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**Evelyn Matekwor Ahulu · Makoto Nakata ·
Masanori Nonaka**

Arum- and *Paris*-type arbuscular mycorrhizas in a mixed pine forest on sand dune soil in Niigata Prefecture, central Honshu, Japan

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Abstract Arbuscular mycorrhizas (AM) are the most widespread mycorrhiza in nature and form two morphologies, *Arum*- and *Paris*-type. The determining factors defining the two different morphologies are not well understood. In this study, the distribution of *Arum*- and *Paris*-type AM was determined in a mixed pine forest. A total of 35 plant species belonging to 20 families and 32 genera were identified and examined for AM colonization and morphological types. AM morphological types in 14 families were confirmed as follows: *Arum*-type in Rosaceae, Oleaceae, Lauraceae, Vitaceae and Compositae, *Paris*-type in Aquifoliaceae, Ulmaceae, Araliaceae, Theaceae, Magnoliaceae, Rubiaceae and Dioscoraceae, and both and/or intermediate types in Caprifoliaceae and Gramineae. Plant families whose AM morphological status was previously unknown were clarified as follows: Polygonaceae and Commelinaceae showed *Arum*-type morphology; Celastraceae, Menispermaceae and Elaeagnaceae had typical *Paris*-type morphology. The proportion of *Arum*-type to *Paris*-type species decreased in the following order: annuals > perennials > deciduous species > evergreen species, and pioneer group > early successional group > late successional group. Evergreen plants had a higher tendency to form *Paris*-type AM than annuals, perennials and deciduous plants. The results indicate that environmental changes, such as shade during plant succession, control the distribution of plant growth forms in mixed pine forest and may also play a part in the distribution of *Arum*- and *Paris*-type morphology. The identity of the plant seems to strongly influence AM morphology, though control by the fungal genome cannot be ruled out.

Keywords *Arum*/*Paris*-type · Host plant/fungal identity · Mixed pine forest · Plant growth form · Plant succession

Introduction

About 80% of angiosperms are reported to have the potential to form arbuscular mycorrhizas (AM) under normal growth conditions (Bonfante-Fasolo 1984). Two AM morphological types, *Arum* and *Paris*, have been identified and are distinguished by the presence or absence of intercellular hyphae within the intercellular spaces of the root cortex, respectively (Smith and Smith 1996, 1997). Generally, *Arum*-type AM occur more commonly in crop plants and *Paris*-types in plants growing in natural ecosystems. Brundrett and Kendrick (1990a, 1990b) proposed that the *Arum*-type is formed in roots that have continuous longitudinal air spaces in their cortices, which probably increases the ease of growth and spread of intercellular hyphae and leads to rapid sequential penetration of cortical cells and growth of arbuscules. Accordingly, it is possible that the occurrence of limited or discontinuous intercellular spaces in roots, or differences between outer and inner cortices, might account for the intermediate AM morphology between *Arum*- and *Paris*-types (Smith and Smith 1997). Contrarily, however, Cavagnaro et al. (2001a) have reported, using wild-type tomato (*Lycopersicon esculentum*), that the colonizing fungus may also influence AM morphology.

In an extensive literature survey, Smith and Smith (1997) found that *Paris*-type AM occur more frequently than *Arum*-type AM, and also noted that this may be related to plant taxonomy. Although it is not yet established that species in one genus form the same AM morphology, only *Ranunculus* is known to have different species within the same genus forming either *Arum*- or *Paris*-type AM. Plant families Compositae and Malvaceae

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E. Matekwor Ahulu · M. Nonaka (✉)
Soil Science Laboratory, Faculty of Agriculture, University of Niigata,
8050 Ikarashi-2,
950–2181 Niigata, Japan
e-mail: nonaka@agr.niigata-u.ac.jp
Tel.: +81-25-2626687
Fax: +81-25-2626854

M. Nakata
Forest Ecology Laboratory, Faculty of Agriculture, University of Niigata,
Japan

appear to be classic *Arum*-types and Aceraceae and Gentianaceae classic *Paris*-types. In a study of AM morphological types in some broad-leaved forests in Japan, Yamato and Iwasaki (2002) also noted that AM plants in the same family usually formed the same AM morphological structure, indicating that plant identity strongly influences AM morphological types.

