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Masahide Yamato · Masahiro Iwasaki

Morphological types of arbuscular mycorrhizal fungi in roots of understory plants in Japanese deciduous broadleaved forests

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Abstract Morphological types of arbuscular mycorrhizal (AM) fungi in roots of understorey plants were examined in three different Japanese deciduous broadleaved forests. In total, 43 species belonging to 33 genera from 27 families were examined for the morphological types of AM. The number of flowering plant species having *Paris*-type AM was greater than those having *Arum*-type AM in each plot. This tendency was more prominent in herbaceous plants than woody plants with nine species having *Paris*-type associations among ten herbaceous plant species examined. Therefore, it is suggested from the ecological point of view that *Paris*-type associations could be advantageous for the herbaceous understorey plants growing slowly in these environments. The influence of plant identity on the morphological types of AM was also discussed by arranging the plants examined with the morphological types in a current plant phylogeny scheme. In this study, some new records on the morphological types of AM in some new plant families were obtained including the first report of a typical *Arum*-type AM in gymnosperms.

Keywords Arbuscular mycorrhiza · Morphological type · *Paris*-type · *Arum*-type · Understory plants

Introduction

The morphology of arbuscular mycorrhizas (AM) is divided into two types, *Arum*- and *Paris*-type (Gallaud 1905; Smith and Smith 1997). In *Arum*-type associations, the hyphae grow intercellularly in the root cortex and penetrate with short side branches into cortical cells to form arbuscules within. In *Paris*-type associations, intracellular hyphal coils frequently having intercalary arbuscules spread cell to cell in the cortex.

Until recently, it has been believed that the *Arum*-type of AM is more common than the *Paris*-type, since most cultivated herbaceous plants that have been used in studies form the *Arum*-type. However, Smith and Smith (1996, 1997) indicated in reviews that the *Paris*-type of AM is found in a rather wide range of plant taxa such as *Paris*, *Parnassia*, *Colchicum* (Gallaud 1905), *Gentiana* (Jacquelinet-Jeanmougin and Gianinazzi-Pearson 1983), *Erythronium*, *Trillium*, *Asarum* (Brundrett and Kendrick 1990b), *Acer* (Yawney and Schultz 1990), etc.

Although physiological or functional differences between the two morphological types have not yet been fully elucidated, it has been shown that the development of *Paris*-type AM is slower than that of *Arum*-type AM (Brundrett and Kendrick 1990a; Cavagnaro et al. 2001a). Brundrett and Kendrick (1990b) discussed that slower colonization of *Paris*-type AM might be beneficial for the host plants to keep the energy supply to the fungi reduced and might be desirable for plants growing slowly in a woodland environment. However, it is necessary to examine the morphological type in a wider range of plants growing in different habitats to support this idea.

In this study, the flowering plants growing on the forest floor whose height was <50 cm were defined as understory plants, and their morphological type of AM was examined in three different deciduous broadleaved forests. The relationship between morphological types of AM and the ecology or taxonomy of the host plants is also discussed.

Materials and methods

Three examination sites (St-M, St-K, St-O) were selected at 3 different deciduous broadleaved forests in Kinki region in Japan as described below.

M. Yamato (✉)
Biological Environment Institute, Kansai Environmental Engineering Center Co., Ltd, 8–4 Ujimatafuri, Uji, Kyoto 611–0021, Japan
e-mail: yamato_masahide@kanso.co.jp
Fax: +81-774-215005

M. Iwasaki
Environmental Harmonization Department, Kansai Environmental Engineering Center Co., Ltd, 1-3-5 Azuchicho, Chuo-ku, Osaka 541–0052, Japan

St-M is located in Mizuho-cho, Funai-gun, Kyoto Prefecture, 210 m above sea level. This site is in a secondary forest in the rainy temperate zone. The vegetation is typical for Japanese red pine (*Pinus densiflora*) and Japanese oak forest. However, most of the red pine trees have already died mainly because of pine wilt disease caused by pinewood nematode (*Bursaphelenchus xylophilus*), which is a phenomenon extensively spread among secondary forests in the western part of Japan (Mamiya 1988). The dominant trees and shrubs are *Quercus variabilis*, *Ilex pedunculosa*, *Lyonia ovalifolia*, *Clethra barbinervis*, and *Eurya japonica*, *Rhododendron macrosepalum*, *Vaccinium Oldhamii*, *Ilex crenata*, respectively.

