Distribution of roots and arbuscular mycorrhizal associations in tropical forest types of Xishuangbanna, southwest China

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Abstract

Root distribution and mycorrhizal associations were compared in primary, secondary and limestone forests in Xishuangbanna, southwest China. Soil cores to a depth of 20 cm were collected at random points from four $50\,m^2$ quadrats in each forest type. Arbuscular mycorrhizal (AM) associations were the only form of mycorrhiza found in all forest types. The primary forest was characterized by high root mass, root lengths and AM colonization levels higher than other forest types. In contrast, secondary forests had greater AM fungal spore numbers and specific root length, indicating that plant species in secondary forests achieved a greater degree of soil exploration with less biomass allocation to roots. Root density, AM colonization and AM fungal spore numbers decreased with soil depth in all forest types. Although the correlation between AM colonization levels and spore numbers was insignificant when all forest types were considered together, significant relationships emerged when each forest type was considered individually. AM colonization and spore numbers were correlated with several root variables.
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1. Introduction

Roots are the primary sinks for carbon acquired in terrestrial net primary productivity (Van Noordwijk, 1993). Primary production allocated to below ground is often greater than that allocated to above ground, and annual carbon and nutrient inputs to the soil from roots frequently equal or exceed those from leaves (Schippers and Olff, 2000). A global estimate indicates around 31×10^9 to 83×10^9 Mg of root biomass in tropical forests (Jackson et al., 1997).

Nutrients such as phosphorus, nitrogen or water are important resources that limit plant growth in tropical soils (Jordan and Herrera, 1981). The importance of these below-ground resources increases as plants compete for these scarce resources (Lauenroth and Burke, 1995; Lauenroth and Coffin, 1992). Plants in tropical soils are adapted to these nutrient-poor environments either by increasing their ability to compete for nutrients through association with soil fungi such as mycorrhizal fungi or by reducing losses of nutrients by minimizing their biomass turnover (Alexander, 1989; Berendse and Elberse, 1990). Most plant species in natural ecosystems depend to various extents on the mycorrhizal fungi for the uptake of nutrients and water from the soil to maintain a steady growth. Arbuscular mycorrhizal (AM) fungi are the predominant type of mycorrhizal fungi in tropical soils that associate with

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a wide range of plant species and are assumed to be non-host specific (Smith and Read, 1997). The distribution and role of AM fungi in tropical plant species is well documented (Alexander et al., 1992; Janos, 1980, 1996; Muthukumar and Udaiyan, 2000; Zangaro et al., 2000). Despite the importance of roots and AM fungi in nutrient cycling, resource capture and global biogeochemistry (Jackson et al., 1997), surprisingly little is known about the patterns of rooting or distribution of AM associations in tropical forests.

Although it is important to understand the rooting and mycorrhizal patterns of individual plant species, it is equally important to identify root and mycorrhizal patterns among plant functional types and across large climatic gradients (Gill and Jackson, 2000). Understanding differences in the distribution of roots and mycorrhizas between different forest types might be helpful in modeling the changes in root and mycorrhizal characteristics that influence the standing vegetation, nutrient availability and nutrient dynamics.

Various studies have been performed to record gross features such as the magnitude and distribution of root biomass in a range of tropical forests, although the differences in measurements and sampling techniques often preclude comparisons of functional significance of these observed patterns (Edwards and Grubb, 1977; Huttel, 1975; Klinge, 1973; Stark and Spratt, 1977). Direct examination of function has frequently been restricted to unique features like fine

roots, root mats or ageotrophic roots (Jackson et al., 1997; Sanford, 1987; Stark and Jordan, 1978). Recent changes in forest cover are altering the abundance and distribution of plant functional types, influencing the below-ground patterns of carbon allocation and nutrient cycling. We hypothesized that substantial differences in plant species composition, structure, disturbance and competition levels should accompany differences in root distribution and mycorrhizal patterns. To test this hypothesis we compared the patterns of root distribution and the intensities of mycorrhizal associations in different forest types of Xishuangbanna, southwest China. In addition we also enumerated AM fungal spore populations, which are usually an indicator for propagule distribution in natural soils.

