

Thangavelu Muthukumar · Sampath Prakash

Arbuscular mycorrhizal morphology in crops and associated weeds in tropical agro-ecosystems

Received: December 7, 2007 / Accepted: December 20, 2008

Abstract Morphological types of arbuscular mycorrhizae (AM) in crops and associated weeds were examined in agro-ecosystems. In total, 48 plant species (8 crops and 40 weeds) belonging to 43 genera in 18 families were examined. The number of plant species with *Arum*-type AM was higher than those with *Paris*-type AM in the examined plants. AM association was absent in 6 weeds, and the average colonization rate was 62.64% in crops and 52.92% in weeds. AM morphology has been reported in 2 crops and 21 weeds for the first time. The influence of plant identity on AM morphology was also analyzed by arranging the examined plants in a current plant phylogenetic scheme. This analysis showed there was a lack of relationship between plant classification and AM morphological type. Actually, the colonization types were not distinguished at the plant family level, but were mostly distinguished at the species level.

Key words Arbuscular mycorrhizae (AM) · *Arum*-type AM · Crops · *Paris*-type AM · Weeds

Introduction

Gallaud (1905) distinguished arbuscular mycorrhizal (AM) morphology into two major morphological classes, *Arum*-type and *Paris*-type, and named them according to the plants in which they were originally observed. *Arum*-type mycorrhizal morphology, which is common in cultivated plants, is characterized by intercellular hyphae and intracellular arbuscules, whereas many plants in natural ecosystems have the *Paris*-type morphology, with intracellular hyphal coils and arbusculate coils. For a long time, the *Arum*-type was regarded as the common type because most experimental studies used crop plants that form *Arum*-type. Mean-

while, Smith and Smith (1997), in their review on AM morphological types, showed that many plants formed *Paris*-type AM in natural ecosystems.

The ability of AM fungi to colonize and provide nutrients to the host plant might differ depending on the colonization type. The feature of *Arum*-type intercellular hyphae, to extend in the intercellular space of the root cortex, can be advantageous for fast colonization spread and nutrient transfer. Brundrett and Kendrick (1990a) showed that the development of *Arum*-type AM is faster than that of the *Paris*-type. It has also been shown that intercellular hyphae are longer lived than arbuscules (Smith and Dickson 1991), thus providing a conduit through which nutrients can move after degeneration of the arbuscules. Brundrett and Kendrick (1990b) also stated that coils tend to remain after arbusculate branches have degenerated and disappeared. However, the other physiological or functional differences between the AM types are yet to be fully ascertained.

Paris-type AM was found to be dominant among herbaceous plants of understory vegetation in Japanese deciduous broad-leaved forests (Yamato and Iwasaki 2002). In contrast, the *Arum*-type was found to be dominant in native plants of remnant natural pine rocky land vegetation in south Florida, USA (Fisher and Jayachandran 2005), pioneer woody plants in an Indonesian oil palm farm (Yamato 2005), weeds on vacant lands in Japan (Yamato 2004), plants in primary, secondary, and limestone forests of Xishuangbanna, southwest China (Muthukumar et al. 2003), and medicinal and aromatic plants in forests, scrubland, and grasslands of Western Ghats, southern India (Muthukumar et al. 2006). Although AM associations in crops and weeds of agro-ecosystems are well known, there are limited reports on AM morphological types of plants in agro-ecosystems (Dickson et al. 2007). Yamato (2004) indicated the predominance of *Arum*-type morphology in weeds growing on vacant land and emphasized the need to examine a wide range of plant species to evaluate the predominance of *Arum*-type morphology in weeds.

The present study was undertaken to test the hypothesis that weeds of agro-ecosystems may also exhibit the predominance of *Arum*-type morphology. We examined many

T. Muthukumar (✉) · S. Prakash
Root and Soil Biology Laboratory, Department of Botany,
Bharathiar University, Coimbatore – 641 046, Tamil Nadu, India
Tel. +91-422-2428306; Fax +91-422-2422387
e-mail: tmkum@yahoo.com

weeds growing in association with crop plants for their AM morphological type as well as the crops. The relationships between AM morphological type and ecological habitat of the host plants were also discussed.

Materials and methods

Study sites

Root and soil samples were collected between November 2005 and December 2006 at five agricultural fields in Coimbatore (I, II, III, IV, V) (11°04' N, 76°93' E, 426 m a.s.l, annual rainfall 500–700 mm) and an agricultural field in Sathyamangalam (VI) (11°29' N, 77°59' E, 540 m a.s.l, annual rainfall 300–600 mm).

Sample collection

Plant roots and soil samples of 8 crops and 40 weeds belonging to 18 families were collected. Ten individuals for each species were randomly sampled. For the weed species, the individuals that were within a 30-cm radius from the crops were sampled. Roots were gently washed and fixed in formalin-acetic acid-alcohol (FAA) and transported to the laboratory for processing. Rhizosphere soil adjacent to roots was collected by shaking the roots. Soil samples collected from individual plants of a species were put into a polythene bag and stored at 4°C until processing. The soil samples were used for assessing soil chemical properties.

