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Arbuscular mycorrhizal fungi associated with common pteridophytes in Dujiangyan, southwest China

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Abstract The colonization and diversity of arbuscular mycorrhizal (AM) fungi associated with common pteridophytes were investigated in Dujiangyan, southwest China. Of the 34 species of ferns from 16 families collected, 31 were colonized by AM fungi. The mean percentage root length colonized was 15%, ranging from 0 to 47%. Nineteen species formed *Paris*-type and 10 intermediate-type AM. In two ferns, only rare intercellular non-septate hyphae or vesicles were observed in the roots and AM type could not be determined. Of the 40 AM fungal taxa belonging to five genera isolated from rooting-zone soils, 32 belonged to *Glomus*, five to *Acaulospora*, one to *Archaeospora*, one to *Entrophospora*, and one to *Gigaspora*. *Acaulospora* and *Glomus* were the dominant genera and *Glomus versiforme* was the most common species. The average AM spore density was 213 per 100 g air-dried soil and the average species richness was 3.7 AM species per soil sample. There was no correlation between spore density and percentage root length colonized by AM fungi.

Keywords Fern · Mycorrhizal colonization · *Paris*-type

Introduction

The ancestors of ferns may have been significant in the evolution of vascular plants. Ferns are still an important component of present-day ecosystems, particularly in tropical and subtropical regions (Ching 1959). They have the potential for bioremediation in severely disturbed areas and some are economically important as medicine and food in regions of China (Ching 1959, 1978).

Arbuscular mycorrhizas (AM) have been found in pteridophytes from about 400 million years ago in the Devonian to Carboniferous periods of the Paleozoic (Hass et al. 1994; Remy et al. 1994). To date, there have been only a few investigations of fern mycorrhizas (Boullard 1957; Hepden 1960; Cooper 1976; Iqbal et al. 1981; Berch and Kendrick 1982; Gemma et al. 1992; Zhao 2000), and these have mainly concentrated on the occurrence of AM fungi in pteridophytes and their evolutionary significance. Studies of species composition of AM fungi in the rooting-zone soils of pteridophytes are few.

AM fungal structures, i.e. arbuscules, hyphal coils, vesicles, and non-septate hyphae, in the roots of plants may have various functions related to both the fungus and the host (Smith and Smith 1996, 1997; Smith and Read 1997). Arbuscular mycorrhizas have been divided into the two classes *Arum*- and *Paris*-type according to the fungal structures occurring in the roots of *Arum maculatum* and *Paris quadrifolia* (Gallaud 1905, communicated reference). In Gallaud's classification, the *Arum*-type is defined on the basis of an extensive intercellular phase of hyphal growth in the root cortex and development of terminal arbuscules on intracellular hyphal branches; the *Paris*-type is defined by the absence of the intercellular phase, the presence of extensive intracellular hyphal coils, and arbuscules as intercalary structures on the coils.

Smith and Smith (1997), reviewing the literature and summarizing the AM types in different taxa of plants (mainly at the family level), proposed that the different AM structures have specialized roles in the transfer of inorganic nutrients and carbon between the partners, depending on the physiology of the symbiosis between different fungus and plant interfaces. In addition to the *Arum*- and *Paris*-types based on the presence or total absence of intercellular hyphae in the root cortex, the authors suggested the existence of an intermediate type ('near *Paris*') showing limited or rare intercellular hyphae

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but extensive intracellular coils in the inner cortex and (where present) intercalary arbuscules. Because of the extensive hyphal coils in the root cortex of ferns examined (Peterson et al. 1981; Pocock and Duckett 1984; Duckett and Ligrone 1991), the *Paris*-type was considered to be dominant in ferns (Smith and Smith 1997). Coiled intracellular hyphae, arbuscules, and vesicles described in the early Devonian fossil *Aglaophyton* (Kidston and Lang 1921) were suggested to indicate a *Paris*-type AM (Smith and Smith 1997).

To better understand the AM status of ferns, it is necessary to carry out further systematic investigation of fern mycorrhizas. The purpose of the present study was to investigate AM fungal structures and morphological types in roots and AM fungal diversity in rooting-zone soils of common pteridophytes from the subtropical region of Dujiangyan, P.R. China.