2. Methods

2.1. Study sites

Xishuangbanna is located in southwestern China bordering Laos and Myanmar ($21°09'$–$22°33'$N and $95°58'$–$101°50'$E) (Fig. 1). The climate is monsoonal dominated by the southwest monsoon with most of the rainfall (85%) falling between May and October. The annual mean temperature is $21.7°C$, and during the coldest month (January) is $15.5°C$; annual precipitation is 1221 mm. Xishuangbanna is cooler

Fig. 1. Geographic location of Xishuangbanna.

compared to the typical rainforest zone, and has lower rainfall. However, the foggy days during the dry season increase the humidity and compensate for the lower rainfall (Zhang and Cao, 1995).

2.1.1. Primary forests

The primary tropical seasonal rainforest is one of the most luxuriant forests in Xishuangbanna on the low hills and flats below 1000 m altitude. It is rich in floral diversity and has a complex forest canopy and structure. The canopy is uneven and consists principally of megaphanerophytes over 40 m. The canopy trees usually develop strong buttresses (e.g. *Shorea chinensis*, *Terminalia myriocarpa*, *Pomentia tomentosa*). In the understorey cauliflorus trees occur frequently (e.g. *Baccaurea ramiflora*, *Ficus auriculata*, *Saurauia* spp.). Many species of cryptogams as well as members of Araliaceae, Areceae, Piperaceae, Moraceae and Orchidaceae comprise the epiphytic and strangler flora.

2.1.2. Secondary forests

Abandoned deforested areas after short-term utilization as farmland or plantations result in regeneration of secondary plant communities. These secondary forests are distributed in dry microenvironments with 50–70% canopy coverage. The plant community is mainly composed of *Bauhinia variegata*, *Colona floribunda*, *Callicarpa* spp., *Oroxylum indicum*, *Kydia calycina*, *Mallotus philippinensis* and *Phyllanthus emblica*. *Digitaria sanguinalis* dominates the herbaceous layer. Shrubs and epiphytes are very rare in these forests. The secondary forest in this study was around 40 years old.

2.1.3. Limestone forests

Steep terrain and boulders projecting from the soil characterize the monsoon forests over limestone in Xishuangbanna. The forest canopy is uneven, usually with huge emergent trees such as *Tetrameles nudiflora*. The understorey is relatively sparse because limestone rocks cover a considerable portion of the ground. The limestone forests in Xishuangbanna are represented by *T. nudiflora* and *Celtis wightii* below 800 m. The lime stone forest is >140-year-old.

More detailed description on the forest characteristics and vegetation types are reported elsewhere (Zhang and Cao, 1995).

2.2. Field sampling

Four 50 m^2 quadrats were marked out in the primary, secondary and limestone forests. Ten intact soil cores (each 50 mm in diameter and 200 mm deep) were collected at random locations from each demarcated quadrat at each site during August 2001. Five of the soil cores were used for extracting roots and the remaining five cores were used for enumerating AM fungal spores and soil characters. The soil cores were separated into 0–10 and 10–20 cm depth sub samples, placed in labeled plastic bags and stored in an insulated container.

2.3. Determination of soil characters

The five soil sub samples (0–20 cm depth) collected from a quadrate was mixed thoroughly and analyzed for pH, total nitrogen (N), phosphorus (P) and extractable potassium (K). Total P was determined colorimetrically with ammonium molybdate and stannous chloride reagents (Jackson, 1971). Total nitrogen (N) was extracted by micro Kjeldahl digestion and measured according to Jackson (1971). Exchangeable potassium (K) was determined after extraction with ammonium acetate (pH 7) and measured on a digital flame photometer (Systronics, Mediflame-127).

2.4. Root extraction and measurements

The roots were extracted from the cores according to Van Noordwijk (1993). The roots were washed from the soil cores immediately upon return from the field. The roots were soaked in water and sieved through 0.3–0.5 mm mesh sieves. The sieved material from the sieves was again mixed with water and the suspended materials decanted. The residues were hand sorted in shallow dishes under water to remove fragments of organic matter and dead roots.

Coarse roots (>2 mm diameter) were separated from fine roots (<2 mm diameter) manually and the diameter and lengths were measured. Root lengths were estimated according to the gridline intersect method (Tennant, 1975) and root diameters were measured using an ocular micrometer. The results are expressed as root length densities per unit volume of soil (cm cm^{-3} soil). The root samples were stored under refrigeration

at all times when they were not being examined or measured. Owing to the high diversity of plant species in the different forest types, we did not attempt to identify roots.

