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Mycorrhiza of plants in different vegetation types in tropical ecosystems of Xishuangbanna, southwest China

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Abstract We examined plants growing in four tropical vegetation types (primary forest, secondary forest, limestone forest and a slash and burn field) in Xishuangbanna, southwest China for mycorrhizal associations. Of the 103 plant species examined (belonging to 47 families), 81 had arbuscular mycorrhizal (AM) associations, while three species possessed orchid mycorrhiza. AM colonization levels ranged between 6% and 91% and spore numbers ranged between 1.36 spores and 25.71 spores per 10 g soil. Mean AM colonization level was higher in primary and secondary forest species than in plant species from limestone forests and a slash and burn field. In contrast, mean AM fungal spore numbers of the primary and limestone forest were lower than in the secondary forest or the slash and burn field. AM fungal spores belonging to *Glomus* and *Acaulospora* were the most frequent in soils of Xishuangbanna. AM fungal colonization and spore numbers were significantly correlated to each other and were significantly influenced by vegetation type.

Keywords Mycorrhiza · Arbuscular mycorrhiza · Spore density · Primary forest · Secondary forest · Limestone forest

Introduction

Mycorrhizal fungi are ubiquitous in terrestrial plant communities, associating with the majority of plant species (Smith and Read 1997). It is assumed that plant species belonging to >80% of plant families are mycorrhizal. However, root systems of the majority of these plant species have not been examined for mycorrhizal association. Tree species of forests and woodlands are either ectomycorrhizal or arbuscular mycorrhizal (AM), whilst herbaceous plants and shrubs in shrublands and grasslands can be ericoid, orchid or AM (Smith and Read 1997). Several recent studies have demonstrated that AM fungi are common and ecologically important in tropical ecosystems, and that co-occurring plant species vary considerably in their germination, growth and flowering response to mycorrhizal colonization along a continuum from highly responsive, obligate mycotrophic species to facultatively mycotrophic and non-responsive species (Johnson et al. 1997).

Xishuangbanna is located in southwestern China, bordering Laos and Myanmar (21°09'–22°33'N and 95°58'–101°50' E), in the upper course of the Mekong River. Xishuangbanna harbors some of the greatest diversity of flora and fauna in China and is of great importance in the maintenance of regional biodiversity (Zhang and Cao 1995). It is estimated that about 16% (5000 species) of the higher plant species in China occur in this 0.2% (19,200 km^2) of the total land area (Li et al. 1996). Among the 5000 plant species in Xishuangbanna, 20% of wild plants are directly used by the people. However, there was a decline of 33% (at an average of 20,000 ha $year^{-1}$) in total forest cover between 1950 and early 1990s. This was mostly due to rapid expansion of the local population, irrational exploitation of forest resources and cultivation practices (Cao and Zhang 1996). Although detailed studies of the vegetation, flora and fauna and the biodiversity of Xishuangbanna are available, little is known about the soil microbial community or their interaction with plant species, especially the types and intensity of mycorrhizal associations. Recently Zhao (2000) reported on the AM association of pteridophytes of the Yunnan province in China. Subsequently, the AM status of 112 angiosperms in Xishuangbanna primary forest was reported (Zhao et al. 2001). In that study, only 56% of the 112 species examined were found to be mycorrhizal.

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Because of their assumed importance, a survey of AM association in the tropical rain forest and successional species in various Xishuangbanna vegetation types was performed to compare the intensity of AM colonization and record the influence of vegetation types or plant taxonomic affinities on mycorrhizal status.

Materials and methods

Study sites

The field sites in Xishuangbanna were located in and around the Xishuangbanna Tropical Botanical Garden (XTBG) (21°41' N and 101°25' E) at an altitude of 570 m a.s.l. The climate is monsoonal dominated by a southwest monsoon, with most of the rainfall (85%) falling between May and October. Xishuangbanna is cool compared with a typical rainforest zone and has low rainfall. The annual mean temperature is 21.7°C, the coldest month being January with 15.5°C; the annual precipitation is 1,221 mm. However, foggy days during the dry season increase the humidity and compensate for the low rainfall (Zhang and Cao 1995).

Three forest types and one slash and burn field were chosen as study sites. The forest types include one primary and one limestone forest and two secondary forests. We chose five sample areas at each site.

Primary forest

The primary tropical seasonal rainforest was located 10 km northwest of XTBG and is one of the most luxuriant forests in Xishuangbanna, on the low hills and flats below 1,000 m altitude. It has a rich floral diversity and 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* (Wang Hsie) H. Zhu, *Terminalia myriocarpa* Heurck et Muell.-Arg., *Pometia tomentosa* (Bl.) Teysm. et Binn.]. Cauliflorus trees occur frequently in the understorey (e.g. *Baccaurea ramiflora* Lour., *Ficus auriculata* Lour., *Saurauia* spp.). Many species of cryptogams as well as members of Araliaceae, Araceae, Piperaceae, Moraceae and Orchidaceae make up the epiphytic and strangler flora (Zhang and Cao 1995).

Secondary forests

The secondary forests in this study were around 40 years old and were located within XTBG. Abandoned deforested areas after short-term utilization as farmlands or plantations have resulted in the 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* (Roxb.) Voigt., *Colona floribunda* (Wall. ex Kurz) Craib, *Callicarpa* spp., *Oroxylum indicum* (L.) Vent., *Kydia calycina* Roxb., *Mallotus philippinensis* (Lam.) Muell.-Arg. and *Phyllanthus emblica* L. *Digitaria sanguinalis* (L.) Scop. dominates the herbaceous layer. Shrubs and epiphytes are very rare in these forests.