Materials and methods

Study sites and sampling procedure

The investigation was conducted at Dujiangyan (N 30°44′, E 103°27′) in the central part of Sichuan Province, subtropical China. Thirty-four common species of pteridophytes were collected in August (summer) 2001 (Table 1) and identified according to Ching (1959, 1978). Three individual roots of each fern species were cleaned and preserved in 50% ethanol.

One rooting-zone soil sample of ca. 500 g was collected from each fern individual to a depth of 20 cm and the three samples from each species mixed evenly. Soil samples were placed in sterilized cotton bags, labeled, and air-dried for 1 week. They were subsequently ground, sieved through a 2-mm sieve, stored at 4°C and processed within 3 months. A total of 31 soil samples were used in this study; three samples were missing.

Root staining

Root samples were rinsed with tap water, cleared in 10% (w/v) KOH (20 min, 92°C), acidified in lactic acid (3 min), and stained (20 min, 92°C) with 0.5% acid fuchsin (Berch and Kendrick 1982). Fifty root fragments (ca. 1 cm long) were mounted on slides in a polyvinyl alcohol solution (Koske and Tessier 1983) and examined with a compound microscope (Olympus BH-2) at ×100–400 for the presence of AM fungal structures. AM types were classified according to Smith and Smith (1997). The percentage of root length colonized by AM fungal structures was determined using the magnified line-intersect method (McGonigle et al. 1990).

Spore separation

Spores were isolated from 100 g air-dried soil taken from each composite sample using the wet-sieving and decanting method of Gerdemann and Nicolson (1963), as modified by Daniels and Skipper (1982). AM fungi were identified following the descriptions of Schenck and Perez (1988), as modified by Morton and Redecker (2001). At least 20 spores of each species were used for identification. Spores were first mounted in water and morphological characteristics measured. Melzer's reagent and cotton blue were used in the identification. The permanent slides were mounted in polyvinyl-lacto-glycerol, sealed with nail varnish, and stored at the Systematic Mycology and Lichenology Laboratory, Institute of Microbiology, Chinese Academy of Sciences, Beijing.

Data analysis

AM fungal composition was evaluated from the isolation frequency (IF), spore density, and species richness associated with each fern species. IF was expressed as the percentage of samples from which spores of a particular genus or species were isolated. The degree of dominance was described as: dominant species (IF >50%), most common species (50–30%), moderately common species (30–10%), and rare species (<10%). Spore density (spores per 100 g air-dried soil) was calculated from direct counts of spores. Species richness was defined as the number of AM fungal species per soil sample (Koske 1987).

The correlation between percentage of root length colonized and spore density was analyzed by linear regression analysis. Goodness of fit was assessed by simple correlation coefficients (r) and degrees of freedom.

Results

Colonization of AM fungi

AM fungal structures, i.e. arbuscules, vesicles, hyphal coils (including arbusculate coils) and intercellular non-septate hyphae, were present in 31 (91%) of 34 fern species examined. The mean percentage of root length colonized was 15%, ranging from 0 to 47%. AM fungal structures were not observed in three species, *Colysis hemitoma* of the Polypodiaceae, *Parathelypteris nipponica* of the Thelypteridaceae, and *Schizoloma heterophyllum* of the Lindsaeaceae (Filicophytina) (Table 1).

AM structures

Arbuscules were present in 16 (47%), hyphal coils in 29 (85%), vesicles in 27 (79%), and intercellular non-septate hyphae in 11 (32%) fern species. Nineteen (56%) fern species formed *Paris*-type and 10 (29%) formed intermediate type AM; two (6%) ferns had only rare intercellular non-septate hyphae or vesicles in the roots and the AM-type could not be determined (Table 1).

AM fungal diversity

Forty taxa of AM fungi were distinguished in 31 rooting-zone soil samples of 31 ferns, of which 28 (70%) were identified at the species level and 12 (30%) at the genus level. Of the 40 taxa, 32 belonged to the genus *Glomus*, five to *Acaulospora*, one to *Archaeospora*, one to *Entrophospora*, and one to *Gigaspora* (Table 2).

Glomus versiforme was the most common species. There were seven moderately common species, i.e. *Acaulospora lacunosa*, *A. laevis*, *Glomus convolutum*, *Glomus dimorphicum*, *Glomus globiferum*, *Glomus heterosporum* (A), and *Glomus mosseae*. The other 32 taxa were rare (Table 2). *Acaulospora* and *Glomus* were the dominant genera. *Archaeospora*, *Entrophospora* and *Gigaspora* were rare. *Paraglomus* and *Scutellospora* species were not found in this study (Table 3).