2.5. Estimation of mycorrhizal colonization

One hundred 1 cm root segments were cleared with 2.5% KOH by heating in a water bath at 90 °C for 90 min, followed by acidification in HCl as previously described (Muthukumar and Udaiyan, 2000), stained with trypan blue (0.05%) in lactoglycerol and mounted on microscopic slides for microscopic evaluation at X 200. Incidence of mycorrhizal colonization per sample was estimated as the percentage of root with AM fungal structures (McGonigle et al., 1990).

2.6. Determination of root biomass and specific root length estimation

Both coarse and fine root fractions were oven dried at 60 °C for 72 h and the dry mass was measured. Root biomass results were expressed as dry weight of roots per unit volume of soil (mg cm^{-3}). Specific root lengths (root length per unit of root biomass, cm g^{-1}) were derived from root length density and root biomass for each sample.

2.7. Enumeration of AM fungal spores

Spores were extracted from 100 g of rhizosphere soil using a modification of the wet-sieving technique (sieves 710–38 μm) (Muthukumar and Udaiyan, 2000). Spores were recovered by filtering the sieved material onto filter paper. The filter paper was then spread over a glass plate and intact spores were counted according to morphologically distinct types and recorded as totals per sample under a dissecting microscope. As intact spore types were found, slides were prepared and diagnostic features were recorded. Color and dimensions of intact spores were assessed under the dissecting microscope using incident illumination. Spores were then mounted on microscopic slides in polyvinyl-lactic acid-glycerol (PVLG) with or without Melzer's reagent, covered with a cover glass and carefully crushed by pressing on the cover slip with a mounting needle. Gentle pressure popped

the spores open, followed by more vigorous crushing with a slight lateral movement to dissociate wall layers. The specimens were identified to genus level using published descriptions (Schenck and Perez, 1990; http://invam.caf.wvu.edu). Although some could be identified to species, generally identification of field-collected spores is often unreliable due to the lack of fine taxonomic characters or the presence of few spores. Therefore the occurrence and statistical analysis of AM fungal spores was restricted to total spore counts. For calculations we considered sporocarps or loose multispore groups as one unit to count.

2.8. Data analysis

Means and standard errors were calculated for root biomass, root length density, specific root length, root diameters, AM colonization and spore numbers using average values of plots for each forest type. Correlation was used to assess the relationships between different root and mycorrhizal variables.

3. Results

3.1. Soil analysis

The soil type is a nutrient deficient ferrasol (Table 1). There were differences in soil pH, N, P and K between forest types. Nutrient contents were maximum in primary forest and least in limestone forest.

3.2. Root diameter

Average fine and coarse root diameters were higher in the primary forest than in other forest types (Table 2). The diameter of coarse roots in the 10–20 cm soil horizon was 31–38% higher compared to the surface horizon (0–10 cm). Similarly, the diameter of the fine roots was also 15–36% higher at the 10–20 cm depth compared to the surface 0–10 cm layer.

3.3. Root biomass

Total biomass (coarse and fine fractions combined) of roots was higher in the primary forest ($\bar{X} = 11.27$ mg cm^{-3}) than in secondary forest ($\bar{X} = 8.10$ mg cm^{-3})

Table 1
Means and standard errors for soil characteristics for different forest types in Xishuangbanna

Forest types	pH	Nutrients (mg kg^{-1})		
		Total nitrogen	Total phosphorus	Exchangeable potassium
Primary	7.4 ± 0.01	83.02 ± 1.98	4.43 ± 0.12	98.42 ± 3.99
Secondary	7.6 ± 0.01	79.54 ± 1.52	3.25 ± 0.08	83.93 ± 3.28
Limestone	8.7 ± 0.03	64.06 ± 4.33	2.65 ± 0.10	65.47 ± 2.35

and limestone ($\bar{X} = 3.76$ mg cm^{-3}) forests (Table 2). Total root biomass also differed with depth in the primary forest, but not in the secondary or limestone forest. The differences with depth however were reflected in these forest types when fine and coarse root fractions were considered separately. Coarse root biomass was higher in the 10–20 cm layer, in contrast to fine roots whose biomass was higher at 0–10 cm depth. Coarse roots constituted the major proportion of the root biomass in all the forest types and depths (Table 2).