Earlier researchers (e.g., Abe and Katsuya 1995; Koske and Halvorson 1981) had shown that plants that colonize lacustrine, inland and maritime sand dunes are closely associated with arbuscular mycorrhizal fungi (AMF). The high incidence of mycorrhizas in natural ecosystems, and the results of several growth experiments, show that successful establishment, growth and survival of dominant plant species that colonize dunes depend on AMF (Newsham et al. 1995).

In Japan, AM associations in relation to enhancement of plant growth have been studied in various grasslands and arable lands (Tawaraya et al. 2001; Tsuchida and Nonaka 2002); however, information on the distribution of AM morphological types in plant species occurring in forest ecosystems is limited. Yamato and Iwasaki (2002) noted that the tendency to form *Paris*-type AM was more prominent in herbaceous plants than in woody plants in Japanese deciduous broad-leaved forests, and suggested that, from the ecological point of view, *Paris*-type AM could be more advantageous for slow-growing herbaceous understorey plants. Brundrett and Kendrick (1990a, 1990b) studied the roots and mycorrhizas of herbaceous woodland plants and found that the rate of mycorrhizal colonization in roots with longitudinal air channels was faster than that in roots lacking longitudinal air channels. They suggested that slow root growth coupled with long root lifespan and gradual mycorrhizal colonization may be the best growth strategy under the low nutrient, high-stress, conditions that usually prevail in natural ecosystems.

Forty years ago, barren coastal sand dunes near Niigata University were planted with pure Japanese black pine (*Pinus thunbergii*) to serve as a windbreak against the strong winds from the Sea of Japan. As a result of plant succession, the pure pine forests have gradually evolved into mixed forests consisting of deciduous trees and understorey vegetation, comprising pioneer, early successional and late successional plants such as grasses (Gramineae), herbs (Compositae), shrub and tree species commonly found in secondary deciduous forests. Fujita and Nakata (2001) have identified 81 plant species within the mixed forest at Niigata University.

The main objective of the present study was firstly to survey the distribution of *Arum*- and *Paris*-type AM in the mixed pine forest at Niigata University, and secondly to examine the relationship between AM type and plant growth forms as well as successional groups.

Materials and methods

Study site

The experimental site was a 25-m^2 plot located in the campus of Niigata University: a 1.4 ha early-to-mid successional mixed stand of Japanese black pine (*P. thunbergii* Parl.), deciduous and evergreen broad-leaved trees in coastal sand dune soil located in the Kaetsu district, Niigata. Niigata Prefecture is located on the northwestern coast of Honshu island, Japan (136–140° E, 36–41° N). The site is about 12 m above sea level and has a yearly average temperature of 13.2°C and precipitation (rain and snow) of 1,778 mm (Japan Meteorological Agency).

Root and soil sampling

Three replicate samples of young seedlings of randomly selected trees, shrubs, herbs and climbers were carefully excavated, making every attempt to ensure that the majority of roots were recovered; only those attributed to a given plant were included in the analysis. Fine roots of mature plants were collected in three replicates by careful digging along a major root from the stem base to the root tips. Samples were collected in May 2001 and September 2002 and stored at 4°C until processing.

Rhizosphere soil at two different depths, 10 and 30 cm, was randomly collected at six locations from the plot and mixed separately. The soil was air-dried and analyzed for chemical properties.