Preparation of roots and AM assessment

The fixed roots were washed free of FAA, cut into 1-cm fragments, cleared in 2.5% KOH (Koske and Gemma 1989), acidified with 5 mol l⁻¹ HCl, and stained with trypan blue (0.5% in lacto-glycerol) overnight. Roots that were pigmented after clearing were bleached in alkaline H₂O₂ before 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 the magnified intersection method (McGonigle et al. 1990).

The AM morphology was classified as *Arum*- or *Paris*-type based on whether the fungal hyphae were present mainly as hyphae running through intercellular spaces or within cells as coils, respectively, following the description by Dickson (2004). Because we examined whole and squashed roots, we could not reliably distinguish among the intermediate subtype morphologies as described and classified by Dickson (2004). However, wherever parallel intracellular running hyphae were found, morphology was designated as the intermediate type.

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).

Results

Soil chemical properties

The soils were either sandy loam or clayey loam (Table 1). The pH varied between 7.6 and 8.2. Electrical conductivity ranged from 0.20 to 0.37 mS cm⁻¹. The amount of total N and P and of exchangeable K varied between 8.9 and 10.7 mg kg⁻¹, 0.37 and 0.63 mg kg⁻¹, and 14.1 and 22.3 mg kg⁻¹ of soil, respectively.

Occurrence of mycorrhizae

In the present study, all the 8 crop species (belonging to 8 genera in 6 families) had mycorrhizal association (Table 2). In contrast, among the examined weeds (belonging to 35 genera in 15 families), AM were absent in *Commelina benghalensis* (Commelinaceae), *Aerva lanata*, *Alternanthera sessilis*, *Celosia argentea* (Amaranthaceae), *Boerhavia diffusa* (Nyctaginaceae), and *Cleome gynandra* (Brassicaceae).

Table 1. Soil characteristics of the fields sampled (mean ± SE)

	Site					
	Coimbatore					Sathyamangalam
	Field I	Field II	Field III	Field IV	Field V	Field VI
Soil type	Sandy loam	Clay loam	Sandy loam	Clay loam	Sandy loam	Sandy loam
pH	7.6 ± 0.01	8.2 ± 0.02	8.1 ± 0.01	7.8 ± 0.03	7.6 ± 0.01	8.1 ± 0.01
EC (mS cm ⁻¹)	0.25 ± 0.01	0.37 ± 0.01	0.20 ± 0.02	0.26 ± 0.01	0.30 ± 0.02	0.28 ± 0.01
Nitrogen (mg kg ⁻¹)	10.7 ± 0.35	9.9 ± 0.32	10.5 ± 0.12	8.92 ± 0.45	10.54 ± 0.84	9.37 ± 0.78
Phosphorus (mg kg ⁻¹)	0.63 ± 0.02	0.37 ± 0.04	0.42 ± 0.03	0.55 ± 0.04	0.52 ± 0.01	0.48 ± 0.02
Potassium (mg kg ⁻¹)	21.72 ± 2.36	21.03 ± 3.58	14.12 ± 1.78	18.36 ± 2.89	22.31 ± 3.54	20.25 ± 1.87

Table 2. Arbuscular mycorrhizal association in crops and weed species (mean \pm SE)