The biomass of the fine root fraction (0–20 cm) was maximum in the primary forest and least in limestone forest. However, the proportional contribution of fine roots to total root biomass was greatest in limestone forest and least in primary forest.

3.4. Root length density

Fine root fraction constituted approximately 94–99% of the total root length density (root length per unit volume of the soil) in all the forest types (Table 3). Fine root density was higher in primary forests than in secondary and limestone forests. In all the forest types, the fine root densities were higher in the upper 0–10 cm depth than at 10–20 cm. The coarse roots constituted the minor proportion of the total root length density; it was higher in the secondary forest than in other forest types and in the 0–10 cm depth in all the forest types.

3.5. Specific root lengths

The specific root lengths of coarse and fine root fractions differed with forest type and depth (Table 3). In the limestone forest the specific root length of the fine root fraction was 54–63% and the coarse root fraction was 30–572% higher than in other forest types. The

variation with depth of specific root length was similar in all forest types.

3.6. AM colonization and spore numbers

There were differences in the intensity of mycorrhizal colonization and root length colonized by different AM fungal structures (Table 4). Total AM colonization (%RLC) was 17 and 119% higher in the primary forest than in the secondary and limestone forest, respectively. The %RLC and root length with AM fungal structures generally decreased with depth.

Average spore numbers (0–20 cm) varied from 15 to 47 spores 100 g^{-1} soil. In the secondary forest the AM fungal spore numbers were 2–3-fold higher than in the primary and limestone forests. Spores were concentrated in the upper soil horizon (0–10 cm) and decreased with depth. Spores belonging to *Acaulospora*, *Glomus* and *Scutellospora* were identified in the soils of different forest types.

3.7. Relationships between root and mycorrhizal variables

Statistical correlations involving root and mycorrhizal variables from different forest types ($n = 120$) suggest that percentage of root length with arbuscules (%RLA) was negatively correlated with the diameter of coarse and fine roots ($r = -0.37$, $P < 0.001$ and $r = -0.30$, $P < 0.01$). Likewise, AM fungal spore numbers were also negatively correlated with the diameter of coarse ($r = -0.76$, $P < 0.001$; $n = 120$) and fine roots ($r = -0.61$, $P < 0.001$), root lengths ($r = -0.49$, $P<0.001$) and coarse root biomass ($r = -0.32$, $P < 0.001$).

Total root biomass (coarse + fine fractions) was positively correlated with percentage root length with hyphae (%RLH) ($r = 0.63$, $P < 0.001$), vesicles

Table 2
Mean values (with standard errors) for root diameter and biomass characteristics of primary, secondary and limestone forests at Xishuangbanna

Forest types	Root diameter (mm)						Root biomass (mg cm^{-3} soil)					
	Coarse			Fine			Coarse		Fine		Total	
	0–10[a]	10–20[a]	Average[a]	0–10[a]	10–20[a]	Average[a]	0–10[a]	10–20[a]	0–10[a]	10–20[a]	0–10[a]	10–20[a]
Primary	7.47 ± 0.19	10.20 ± 0.97	8.89 ± 0.26	1.52 ± 0.04	1.74 ± 0.08	1.63 ± 0.07	8.38 ± 1.03	10.24 ± 1.01	2.35 ± 0.04	1.57 ± 0.01	10.73 ± 1.32	11.80 ± 2.35
Secondary	4.89 ± 0.97	6.42 ± 0.88	5.66 ± 0.99	1.10 ± 0.06	1.50 ± 0.02	1.30 ± 0.05	5.99 ± 0.57	7.17 ± 0.17	1.95 ± 0.05	1.00 ± 0.01	7.94 ± 1.03	8.27 ± 0.93
Limestone	6.15 ± 0.29	8.49 ± 0.38	7.32 ± 0.83	1.39 ± 0.04	1.65 ± 0.02	1.52 ± 0.02	2.51 ± 0.08	3.07 ± 0.08	1.23 ± 0.02	0.72 ± 0.02	3.74 ± 1.53	3.79 ± 1.62

[a] Depth.