Table 1 Chemical properties of the study plot soil

Depth of soil sample	0–10 cm	10–30 cm
pH (H_2O)	5.9	5.6
pH (KCl)	4.2	4.0
EC (S m^{-1})	3.3	2.6
C (g kg soil^{-1})	15.2	7.7
N (g kg soil^{-1})	1.0	0.6
C/N	15.2	12.9
Available P (µg kg soil^{-1}) (0.002 *N* H_2SO_4 extractable)	40.0	4.0
CEC (mol$_c$ kg^{-1})	1.60	1.17
Ca (mol$_c$ kg^{-1}) (exchangeable)	0.05	0.02
K (mol$_c$ kg^{-1}) (exchangeable)	0.03	0.04
Mg (mol$_c$ kg^{-1}) (exchangeable)	0.27	0.14

Clearing and staining of roots

Root samples were cleared and stained according to the methods outlined by Phillips and Hayman (1970). Samples of 30 stained 5 mm root fragments from three replicates of each plant species were examined microscopically to identify AM fungal colonization using the magnified intersect technique (McGonigle et al. 1990).

Results

Soil chemical properties

The soil in the study plot is nutrient-poor and acidic (Table 1). EC values were low and there was a low carbon (C) and nitrogen (N) content with extremely low available phosphorus (P) content.

Vegetation composition of the study plot

The plot contained 35 plant species belonging to 20 families, and 32 genera were identified. The different plant growth forms identified included annual and perennial herbs, perennial, deciduous and evergreen climbers, deciduous and evergreen shrubs and trees. Plant successional groups (pioneer, early successional and late successional) were identified. The classification of each plant successional stage was based on the main growing habitat of each species (Kitamura and Murata 1974a, 1974b, 1979; Kitamura et al. 1974a, 1974b) and the criteria used are shown in Table 2. Dominant plant species included *Lonicera morrowii* (early successional deciduous shrub), *Rubus parvifolius* and *Rosa multiflora* (pioneer deciduous shrub), *Celtis sinensis* var. *japonica*, *Euonymus alatus* f. *ciliatodentatus*, *Ilex crenata*, *Prunus lannesiana* var. *speciosa* and *Osmanthus heterophyllus* (non-pioneer deciduous and evergreen shrubs and trees), *Parthenocissus tricuspidata* (early successional deciduous climber), *Artemisia princeps*, *Pennisetum alopecuroides*, *Miscanthus sinensis* (pioneer perennial herbs) and *Solidago virgaaurea* var. *asiatica* (early successional perennial herb).

Occurrence and distribution of AM morphological types

In the present study, 34 out of 35 plant species identified were colonized by AM fungi. It was possible to discriminate between *Arum*- and *Paris*-types at plant family level: *Arum*-types were found in Rosaceae, Oleaceae, Lauraceae, Vitaceae, Compositae, Commelinaceae and Polygonaceae, and *Paris*-type was found in Aquifoliaceae, Ulmaceae, Araliaceae, Theaceae, Magnoliaceae, Rubiaceae, Dioscoraceae, Elaeagnaceae, Celastraceae and Menispermaceae (Table 3). Both *Arum*- and *Paris*-types were found in Gramineae, and *Paris*-types and intermediate types in Caprifoliaceae (Table 3). Roots of three individual plants of *Rhus javanica*, (Anacardiaceae) showed no AM colonization (Table 3).

Plant families whose AM morphological status was previously unknown were found as follows: Polygonaceae and Commelinaceae had *Arum*-type morphology and the *Paris*-type was seen in Celastraceae, Menispermaceae and Elaeagnaceae (Fig. 1a–d). *Lonicera morrowii* (deciduous shrub) was the only species that had both intercellular hyphae and hyphal coils in the inner root cortex, indicating an intermediate between the *Arum*- and *Paris*-type morphologies (Table 3).

Influence of plant growth forms on AM morphology

Distribution of *Arum*- and *Paris*-type AM in the mixed pine forest correlated with plant growth characteristics (Fig. 2). The *Arum*-type was observed in 100% of the annuals, 70 and 30% of the perennials formed *Arum*- and *Paris*-type AM, respectively, and of the evergreen plants the proportion of *Arum*- and *Paris*-type AM was 30 and 70%, respectively. In the deciduous group, 38.5% formed *Arum*-type and 46.2% *Paris*-type morphology (Fig. 2). The proportion of *Arum*-type AM plants decreased according to the following trend: annuals > perennials > deciduous > evergreen, while the *Paris*-type increased in the same order.