Plant species	Field ^a	Associated crop species	AM fungal colonization ^b			
			% RLH	% RLA	% RLV	% RLTC
Crops						
<i>Areca catechu</i> (AC)	I		56.64 \pm 11.85	10.58 \pm 7.24	1.28 \pm 1.28	68.28 \pm 15.87
<i>Cajanus cajan</i> (CC)	II		27.41 \pm 3.92	3.28 \pm 1.96	5.36 \pm 3.52	36.05 \pm 5.40
<i>Cocos nucifera</i> (CN)	I		31.37 \pm 7.13	9.70 \pm 9.70	8.97 \pm 2.54	50.03 \pm 11.86
<i>Manihot esculanta</i> (ME)	II		53.55 \pm 6.01	10.10 \pm 6.09	1.17 \pm 1.17	64.73 \pm 11.45
<i>Musa paradisiaca</i> (MP)	III		41.57 \pm 5.15	22.63 \pm 8.49	12.50 \pm 6.82	76.69 \pm 9.57
<i>Saccharum officinarum</i> (SO)	V		36.85 \pm 6.02	1.26 \pm 0.72	20.58 \pm 5.84	58.69 \pm 0.47
<i>Vitis vinifera</i> (VV)	IV		39.80 \pm 2.74	14.26 \pm 9.26	8.59 \pm 0.01	62.67 \pm 17.08
<i>Zea mays</i> (ZM)	VI		43.19 \pm 5.19	27.70 \pm 6.95	13.10 \pm 2.36	83.99 \pm 1.78
Weeds						
<i>Acalypha indica</i>	III	MP	33.83 \pm 3.81	7.15 \pm 1.63	3.93 \pm 1.06	44.91 \pm 5.38
	V	SO	34.41 \pm 4.28	13.19 \pm 3.15	3.79 \pm 1.01	51.39 \pm 6.15
<i>Achyranthes aspera</i>	II	CC	20.57 \pm 8.10	26.79 \pm 14.54	6.45 \pm 0.80	53.81 \pm 14.07
<i>Aerva lanata</i>	II	CC	–	–	–	–
<i>Ageratum conyzoides</i>	I	AC	34.21 \pm 5.16	5.21 \pm 1.05	6.18 \pm 1.81	45.60 \pm 4.31
	II	CC	37.13 \pm 4.31	9.05 \pm 2.31	8.28 \pm 2.35	54.46 \pm 6.18
<i>Alternanthera sessilis</i>	I	AC	–	–	–	–
<i>Amaranthus viridis</i>	I	CN	10.56 \pm 1.37	2.35 \pm 1.11	3.52 \pm 1.06	16.45 \pm 3.38
<i>Bidens pilosa</i>	I	AC	16.78 \pm 3.86	9.89 \pm 1.38	15.21 \pm 2.15	41.88 \pm 3.86
	II	CC	16.28 \pm 1.21	11.21 \pm 1.97	17.31 \pm 1.87	44.80 \pm 4.39
	III	MP	16.05 \pm 2.38	10.79 \pm 1.82	16.47 \pm 1.92	43.31 \pm 3.97
<i>Boerhavia diffusa</i>	II	ME	–	–	–	–
<i>Borreria ocyroides</i>	VI	ZM	23.57 \pm 4.86	26.76 \pm 1.14	6.99 \pm 2.25	57.32 \pm 6.00
<i>Brachiaria ramosa</i>	VI	ZM	40.00 \pm 4.62	21.33 \pm 2.91	–	61.33 \pm 3.71
<i>Celosia argentea</i>	VI	ZM	–	–	–	–
<i>Chloris barbata</i>	II	CC	52.00 \pm 3.06	4.00 \pm 2.09	–	59.33 \pm 5.70
<i>Cleome gynandra</i>	VI	ZM	–	–	–	–
<i>Commelina benghalensis</i>	III	MP	–	–	–	–
<i>Corchorus trilocularis</i>	II	CC	43.33 \pm 2.91	2.67 \pm 1.76	9.33 \pm 1.76	55.33 \pm 3.53
<i>Croton bonplandianum</i>	I	AC	36.01 \pm 5.96	8.00 \pm 1.15	7.32 \pm 2.53	66.00 \pm 7.02
<i>Cynodon dactylon</i>	VI	ZM	41.62 \pm 7.03	10.00 \pm 3.06	12.38 \pm 3.81	64.00 \pm 8.08
<i>Dactyloctenium aegyptium</i>	II	CC	32.00 \pm 9.02	4.00 \pm 3.06	5.33 \pm 3.50	41.33 \pm 11.62
<i>Datura metel</i>	III	MP	58.01 \pm 15.10	4.03 \pm 1.33	13.33 \pm 2.67	58.67 \pm 2.40
<i>Dipteracanthus prostratus</i>	II	ME	30.51 \pm 5.46	8.83 \pm 1.97	18.07 \pm 2.67	60.67 \pm 1.33
<i>Eclipta prostrata</i>	V	SO	40.67 \pm 4.67	13.33 \pm 6.67	8.01 \pm 7.02	62.00 \pm 4.62
<i>E. alba</i>	V	SO	26.41 \pm 9.38	10.39 \pm 4.60	5.38 \pm 1.38	42.17 \pm 18.83
<i>Eragrostis amabilis</i>	VI	ZM	36.58 \pm 16.71	1.83 \pm 0.67	10.47 \pm 5.38	48.88 \pm 21.58
<i>Euphorbia cyathophora</i>	V	SO	45.31 \pm 7.86	14.69 \pm 1.05	14.67 \pm 5.21	74.67 \pm 8.97
<i>E. heterophylla</i>	II	ME	39.14 \pm 3.11	6.41 \pm 6.41	3.82 \pm 1.15	49.37 \pm 8.44
<i>E. hirta</i>	I	AC	12.58 \pm 2.81	7.38 \pm 1.16	13.26 \pm 3.15	33.22 \pm 9.65
<i>Indigofera tinctoria</i>	IV	VV	36.29 \pm 5.67	12.05 \pm 1.07	–	59.33 \pm 7.06
<i>Justicia tranquebarensis</i>	II	CC	38.62 \pm 5.29	8.67 \pm 5.93	7.38 \pm 1.26	54.67 \pm 0.67
<i>Lantana camara</i>	II	ME	34.41 \pm 3.71	6.95 \pm 1.76	7.32 \pm 1.56	52.00 \pm 5.03
<i>Mukia maderaspatana</i>	I	CN	42.19 \pm 6.57	14.67 \pm 0.67	10.48 \pm 2.21	67.33 \pm 6.77
<i>Ocimum americanum</i>	I	CN	36.86 \pm 5.40	6.00 \pm 3.46	13.81 \pm 4.15	56.67 \pm 3.71
<i>O. basilicum</i>	II	CC	13.89 \pm 0.93	6.89 \pm 2.59	6.43 \pm 1.19	27.21 \pm 12.95
<i>Parthenium hysterophorus</i>	II	ME	29.00 \pm 0.78	10.39 \pm 0.49	10.42 \pm 2.75	49.80 \pm 3.37
<i>Pavonia zeylanica</i>	V	SO	21.67 \pm 3.34	57.73 \pm 7.55	1.65 \pm 0.95	81.05 \pm 4.91
<i>Phyla nodiflora</i>	I	CN	44.00 \pm 4.16	16.00 \pm 4.16	–	60.00 \pm 2.00
<i>Solanum nigrum</i>	VI	ZM	22.22 \pm 5.16	9.79 \pm 4.99	4.30 \pm 3.34	36.31 \pm 12.19
<i>S. torvum</i>	II	ME	35.27 \pm 4.43	3.97 \pm 2.31	3.10 \pm 1.05	42.34 \pm 3.39
<i>Tephrosia purpurea</i>	I	AC	49.33 \pm 5.46	16.03 \pm 4.62	–	65.33 \pm 1.76
<i>Tridax procumbens</i>	V	SO	26.14 \pm 9.49	8.50 \pm 3.98	6.54 \pm 3.64	41.18 \pm 11.93
<i>Vernonia pulneyensis</i>	I	AC	18.21 \pm 0.85	41.16 \pm 18.38	0.68 \pm 0.09	60.05 \pm 17.42

