 cm, and again increased in the soil layer of 60 ~ 80 cm (Fig 1a). It can be seen that the fine roots of the two species in the mixed forest show a vertical stratification in the 10 ~ 80 cm soil layer. The root density of Chinese fir in the pure stand peaked in the depth of 10 ~ 20 cm, and decreased thereafter with the increase of soil depth, with 47.3% of the fine roots being detected from the surface to the depth of 20 cm (Fig 1a).

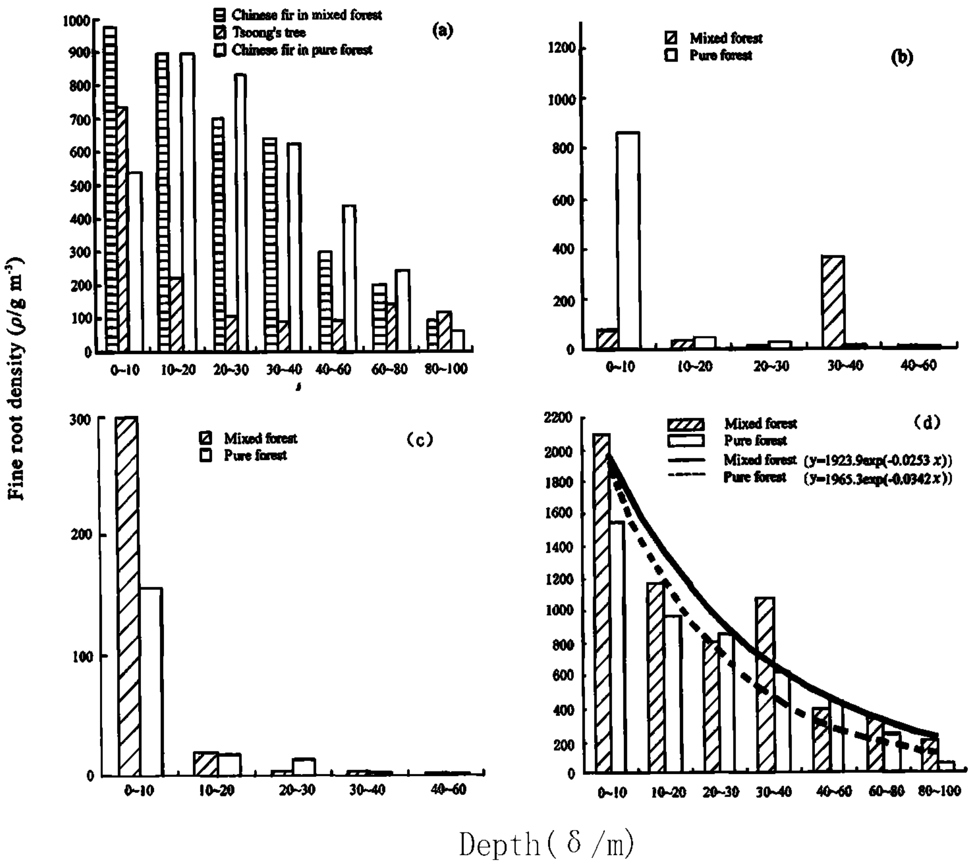

Fig 1　Vertical distribution of fine roots in the mixed and pure forests
(a) Vertical distribution of fine roots of tree species; (b) Vertical distribution of fine roots of shrub species; (c) Vertical distribution of fine roots of herbage species; (d) Vertical distribution of total fine roots

Fine roots of the shrubs in the mixed forest were rare in soil layer of 0 ~ 30 cm, and reached a maximum in the 30 ~ 40 cm layer, with a percentage of 74.0%, while those in the pure forest were packed in the soil layer of 0 ~ 10 cm, with a high percentage of 91.1% (Fig 1b). Fine roots of the herbages in the mixed and pure forests were both concentrated in the 0 ~ 10 cm layer, with a proportion of 90.9% and 81.3% respectively, then decreased rapidly in the deeper layer (Fig 1c).

The densities of total fine roots in the mixed and pure forest were both highest in the depth of 0 ~ 10 cm, and decreased gradually with the increase of soil depth except for an increase at the depth of 30 ~ 40 cm in the mixed forest (Fig 1d). About 49.2% of total fine roots occurred in the 0 ~ 20 cm soil layer in the mixed forest, compared with 44.5% in the pure forest.