Table 3

Mean values (with standard errors) for root length density and specific root length in primary, secondary and limestone forests in Xishuangbanna

Forest types	Root length density (cm cm^{-3} soil)						Specific root length (cm g^{-1})					
	Coarse		Fine		Total		Coarse		Fine		Total	
	0–10[a]	10–20[a]	0–10[a]	10–20[a]	0–10[a]	10–20[a]	0–10[a]	10–20[a]	0–10[a]	10–20[a]	0–10[a]	10–20[a]
Primary	0.03 ± 0.001	0.02 ± 0.001	1.90 ± 0.01	1.75 ± 0.02	1.93 ± 0.01	1.77 ± 0.02	3.96 ± 1.32	1.91 ± 0.95	844.01 ± 50.56	1128.96 ± 30.15	182.11 ± 10.80	166.90 ± 10.12
Secondary	0.09 ± 0.001	0.07 ± 0.001	1.49 ± 0.02	1.42 ± 0.04	1.58 ± 0.02	1.49 ± 0.04	15.18 ± 2.86	10.60 ± 1.39	770.61 ± 63.15	1315.68 ± 36.83	196.78 ± 15.38	180.14 ± 10.61
Limestone	0.05 ± 0.001	0.04 ± 0.001	1.45 ± 0.10	1.42 ± 0.01	1.50 ± 0.01	1.41 ± 0.01	20.37 ± 2.58	13.22 ± 3.83	1194.58 ± 38.83	2015.14 ± 56.19	406.85 ± 10.31	389.22 ± 11.36

[a] Depth.

Table 4
Mean values (with standard errors) for arbuscular mycorrhizal characteristics of different forest types in Xishuangbanna

Forest types	AM fungal colonization								Spore number ($100 g^{-1}$ soil)	
	%RLH[a]		%RLA[a]		%RLV[a]		%RLC[a]			
	0–10	10–20	0–10	10–20	0–10	10–20	0–10	10–20	0–10	10–20
Primary	18.10 ± 1.38	20.04 ± 1.72	32.12 ± 2.73	12.12 ± 1.39	5.01 ± 1.38	13.01 ± 1.52	62.10 ± 4.38	46.05 ± 5.30	18.12 ± 2.86	12.08 ± 1.32
Secondary	15.01 ± 1.08	9.01 ± 3.58	26.08 ± 2.06	18.15 ± 4.72	12.06 ± 1.26	10.03 ± 1.03	52.65 ± 6.38	37.10 ± 3.05	53.21 ± 4.32	41.25 ± 6.31
Lime stone	12.80 ± 1.38	7.50 ± 3.28	15.31 ± 5.12	3.20 ± 3.33	4.18 ± 1.38	7.12 ± 2.08	31.91 ± 7.93	17.51 ± 6.26	32.08 ± 4.93	23.50 ± 5.38

[a] %RLH, %RLA, %RLV and %RLC, percent root length with hyphae, arbuscules, vesicles and total colonization, respectively.

(%RLV) ($r = 0.44$, $P < 0.001$), %RLA ($r = 0.50$, $P < 0.001$), %RLC ($r = 0.73$, $P < 0.001$) and negatively with spore numbers ($r = -0.28$, $P < 0.01$). In contrast specific root length concentration was significantly and negatively correlated with %RLC ($r = -0.71$, $P < 0.001$), %RLH ($r = -0.48$, $P < 0.001$), %RLA ($r = -0.52$, $P < 0.001$) and %RLV ($r = -0.50$, $P < 0.001$).

4. Discussion

4.1. Root characteristics

The characteristics of roots, which are a major component of tropical forest ecosystems, differed between the forest types studied. The root biomass estimates for the primary forest are 1.5 to 4.9-fold lower than those reported for primary forests from other parts of the world (Hopkins et al., 1996; Klinge and Herrera, 1978). Similarities in root characteristics can be expected with similar species composition and a given set of climatic and environmental variables. So as different plant species develop different adaptations for their survival in a given environment, meaningful comparisons between root characteristics and their distribution in tropical forests under varied environmental conditions are difficult. Further, root biomass production depends on the species composition and ecological conditions (Goff and Ottorini, 2001). However, the root estimates recorded in the secondary forest are comparable to the few estimates for other tropical secondary forests (Berish, 1982; Hopkins et al., 1996; Raich, 1983), but comparisons of secondary forests are also difficult due to the confounding influence of forest age and structure. The relatively high root biomass in the primary forest was a reflection of the increased allocation of resources by the existing plant species to the roots, which is necessary to access nutrients and water for the large aboveground biomass. Lower soil depths (10–20 cm) had consistently higher root biomass and a greater proportion of the root biomass in the coarse fraction.