Limestone forest

Steep terrain and boulders projecting from the soil characterize the monsoon forest over limestone in Xishuangbanna. The forest is located 1 km north of XTBG and the canopy is uneven, usually with huge emergent trees such as *Tetrameles nudiflora* R.Br. The understorey is relatively sparse because a considerable proportion of the ground is covered by limestone rocks. These forests of Xishuangbanna are represented by the formation of *Tetrameles nudiflora* and *Celtis wightii* Planch. on the limestone mountains below 800 m.

Slash and burn field

Forest lands are widely cleared by felling and burning for cultivation. Burning, a common practice in shifting cultivation, releases minerals from the vegetation into the soil. The crops are raised either on a non-rotation basis for 1 year or on a rotation basis for 2–5 years. The lands are then abandoned for 8–12 years, which results in the invasion of weeds (Cao and Zhang 1996). The site in the present study was abandoned 3–4 years ago and was located 15 km northwest of XTBG.

Sample collection

Plant roots and soil samples were collected during August 2001. Care was taken during collection of individual plants that roots could be positively identified as belonging to a particular plant. For this, herbs were usually dug out and samples of trees or shrubs were made usually from saplings if available or the roots were traced back to the stem. Most of the collections were from the primary and secondary forests, with limited collections from limestone forest and the slash and burn field. Roots were gently washed and fixed in FAA (formalin-acetic acid-alcohol) and transported to the laboratory for processing. Rhizosphere soil shaken from roots and adjacent to roots was collected. Soil samples collected from individual plants of a species were packed in polythene bags and stored at 4°C until processing. The soil samples were used for assessing soil chemistry and the enumeration and extraction of AM fungal spores. Plant nomenclature and authorities follow Li et al. (1996).

Preparation of roots and AM assessment

Fixed roots were washed free of FAA and examined under a dissection microscope (×20) for AM fungal spores attached to roots. After examination, the roots were cut into 1-cm fragments, cleared in 2.5% KOH (Koske and Gemma 1989), acidified with 5 N HCl and stained with acid fuchsin (0.5% in lactoglycerol) overnight. Roots that remained dark after clearing were bleached in alkaline H_2O_2 prior to acidification. The stained roots were examined with a compound microscope (×200–400) for AM fungal structures and the percentage of root length colonization was estimated according to a magnified intersection method (McGonigle et al. 1990).

Plant species were classified as consistently and inconsistently mycorrhizal according to Koske et al. (1992). If the root system of each individual of a species examined had mycorrhizal colonization, the species was designated consistently mycorrhizal. If root systems of only some individuals for a species were colonized, the species was classified as inconsistently mycorrhizal, and if every individual root system lacked mycorrhizae, the species was categorized as non-mycotrophic.

Determination of soil characters

Soil pH was determined in 1:1, soil: water soon after the soil samples was brought to the laboratory. The total nitrogen (N), and total phosphorus (P) were determined according to Jackson (1971) and exchangeable potassium (K) was determined after extraction with ammonium acetate (Jackson 1971).

Enumeration and isolation of AM fungal spores

One hundred gram of soil was dispersed in 1 l water and the suspension was decanted through 710- to 38-μm sieves. The residues in the sieves were washed into beakers. The sievates were dispersed in water and filtered through gridded filter papers. Each filter paper was then spread on a petri dish and scanned under a dissection microscope at × 40 magnification and all intact spores (non-collapsed spores with cytoplasmic contents and free from parasitic attack) were counted. Sporocarps and spore clusters were considered as one unit. Intact AM fungal spores were transferred using a wet needle to polyvinyl alcohol-lactoglycerol with or without Melzers reagent on a glass slide for identification. Spores were identified from spore morphology and subcellular characters and compared to original descriptions (Schenck and Perez 1990). Spore morphology was also compared to the culture database established by INVAM (http://invam.cag.wvu.edu).

Statistical analysis

One-way analysis of variance (ANOVA) was used to test the influence of vegetation on AM fungal colonization and spore numbers and to test whether differences in mycorrhizal intensity exist between plant families (Zar 1984). In order to meet the assumption of the normal distribution, data on percent mycorrhizal colonization were arcsin transformed and spore numbers log transformed [In (x+1)] before statistical analysis. The relationship between AM colonization levels and spore numbers was tested by correlation (Pearson) analysis.