3.3　Annual fine root production and nutrient return

Annual net production of fine roots in the mixed stand was up to 4.124 t hm^{-2}, 16.9% higher than that of pure stand (Tab 2). The annual turnover rate of Tsoong' tree was 1.16, compared with 0.96 of Chinese fir ($P < 0.05$). Undergrowth had a higher turnover rate of fine roots than its respective tree stratum ($P<0.05$). The annual turnover rate of total fine roots in mixed stand was 1.07, being similar to that in the pure stand (1.06; $P>0.1$).

Tab 2 Annual turnover rate, mortality and annual return of nutrients of fine roots ($\bar{x}\pm s$)

Items	Mixed stand					Pure stand		
	Tree stratum			Undergrowth	Total	Tree stratum	Undergrowth	Total
	Chinese fir	Tsoong' tree	Subtotal					
Turnover rate	0.96±0.10	1.16±0.14	1.02±0.10	1.46±0.16	1.07±0.13	0.95±0.09	1.52±0.17	1.06±0.11
Annual prodution	2.569±0.436	0.687±0.101	3.256±0.503	0.868±0.144	4.124±0.579	2.504±0.372	1.024±0.163	3.528±0.533
Annual mortality (ρ_A/ t hm^{-2})	1.461±0.209	0.348±0.054	1.809±0.219	0.310±0.046	2.119±0.291	1.519±0.234	0.375±0.062	1.894±0.250
Annual return of N (ρ_A/ kg hm^{-2})	11.529±1.334	4.17±0.520	15.699±.537	2.860±0.344	18.559±2.065	11.503±1.433	3.612±0.482	15.115±1.614
Annual return of P (ρ_A/ kg hm^{-2})	0.675±1.414	0.353±0.551	1.028±1.629	0.537±0.364	1.565±2.189	0.678±1.519	0.697±0.511	1.375±1.711

In the mixed stand, annual mortality of fine roots, and the return of N, P, amounted to 2.119 t hm^{-2}, 18.559 kg hm^{-2} and 1.565 kg hm^{-2}, being 1.21, 1.23 and 1.14 times as much as that in the pure stand, respectively (Tab 2). As far as the percentage of nutrient return through fine roots turnover in mixed stand is concerned, Chinese fir accounted for 62.1% of total N return and 43.1% of total P return, and Tsoong' tree accounted for 22.5% and 22.6%, and undergrowth accounted for 15.4% and 34.3% respectively. Correspondingly, 76.10% of total N return and 49.3% of total P return were contributed by Chinese fir, and 23.9% of N and 50.7% of P were contributed by undergrowth in the pure forest. For both tree species, 70% of annual nutrient return via fine roots was contributed by those <0.5 mm in diameter.

Tab 3 Fine root density and soil factors in the mixed and pure forests ($\bar{x}\pm s$)

Stand	Depth (δ/cm)	Root density	Bulk density	Non-capillary porosity	>0.25 mm waterstable aggeregate	Moisture content	Humic C	Total N	Total P	Hydrolysable N	Available P	pH
		ρ/g m^{-3}		w/%			w/mg kg^{-1}					
Mixed forest	0~20	1612 ±35.2	1.21 ±0.05	10.24 ±0.50	25.96 ±2.37	32.911 ±4.461	8.595 ±0.416	1.18 ±0.02	0.252 ±0.005	106.8 ±4.9	5.42 ±0.40	5.23 ±0.25
	20~40	915.7 ±22.0	1.336 ±0.015	9.73 ±0.603	23.38 ±2.284	28.529 ±3.829	5.652 ±0.702	0.747 ±0.031	0.238 ±0.010	73.5 ±4.041	3.44 ±0.200	4.88 ±0.11
	40~60	341.7 ±35.4	1.373 ±0.016	8.45 ±0.351	21.34 ±1.249	27.307 ±3.107	3.67 ±0.153	0.447 ±0.010	0.211 ±0.021	56.91 ±6.557	2.31 ±0.150	4.83 ±0.09
Pureforest	0~20	1260.5 ±76.9	1.221 ±0.015	6.56 ±0.351	18.21 ±2.278	26.488 ±4.835	6.326 ±0.251	1.03 ±0.112	0.195 ±0.014	86.21 ±2.646	4.92 ±0.306	4.87 ±0.126
	20~40	748 ±26.5	1.421 ±0.038	5.77 ±0.420	16.85 ±2.354	24.344 ±3.451	3.581 ±0.173	0.58 ±0.028	0.17 ±0.005	55.62 ±5.000	3.28 ±0.252	4.82 ±0.081
	40~60	438 ±20.0	1.534 ±0.068	3.83 ±0.252	14.24 ±2.133	23.021 ±3.739	2.745 ±0.289	0.367 ±0.013	0.165 ±0.009	49.2 ±3.215	1.06 ±0.500	4.9 ±0.146