Arum- and *Paris*-type AM morphology in relation to plant successional groups

Plant species within the study plot were grouped into three plant successional groups (pioneer, early successional and late successional) (Table 3). Within the pioneer group, seven species had *Arum*-type and two *Paris*-type AM (Table 3, Fig. 3). The proportion of *Arum*-type AM plants decreased according to the following trend: pioneer > early successional > late successional, while *Paris*-types increased in the same order. Distribution of the different plant growth forms (annuals, perennials, deciduous and evergreen) within the successional groups identified is shown in Fig. 4: pioneer plants (two annuals, four perennials and three deciduous species), early successional plants (six perennials, eight deciduous and one evergreen

Table 2 Criteria for classification of successional stages of plants in the mixed pine forest

Successional stage	Main growth habitat
Pioneer species	Barren, grassland and roadside
Early successional species	Forest edge, sunny forest and sunny forest floor
Late successional species	Forest and shady forest floor

Table 3 Arbuscular mycorrhiza (AM) morphological status of representative plant species in a mixed pine forest at Niigata University. Plant species authority (Ohwi (1975); *A Arum*-type, *I* intermediate-type,*P Paris*-type

Family	Species	Growth form	AM type	Successional groups
Rosaceae	*Prunus lannesiana* var. *speciosa*	Deciduous tree	A	Early successional
	Rosa multiflora	Deciduous shrub	A	Pioneer
	Prunus verecunda	Deciduous tree	A	Early successional
	Rubus parvifolius	Deciduous shrub	A	Pioneer
Oleaceae	*Osmanthus heterophyllus*	Evergreen tree	A	Late successional
	Ligustrum japonicum	Evergreen shrub	A	Late successional
Caprifoliaceae	*Lonicera morrowii*	Deciduous shrub	I	Early successional
	Viburnum dilatatum	Deciduous shrub	P	Early successional
Aquifoliaceae	*Ilex crenata*	Evergreen shrub	P	Late successional
	Ilex integra	Evergreen tree	P	Late successional
Ulmaceae	*Celtis sinensis* var. *japonica*	Deciduous tree	P	Early successional
Araliaceae	*Hedera rhombea*	Evergreen climber	P	Late successional
	Dendropanax trifidus	Evergreen tree	P	Late successional
Elaeagnaceae[a]	*Elaeagnus multiflora* var. *hortensis*	Deciduous shrub	P	Early successional
Theaceae	*Ternstroemia gymnanthera*	Evergreen tree	P	Early successional
	Camellia japonica	Evergreen tree	P	Late successional
Anacardiaceae	*Rhus javanica*	Deciduous tree	-	Early successional
Magnoliaceae	*Magnolia kobus*	Deciduous tree	P	Late successional
Celastraceae[a]	*Euonymus alatus* f. *ciliatodentatus*	Deciduous shrub	P	Late successional
	Euonymus japonicus	Evergreen shrub	P	Late successional
Lauraceae	*Neolitsea sericea*	Evergreen tree	A	Late successional
Vitaceae	*Parthenocissus tricuspidata*	Deciduous climber	A	Early successional
	Ampelopsis brevipedunculata	Perennial climber	A	Early successional
Menispermaceae[a]	*Cocculus trilobus*	Deciduous climber	P	Pioneer
Rubiaceae	*Paederia scandens* var. *mairei*	Perennial climber	P	Early successional
Dioscoreaceae	*Dioscorea tokoro*	Perennial climber	P	Early successional
Gramineae	*Miscanthus sinensis*	Perennial herb	P	Pioneer
	Briza maxima	Annual herb	A	Pioneer
	Pennisetum alopecuroides	Perennial herb	A	Pioneer
	Eragrostis curvula	Perennial herb	A	Pioneer
	Oplismenus undulatifolius	Perennial herb	A	Early successional
Compositae	*Solidago virga-aurea* var.*asiatica*	Perennial herb	A	Early successional
	Artemisia princeps	Perennial herb	A	Pioneer
Commelinaceae[a]	*Commelina communis*	Annual herb	A	Pioneer
Polygonaceae[a]	*Polygonum filiforme*	Perennial herb	A	Early successional

[a] New records of AM type

species) and late successional plants (two deciduous and nine evergreen species). All annual plants species were included in the pioneer group, whereas most evergreen plants species were in the late successional group. Perennial and deciduous plants species were mainly in the pioneer and early successional groups.