St-K is located in Kanaibara Kinomoto-cho Shiga Prefecture, 890 m above sea level. This site is in a primary forest in the cool temperate zone. The vegetation is typical for beech forest with the dominant species, *Fagus crenata*, *Acer sieboldianum*, *Prunus grayana* and *Acer tschonoskii* as the tree layer, and *Lindera triloba*, *Clethra barbinervis* and *Lindera umbellata* as the shrub layer.

St-O is located in Okuyoshino, Totsukawa-mura, Nara Prefecture, 970 m above sea level. This site is in a secondary forest in the cool temperate zone. The vegetation is typical for Japanese oak forest with the dominant species, *Quercus mongolica*, *Lindera erythrocarpa*, *Hydrangea paniculata* and *Meliosma myriantha* as the tree layer, and *Lindera umbellata*, *Actinidia arguta*, *Schizopharagma hydrangeoides* and *Viburnum erosum* as the shrub layer.

In each site, a sampling plot of 100 m^2 (10 m×10 m) was established. Specimens were collected for all of the understory plant species and examined for mycorrhiza formation. The collected plant roots were fixed and preserved in formalin-acetic acid-alcohol. The roots were stained using the method of Brundrett et al. (1984) with a slight modification. The roots were cleared by autoclaving at 121°C for 15 min in 10% KOH and stained with 0.1% Chlolazol black E at 90°C for 90 min. The stained roots were squashed and observed under a Nomarski interference-contrast microscope (Leica; Leitz, Wetzlar). At least 20 cm of colonized root from three individuals was examined for each species in each plot to discern the morphological type of AM.

The classification of flowering plants used here corresponds to that of the Angiosperm Phylogeny Group (APG 1998). The relationship between classification of the plants and morphological types of AM is shown according to a current plant phylogeny scheme (Soltis et al. 2000).

Results and discussion

All of the understory plants found at each plot were colonized by some kinds of mycorrhizal fungi.

No plants having both or intermediate types of AM were found in this study, thus, all of the examined plant species colonized by AM fungi can be divided into two groups with *Arum*- or *Paris*-type AM within the survey.

In the plot St-M, 26 species of understory plants covered about 20% of the plot area. Among them, 15 species were colonized by AM fungi, in which *Arum*- and *Paris*-type were found in four and 11 species, respectively (Table 1).

In the plot St-K, 25 species covered about 20% of the plot area with 23 species being colonized by *Arum*- and *Paris*-type AM, i.e. seven and 16 species, respectively (Table 1).

In the plot St-O, 21 species covered only about 5% of the plot area with 20 species colonized by eight *Arum*- and 12 *Paris*-type AM fungi (Table 1).

In all of the three plots, the *Paris*-type was more frequently found than the *Arum*-type in each level of plant taxonomy, from species to family (Table 1). Overall, this tendency was more prominent in herbaceous than woody plants. Only one species (*Smilacina japonica*) showed the *Arum*-type among ten herbaceous plant species examined. Although ferns were not examined in this study, they were found in all of the plots, and are also known to form *Paris*-type AM (Smith and Smith 1997). In contrast, O'Connor et al. (2001) found the *Arum*-type in all of the 21 species of herbaceous AM plants growing with no shading in Australian desert. Furthermore, it is well known that *Arum*-type AM is formed in most cultivated plants, which are usually grown in sunlight. These facts indicate that the *Paris*-type AM is advantageous for herbaceous understory plants growing slowly with low light intensity and a low level of nutrient availability, since they grow slowly through their whole life cycle.