^aAs in Table 1^b% RLH, % RLA, % RLV, and % RLTC: root length with hyphae/hyphal coils, arbuscules/arbusculate coils, intercellular/intracellular vesicles, and total colonization, respectively

Distribution of AM morphological types

AM morphology has been recorded in 23 plant species for the first time. The *Arum*-type mycorrhizae were characterized by the presence of intercellular hyphae, vesicles, and intracellular arbuscules (Fig. 1). Hyphal coils, when present,

were restricted to a few cells near the penetration point. The *Paris*-type was characterized by extensive intracellular hyphal coils, arbusculate coils, and intracellular vesicles. Among the 8 crop species examined, 3 had *Arum*-type, 3 had *Paris*-type, and 2 had intermediate-type AM morphology (Fig. 2). Among the 34 mycorrhizal

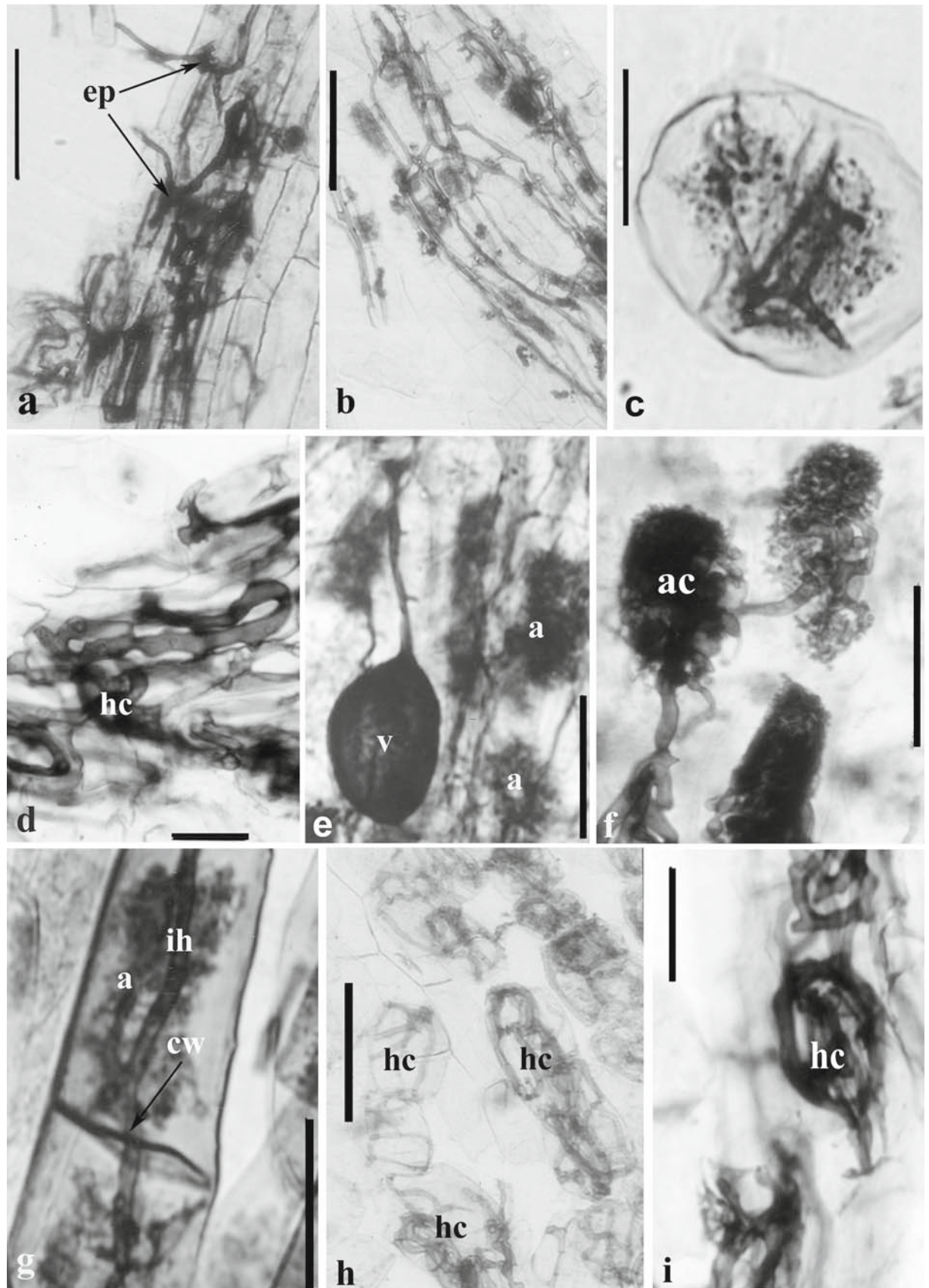


Fig. 1. Micrograph showing morphology of mycorrhizal association in crops and weeds. **a** Entry point (*ep*) with appressorium in *Ageratum conyzoides*. **b** Intercellular hyphae and arbuscules in *Vernonia pulneyensis*. **c** Arbusculate coil in *Saccharum officinarum*. **d** Hyphal coils (*hc*) in *Dactyloctenium aegypticum*. **e** Vesicle (*v*) and arbuscules (*a*) in

Cocos nucifera. **f** Arbusculate coil (*ac*) and hyphal coils in *Tephrosia purpurea*. **g** Intracellular hyphae (*ih*), arbuscule (*a*), and cell wall (*cw*) in *Zea mays*. **h** Hyphal coils (*hc*) in *Musa paradisiaca*. **i** Hyphal coils (*hc*) in *Indigofera tinctoria*. Bars **a, b, f, h, i** 100 μ m; **c-e, g** 50 μ m

Order	Family	Species	AM type	Previous report
Arecales	Arecaceae	<i>Areca catechu</i>	Intermediate	Intermediate ¹⁰
		<i>Cocos nucifera</i>	Arum	Arum ^{5,10}
Poales	Poaceae	<i>Brachiaria ramosa</i> *	Arum	
		<i>Dactyloctenium aegyptium</i>	Arum	Paris ⁶
		<i>Cynodon dactylon</i>	Arum	Arum ¹⁰
		<i>Chloris barbata</i>	Arum	Arum ⁶
		<i>Eragrostis amabilis</i> *	Arum	