Tab 4 Correlation coefficients (r) between soil factors and fine root density in the mixed forest and pure forest

Stand	Indice	Bulk density	Non-capillary porosity	>0.25 mm waterstable aggregate	Moisture content	Humic C	Total N	Total P	Hydrolysable N	Available P	pH
Mixed	r	−0.7760	0.6817	0.5768	0.6817	0.8416	0.8904	0.4109	0.6369	0.5566	0.4153
forest	F	9.4603**	6.3073*	4.8231*	5.5491*	13.032**	17.9287**	3.9905	4.754*	3.505	3.9731
Pure	r	−0.7216	0.7209	0.6267	0.6542	0.8166	0.8689	0.3769	0.6424	0.4792	0.3301
forest	F	7.5875**	5.9707*	5.5993*	4.7672*	11.0133**	15.7211**	3.5457	4.6639*	3.9611	3.4493

$n=54$; $F_{0.05(1,54)}=4.018$; $F_{0.01(1,54)}=7.13$; $^{*}P<0.05$, $^{**}P<0.01$

3.4 Effects of soil factors on root distribution

The fine root densities and soil chemical and physical factors in both of the two forests are listed in table 3. The fine root density are significantly correlated with the soil factors except for the total P, available P and pH, and the highest coefficients are shown with the total N and humic C (Tab 4).

4 DISCUSSIONS

4.1 Biomass and nutrient content in fine roots

The observation of a higher fine root biomass in the mixed forest than that in the pure forest was in lined with the finding of Liao *et al*. (1995) for a mixed forest of Chinese fir and *Michelia macclurei* and a pure Chinese fir plantation in Huitong [11], which may be an important cause for the higher stand productivity in the mixed forest.

A wide range of standing crop of fine roots from 3 ~ 100 t hm^{-2} has been reported by Vogt *et al*. (1986)[12]. However, for forest stands over 10 years of age, the published fine root biomass values for different forest types of the world range between 400 and 6 000 kg hm^{-2}[13]. The annual mean fine root biomass in our study lies in the middle of the global range. Also, our values are comparable to those reported for a Chinese fir-*Michelia* macclurei mixed forest and a pure Chinese fir forest in Huitong in north subtropics [11]. With respect to total (above- and below-ground) stand biomass, fine roots ($d < 2.0$ mm) represented a relatively small proportion in both of the forests we studied: 2.1% of total biomass in the mixed forest and 2.3% in the pure forest. Similar values have been found by numerous other researchers in a wide array of forest types [14, 15].

The proportions of the dead to total fine root biomass in our studies were less than those observed in most of plantations (45% ~ 80%) [1, 16, 17], but they were similar to those reported by Liao *et al*. (1995) [11]. Several factors may explain the observed differences in the proportion of dead to total fine root biomass: (i) seasonal time of sampling: dead fine root biomass may fluctuate considerably throughout the season; (ii) the age of the stand; (iii) nutrient status of the site; and (iv) moisture and temperature status of the site.

The contribution of different diameter classes of fine roots to total fine root biomass and turnover in forests differs greatly. The percentages of roots < 0.5 mm in diameter in total root (< 2 mm) biomass observed in our study are similar to other studies. Hendrick *et al*. (1993) reported that the percentage of the total fine root (<2 mm) biomass accounted for by roots < 0.5 mm in diameter was higher than 70% [15]; McClaughterty *et al*. (1982) showed that the mass of roots < 0.5 mm represented about one half to two thirds of the total mass of all roots < 3.0 mm [10]. It suggested that roots < 0.5 mm were the main pool of dry matter for fine roots.