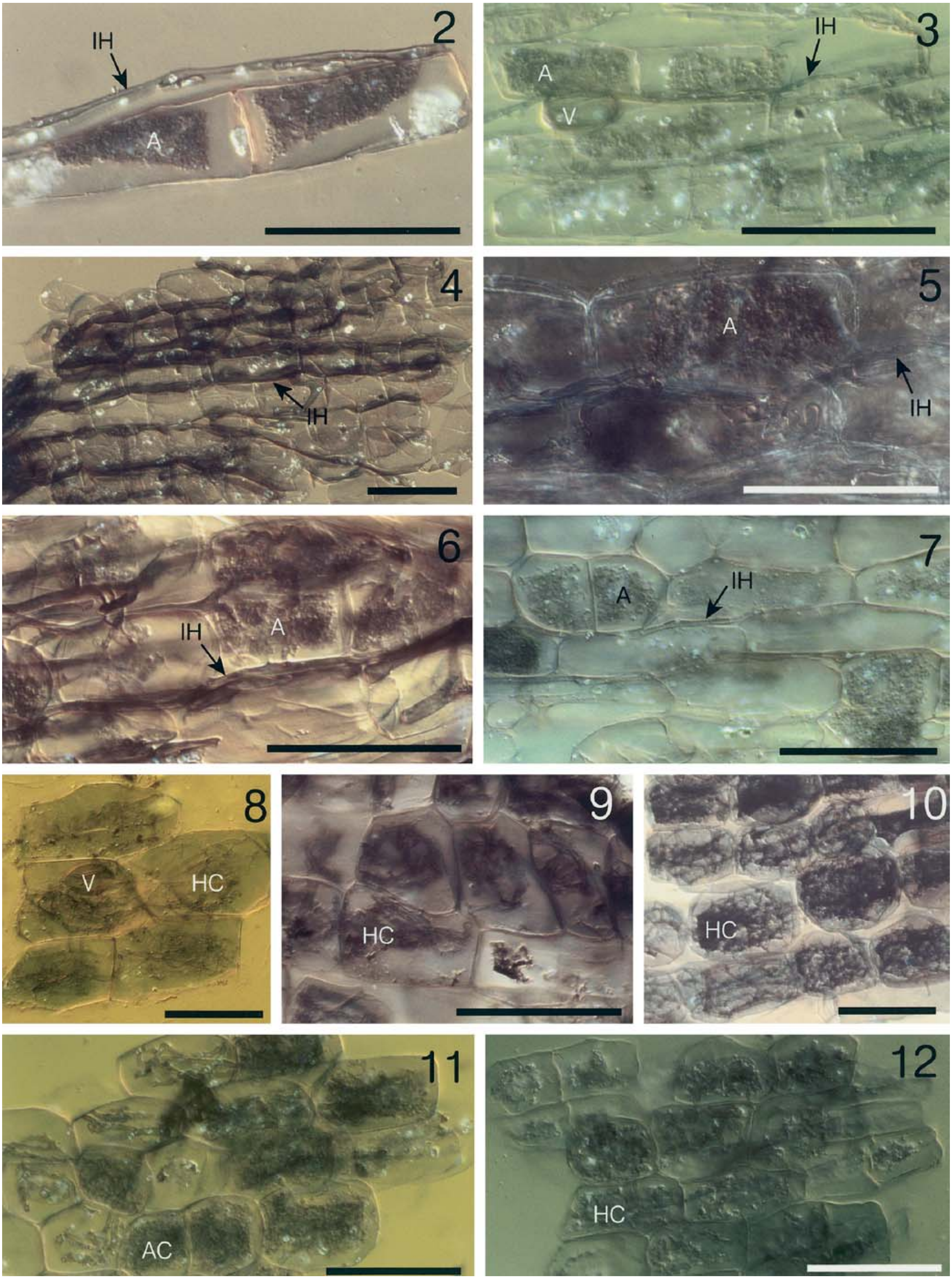
It has been shown that the morphological types of AM are controlled by host plants. Gerdemann (1965) demonstrated that the same species of AM fungi formed the *Paris*-type in *Liriodendron* and the *Arum*-type in maize, respectively. Similarly, Jacquelinet-Jeanmougin and Gianinazzi-Pearson (1983) showed that the *Paris*-type in *Gentiana* was formed by the same AM fungus which formed the *Arum*-type in *Allium*. Brundrett and Kendrick (1990b) suggested that the types are determined by the presence of continuous longitudinal airspaces in the root cortex, i.e. the *Arum*-type is formed in their presence and the *Paris*-type is formed in their absence. However, the effect of fungal identity on the morphological types of AM, which was indicated by Smith and Smith (1997), was also demonstrated by Cavagnaro et al. (2001b). They found both morphological types of AM were formed in *Lycopersicon esculentum* (wild type tomato) depending on the fungal species of AM inoculated. They suggested that the differences in mechanical