		<i>Saccharum officinarum</i> *	Paris	
		<i>Zea mays</i>	Intermediate	Arum ^{2,3} , Paris ⁵
Commelinales	Commelinaceae	<i>Commelina benghalensis</i>	NM	Mycorrhizal ⁷
Zingiberales	Musaceae	<i>Musa paradisiaca</i>	Paris	Paris ⁹
Caryophyllales	Amaranthaceae	<i>Achyranthes aspera</i> *	Arum	
		<i>Aerva lanata</i>	NM	
		<i>Alternanthera sessilis</i>	NM	
		<i>Amaranthus viridis</i>	Arum	Arum ⁹
		<i>Celosia argentea</i>	NM	
	Nyctaginaceae	<i>Boerhavia diffusa</i>	NM	Mycorrhizal ⁴
Vitales	Vitaceae	<i>Vitis vinifera</i> *	Arum	
Malpighiales	Euphorbiaceae	<i>Acalypha indica</i>	Arum	Arum ⁹
		<i>Croton bonplandianum</i> *	Arum	
		<i>Euphorbia cyathophora</i> *	Intermediate	
		<i>Euphorbia heterophylla</i> *	Arum	
		<i>Euphorbia hirta</i>	Arum	Arum ⁵ , Paris ⁶
		<i>Manihot esculenta</i> *	Paris	
Fabales	Fabaceae	<i>Cajanus cajan</i>	Arum	Arum ⁵
		<i>Tephrosia purpurea</i> *	Paris	
		<i>Indigofera tinctoria</i> *	Paris	
Cucurbitales	Cucurbitaceae	<i>Mukia maderaspatana</i> *	Arum	
Brassicales	Brassicaceae	<i>Cleome gynandra</i>	NM	
Malvales	Malvaceae	<i>Corchorus trilocularis</i> *	Paris	
		<i>Pavonia zeylanica</i> *	Arum	
Gentinales	Rubiaceae	<i>Borreria ocyroides</i> *	Paris	
Lamiales	Acanthaceae	<i>Justicia tranquebarensis</i> *	Arum	
		<i>Dipteracanthus prostratus</i> *	Intermediate	
	Lamiaceae	<i>Ocimum basilicum</i>	Arum	Arum, Intermediate ¹
		<i>Ocimum americanum</i> *	Arum	
Verbenaceae	<i>Lantana camara</i>	Intermediate	Paris ⁵	
	<i>Phyla nodiflora</i> *	Arum		
Solanales	Solanaceae	<i>Datura metel</i>	Arum	Arum ⁹
		<i>Solanum nigrum</i> *	Paris	
		<i>Solanum torvum</i> *	Arum	
Asterales	Asteraceae	<i>Ageratum conyzoides</i>	Arum	Arum ⁸
		<i>Bidens pilosa</i>	Arum	Arum ^{5,8}
		<i>Eclipta alba</i> *	Arum	
		<i>Eclipta prostrata</i>	Arum	Arum ⁸
		<i>Parthenium hysterophorus</i>	Arum	Arum ¹⁰
		<i>Tridax procumbens</i>	Arum	Arum ⁹
		<i>Vernonia pulneyensis</i> *	Arum	