We found that the diameter of roots tends to increase with depth in all the forest types and speculate that root diameter is an adaptation to the degree of compaction of the soil horizon. Fitter (1996) concluded that thick roots can exert greater force on the soil

and might have greater ability to penetrate compact soils than roots with smaller diameter. The vertical distribution of fine roots was similar to that observed by others (Bruke and Raynal, 1994; Cavalier, 1992; Farrish, 1991; Hendrick and Pregitzer, 1996) with more than half of the fine roots occurring in the top 10 cm. Further, the different forest types in the present study had an average of 17–25% of total root biomass in fine roots in the upper 20 cm of the soil profile. These estimates of root biomass in fine roots are lower than those estimated for the upper 20 cm of deciduous and evergreen tropical forests (42–57%) (Jackson et al., 1997) and Australian forest types (22–32%) (Hopkins et al., 1996). The fine root fraction dominated the root length comprising >95% of the total root length in all forest types. This is in accordance with Hopkins et al. (1996) who also found maximum contribution to root length by the fine root fraction in Australian primary and secondary forests. The high root lengths in the primary forest indicate that the exploration of the soil was more extensive and complete in this forest than in others. Differences were also evident in the root density between depths, with the upper soil horizon (0–10 cm) being thoroughly explored. Since soil water and nutrients are concentrated near the soil surface (Hayes and Seasted, 1989; Sala et al., 1992), the concentration of roots near the soil surface is a critical feature that allows for the acquisition of below-ground resources and consequently plant survival.

The secondary and limestone forest species were more efficient in converting biomass into root fractions as evidenced by the specific root length, when compared to the primary forest. The specific root lengths of secondary and limestone forests were 8 and 128% higher than for the primary forest and especially the specific root lengths in the fine root fraction were 8–63% higher in the primary forest. These results do support the view that species from nutrient-poor habitats are better competitors for nutrients (Elberse and Berendse, 1993; Tilman, 1985). Species in this nutrient deficient soils appear to invest more in root systems as suggested by Gleeson and Tilman (1994) and had higher specific root lengths as suggested by Elberse and Berendse (1993). Typically secondary forest succession is characterized by shifts in the biomass allocation of the plant community (Ewel, 1971). In young secondary forests, relatively more biomass is allocated

to the resource acquiring tissues (roots and leaves) and in the later stages it is allocated more towards structural materials (woody stems and coarse roots) (Guariguata and Ostertag, 2001).

4.2. Mycorrhizal colonization

The high mycorrhizal incidence in the forest types studied here was not unexpected. Most studies on tropical forests have recorded the dominance of AM associations (Alexander et al., 1992; Janos, 1980; Muthukumar and Udaiyan, 2000; St. John and Uhl, 1983; Zhao et al., 2001), with the exceptions of the dipterocarps in Asia (Alexander, 1989) and some legume-dominated forests in Cameroon (Newbery et al., 1988), where ectomycorrhizal associations predominate. The forest types studied here were dominated by AM associations in contrast to the rainforest in North Queensland, Australia, where AM mycorrhizas predominated in the primary forests and ectomycorrhizas in the secondary forests (Hopkins et al., 1996).

The moderate to high total colonization levels (18–62%) reflects the high mycotrophic nature of the plant community in these forest types. A decrease in AM colonization levels and root length with AM fungal structures is consistent with the view that mycorrhizal colonization decreases with depth (Abbott and Robson, 1991). However, this contradicts the results of Ingleby et al. (1997), which failed to detect any decrease in mycorrhizal colonization levels with increasing soil depth in a legume tree plantation in Senegal. Similarly Moyersoen et al. (1998) also failed to find variations in AM colonization levels with soil depth in rainforest in Korup National Park, Cameroon. Further, mycorrhizal variables in the present study were strongly related to root length and their mass. Mycorrhizal colonization in roots occupying a defined volume of soil will depend on a balance between root and fungal activity (Koide, 1993) which is influenced by several factors including soil properties, root phenology, predation, local disturbance and propagule availability (Brundrett, 1991).