Table 1 The number of each morphological type of arbuscular mycorrhizal (AM) fungi, i.e. *Arum- and Paris-*type, in each plant classification level, from species to family, in each plot

Plot	Plant taxonomy	Total		Woody plants		Herbs	
		Arum	*Paris*	*Arum*	*Paris*	*Arum*	*Paris*
St-M	Family	4	9	4	6	0	3
	Genus	4	10	4	6	0	4
	Species	4	11	4	7	0	4
St-K	Family	6	12	6	10	1	2
	Genus	7	12	7	10	1	2
	Species	7	16	7	14	1	2
St-O	Family	6	9	6	5	0	4
	Genus	7	11	7	5	0	6
	Species	8	12	8	5	0	7

orders	species	plant habits	plots	morphological types of AM	families	morphological types of AM in previous studies
gymnosperm						
Taxales	*Cephalotaxus harringtonia*	wood	K O	*Paris**	Cephalotaxaceae	
Taxodiales	*Cryptomeria japonica*	wood	O	*Paris*	Taxodiaceae	*Paris* [2,6]
	Chamaecyparis obtusa	wood	M	*Arum**	Cupressaceae	
angiosperm						
Rosales	*Rubus palmatus*	wood	O	*Arum*	Rosaceae	*Arum* [1, 2, 10, 16]
	Prunus grayana	wood	M K	*Arum*		
	Sorbus alnifolia	wood	K	*Paris**		
	Sorbus commixta	wood	K	*Paris**		
Malpighiales	*Viola violacea*	herb	O	*Paris*	Violaceae	*Paris* [2, 10]
	Viola grypoceras	herb	O	*Paris*		
Sapindales	*Skimmia japonica*	wood	K O	*Arum*	Rutaceae	Both and Intermediate[1, 3, 5]
	Acer crataegifolium	wood	M	*Paris*	Sapindaceae	*Paris* [1, 9, 10, 14, 19, 22]
	Acer rufinerve	wood	K	*Paris*		
	Acer sieboldianum	wood	K	*Paris*		
	Acer distylum	wood	K	*Paris*		
	Acer tschonoskii	wood	K	*Paris*		
	Rhus trichocarpa	wood	M K O	*Paris**	Anacardiaceae	*Arum* [23]
Saxifragales	*Hydrangea hirta*	wood	O	*Arum**	Saxifragaceae	*Paris* [2]
	Hydrangea paniculata	wood	K O	*Arum**		
	Schizophragma hydrangeoides	wood	K O	*Arum**		
	Hamamelis japonica var. obutusata	wood	K	*Paris*	Hamamelidaceae	*Paris* [1]
Lamiales	*Callicarpa mollis*	wood	O	*Arum*	Verbenaceae	Both[5, 23]
Gentianales	*Mitschella undulata*	herb	K	*Paris*	Rubiaceae	Both[2, 5, 10]
	Swertia bimaculata	herb	O	*Paris*	Gentianaceae	*Paris* [1, 10, 12, 13, 15, 21]
	Tripterospermum japonicum	herb	M K O	*Paris*		
	Gentiana zollingeri	herb	O	*Paris*		
Dipsacales	*Abelia spathulata*	wood	M	*Arum**	Linnaenaceae	
	Viburnum diatatum	wood	O	*Paris**	Adoxaceae	
	Viburnum furcatum	wood	K	*Paris**		
Apiales	*Acanthopanax sciadophylloides*	wood	M K	*Paris*	Araliaceae	*Paris* [5, 18]
Aquifoliales	*Irex crenata*	wood	M K	*Paris**	Aquifoliaceae	
	Irex pedunculosa	wood	M	*Paris**		
Cornales	*Aucuba japonica*	wood	K	*Arum**	Cornaceae	*Paris* [10]
Ericales	*Clethra barvinervis*	wood	K	*Paris*	Clethraceae	*Paris* [25]
	Ardisia japonica	wood	M	*Paris*	Myrsinaceae	*Paris* [1]
Ranuncuales	*Akebia trifoliata*	wood	O	*Arum**	Lardizabaceae	
Liliales	*Smilax china*	herb	M O	*Paris*	Smilacaceae	*Paris* [24]
	Disporum smilacinum	herb	M O	*Paris*	Liliaceae	*Paris* [17, 20]
	Heloniopsis orientalis	herb	M	*Paris*		
Asparagales	*Smilacina japonica*	herb	K	*Arum*	Convallariaceae	*Arum* [2, 17]
Poales	*Pleioblastus chino var. viridis*	wood	O	*Paris*	Poaceae	Both and Intermediate[4, 5, 7, 10, 26]
Laurales	*Lindera umbellata*	wood	M O	*Arum**	Lauraceae	
	Lindera triloba	wood	K	*Arum**		
Magnoliales	*Magnolia salicifolia*	wood	M K	*Paris*	Magnoliaceae	*Paris* [1, 8, 11]