Observations on fine roots of undergrowth have seldom been conducted separately, thus, their contributions to root turnover and nutrient cycle remains unclear. Finer *et al*. (1997) found that understorey species accounted for 20% ~34% of the root biomass [18], which was a little higher than that in our study (14.1% in mixed forest and 19.0% in pure forest). The contribution of understorey species to total fine root biomass is correlated with tree canopy status and changes in understorey light availability [18]. A higher value in the pure forest might be the result of a higher undergrowth coverage (0.95 vs. 0.80), which is due to the lower canopy density (0.80 vs. 0.95).

4.2 Vertical distribution

Root partitioning among co-existing species is still poorly understood, but a recent paper by Brisson *et al*. (1994) has shown that there exists a strong intraspecific competition for rooting space for creosotebush (*Larrea tridentate*) shrubs in the Chihuahuan desert of New Mexico, USA [19]. The spatial distribution of plant roots in the soil is a complex dynamic process that changes in response to the changing morphological, physiological and ecological state of plants and in response to the spatial and temporal distribution of soil resources [19].

Our data show that the two co-existing tree species in the mixed forest differ clearly with respect to root distribution along the soil profile in a shared soil volume (Fig 1a). This is consistent with the findings of a vertical stratification of the fine roots of two co-existing tree species in the mineral soil under a mixed Pinus-Picea and a Pinus-Fagus stands [2]. In a mixed oak-beech forest, Buttner *et al*. (1994) found that oak fine roots were more superficially distributed than beech roots in the organic layers, indicating a vertical stratification of the root systems of the two species [3]. Our results showed that the vertical stratification existed not only between trees, but also between trees and undergrowth species (Fig 1a, b, c). The different proportion of roots found in the different soil layers among species could be seen as an acclimatization for the coexistence of different plant species in order to minimize competition for water and nutrients[18].

The fine roots of the two tree species in the mixed forest were both concentrated at surface soil of 0 ~ 20 cm, especially those of Tsoong' tree, which may be due to the more accumulation of nutrient in surface soil of mixed stand. A reduction in abundance of fine roots for Tsoong' tree in deeper soil indicated the weakness of this species in competition for nutrients with Chinese fir when there existed a nutrient depression, especially in 20 ~ 40 cm soil layer.

Numerous studies[1, 2] have shown that the majority of forest tree roots are located in the upper 50 cm of a soil profile with most of the absorbing roots in the top 20 cm. Similar results were obtained during this study for Chinese fir and Tsoong' tree in the mixed forest. Several reports stated that high concentration of fine roots in the surface soil layers of the forest is related to higher nutrient concentrations and more moisture retention because of plant litter on the surface soil, particularly during periods of active growth [1]. The leaf litter forms a shelter for the surface roots by providing a moist microclimate for the development of new roots. Further, a shallow-rooted system was adapted for the uptake of nutrients from detritus, stemflow and rainfall as implied in the direct nutrient cycling and nutrient trapping theories. However, Buttner *et al*. (1994) reported that the superficial distribution could be a consequence of the highly acidic soil profile which forces the trees to concentrate fine root growth in the nutrient-rich organic horizons [3].

In the pure forest, however, the bulk of fine roots of Chinese fir occurred at a deeper depth than those in the mixed forest. The subsoil colonization of fine roots in the pure forest may be due to one or more of the following: (i) the athelopathic substances produced by the litter of Chinese fir in forest floor; (ii) the competition from fine roots of shrubs. The decomposition product of the mixture of fallen litter of Chinese fir and Tsoong's tree was likely to be less or no harmful to the growth of fine roots in the mixed forest. A low crown density in the pure forest increased the light availability for undergrowth shrub species, thus, a strong belowground competition between shrubs and Chinese fir occurred in the superficial soil layer. Liao *et al*. (2001) found that the distribution of fine roots of Chinese fir got deeper in the soil layer with the increase of replanting generations [20]. They owed this perology to soil degradation resulted from the management disturbances such as harvesting, slash, burning, etc. Following a cycle of slash and burn land preparation, losses of nutrients occurred, and inorganic ions were susceptible to leaching. Thus, the development of a superficial fine-root system was certainly important in nutrient conserving, especially in the repeating monoculture of Chinese fir.

A negative exponential equation fits the declining pattern of root density with the increase of soil depth very well for both of the two forests (Fig 1d). A negative exponential distribution of fine root biomass density along the soil profile was also observed in other studies [21 ~ 23].