Discussion

Occurrence and distribution of AM morphological types in the mixed pine forest

The high incidence of plants colonized by AM fungi confirms the ubiquity of AM associations in nutrient-poor sand dune ecosystems (Louis 1990). Factors involved in determining the formation of *Arum*- and *Paris*-type morphologies, however, remain unclear. With the exception of two families, species within a majority of eight out of ten families (Rosaceae, Oleaceae, Aquifoliaceae, Araliaceae, Theaceae, Celastraceae, Vitaceae and Compositae), formed the same AM morphology, in accordance with earlier observations (Smith and Smith 1997; Yamato and Iwasaki 2002), indicating that AM morphology is strongly influenced by the identity of the host plant. Gerdemann (1965) showed that the same AM fungus that formed the *Arum*-type in *Zea mays* also formed the *Paris*-type in *Liriodendron tulipifera*. A similar result was observed by Jacquelinet-Jeanmougin and Gianinazzi-Pearson (1983) using *Allium cepa* and *Gentiana lutea*, respectively. *Glomus mosseae* and *G. viscosum*, which are known to form *Arum*-type AM in many plant species

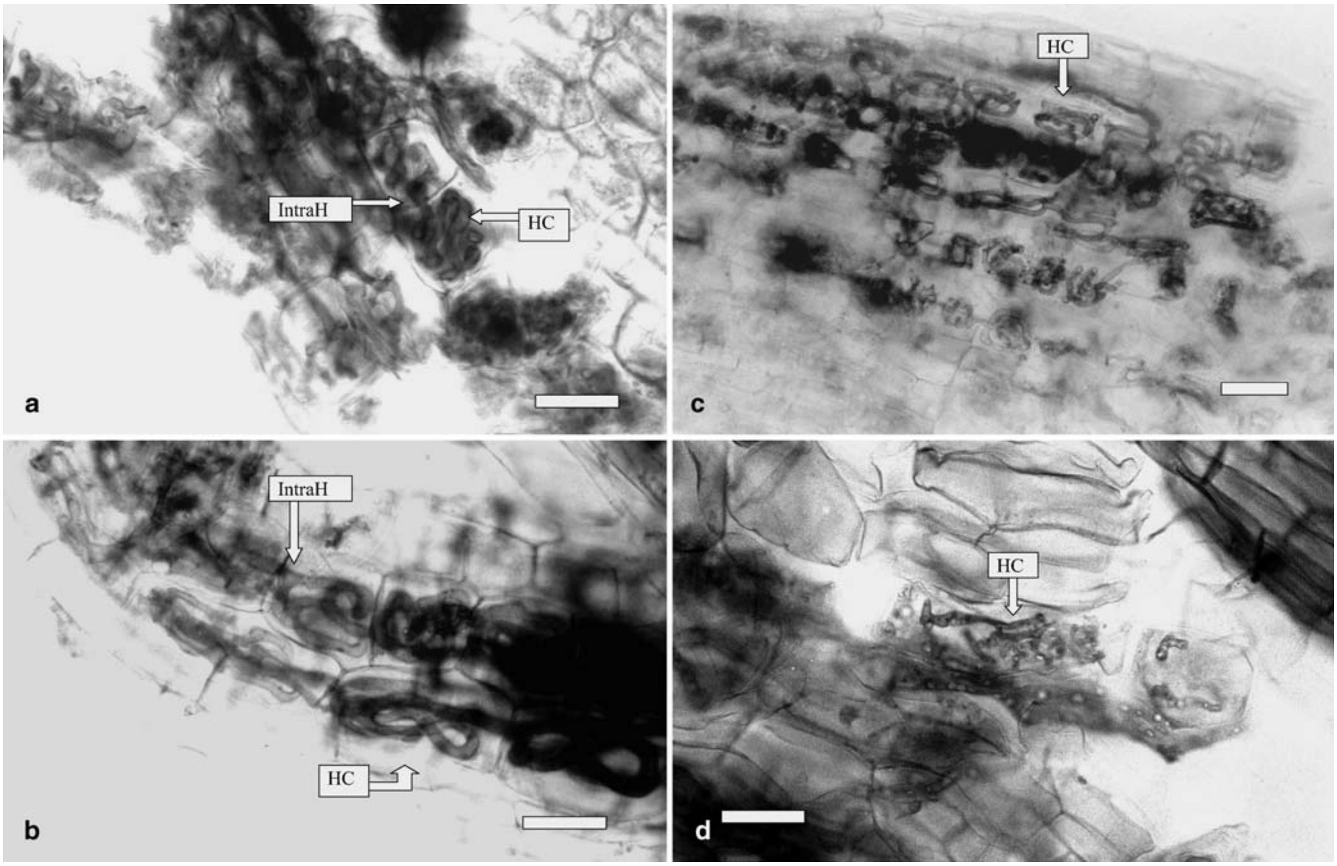