Fig. 1 Morphological types of arbuscular mycorrhizal (AM) fungi examined in this study with a current plant phylogeny scheme. The ordinal names correspond to those used in APG (1998). The applied phylogeny is that of Soltis et al. (2000), which is inferred from 18S rDNA, *rbc*, and *atpB* sequences. The morphological types of AM of each plant family in the previous studies are also shown. *New record of the morphological type of AM in each plant family,[1]Janse (1897), [2]Gallaud (1905), [3]McLukie and Burges (1932), [4]Endrigkeit (1937), [5]Johnston (1949), [6]Konoe (1957), [7]Nicolson (1959), [8]Gerdemann(1965), [9]Kessler (1966), [10]Steltz (1968), [11]Kinden and Brown (1975), [12]Gay et al. (1982), [13]Jacquelinet-Jeanmougin and Gianinazzi-Pearson (1983), [14]Frankland and Harrison (1985), [15]Kuhn and Weber (1986), [16]Brundrett et al. (1990), [17]Brundrett and Kendrick (1990b), [18]Whitbread et al. (1996), [19]Yawney and Schultz (1990), [20]Widden (1996), [21]Imhof and Weber (1997), [22]Smith et al. (1997), [23]Smith and Smith (1997), [24]Bedini et al. (2000), [25]Kubota et al. (2001), [26]O'Connor (2001)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and enzymatic characteristics of different fungal species might affect the morphology of AM. They also indicate a possibility that the *Arum*-type AM in plants with narrow air spaces may depend on thinner hyphae or their plasticity to invade the space. However, even though the fungal identity could determine the morphological types of AM in some cases, it still seems likely that only a single type is found in a plant in most cases, which indicates the morphological types of AM depend on the characteristics of plants rather than those of fungi.