4.3 Annual fine root production and nutrient return

Our estimates of fine root production lies in the range of 1.4 t hm^{-2} to 11.5 t hm^{-2} obtained from worldwide forest ecosystems [16]. Although fine roots contribute only a very low proportion to total stand biomass, they account for 30% ~ 80% of total stand net primary production [1, 12, 24]. In this study, though fine roots occupied only 2.1% ~ 2.3% of the total stand biomass, they accounted for 20.9% ~ 22.9% of the total stand net primary production [25], which was higher than those in the broad—leaved Korean pine forest of Changbai mountain (19.4%) [26], in monsoon broad-leaved evergreen forest (16.8%) and in coniferous and broad-leaved mixed forest in Dinghu mountain (17.4%) [27]. The variations therein may be related to the difference in site conditions and tree species.

Fine root turnover was related to a nutrient absorptive strategy, that is, new roots should occur frequently at a new position as a substitution for senescing roots to meet with the variational status of soil water and nutrient in prevention of excessive respiratory consumption of ineffective roots [28]. It was reported that differences in turnover rate of fine roots among species were related to biological characteristics, climatic conditions, life span and disturbance from forest managements [11]. It can be seen from table 2 that the turnover rates for both Tsoong' tree and Chinese fir fell into the upside of the range of 0.5 ~ 1.20 reported in other studies [29], which showed that both of the two species in the middle-subtropics had a relative high fine roots turnover rate.

It is widely recognized that the turnover and decomposition of fine roots may contribute substantially more to soil carbon and nutrient pools than those of aboveground litter-fall [12, 14, 15]. Researches showed that annual input of C via fine roots（d< 2 mm）accounted for 25% ~80% of total soil C pool [10]. Hendrick *et al*.（1993）reported that, in two sugar maple forests, fine root turnover dominated nutrient inputs to the soil, accounting for approximately 48% ~58% of N cycled annually [15]. In some ecosystems, the input of nitrogen to soil through fine roots turnover had been reported as 18% ~58% greater than through litterfall aboveground [12]. Li *et al*.（1998）reported that N return from fine root accounted for 49.5% of the total annual N return in stand, 3.1% more than that of litterfall, 42.3% P and 28.9% Mg, slightly less than those of litterfall [30].

In this paper, annual fine root mortality in mixed stand and pure stand were 31.4% and 27.8% of annual litterfall above ground, respectively. Annual return of N, P from fine roots of mixed stand accounted respectively for 38.3% and 67.4% of those from litterfall. It was showed that nutrient return from fine roots was an important source to the soil nutrient pool, especially for P.

Surprisingly, roots of <0.5 mm in diameter accounted for a large proportion of the carbon and nutrients in fine root standing crops, as well as fine root production and mortality. These roots played a major role in the carbon and nutrient cycles of plantation forests, and care should be taken to fully recover very fine roots in future studies.

4.4 Effects of soil factors on root distribution

Soil conditions can adversely affect root growth and in some circumstances can reduce crop yield, so much attention has been directed towards understanding the mechanisms underlying these responses. This has also led to a greater recognition of the interactions between soil factors and root growth. However, the influence of soil factors on root growth remains unclear. This may be attributable to the lack of knowledge on soil conditions in different studies.

The soil where fine roots occurred densely might become more porous because of the mechanical penetration during growth periods of fine roots and the plenty of small root pores remained after root disappearance; inversely, more porous soil is certainly suitable for fine root growth. In addition, the soil humus produced by root decomposition and root excretion is a good agglutinant for soil, especially for subsoil, to form aggregates. These were confirmed by the significant correlations of root density with bulk density, non-capillary porosity and the content of >0.25 mm water-stable aggregate（Tab 4）. A negative correlation between root density and bulk density was also reported elsewhere. Shierlaw *et al*.（1984）reported that the root lengths of annual ryegrass and maize were decreased by half when the soil bulk density increased from 1 200 g cm^{-3} to 1 550 g cm^{-3} [31].