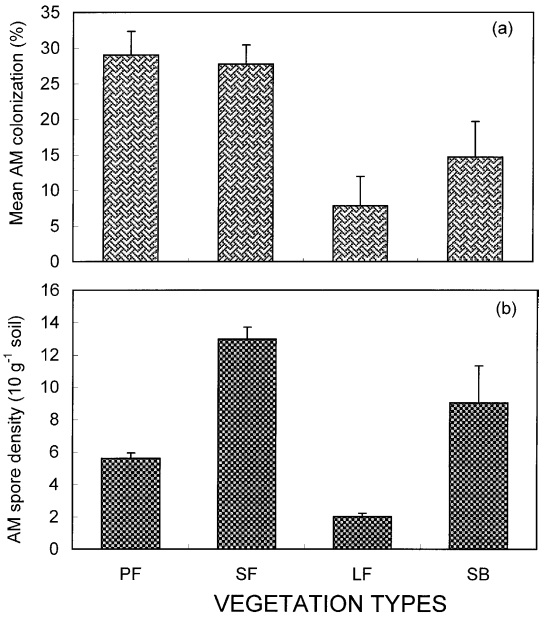

Fig. 1 Mean arbuscular mycorrhizal (AM) fungal colonization (**a**) and AM fungal spore numbers (**b**) in different vegetation types in Xishuangbanna. The error bars indicate ± 1 SE (*LF* Limestone forest, *PF* primary forest, ,*SB* slash and burn field, *SF* secondary forest)

Results

The soil type of study sites is a nutrient-deficient ferrasol and, as in most parts of the tropics, has a pH range of 7.4–8.7. The total soil N, P and exchangeable K were 640.61–830.26 mg kg^{-1}, 265.72–433.18 mg kg^{-1} and 654.78–984.26 mg kg^{-1}, respectively.

The roots of 394 plants representing 103 species, 91 genera and 47 families were examined for mycorrhizal associations (Table 1). Eighty-four of the 103 plant species had AM association. The presence of coenocytic hyphae, intercellular hyphae or intracellular hyphal coils, arbuscules, and/or vesicles in the root cortex was used to assign AM fungal colonization. The AM colonization ranged between 6% (*Macaranga denticulata*, Euphorbiaceae) and 91% (*Canavalia gladiata*, Papilionaceae). Orchid mycorrhizae characterized by pelotons occurred in *Anoectochilus burmannicus*, *Anoectochilus roxburghii* and *Malaxis latifolia* (Orchidaceae) from primary forest. No other types of mycorrhizae were found in the vegetation types studied. Twelve of the plant species sampled lacked mycorrhizal structures. We did not observe any fungal structures in *Achyranthes aspera*, *Amaranthus spinosus* (Amaranthaceae), *Trevesia palmata* (Araliaceae), *Commelina* sp. (Commelinaceae), *Kyllinga brevifolia* (Cyperaceae), *Castanopsis indica*, *Lithocarpus leucostachyus* (Fagaceae), *Melastoma affine* (Melastomaceae), *Melia toosanden* (Meliaceae), *Piper* sp. (Piperaceae), *Homalium laoticum* (Samydaceae) or *Gironniera subequalis* (Ulmaceae). However, hyphae and *Glomus*-type vesicles (not arbuscules) were found in seven species: *Cyperus iria*, *Cyperus rotundus* (Cyperaceae), *Euphorbia hirta* (Euphorbiaceae), *Garcinia xanthochymus* (Guttiferae), *Chisocheton siamensis* (Meliaceae), *Lepisanthes senegalensis* (Sapindaceae) and *Solanum torvum* (Solanaceae). Fifty-one species were consistently mycorrhizal with every root system examined possessing a mycorrhizal association, and 33 species were inconsistently mycorrhizal.

Fewer than 15% of the mycorrhizal species had typical Paris-type colonization, characterized by broad coenocytic hyphal coils with the rare occurrence of arbuscules with limited morphology and intracellular vesicles. A plant species was assigned as Paris-type only if the cortical hyphal coils were accompanied by either intraradical or extraradical spores attached to roots. Around 85% of plants had Arum-type AM colonization characterized by intercellular hyphae, vesicles and intracellular arbuscules. AM fungal spores were found attached to roots in 42 root samples belonging to 23 species. AM fungal spores were isolated from 165 of the 292 soil samples collected. AM fungal spore numbers in the rhizosphere soils ranged between 1.36 spores per 10 g soil (*Bwsenaceae grawga*, Begoniaceae) and 25.71 spores per 10 g soil (*Crassocephalum cerpioides*, Compositae). In the present survey, AM fungal spores belonging to four genera, namely *Acaulospora*, *Gigaspora*, *Glomus* and *Scutellospora*, were isolated and their frequencies of occurrence were as follows: *Glomus* (93%), *Acaulospora* (53%), *Gigaspora* (23%) and *Scutellospora* (18%).

The mean mycorrhizal colonization and average spore numbers for each vegetation type were calculated by averaging colonization and spore numbers of all the species collected in each vegetation type. Plants in

Table 1 The arbuscular mycorrhizal (AM) status of angiosperms in different vegetation types (VegT) in Xishuangbanna. The AM types (AMT) Paris (P) and Arum (A) are indicated. Mycorrhizae of the Orchidaceae were characterized by peltons. AM fungal spore numbers are shown with coefficients of variation (%) in parentheses (*LF* Limestone forest, *PF* primary forest, *M/N* number of individuals with AM association relative to the total number of individuals examined, *%RLA* percent root length with arbuscules ± SE, *%RLC* percent root colonization ± SE,*%RLH* percent root length with hyphae ± SE, *%RLV* percent root length with vesicles ± SE, *SB* slash and burn field, *SF* secondary forest)