Fig. 1a–d Photomicrographs of arbuscular mycorrhiza (AM) morphological types in roots of plants in the mixed pine forest. *HC* Hyphal coil, *IntraH* intracellular hyphae. **a** *Euonymus alatus* f. *ciliatodentatus*. **b** *Euonymus japonicus*. **c** *Cocculus trilobus*. **d** *Elaeagnus multiflora* var. *hortensis*. *Bars* **a**, **b**, **d** 50 µm; **c** 100 µm

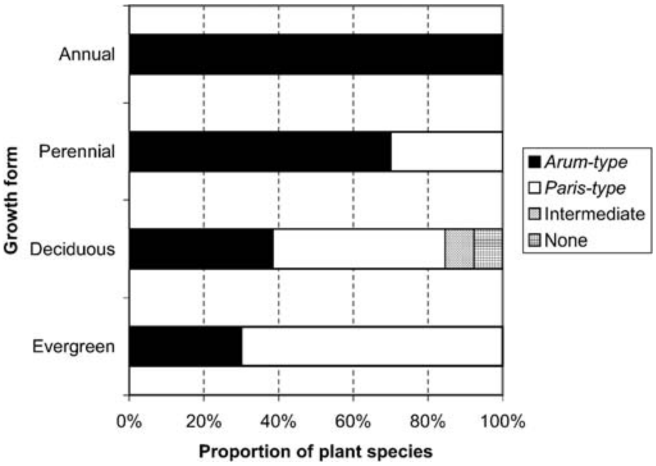

Fig. 2 Proportion of AM types in each plant growth form

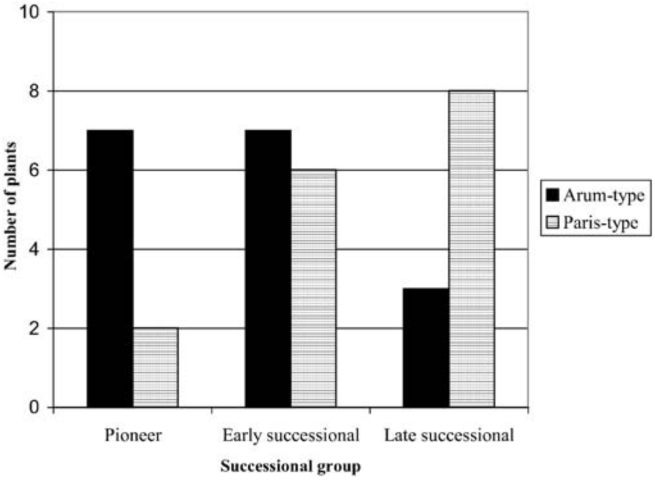

Fig. 3 Distribution of *Arum*- and *Paris*-type AM in successional groups

produced *Paris*-type AM in *Smilax aspera*, which also forms *Paris*-type in nature (Bedini et al. 2000). It has been noted that differences in cell wall structure and modifications produced during fungal colonization may be important in determining AM morphology in different plant species (Bonfante-Fasolo and Fontana 1985). Brundrett and Kendrick (1990a, 1990b) suggested that the presence or absence of continuous longitudinal air spaces in the root cortex may be the factor determining formation of either the *Arum*- or *Paris*-types, respectively. However, Imhof and Weber (1997, 2000) noted that *Voyria obconica* formed *Paris*-type AM in spite of the presence of clear intercellular spaces in the root cortices.