¹Dickson (2004), ²Gerdemann (1965), ³Greny (1973), ⁴Jain et al. (1997), ⁵Johnston (1949), ⁶Louis (1990), ⁷Muthukumar and Udaiyan (2000), ⁸Muthukumar et al. (2003), ⁹Muthukumar et al. (2006), ¹⁰Sengupta and Chaudhuri (2002)

Fig. 2. Morphological types of arbuscular mycorrhizal (AM) fungi examined in the study in a current plant phylogeny scheme that is inferred from 18S rDNA, *rbcl*, and *atpB* sequences (Soltis et al. 2000). The ordinal names correspond to those used in the Angiosperm Phy-

logeny Group (2003). The morphological types of each plant species in the previous studies are also shown. Crop species are indicated in *bold*. *First record of the morphological type of AM in the plant species

weeds, *Arum*-type, *Paris*-type, and intermediate-type AM morphology was present in 26, 5, and 3 species, respectively.

Extent of AM colonization

There were large differences in patterns of colonization between crops and weeds. Percentage root length colonized by hyphal coils, inter- or intracellular hyphae, arbusculate coils, arbuscules, and inter- or intracellular vesicles is shown for all plant species examined (Table 2). The colonization rate ranged from 36% (*Cajanus cajan*, Fabaceae) to 84% (*Zea mays*, Poaceae) in crops; similarly, that in weeds ranged from 27% (*Ocimum basilicum*, Lamiaceae) to 81% (*Pavonia zeylanica*, Malvaceae). Average AM colonization rate was higher in crops (62.64%) compared to weeds (52.92%, excluding the nonmycorrhizal species). As arbuscules or arbusculate coils were present in all the mycorrhizal crop and weedy species, vesicles were absent in *Chloris barbata*, *Brachiaria ramosa* (Poaceae), *Indigofera tinctoria*, *Tephrosia purpurea* (Fabaceae), and *Phyla nodiflora* (Verbenaceae).

Distribution of AM in plant families

Although the colonization types were mostly discriminated at plant species level, it was not possible to discriminate between *Arum*-type and *Paris*-type at the plant family level, except for Asteraceae (Fig. 2). Most plant families contained species with more than one AM type, and these findings were similar to those observed earlier (Fig. 2).

Discussion

In the present study, all the crops and 90% of the weeds (34 of 40) were mycorrhizal. A similar high incidence of mycorrhizae in weeds has been reported in other studies (Anwar and Jalaluddin 1994; Jain et al. 1997; Yamato 2004). Plants devoid of mycorrhizal association in the present study are in the families that have been grouped as the nonmycorrhizal families, i.e., Amaranthaceae, Brassicaceae, and Commelinaceae (Tester et al. 1987; Peat and Fitter 1993). Meanwhile, AM association has been reported in *Boerhavia diffusa* (Nyctaginaceae) and *Commelina benghalensis* (Comelinaceae) (Jain et al. 1997; Muthukumar and Udaiyan 2000), which lacked AM in the present study.

Arum-type colonization was dominant among the plants examined, which is in accordance with the studies that showed *Arum*-type AM dominance in weeds (Smith and Smith 1997; Yamato 2004; Dickson et al. 2007). Predominance of *Arum*-type colonization was also frequent among AM plants examined in natural ecosystems (O'Connor et al. 2001; Muthukumar et al. 2003, 2006). One of the most conspicuous environmental factors that affects photosynthetic activity and plant growth is light intensity. It is also well known that most cultivated herbs grown without any

shading form *Arum*-type AM (Smith and Smith 1990). Yamato (2004) suggested that *Arum*-type colonization is appropriate for fast-growing plant species because root growth rates in these plants also tend to be relatively high. The high spreading rate of colonization in *Arum*-type (Brundrett and Kendrick 1990a) may be one reason for the aptitude of the *Arum*-type in fast-growing plants, as indicated by Brundrett and Kendrick (1990b).