Table 1 Arbuscular mycorrhizal (AM) fungal status in roots and diversity in rooting zone soils of pteridophytes. Relative development of structures shown as: ++ always present in significant numbers, + always present, *(+)* very rare; only present after cortical colonization, – not detected, *ND* not determined, *NO* no soil samples (*Length* AM root length %, *NS* intercellular non-septate hyphae, *coils* hyphal coils, *A* arbuscules, *V* vesicles, *type* Arum, Paris or intermediate, *density* spore density per 100 g air-dried soil, *number* species number per soil sample)

Host	Length	NS	Coils	A	V	Type	Density	Number
Lycophytina								
Selaginellaceae								
Selaginella davidii Franch.	9	–	(+)	–	(+)	P	144	6
S. moellendorfii Hieron.	20	(+)	(+)	–	++	I	NO	
Sphenophytina								
Equisetaceae								
Equisetum hiemale L.	21	–	+	(+)	(+)	P	201	4
E. ramosissimum Desf.	22	–	+	(+)	(+)	P	497	5
Filicophytina								
Botrychiaceae								
Botrychium lanuginosum Wall.	29	–	+	–	+	P	214	5
B. ternatum (Thunb.) Sw.	26	–	++	–	+	P	2	1
Ophioglossaceae								
Ophioglossum vulgatum L.	16	–	(+)	–	(+)	P	13	1
Osmundaceae								
Osmunda japonica Thunb.	13	–	+	–	(+)	P	130	2
Aspidiaceae								
Ctenitis mariformis (Rosenst.) Ching	10	–	+	–	–	P	2	1
Athyriaceae								
Allantodia chinensis (Bak.) Ching	9	(+)	(+)	(+)	(+)	I	66	4
Athyrium wardii (Hook.) Makino	4	–	+	(+)	(+)	P	56	1
Callipteris esculenta (Retz.) J. Sm.	1	–	+	(+)	(+)	P	64	4
Cystopteris pellucida (Franch.) Ching	47	–	++	+	+	P	270	5
Diplazium donianum (Mett.) Tard.-Blot	16	–	+	–	(+)	P	60	2
D. lanceum (Thunb.) Presl	5	–	++	+	+	P	796	4
Blechnaceae								
Woodwardia orientalis Sw.	15	(+)	(+)	(+)	(+)	I	266	4
Dennstaedtiaceae								
Microlepia marginata (Houtt.) C. Chr.	2	–	–	–	(+)	ND	388	4
Dryopteridaceae								
Arachniodes rhomboidea (Wall.) Ching	18	(+)	+	(+)	(+)	I	239	6
A. festina (Hance) Ching	18	+	(+)	(+)	–	I	197	6
A. simplicior (Makino) Ohwi	13	–	(+)	–	++	P	9	1
Cyrtomium falcatum (L. f.) Presl	1	(+)	–	–	–	ND	466	5
Dryopteris fuscipes C. Chr.	28	++	++	(+)	+	I	NO	
Gleicheniaceae								
Dicranopteris dichotoma (Thunb.) Bernh.	34	–	+	–	++	P	342	10
Lindsaeaceae								
Lindsaea cultrata (Willd.) Sw.	19	+	(+)	+	(+)	I	791	4
Schizoloma heterophyllum (Dry.) J. Sm.	0	–	–	–	–	–	464	4
Stenoloma chusanum (L.) Ching	26	++	(+)	(+)	+	I	124	4
Lygodiaceae								
Lygodium japonicum (Thunb.) Sw.	35	(+)	+	(+)	++	I	20	2
Polypodiaceae								
Colysis hemitoma (Hance) Ching	0	–	–	–	–	–	204	3
Pteridaceae								
Pteridium aquilinum (L.) Kuhn	6	–	+	–	(+)	P	304	4
Pteris aspericaulis Wall.	6	–	++	(+)	+	P	NO	
P. vittata L.	9	–	(+)	–	(+)	P	40	2
Thelypteridaceae								
Dictyocline wilfordii (Hook.) J. Sm.	34	+	+	+	+	I	208	7
Metathelypteris hattori (H. Ito) Ching	1	–	(+)	–	–	P	4	1
Parathelypteris nipponica (Franch. et Sav.) Ching	0	–	–	–	–	–	15	2
Average	15	-	-	-	-	-	213	3.7