Family and species	VegT	M/N	AMT	AM colonization				Spore number per 10 g soil
				%RLH	%RLA	%RLV	%RLC	
Acanthaceae								
Pseudoranthemum palatiferum (Nees) Radlk.	SF	2/2	A[a]	23.15±6.36	12.15±3.82	13.15±5.31	48.38±13.26	6.52 (39.72)
Agrostidoideae								
Digitaria chinensis Hornem.	PF	2/3	A	6.83±1.52	3.82±1.57	10.38±1.59	21.13±6.38	7.93 (33.20)
D. violascens Link.	SF	2/2	A[a]	9.26±1.58	1.32±1.02	13.56±3.95	21.21±4.83	9.32 (49.47)
Eleusine indica (L.) Gaertn.	SF	1/3	A	3.28±1.53	4.32±1.98	3.95±4.62	11.58±3.26	10.25 (70.13)
Imperata cylindrica (L.) Beauv.	SF	3/3	P[a]	15.71±3.54	–	4.83±1.82	20.64±8.12	13.46 (65.88)
Microstegium ciliatum (Trin.) A.Camus	SF	3/4	A	12.38±3.26	3.21±1.08	12.16±3.58	27.75±4.38	14.21 (54.33)
Thysanolaena maxima (Roxb.) O.Ktze.	SF	1/3	P?	14.84±1.87	–	5.26±1.03	20.11±5.38	15.83 (42.78)
Amaranthaceae								
Achyranthes aspera L.	PF	0/3	–	–	–	–	–	3.26 (206.68)
Amaranthus spinosus L.	SB	0/3	–	–	–	–	–	7.35 (35.82)
Annonaceae								
Goniothalamus griffithii Hook.f. et Thoms.	SF	2/2	P[a]	39.20±3.42	–	18.32±4.16	57.53±6.07	6.25 (87.12)
Apostasiaceae								
Apostasia odorata Bl.	SB	3/3	–	9.87±1.26	2.58±1.01	5.26±1.32	17.72±3.59	8.83 (21.39)
Araceae								
Alocasis macrorrhiza (L.) Schott	PF	2/3	A	13.58±4.32	8.93±1.36	12.26±1.92	34.78±6.32	3.93 (55.53)
Amorphophallus bannaensis H.Li	SF	3/3	A	14.95±3.98	12.15±3.95	10.26±5.12	33.38±5.97	4.52 (41.39)
Rhaphidophora decursiva (Roxb.) Schott	PF	2/2	A	12.93±3.26	5.05±1.03	11.08±3.18	29.08±6.28	5.32 (31.10)
Araliaceae								
Trevesia palmata (Roxb.) Vis.	SF	0/3	–	–	–	–	–	13.58 (54.59)
Begoniaceae								
Begonia angustinei Hemsl.	PF	2/2	A	3.83±.52	1.92±1.58	6.26±1.32	12.01±3.58	2.15 (89.46)
B. cathayana Hemsl.	LF	2/2	A	7.38±1.26	2.03±1.01	10.38±2.45	20.78±4.12	1.36 (95.67)
Commelinaceae								
Commelina sp.	PF	0/3	–	–	–	–	–	4.26 (56.11)
Compositae								
Ageratum conyzoides L.	PF	2/2	A[a]	5.32±2.36	4.92±1.32	13.86±2.93	24.12±6.12	3.21 (188.56)
Bidens bipinnata L.	SF	4/4	A	6.87±1.28	13.58±6.97	23.58±6.87	44.13±7.28	7.95 (54.84)
B. pilosa L.	SF	2/3	A	23.58±6.32	10.28±2.38	10.18±2.08	44.10±9.36	13.53 (80.39)
Crassocephalum crepidioides (Benth.) S.Moore	SB	5/5	A	19.87±20.38	10.19±3.85	13.85±4.61	43.93±8.26	25.71 (63.40)
Eupatorium coelesticum L.	PF	3/3	A	13.95±2.31	9.58±1.38	23.17±4.26	46.73±9.21	4.86 (44.55)
E. odoratum L.	PF	3/3	A	11.18±3.21	9.38±2.46	13.38±2.31	33.95±6.26	5.93 (30.08)
Spilanthes callimorpha A.H.Moore	SF	2/2	A[a]	25.32±4.38	18.36±1.35	14.32±3.82	58.03±7.21	15.48 (33.35)
Synedrella nudiflora (L.) Gaertn.	SF	4/4	A	30.26±6.26	11.38±5.21	15.26±4.08	56.53±8.91	12.19 (62.67)
Tithonia diversifolia A. Gray	SF	4/4	A	23.91±5.28	9.26±2.38	13.95±3.01	47.11±9.29	16.63 (23.45)
Cyperaceae								
Cyperus iria L.	PF	0/3	–	7.26±1.38	–	5.29±1.28	–	3.28 (99.80)
C. rotundus L.	SB	0/5	–	3.25±1.25	–	8.26±2.31	–	12.32 (28.68)
Kyllinga brevifolia Rottb.	PF	0/3	–	–	–	–	–	3.83 (57.89)
Ebenaceae								
Diospyros nigrocartex C.Y. Wu ex Wu et Li	PF	2/3	A	13.32±2.36	9.26±1.52	6.08±1.31	28.67±6.32	4.95 (48.29)
Elaeocarpaceae								
Elaeocarpus austro-yunnanensis Hu	PF	2/2	A	8.56±2.15	10.32±3.48	7.32±3.15	26.20±5.87	5.62 (49.07)

Table 1 (continued)