Attempts to correlate tree root activity to soil water availability have yielded controversial results. Our results were similar to Persson（1983）and Ares *et al*.（1992）who found a negative impact of water shortage on tree root biomass, root growth [1~2]. However, this contrast with studies that there are minor or no reduction of root activity or biomass of fine root under the condition of water shortage [21]. According to Mallonen *et al*.（1998）, soil pH can exert a great influence on root distribution [17]. They found that the solubility of Al increases sharply in acid soils at pH values below 5.5, and can cause toxic effects and poor root growth. But no significant correlation between root density and soil pH value has been observed in our study though most of the pH values less than 5.0.

Ares *et al*.（1992）and Heilman *et al*.（1994）both found [2, 32] that, among soil factors, the organic matter content provided the best correlation with root density. A very strong correlation between root density and humic C was also detected in our study. This may explain the frequent occurrence of fine roots in combination with organic detritus, the relatively dense distribution of fine roots in cumulic soils as well as the more sharp decrease in soils with less organic matter content at lower depths.

How the soil nutrients can affect the root distribution has seldom been done. Heilman *et al*.（1994）reported that the distribution of fine roots in the stratified soil profile was correlated with soil Kjeldahl N with a determination coefficient of 0.73 [32]. Our study found a correlation of root density with soil total N and hydrolysable N, with the total N showing the best correlation（Tab 4）. It implied that fine root had strong tropisms for soil N, and their growth might be restrained in soils where there is low N availability. However, no significant effect of soil total P or available P on root distribution has been detected in our study. This is out of expectations in view that P availability has been usually considered as an important factor that restrict tree growth.

From our results, it can be deduced that, in general, the growth or distribution of fine roots in the subtropical mountainous area can be predicted by a combination of soil bulk density, N availability, humic C and moisture content. However, how can this prediction run well needs a vast of further studies.

References

1 Persson H. The distribution and productivity of fine roots in boreal forests. *Plant &Soil*, 1983, **71**: 87~101

2 Ares A, Peinemann N. Fine-root distribution of coniferous plantations in relation to site in southern Buenos Aires, Argentina. *Can J For Res*, 1992, **22**: 1575~1582

3 Buttner V, Leuschner C. Spatial and temporal patterns of fine root abundance in a mixed oak-beech forest. *For Ecol Manag*, 1994, **70**: 11~21

4 Meier CE, Grier CC, Cole DW. Below and above ground N and P use by *Abies amabilis* stands. *Ecology*, 1985, **66**: 1928~1942

5 Nambiar EKS. Do nutrients retranslocate from fine roots? *Can J For Res*, 1987, **17**: 913~918

6 Chen GS(陈光水), Lin RY(林瑞余), Lu JM(卢镜铭), Chen YX(陈银秀), Yang YS(杨玉盛). Seasonal dynamics of ash content and caloric value for fine roots of mixed forest of Chinese fir and *Tsoongiodendron odorum*. *J Fujian Colleg For*(福建林学院学报), 2001, **21**(4): 332~335

7 Chen GS(陈光水). Studies on ecology of fine roots in the community of mixed forest of Chinese fir and *Tsoongiodendron odorum*: [Master Thesis]. Nanping, China. Fujian College of Forestry(福建林学院硕士学位论文), 2001

8 Department of Science and Technology of the Ministry of Forestry (林业部科技司). The Collective of Forestry Criteria (Ⅲ). Beijing: Chinese Forestry Press, 1992

9 Yang YS(杨玉盛), Li ZW(李振问), Yu XT(俞新妥), He ZM (何宗明). Study on changes of soil fertility as affected by the replacement of broad-leaved stand by Chinese fir stand in Nanping. *Acta Phytoecol Sin*(植物生态学报), 1994, **18**(3): 236~242

10 McClaugherty CA, Aber JD. The role of fine roots in the organic matter and nitrogen budgets of two forested ecosystems. *Ecology*, 1982, **63**: 1481~1490

11 Liao LP(廖利平), Chen CY(陈楚莹), Zhang JW(张家武). Turnover of fine roots in pure and mixed Chinese fir and Michelia macclurei forest. *Chin J Appl Ecol*(应用生态学报), 1995, **6**(1): 7~10

12 Vogt KA, Grier CC, Vogt DJ. Production, turnover and nutrient dynamics of above- and below-ground detritus of world forests. *Advances in Ecol Res*, 1986, **15**: 303~377

13 Srivastava SK, Singh KP, Upadhyay RS. fine root growth dynamics in teak (*Tectona grandis* Linn. F.). *Can J For Res*, 1986, **16**: 1360~1364