In the present study, *S. officinarum*, *M. paradisiaca*, and *M. esculenta* had *Paris*-type morphology among the crop species. Although the AM formation in *S. officinarum* and *Vitis vinifera* is well known (Tholkappian et al. 2004; Reddy et al. 2000), this is the first report on the colonization types in these crops. In this study, AM morphology has been reported in 21 weeds for the first time. Furthermore, several discrepancies were noted in the present study from those results reported in earlier studies. *Zea mays* has been reported to possess *Arum*-type (Gerdemann 1965; Greny 1973) or *Paris*-type (Johnston 1949) morphology. However, in the present study AM colonization in *Z. mays* was characterized by both inter- and intracellular hyphae running parallel with arbuscules, suggesting an intermediate-type (I3), as defined by Dickson (2004). Similarly, *Arum*-type and intermediate-type were found in *Dactyloctenium aegyptium* (Louis 1990) and *Lantana camara* (Johnston 1949), respectively, in which the *Paris*-type had been previously reported.

It has been shown that AM morphological type is controlled by the host plant (Jacquelinet-Jeanmougin and Gianinazzi-Pearson 1983). A strong link between plant identity and AM morphology was also shown in the present study, wherein AM morphological type was determined at the species level. This result suggests that plant identity strongly influences AM morphology. However, morphological types were not discriminated at the plant family level except for Asteraceae. In some cases, different AM morphological types were found in a genus. For example, *Solanum nigrum* and *S. torvum* exhibited *Paris*-type and *Arum*-type, respectively. Smith and Smith (1997), in their review on AM morphological types, also reported the coexistence of both types in certain families such as Arecaceae, Poaceae, Euphorbiaceae, Fabaceae, Rubiaceae, Lamiaceae, and Solanaceae. Effects of the fungal species may also be the reason for this inconsistency. Actually, the effect of fungal species on AM morphological type was clearly shown by Cavagnaro et al. (2001b), in which both AM morphological types were formed in *Lycopersicon esculentum* (wild-type tomato), depending on the fungal species. Similarly, Dickson (2004) also showed that certain plants were consistent in AM morphology when colonized by different AM fungi, while others exhibited AM morphology dependent on the fungal species. These findings clearly indicated that AM morphology is dependent on both individual plant species and the AM fungus. Therefore, it is probable that AM morphological type is determined by both host and fungal identity, but some plants seem to be inclined to form one morphological type. Additionally, environmental factors such as temperature, light intensity, and soil moisture content may influence AM morphology, as assumed by

Cavagnaro et al. (2001a,b), because these factors affect the growth and the morphology of roots.