Table 2 The isolation frequency (*IF*, ≥10%) and spore density (*Density*, per 100 g air-dried soil, mean ± SE) of AM fungal species. Rare species isolated in present investigation: *Acaulospora foveata* Trappe & Janos, *A. scrobiculata* Trappe, *Acaulospora* sp.; *Archaeospora leptoticha* (Schenck & Smith) Morton et Redecker; *Entrophospora infrequens* (Hall) Ames & Schneider; *Gigaspora* sp.1; *Glomus aggregatum* Schenck & Smith, *G. albidum* Walker & Rhodes, *G. australe* (Berkeley) Berch, *G. caledonium* (Nicolson & Gerdemann) Trappe & Gerdemann, *G. chimonobambusae* Wu & Liu, *G. claroideum* Schenck & Smith, *G. clarum* Nicolson & Schenck, *G. clavisporum* (Trappe) R. T. Almeida & N. C. Schenck, *G. delhiense* Mukerji, Bhattacharjee & Tewari, *G. dolichosporum* Zhang & Wang, *G. formosanum* Wu & Chen, *G. gibbosum* Blaszkowski, *G. hoi* Berch & Trappe, *G. manihotis* Howeler, Sieverding & Schenck, *G. monosporum* Gerdemann & Trappe, *G. pachycaulis* Wu & Chen, *Glomus* sp.1, *Glomus* sp.2, *Glomus* sp.3, *Glomus* sp.4, *Glomus* sp.5, *Glomus* sp.6, *Glomus* sp.7, *Glomus* sp.8, *Glomus* sp.9, and *Glomus* sp.10

Species	F	Density
Acaulospora lacunosa Morton	16.13	4.26±2.19
A. laevis Gerd. & Trappe	29.03	8.26±4.95
Glomus convolutum Gerd. & Trappe	19.35	4.45±2.71
G. dimorphicum Boyetchko & Tewari	22.58	11.84±6.02
G. globiferum Koske & Walker	12.9	3±2.25
G. heterosporum (A) Sm. & Schenck	22.58	14.55±6.95
G. mosseae (Nicol. & Gerd.) Gerd. & Trappe	16.13	28.1±20.55
G. versiforme (Karsten) Berch	45.16	39.58±12.54

Table 3 The isolation frequency (*IF, %*), spore density (*Density*, per 100 g air-dried soil, mean ± SE) and species richness (*Richness*, mean ± SE) of the five AM fungal genera

Genus	IF	Density	Richness
Acaulospora	64.52	26±8.67	0.68±0.1
Archaeospora	6.45	1.19±1.07	0.03±0.03
Entrophospora	3.23	0.26±0.26	0.03±0.03
Gigaspora	6.45	0.55±0.38	0.06±0.04
Glomus	87.1	173.78±30.4	2.29±0.23

The average spore density of AM fungi was 213 spores per 100 g air-dried soil, ranging from 2 to 796, and the average species richness was 3.7 species per soil sample, ranging from 1 to 10 (Table 1). The most common species, *Glomus versiforme*, had the highest spore density (Table 2). The dominant genus *Glomus* had the highest spore density and species richness, followed by the second dominant genus *Acaulospora* (Table 3).

There was no correlation between percentage root length colonized by AM fungi and spore density in rooting-zone soil ($r = 0.086$, $P > 0.05$) (results not shown).

Discussion

AM fungal structures were observed in 91% of the pteridophytes sampled in Dujiangyan, subtropical China in the present study. This finding is very different from the results of Zhao (2000), who investigated 256 fern species and reported very low occurrence (17%) of AM fungi in a tropical region of Yunnan, southwest China. However, only arbuscules were recorded as the colonization criterion of AM fungi, whereas the presence of arbuscules, vesicles, hyphal coils, and intraradical non-septate hyphae in the roots is considered elsewhere to be evidence of colonization by AM fungi (Duckett and Ligrone 1991; Gemma et al. 1992; Smith and Read 1997). Higher AM fungal colonization (more than 74%) was found for ferns elsewhere (Boullard 1957; Cooper 1976; Berch and Kendrick 1982; Gemma et al. 1992).