Family and species	VegT	M/N	AMT	AM colonization				Spore number per 10 g soil
				%RLH	%RLA	%RLV	%RLC	
Euphorbiaceae								
Alchornea tiliaefolia (Benth.) Muell.-Arg.	SF	2/2	A	13.58±3.86	5.28±1.32	9.86±2.83	28.73±4.38	19.32 (28.25)
Baccaurea ramiflora Lour.	PF	1/3	A	1.25±0.98	3.89±1.06	13.26±4.83	18.41±4.63	4.98 (71.65)
Breynia fruticosa (L.) Hook.f.	PF	2/2	A	6.83±2.15	13.18±1.26	10.89±3.52	30.92±9.32	5.83 (46.57)
Cleidion bracteosum Bl.	PF	1/3	A	3.26±1.83	3.89±1.26	11.26±2.31	18.41±3.63	4.95 (47.59)
Cleistanthus sumatranus (Miq.) Muell.-Arg.	LF	1/4	A	2.38±0.93	8.26±1.95	6.38±1.58	17.02±4.38	2.13 (83.57)
Croton kongensis Gagnep.	PF	2/2	A[a]	3.82±1.36	7.95±2.01	10.32±3.11	22.09±7.15	4.18 (46.01)
Euphorbia hirta L.	SB	0/3		3.79±2.12	–	7.21±1.58	–	6.32 (43.30)
Macaranga denticulata (Bl.) Muell.-Arg.	SB	1/3	A	1.38±0.92	0.93±0.03	3.56±0.87	5.88±0.93	5.26 (45.44)
Phyllanthus asteranthus Croiz.	PF	2/3	A	4.38±1.21	3.83±1.06	12.38±1.87	20.58±6.52	3.25 (68.22)
Fagaceae								
Castanopsis indica (Roxb.) A. DC.	SF	0/3	–	–	–	–	–	–
Lithocarpus leucostachyus A. Camus	PF	0/5	–	–	–	–	–	–
Guttiferae								
Garcinia xanthochymus Hook.f. ex T.Anders.	LF	0/2	–	10.38±2.58	–	8.39±2.62	–	–
Hypoxidaceae								
Curculigo capitullata (Lour.) O. Ktze	SF	3/3	A	13.86±3.82	12.12±4.32	20.38±7.36	46.36±9.38	15.92 (41.56)
Icacinaceae								
Pittosporopsis kerrii Craib	SF	2/2	A	10.32±3.26	3.85±1.05	7.93±1.83	22.10±4.05	14.32 (51.95)
Labiatae								
Elsholtzia blanda (Benth.) Benth.	PF	2/2	A	12.38±3.26	15.26±5.12	18.32±5.16	45.96±8.38	7.32 (26.66)
Lauraceae								
Cryptocarya yunnanensis H.W. Li	PF	1/3	P[a]	11.68±3.32	–	14.32±1.38	26.03±4.32	5.89 (37.05)
Phoebe lanceolata (Wall. ex Nees) Nees	SF	2/4	P[a]	15.74±2.29	–	10.82±1.59	26.57±9.01	16.26 (51.05)
Lobeliaceae								
Pratia nummularia (Lam.) A.Br. et Aschers.	PF	1/2	A	12.38±3.69	15.26±3.05	14.11±2.68	41.75±5.27	5.32 (31.37)
Magnoliaceae								
Magnolia henryi Dunn	PF	4/4	P[a]	27.30±4.26	–	20.19±1.58	47.50±6.83	7.29 (87.24)
Melastomaceae								
Melastoma affine D. Don	SF	0/2	–	–	–	–	–	10.93 (38.95)
Meliaceae								
Chisocheton siamensis Craib	PF	0/2	A[a]	8.38±3.25	–	9.82±2.31	–	4.32 (45.18)
Lansium domesticum Jack	PF	2/2	A	3.86±1.96	5.82±1.32	20.86±4.15	30.55±9.31	6.23 (29.96)
Melia azedarach L.	PF	4/4	A	13.82±4.36	18.32±2.58	30.63±2.58	62.79±6.58	5.13 (53.02)
M. toosanden Sieb. et Zucc.	LF	0/2	–	–	–	–	–	2.18 (68.76)
Moraceae								
Ficus hirta Vahl	SF	2/2	P[a]	35.84±5.03	–	16.15±2.31	51.98±10.13	18.97 (39.67)
Myristicaceae								
Horsfieldia tetratepala C.Y. Wu et W.T. Wang	PF	2/2	A[a]	9.87±1.38	3.92±1.16	23.15±6.26	36.96±8.31	7.91 (54.53)
Myrsinaceae								
Ardisia tenera Mez	PF	1/3	A	7.95±2.03	13.26±3.15	14.68±3.95	35.90±4.36	6.28 (47.99)
Measa indica (Roxb.) A. DC.	PF	2/2	P[a]	21.73±3.32	–	9.87±2.31	31.63±7.65	3.82 (70.73)
Myrtaceae								
Syzygium sp.	SF	2/3	P[a]	20.65±3.81	–	2.38±0.91	23.05±7.32	18.28 (40.36)
S. latilimbum Merr. et Perry	PF	3/3	P[a]	30.40±6.15	–	5.82±1.36	36.25±8.18	7.82 (87.49)
Oleaceae								
Jasminum wangii Kobuski	SF	2/3	A	10.83±3.15	13.82±1.56	23.82±1.57	48.48±8.93	11.28 (58.66)