14 Arthur MA, Fahey TJ. Biomass and nutrients in an Engelmann spruce-subalpine fir forest in north central Colorado: pools, annual production, and internal cycling. *Can J For Res*, 1992, **22**: 315~325

15 Hendrick RL, Pregitzer KS. The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. *Can J For Res*, 1993, **23**: 2507~2520

16 Santantonio D, Grace JC. Estimating fine-root production and turnover from biomass and decomposition data: a compartment-flow model. *Can J For Res*, 1987, **17**: 900~908

17 Mallonen K, Helmisaari HS. Seasonal and yearly variations of fine-root biomass and necromass in a Scots pine (*Pinus sylvestris* L.) stand. *For Ecol Manag*, 1998, **102**: 283~290

18 Finer L, Messier C, de Grandpre L. Fine-root dynamics in mixed boreal conifer-broad-leaved forest stands at different successional stages after fire. *Can J For Res*, 1997, **27**: 304~314

19 Brisson J, Reynolds JF. The effect of neighbours on root distribution in a creosotebush (*Larrea tridentate*) population. *Ecology*, 1994, **75**: 1693~1698

20 Liao LP(廖利平), Deng SJ(邓仕坚), Yu XJ(于小军), Han SJ(韩世杰). Growth, distribution and exudation of fine roots of Chinese fir trees grown in continuously cropped plantations. *Acta Ecol Sin*(生态学报), 2001, **21**(4): 569~573

21 Vogt KA, Edmonds RL, Grier CC. Seasonal changes in biomass and vertical distribution of mycorrhizal and fibrous-textured conifer fine roots in 23- and 180-year-old subalpine *Abies amabilis stands*. *Can J For Res*, 1981, **11**: 223~229

22 Cheng W, Coleman DC, Box JE. Root dynamics, production and distribution in agroecosystems on the Georgia piedmont using minirhizotrons. *J Appl Ecol*, 1990, **27**: 592~604

23 Parker MM, Van Lear DH. Soil heterogeneity and root distribution of mature loblolly pine stands in Piedmont Soils. *Soil Sci Soc Am J*, 1996, **60**: 1920~1925

24 Sundarapandian SM, Swamy PS. Fine root biomass distribution and productivity patterns under open and closed canopies of tropical forest ecosystems at Kodayar in western Ghats, South India. *For Ecol Manag*, 1996, **86**: 181~196

25 Chen GS(陈光水), Yang YS(杨玉盛), Liu JB(刘剑斌), He ZM(何宗明), Xie JS(谢锦升). Net primary productivity in mixed forest of *cunninghamia lanceolata and tsoongiodendron odorum*. *Sci Silv Sin*(林业科学), 2001, **37**(Suppl): 143~147

26 Shan JP(单建平)，Tao DL(陶大立)，Wang S(王森)．Fine roots turnover in a broad-leaved Korean pine forest of Changbai mountain. *Chin J Appl Ecol*(应用生态学报)，1993，**4**：241～245

27 Wen DZ(温达志)，Wei P(魏平)，Kong GH(孔国辉)．The productivity and turnover of fine roots of southern subtropical forest in Dinghu Mountains．*Acta Bot Sin*(植物学报)，1999，**23**(4)：36～369

28 Bartsch N. Responses of root systems of young *Pinus sylvestris* and Picea-abies plants to water deficits and soil acidity. *Can J For Res*，1987，**17**：805～815

29 Shan JP(单建平)，Tao DL(陶大立)．Overseas researches on tree fine root. *Chin J Ecol*(生态学杂志)，1992，**11**(4)：4～49

30 Li LH(李凌浩)，Lin P(林鹏)，Xing XR(刑雪荣)．Fine root biomass and production of *Castanopsis eytei* forests in Wuyi Mountains. *Chin J Appl Ecol*(应用生态学报)，1998，**9**(4)：337～340

31 Shierlaw J，Alston L. Effect of soil compaction on root growth and uptake of phosphorus．*Plant & soil*，1984，**77**：15～28

32 Heilman PE，Ekuan G，Fogle D. Above- and below-ground biomass and fine roots of 4-year-old hybrids of *Populus trichocarpa* × *Populus deltoides* and parental species in short-rotation culture. *Can J For Res*，1994，**24**：1186～1192