The AM colonization levels in the secondary forest were lower compared to the primary forest, indicating the influence of disturbance on mycorrhizas. As the root biomass recovers, it is likely that AM fungal communities will also recover. There are

however, few experimental investigations on mycorrhizal associations during secondary forest succession. It is well-known that land disturbance may decrease fungal communities (Allen et al., 1998) or affect mycorrhizal propagules (Fischer et al., 1994). These few studies do indicate a fungal succession in which some species of AM fungi persist and dominate presumably due to their ability to tolerate various soil conditions (Abbott and Robson, 1991).

4.3. Spore numbers

Spores of AM fungi were concentrated mostly in the soil surface layer (0–10 cm), which supports the view that spore production is at a maximum near the soil surface (Abbott and Robson, 1991; Ingleby et al., 1997). Though the spore numbers were not related to AM fungal colonization levels when all the forest types were considered together; significant relationships emerged when the forest types were considered separately (primary forest: $r = 0.35$; $P < 0.002$, secondary forest: $r = 0.41$; $P < 0.001$ and limestone forest: $r = 0.49$; $P < 0.001$, $n = 40$). This clearly indicates that local environmental conditions override mycorrhizal colonization and spore production in these forests. The primary forest had the lowest spore numbers of all the forest types in spite of high colonization being recorded there. This clearly shows that spores may be relatively unimportant as propagules in this ecosystem. In undisturbed soils or soils with minimal disturbance, colonization of new roots is likely to be achieved primarily via the soil hyphal networks and senescing mycorrhizal roots in the soil (Jasper et al., 1989).

4.4. Soil nutrient effects on root and AM variables

Nutrient pools are important controlling factor in determining the amount of root biomass (especially fine roots) and mycorrhizal association maintained on a site (Brundrett et al., 1996; Vogt et al., 1996). The soils of the primary forest in the present study had the maximum nutrient content followed by soils of the secondary and limestone forests. This is in accordance with studies that have noted an increase in soil nutrients with forest age (Lamb, 1980; Williams-Linera, 1983; Werner, 1984; Silver et al., 1996), but contradicts studies where a decrease has been noted (Uhl

and Jordan, 1984). The amount of nutrients in the soil can change over the course of succession and soil is an important nutrient capital for forest regrowth after clearance (Brown and Lugo, 1990). As vegetation develops, the nutrient levels in the soil at any given time will be a balance between (a) retention of nutrients in biomass, (b) turn over and decomposition of biomass which adds nutrients to the soil, and (c) leaching of nutrients out of the zones of plant root accessibility. The recovery of soil to its previous functions varies with forest type (Brown and Lugo, 1990), soil type (Allen, 1985; Neill et al., 1997) and the type and intensity of past land use (Buschbacher et al., 1988; Neill et al., 1997).

The impact of soil nutrients on root morphology and mycorrhizal associations should not be underestimated, as nutrient uptake by plants is related to the availability of nutrients in the soil. Clearly, roots with greatest interface with the soil have the greatest nutrient uptake potential but this is balanced against the cost to the plant for growing and maintaining roots (Fitter, 1987). Low nutrient availability in the soil has been shown to increase specific root lengths and root fineness (Fitter, 1987). This is evident in the present study where limestone forest with the least soil nutrient levels had the maximum specific root length values reflecting the fineness of the roots produced (Fitter, 1985). Presumably, the high specific root length allows maximum surface area for nutrient uptake. As forests mature and mycorhizas compensate for low nutrient availability, specific root length would be expected to decrease as observed in the present study where primary forest with maximum AM colonization levels had the lowest specific root length values. This observation is further supported by the existence of an inverse relationship between specific root length and AM colonization levels.

The patterns of root distribution and mycorrhizal associations are crucial for our understanding of forest dynamics, as these estimates are important parameters in determining the availability of soil resources to plants. The present study clearly indicated differences in root distribution and intensities of AM association in the three forest types in Xishuangbanna. However, caution must be exercised in the extent of generalizations made concerning root distribution and intensities of AM association in different forest types since our analyses are based upon one forest in each type. Further studies involving more forests of different types and ages would be useful for further understanding of rooting and mycorrhizal patterns in forests of Xishuangbanna.

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