Table 1 (continued)

Family and species	VegT	M/N	AMT	AM colonization				Spore number per 10 g soil
				%RLH	%RLA	%RLV	%RLC	
Onagraceae								
Ludwigia prostrata Roxb.	SF	1/3	P[a]	9.10±2.98	–	1.28±1.32	10.38±3.15	13.43 (16.51)
Orchidaceae								
Anoectochilus burmannicus Rolfe	PF	3/3	–	–	–	–	–	–
A. roxburghii (Wall.) Lindl.	SF	3/3	–	–	–	–	–	–
Malaxis latifolia J.E.Sm.	PF	2/2	–	–	–	–	–	–
Papilionaceae								
Campylotropis rockii Schindl.	PF	4/4	A	13.85±1.26	36.58±6.83	23.95±6.83	74.39±9.38	8.26 (94.92)
Canavalia gladiata (Jacq.) DC.	PF	3/3	A	18.57±6.26	39.52±5.26	32.83±7.26	90.92±10.01	7.83 (30.75)
Craspedolobium schochii Harms	PF	2/2	A[a]	33.58±6.95	43.21±9.83	12.32±3.58	89.15±10.15	6.92 (43.94)
Dalbergia obtusifolia (Baker) Prain	SF	2/2	A	12.83±3.05	39.82±8.15	23.15±6.32	75.83±9.86	5.38 (62.04)
Millettia leptobortrya Dunn	SF	2/2	A[a]	13.98±2.98	30.15±9.32	38.92±6.21	83.05±6.83	17.31 (43.79)
Piperaceae								
Piper sp.	PF	0/2	–	–	–	–	–	3.26 (57.26)
P. longum L.	PF	1/3	A	1.28±0.95	0.98±0.31	5.26±1.09	7.52±1.38	4.38 (54.57)
P. sarmentosum Roxb ex Hunter	PF	2/3	A	1.32±0.70	3.25±1.26	2.38±1.03	6.96±1.08	2.36 (115.96)
Rosaceae								
Rubus rufus Focke var. *palmatifidus* Card.	PF	3/3	A	13.58±2.85	15.26±3.85	12.18±4.36	41.02±6.83	3.83 (77.78)
Rubiaceae								
Canthium parvifoliam Roxb.	PF	2/3	A	10.86±1.53	9.86±3.25	13.85±2.58	34.58±6.01	3.97 (53.66)
Chesalia curviflora Thw.	SF	2/2	A[a]	13.52±1.28	3.82±1.03	9.16±3.85	26.50±4.12	3.83 (60.93)
Geophila herbacea (L.) O. Ktze.	SF	2/2	A	13.58±2.36	7.15±3.15	15.21±5.26	35.94±6.19	18.32 (33.66)
Hedyotis costata Roxb.	SF	3/3	A	6.03±1.52	13.86±3.83	15.97±3.82	35.86±6.07	16.32 (46.49)
Lasianthus hookeri C.B. Clarke ex Hook.f.	SF	3/4	A[a]	5.26±2.31	8.92±1.26	13.21±4.36	27.39±5.38	17.38 (43.96)
Morinda lucida Benth.	PF	2/3	A	10.28±3.26	5.28±1.36	20.32±4.38	35.89±7.38	5.26 (43.47)
Ophiorrhiza austro-yunnanensis Lo	PF	2/3	A	13.86±4.26	15.95±4.26	10.08±2.31	39.90±7.15	14.92 (59.09)
Prismatomeria tetrandra (Roxb.) K. Schum.	SF	2/3	A	7.89±4.38	13.52±3.28	12.15±1.36	37.38±8.31	13.26 (54.56)
Psychotria henryi Levl.	SF	3/3	A	10.29±3.26	14.93±3.28	12.15±1.36	37.38±8.31	13.26 (54.60)
Samydaceae								
Homalium laoticum Gagnep.	PF	0/2	–	–	–	–	–	–
Sapindaceae								
Lepisanthes senegalensis (Poir.) Leenh.	SF	0/2	–	5.39±1.54	–	3.86±1.12	–	4.91 (28.41)
Pometia tomentosa (B1.) Teysm. et Binn.	PF	4/5	A	4.83±1.26	10.32±2.31	17.83±3.56	35.17±5.32	3.21 (31.97)
Smilaceae								
Smilax corbularia Kunth	SF	2/2	–	10.26±3.28	13.21±3.82	14.96±4.18	38.43±4.36	13.97 (23.89)
S. hypoglauca Benth.	PF	2/3	–	13.28±4.21	14.99±4.86	10.93±4.85	39.22±8.31	7.26 (55.11)
S. indica Vitm.	PF	1/2	–	9.15±2.62	10.29±3.96	15.82±3.62	35.26±7.31	5.32 (49.71)
Solanaceae								
Solanum torvum Sw.	SB	0/3	–	15.26±3.15	–	5.36±1.38	–	1.26 (134.72)
Sterculiaceae								
Pterospermum menglunense Huse	PF	3/3	A	10.26±3.83	12.56±4.36	10.89±4.15	33.71±7.31	6.03 (37.92)
Tetramelaceae								
Tetrameles nudiflora R.Br	LF	3/3	A[a]	12.56±4.32	6.93±1.38	10.32±1.61	29.81±4.81	2.36 (77.80)
Theaceae								
Pyrenaria cheliensis Hu	PF	3/3	–	13.26±3.83	6.27±1.38	13.97±4.36	33.52±8.21	8.08 (49.52)
Ulmaceae								
Celtis wightii Planch.	LF	2/3	P[a]	10.95±3.18	–	2.36±1.01	13.31±8.02	8.02 (43.62)
Gironniera subaequalis Planch.	PF	0/5	–	–	–	–	–	–
Urticaceae								
Boehmeria zollingeriana Wedd.	SB	1/2	A	12.31±5.26	3.21±1.08	5.36±1.32	20.89±5.41	7.28 (26.42)
Elatostema parvum (Bl.) Miq.	PF	2/3	A	6.83±1.26	2.86±1.38	10.27±1.59	19.47±6.38	9.32 (47.02)