Cavagnaro et al. (2001a) found both *Arum*- and *Paris*-type morphology when *L. esculentum* (wild-type tomato) was inoculated with different AM fungal species. There

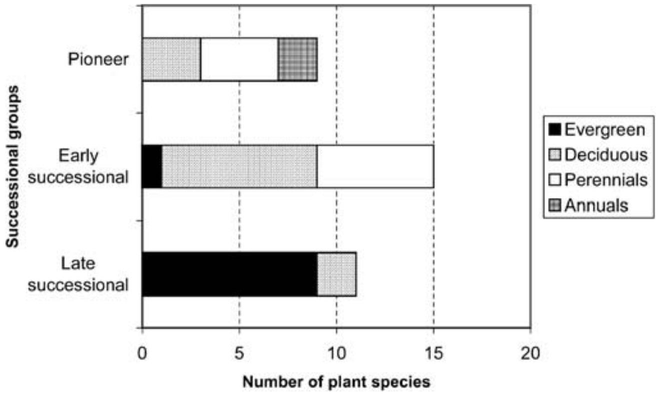

Fig. 4 Distribution of plant growth forms in successional groups

were variations in each of the morphological groups, such as different ratios of hyphal and arbusculate coils, in the *Paris*-type AM formed by pure cultures of AM fungal species *Glomus coronatum*, *Gigaspora margarita* and *Scutellospora calospora*. Cavagnaro et al. (2001a) reasoned that if hyphal and arbusculate coils have dissimilar roles, then the differences in ratios could reflect differences in functionality. Furthermore, they noted that environmental factors, such as soil phosphorus, temperature and light, as well as molecular activity at the interfaces of the morphological structures could influence AM morphology. In a study of ten AM fungi, Abbott (1982) stated that each fungi formed characteristic infection patterns in roots of *Trifolium subterraneum* and many of the fungi could be distinguished from each other at the generic level. There were features of both *Arum*- and *Paris*-types. She attributed the differences in AM morphology to differences in the ability of the fungi to penetrate the various cell types within the root, and concluded that the prominent characteristics of each fungus within a root may be independent of host morphology and nutrition. As also noted by Cavagnaro et al. (2001a), it could be that although the host plant strongly influences formation of either *Arum*- and *Paris*-type AM, the fungal genome can also exert control at the morphological level. In our study, AM morphology of individual plants of the same species was consistent. This indicates that genetic factors pertaining to the host plant strongly influence AM morphology, as it has been proved that more than one AM fungal species can colonize the roots of an individual plant (Helgason et al. 1999; Van Tuinen et al. 1998). Plant families such as Caprifoliaceae, Gramineae (Smith and Smith 1997), and the genus *Sorbus* in Rosaceae (Yamato and Iwasaki 2002) may be exceptions to the rule.

Species of Polygonaceae (Gange et al. 2002), Celastraceae (Brundrett et al. 1995) and Menispermaceae (Logan et al. 1989) have been reported as AM but their AM morphological affiliations have not been categorically stated. We found intercellular hyphae and vesicles with no arbuscules in *Polygonum filiforme* (Polygonaceae) and *Commelina communis* (Commelinaceae), which is reported as non-AM (Brundrett et al. 1995). *Elaeagnus multiflora* var. *hortensis* (Elaeagnaceae), an actinorhizal plant, *Euonymus alatus* f. *ciliatodentatus*, *E. japonicus* (Celastraceae) and *Cocculus trilobus* (Menispermaceae) formed typical *Paris*-type AM morphology with intracellular hyphal coils in their inner root cortices.