In order to infer the influence of plant identity on the morphological types of AM, the plants examined were arranged in relation to morphological types of AM in a current plant phylogeny scheme (Fig. 1). This phylogeny scheme is inferred from 18S rDNA, *rbcL*, and *atpB* sequences (Soltis et al. 2000) using the classification of APG (1998). This new classification system seems to be more reasonable than the classic one from the view point of morphological types of AM. For instance, both morphological types of AM were found in plants belonging to Liliaceae in the classic classification; the Liliaceae is divided into the orders, Asparagales, Discoreales (Burmanniales) and Liliales in the new classification (Dahlgren et al. 1985; APG 1998), where *Arum*-type Asparagales was discriminated from the other *Paris*-type orders (Smith and Smith 1997). In this study, *Smilacina* (Convallariaceae) in Asparagales was found to be an *Arum*-type AM in accordance with a previous study (Brundrett and Kendrick 1990b). Morphological types of AM were mostly discriminated in a family level except for Rosaceae (Fig. 1), which suggests that the plant identity strongly influences the morphology of AM, although the contribution from AM fungi was not evaluated because there was no identification of colonized fungi in this study. Further study is required to understand the contribution of plants and fungi to the morphological types of AM.

New records on the morphological type of AM in some plant families were obtained (Fig. 1), such as *Arum*-type in Cupressaceae, Saxifragaceae, Linnaenaceae, Cornaceae, Lardizabaceae and Lauraceae (Figs. 2, 3, 4, 5, 6, 7); and *Paris*-type in Cephalotaxaceae, Rosaceae, Anacardiaceae, Adoxaceae and Aquifoliaceae (Figs. 8, 9, 10, 11, 12). The morphological type of AM in gymnosperms has been described as *Paris*-type with only one exception, *Gingko biloba*, which shows abundant intracellular hyphal coils and rare intercellular hyphae (Bonfante-Fasolo and Fontana 1985). Thus, this was described as “near-*Paris*-type” by Smith and Smith (1997). However, *Chamaecyparis obtusa* was found to have *Arum*-type AM in this study, which is the first report of typical *Arum*-type AM in gymnosperms as far as we know.

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◀ **Fig. 2** Micrograph showing morphology of mycorrhizal associations in roots of the understory plant, *Chamaecyparis obtusa* (Cupressaceae); *bar*=100 µm. *A* Arbuscule, *IH* intercellular hyphae

Fig. 3 Micrograph showing morphology of mycorrhizal associations in roots of the understory plant, *Hydrangea paniculata* (Saxifragaceae); *bar*=100 µm. *V* Vesicle; for other abbreviations, see Fig. 2

Fig. 4 Micrograph showing morphology of mycorrhizal associations in roots of the understory plant, *Abelia spathulata* (Caprifoliaceae); *bar*=100 µm

Fig. 5 Micrograph showing morphology of mycorrhizal associations in roots of the understory plant, *Aucuba japonica* (Cornaceae); *bar*=1 µm. For abbreviations, see Fig. 2

Fig. 6 Micrograph showing morphology of mycorrhizal associations in roots of the understory plant, *Akebia trifoliata* (Lardizabalaceae); *bar*=1 µm. For abbreviations, see Fig. 2

Fig. 7 Micrograph showing morphology of mycorrhizal associations in roots of the understory plant, *Lindera umbellata* (Lauraceae); *bar*=1 µm

Fig. 8 Micrograph showing morphology of mycorrhizal associations in roots of the understory plant, *Cephalotaxus harringtonia* (Cephalotaxaceae); *bar*=100 µm. *HC* Hyphal coil; for other abbreviations, see Fig. 3

Fig. 9 Micrograph showing morphology of mycorrhizal associations in roots of the understory plant, *Sorbus commixta* (Rosaceae); *bar*=100 µm. For abbreviations, see Fig. 8

Fig. 10 Micrograph showing morphology of mycorrhizal associations in roots of the understory plant, *Rhus trichocarpa* (Anacardiaceae); *bar*=100 µm. For abbreviations, see Fig. 8

Fig. 11 Micrograph showing morphology of mycorrhizal associations in roots of the understory plant, *Viburnum diatatum* (Caprifoliaceae); *bar*=100 µm. *AC* Arbuscular hyphal coils

Fig. 12 Micrograph showing morphology of mycorrhizal associations in roots of the understory plant, *Irex crenata* (Aquifoliaceae); *bar*=100 µm. For abbreviations, see Fig. 8

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