Table 1 (continued)

Family and species	VegT	M/N	AMT	AM colonization				Spore number per 10 g soil
				%RLH	%RLA	%RLV	%RLC	
Verbenaceae								
Clerodendron japonicum (Thunb.) Sweet	PF	2/2	A	13.82±6.58	14.32±5.36	6.32±2.38	34.48±9.31	6.21 (70.37)
Xanthophyllaceae								
Xanthophyllum siamensis Craib	SF	2/3	A	12.38±1.58	13.26±1.36	7.28±5.21	39.93±8.31	13.29 (50.18)
Zingiberaceae								
Amomum villosum Lour.	PF	5/5	A	33.52±6.32	10.52±1.38	6.05±1.38	50.05±7.81	8.26 (87.98)
Costus speciosus (Koenig) Sm.	SB	3/3	A	23.58±5.32	6.87±2.36	13.28±1.26	43.75±8.31	9.85 (167.35)

[a] AM fungal spores were attached to roots

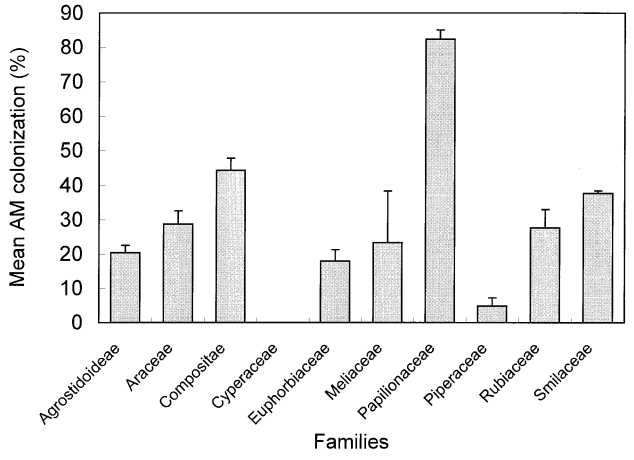

Fig. 2 Intensity of mycorrhiza in selected plant families in Xishuangbanna. The error bars indicate ± 1 SE

primary forests had high levels of colonization (Fig. 1a). In contrast, maximum spore numbers occurred in secondary forest soils (Fig. 1b). Vegetation types significantly influenced colonization levels ($F_{3,99}$ = 3.13; P<0.05) and spore numbers ($F_{3,92}$ = 31.95; P<0.001). Three or more plant species from ten selected plant families were assessed for the role of plant taxonomic position on plant mycorrhizal status. Colonization levels tended to vary significantly between plant families ($F_{9,51}$ = 30.07; P<0.001) (Fig. 2), with the highest colonization levels in members of Papilionaceae. A statistically significant relationship existed between AM fungal colonization levels and spore numbers (r = 0.532; P<0.000; n= 103).

Discussion

Our study further elucidates the AM status of plants in Xishuangbanna. The extent of mycotrophy in Xishuangbanna plants is similar to or higher than that reported for plants in natural communities from other regions of the world (Table 2). To our knowledge, many reports of mycorrhiza in the present survey are the first published reports for some of these plant species. An important consideration in this study was the distribution of AM types in the plant species examined. Although, the Paris-

Table 2 A comparison of some published estimates of mycorrhizal incidence in plant communities (*M* Mycorrhizal, *NM* non-mycorrhizal)

Country	Vegetation type	Species examined	Mycorrhizal incidence		Reference
			M	NM	
Australia	Forests	109	82	27	Brundrett and Abbott (1991)
	Undisturbed woodlands	55	45	10	Reddell and Milnes (1993)
	Woodland	32	21	11	Bellgard (1991)
	Heathland	47	31	16	–
China	Primary, secondary, limestone forests, slash and burn field	103	84	19	Present study
	Tropical rain forest	112	63	49	Zhao et al. (2001)
India	Tropical forest, scrubland, grassland, plantations, agricultural sites	329	174	155	Muthukumar and Udaiyan (2000)
	Forest, grassland, mangroves, usar lands, cultivated lands	737	372	365	Ragupathy and Mahadevan (1993)
South Africa	Tropical shrub lands	332	241	91	Allsopp and Stock (1993)
U.S.A	Coastal strand, shrub land, forests, cultivated lands	147	122	25	Koske et al. (1992)