References

- Anwar QMK, Jalaluddin M (1994) Significance of VAM fungi in weeds of wheat. *Mycorrhiza News* 5:9–11
- Brundrett M, Kendrick B (1990a) The roots and mycorrhizas of herbaceous woodland plants I. Quantitative aspects of morphology. *New Phytol* 114:457–468
- Brundrett M, Kendrick B (1990b) The roots and mycorrhizas of herbaceous woodland plants II. Structural aspects of morphology. *New Phytol* 114:469–479
- Cavagnaro TR, Gao L-L, Smith FA, Smith SE (2001a) Morphology of arbuscular mycorrhizas is influenced by fungal identity. *New Phytol* 151:469–475
- Cavagnaro TR, Smith FA, Lorimer MF, Haskard KA, Ayling SM, Smith SE (2001b) Quantitative development of *Paris*-type arbuscular mycorrhizas formed between *Asphodelus fistulosus* and *Glomus coronatum*. *New Phytol* 149:105–113
- Dickson S (2004) The *Arum-Paris* continuum of mycorrhizal symbioses. *New Phytol* 163:187–200
- Dickson S, Smith FA, Smith SE (2007) Structural differences in arbuscular mycorrhizal symbioses: more than 100 years after Gallaud, where next? *Mycorrhiza* 17:375–393
- Fisher JB, Jayachandran K (2005) Presence of arbuscular mycorrhizal fungi in South Florida native plants. *Mycorrhiza* 15:580–588
- Gallaud I (1905) Etudes sur les mycorrhizes endotrophes. *Rev Génér Bot* 17:5–48, 66–83, 123–136, 223–239, 313–325, 425–433, 479–500
- Gerdemann JW (1965) Vesicular-arbuscular mycorrhizae formed on maize and tuliptree by *Endogone fasciculata*. *Mycologia* 57:562–575
- Greny A (1973) Étude anatomo-morphologique des endomycorrhizes constituées par le Maïs, l'Avoine, le Blé, l'Orge et diverses Graminées prairiales et adventices. Mémoire présentée au Conservatoire des Arts et Métiers pour obtenir le Diplôme d'Ingenieur C.N.A.M., Paris
- Jackson ML (1971) Soil chemical analysis. Prentice-Hall, New Delhi
- Jacquelinet-Jeanmougin S, Gianinazzi-Pearson V (1983) Endomycorrhizas in the Gentianaceae. I. The fungus associated with *Gentiana lutea* L. *New Phytol* 95:663–666
- Jain RK, Hasan N, Singh RK, Pandey PN (1997) Vesicular arbuscular mycorrhizal (VAM) associations in some weeds of forage legumes. *Mycorrhiza News* 5:9–11
- Johnston A (1949) Vesicular-arbuscular mycorrhiza in sea island cotton and other tropical plants. *Trop Agric* 26:118–121
- Koske RE, Gemma JN (1989) A modified procedure for staining roots to detect VA mycorrhizae. *Mycol Res* 92:486–488
- Louis I (1990) A mycorrhizal survey of plant species colonizing coastal reclaimed land in Singapore. *Mycologia* 82:772–778
- McGonigle TP, Miller MH, Evans DG, Fairchild GL, Swan JA (1990) A method which gives an objective measure of colonization of roots by vesicular-arbuscular mycorrhizal fungi. *New Phytol* 115:495–501
- Muthukumar T, Udaiyan K (2000) Arbuscular mycorrhizas of plants growing in the western Ghats region, Southern India. *Mycorrhiza* 9:297–313
- Muthukumar T, Sha L, Yang X, Cao M, Tang J, Zheng Z (2003) Mycorrhiza of plants in different vegetation types in tropical ecosystems of Xishuangbanna, southwest China. *Mycorrhiza* 13:289–297
- Muthukumar T, Senthilkumar M, Rajangam M, Udaiyan K (2006) Arbuscular mycorrhizal morphology and dark septate fungal association in medicinal and aromatic plants of Western Ghats, Southern India. *Mycorrhiza* 17:11–24
- O'Connor PJ, Smith SE, Smith FA (2001) Arbuscular mycorrhizal association in the southern Simpson Desert. *Aust J Bot* 49:493–499
- Peat H, Fitter H (1993) The distribution of arbuscular mycorrhizas in the British Flora. *New Phytol* 125:845–854
- Reddy CN, Bharati BK, Rajkumar HG, Sunanda DN (2000) Infectivity and efficacy of four native vesicular-arbuscular mycorrhizal fungi on sugar cane (c.v. 0419). *Mycorrhiza News* 16:9–12
- Sengupta A, Chaudhuri S (2002) Arbuscular mycorrhizal relations of mangrove plant community at the Ganges River estuary in India. *Mycorrhiza* 12:169–174
- Smith FA, Smith SE (1997) Structural diversity in (vesicular)-arbuscular mycorrhizal symbioses. *New Phytol* 137:373–388
- Smith SE, Dickson S (1991) Quantification of active vesicular-arbuscular mycorrhizal infection using image analysis and other techniques. *Aust J Plant Physiol* 18:637–648
- Smith SE, Smith FA (1990) Structure and function of the interface of in biotrophic symbiosis as they relate to nutrient transport. *New Phytol* 114:1–38
- Soltis DE, Soltis PS, Chase MW, Most ME, Albach DC, Zanis M, Savolonen V, Hahn WH, Hoot SB, Fay MF, Axtell M, Swensen SM, Prince LM, Kress WJ, Nixon KC, Farris JS (2000) Angiosperm phylogeny inferred from 18S rDNA, *rbcL*, and *atpB* sequences. *Bot J Linn Soc* 133:381–461
- Tester M, Smith SE, Smith FA (1987) The phenomenon of “non-mycorrhizal” plants. *Can J Bot* 65:419–431
- The Angiosperm Phylogeny Group (2003) An update of the Angiosperm Phylogeny Group classification for the orders families of flowering plants: APG II. *Bot J Linn Soc* 141:399–346
- Tholkappian P, Sivasarvanan A, Sundaram MD (2004) Effect of phosphorus level on the mycorrhizal colonization, growth, yield, and nutrient uptake of cassava (*Manihot esculenta* Crantz) in alluvial soils of coastal Tamil Nadu. *Mycorrhiza News* 11:15–18
- Yamato M (2004) Morphological types of arbuscular mycorrhizal fungi in roots of weeds on vacant land. *Mycorrhiza* 14:127–131
- Yamato M (2005) Morphological types of arbuscular mycorrhizas in pioneer woody plants growing in an oil palm in Sumatra, Indonesia. *Mycoscience* 46:66–68
- Yamato M, Iwasaki M (2002) Morphological types of arbuscular mycorrhizal fungi in roots of understory plants in Japanese deciduous broadleaved forests. *Mycorrhiza* 12:291–296