In 'lower' pteridophytes (non-Filicophytina), hyphal coils were always present in *Equisetum hiemale* and *E. ramosissimum* of the Equisetaceae (Sphenophytina) and in *Selaginella davidii* and *S. moellendorfii* of the Selaginellaceae (Lycophytina). All formed *Paris*-type AM except *S. moellendorfii,* which was considered to be of the intermediate type due to the rare intercellular non-septate hyphae observed in the present study. Similar results were found in previous studies. Hyphal coils and arbuscules were present in the gametophyte cells of *Lycopodium cernuum* of the Lycopodiaceae (Lycophytina) (Duckett and Ligrone 1991), which were also considered to be *Paris*-type AM, which is dominant in 'lower' pteridophytes (Smith and Smith 1997).

In 'higher' pteridophytes (Filicophytina), hyphal coils were extensive in root cortex (83.3% of 30 higher ferns). The *Paris*-type (57% of 30 higher ferns) was also dominant, except that intercellular non-septate hyphae were observed in 10 (33%) out of 30 ferns, which formed intermediate type AM. *Paris*-type structures. This included hyphal coils, vesicles, and the remnants of arbuscules in *Ophioglossum* and the related genus *Botrychium*, which have been found previously (Gallaud 1905, communicated reference; Boullard 1957). Similar *Paris*-type structures were present in three species, i.e. *B. ternatum* and *B. lanuginosum* of the Botrychiaceae and *O. vulgatum* of the Ophioglossaceae, in the present study.

The different AM structures may have specialized roles in transfer of inorganic nutrients and organic carbon between the partners of the symbiosis (Smith and Read 1997; Smith and Smith 1997), but we know little about either the functions or the relationship between their diversity and roles in different ecosystems.

The number of AM fungal taxa (40) isolated in the present study was higher than in previous investigations. For example, 23 AM fungal species associated with 25 plant species were found in a grassland ecosystem using trap culture (Bever et al. 1996). Far fewer AM fungi (10 species) were found in a temperate grassland soil and even less in cultivated soils (Johnson 1993). Twenty-three AM fungal taxa were isolated in the rooting zone of three major plant species growing on the Atlantic coast from New Jersey to Virginia (Koske 1987), and only 16 taxa were isolated from soils in a tropical rain forest of Mexico (Guadarrama and Álvarez-Sánchez 1999). A total of 17 AM fungal taxa were found in soils from agricultural fields by both direct spore isolation and trap culture with different plants (Jansa et al. 2002). It is highly likely that the high AM fungal number found in the present investigation was due to the collection of soil samples from various habitats and from more fern species.

In the subtropical ecosystem investigated, *Acaulospora* and *Glomus* were dominant in the rooting-zone soils, and 99% of the AM fungal spores belonged to these two genera. Similar results have been obtained in tropical rain forests of Xishuangbanna in southwest China (Zhao et al. 2001) and of Veracruz in Mexico (Guadarrama and Álvarez-Sánchez 1999), as well as from temperate to tropical regions on the south and east coasts of China (Zhang et al. 1998).

Our results showed no correlation between spore density and percentage of root length colonized by AM fungi, and there was a wide range of spore density (2–796 spores per 100 g air-dried soil) in the rooting-zone soils of mycorrhizal plants. Similar results were obtained in previous studies (Molina et al. 1978; Friese and Koske 1991; Zhao et al. 2001; Liu and Wang 2003). The relationship between spore number and percentage of root length colonized by AM fungi is complicated and may be influenced by many environmental and biological factors (Smith and Smith 1996; Liu and Wang 2003). There are two possible explanations for our results. Firstly, the roots associated with AM fungi may have decayed before sampling. Secondly, it is likely that some spores included in the counts were not viable, or were present in clusters that would function as one (inseparable) infective propagule in field soil (Jasper et al. 1991; Jansa et al. 2002).

A high spore density of AM fungi (up to 464 spores per 100 g air-dried soil) was recorded even in the rooting-zone soil collected from the non-mycorrhizal fern in the present study. This may be the result of interwoven roots from different plants in the same field sample; mycorrhizal plants may influence AM fungal spore number in the rooting zone of non-mycorrhizal plants (Zhao et al. 2001).

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