type has been reported to be more frequent in wild angiosperms (Smith and Smith 1997), less than 15% of the plants in the present study had this type of association. We found typical Arum-type in plants belonging to families like Euphorbiaceae, Papilionaceae, Mimosaceae, Meliaceae, Rubiaceae, Sterculiaceae and Verbenaceae, where both AM types and intermediate types of AM tend to occur. Arbuscules, which have only a short life-span in actively growing roots (Alexander et al. 1988), are essential in order to designate a plant species as being AM. We observed arbuscules in *Pittosporopsis kerrii* (Icacinaceae), *Phoebe lanceolata* (Lauraceae), *Terameles nudiflora* (Tetramelaceae) and *Celtis wightii* (Ulmaceae), which were designated only as being possible mycorrhizal species by Zhao et al. (2001). This discrepancy may be related to the sampling season, since the present study was carried out during the wet period (August) when plant and root growth occurs, as against the dry season (January) sampling by Zhao et al. (2001). The appearance of arbuscules in some host species may be brief and correspond to the nutrient demand of the host, as found by Mullen and Schmidt (1993) for *Ranunculus adoneus*.

The proportion of non-mycorrhizal plant species in Xishuangbanna is low (18%) compared with other vegetation types world wide (25%–50%) (Bellgard 1991; Brundrett and Abbott 1991; Allsopp and Stock 1993; Ragupathy and Mahadevan 1993; Muthukumar and Udaiyan 2000; Zhao et al. 2001). However, around 50% of the plant species examined in the slash and burn field were non-mycorrhizal. As the non-mycorrhizal trait is frequently associated with high levels of ecosystem disturbance (Brundrett 1991), this observation is tenable. Orchid mycorrhiza were observed in all three orchid species from the primary forest. Koske et al. (1992) also reported orchid mycorrhiza in all the species examined from lowland forests in Hawaii. Plants lacking a mycorrhizal association in the present survey have been reported as such before and are grouped into certain presumed non-mycorrhizal families like the Amaranthaceae, Commelinaceae and Cyperaceae (Tester et al. 1987; Peat and Fitter 1993). However, other plant species like *Castanopsis indica*, *Chisocheton siamensis*, *Euphorbia hirta*, *Garcinia xanthochymus*, *Gironniera subaequalis*, *Homalium laoticum*, *Lepisanthes senegalensis*, *Lithocarpus leucostachyus*, *Melastoma affine*, *Melia toosanden*, *Piper* sp., *Solanum torvum* and *Trevesia palmata*, which lacked AM colonization, normally belong to mycorrhizal families. Vesicle-like structures and hyphae, without arbuscules, were detected in eight plant species. Although vesicles of AM fungi from the Glomineae usually occur in AM roots after arbuscule development, and *Glomus*-type vesicles and hyphae have been reported earlier in presumed non-mycorrhizal hosts like *Cyperus iria* and *Cyperus rotundus* (Koske et al. 1992; Giovannetti and Sbrana 1998; Muthukumar and Udaiyan 2000), these plants cannot be termed mycorrhizal in the absence of arbuscules.

AM fungal spore numbers in the primary forest ranged between 1.36 and 9.32 per 10 g soil, which is low compared with 5.5 to 19.08 per 10 g spores reported by Zhao et al. (2001). This low density of AM fungal spores is in accordance with reports from humid tropical forests, where spore numbers tend to be relatively low or infrequent (Janos 1980; Fischer et al. 1994). Generally, AM fungal spores in natural soils are frequently dead or parasitized and are merely spore cases (Muthukumar and Udaiyan 1999). The spore numbers reported in the present study are values for only intact and healthy spores. In addition, AM fungal sporulation is influenced by an array of environmental, host and fungal factors, and spore numbers tend to decrease during root growth but to increase during root inactivity or senescence (Brundrett 1991). In the present survey, AM fungal spores were present in the rhizospheres of non-mycorrhizal hosts. In natural soils, roots of adjacent plants often grow in close proximity and are interwoven, so spores in the rhizosphere of a host could come from AM fungi colonizing a companion plant species (Muthukumar and Udaiyan 2000). In a tropical Mexican wet forest, Guadarrama and Alvarez-Sanchez (1999) reported that disturbance, but not seasonality, affected the abundance and richness of AM fungal spores. This contradicts the present observation, where AM fungal spore numbers in the primary forest and lime stone forest tended to be lower than in secondary forest and the slash and burn field. However, as Zhao et al. (2001) suggested, the uneven spatial distribution of AM fungal spores and the complex structure of the underground root component should be considered as a major factor affecting spore densities of AM fungi.

The highly significant positive correlation between percent root length colonization and AM fungal spore numbers contradicts several previous reports in which the lack of a demonstrable relationship was reported between these mycorrhizal variables (Brundrett 1991; Zahka et al. 1995; Brundrett et al. 1996). However, this observation is consistent with another study in natural soils (Muthukumar and Udaiyan 2000). AM fungal spores belonging to *Glomus* and *Acaulospora* were frequent. This is in accordance with observations that species of *Glomus* and *Acaulospora* can dominate tropical soils (Guadarrama and Alvarez-Sanchez 1999; Muthukumar and Udaiyan 2000; Zhao et al. 2001). Although, in the present survey, we could identify certain AM fungal spores to the species level, most of these are yet to be characterized, since field-collected spores usually lack fine distinguishable taxonomic characters and identification is often unreliable (Walker 1992). Further studies are in progress to characterize the different AM fungal species in various vegetation types in Xishuangbanna.

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