Arum- and *Paris*-type AM morphology in relation to plant growth form and succession

Competition and modification of the abiotic environment, the main processes that act to produce the various successional stages of species dominance and climax in a plant community, can be detrimental to the plants involved (Pidwirny 2000). Conventional changes such as shade, moderate temperature and humid conditions resulting in exclusion of many fast-growing, light-loving annual, perennial and deciduous species. New colonists, such as deciduous and evergreen species that are adapted to low light conditions, usually grow slowly and have *Paris*-type AM. AMF activity has also been known to influence the order of plant succession (Koske and Gemma 1992; Francis and Read 1994). Greipsson and El-Mayas (2000) studied the occurrence of AMF in natural and reclaimed sand dunes in Iceland and noted that the pattern of colonization seemed to confirm the model that links plant succession with mycorrhizal status. Soils lacking AMF propagules are generally first colonized by non-AM plants followed by facultative AM plants, and AM-dependent plants are the last to arrive as AMF propagules become established (Allen and Allen 1980; Janos 1980). Burrows and Pfleger (2002) noted that increasing plant species richness was correlated with increases in AMF sporulation and species numbers as well as changes in AMF community composition in a natural ecosystem. They suggested that these increases could be due to the direct effects of increased numbers of plant species on the AMF community or they may be mediated through factors such as plant biomass. In the present study, environmental changes, such as shade during plant succession in the mixed pine forest, may control the distribution of plant growth forms and could also play a part in the proportion of *Arum*- to *Paris*-type AM plants.

Fujita and Nakata (2001) studied changes in vegetation and soil properties caused by a mixture of deciduous broad-leaved trees in the Japanese black pine forest at Niigata University. They noted that the pure pine stands had graminaceous species that prefer mainly sands, whereas the mixed stands contained many saplings of evergreen broad-leaved trees, and attributed the differences to alteration of the light and soil conditions at the forest floor by the mixture of deciduous broad-leaved trees. In our study of the same forest we noted that a majority of the pioneer plants, consisting mainly of annual and perennial herbs, formed *Arum*-type AM whereas a majority of the late successional plants, mostly evergreen shrubs and trees, formed *Paris*-type AM. The proportion of *Arum*-type AM in each growth form decreased as follows: annual > perennial > deciduous > evergreen, and

Paris-type AM increased in the same order. Plant succession has been known to follow the same order to attain a climax. In a similar study, Yamato and Iwasaki (2002) found *Paris*-type AM in nine out of ten herbaceous understorey plants of some Japanese deciduous forests, and noted that *Paris*-type AM were more frequently found than *Arum*-types in each level of plant taxonomy from species to family. A majority of the herbs that we examined formed *Arum*-type AM and there were more *Paris*-type than *Arum*-type AM plant families in the study plot; however, there was only a small difference between the number of *Paris*-type plants and *Arum*-type plants. O'Connor et al. (2001) found *Arum*-type AM in 21 herbaceous plant species growing in an Australian desert. The differences in distribution of *Arum*- and *Paris*-type AM at different sites could be the result of differences in plant successional stages at the different sites.

Arum-type morphology has been associated with cultivated plants (Smith and Smith 1997), which are usually fast-growing, and do well in sunlight, while *Paris*-type plants seem to be shade-loving and slow-growing (Brundrett and Kendrick 1990a, 1990b; Yamato and Iwasaki 2002). This suggests that the composition of plant communities at any successional stage is under the influence of the prevailing environmental conditions, and that these could affect the distribution of *Arum*- and *Paris*-type morphologies at different plant successional stages. The continuously changing environmental conditions within forest communities effectively influence dominant plant growth forms and the root anatomy of plant species could influence the proportions of *Arum*- and *Paris*-type plants at any particular successional stage. This probably explains why *Paris*-type AM have been noted to occur more frequently in natural forest ecosystems (Smith and Smith 1997; Yamato and Iwasaki 2002). Development of *Paris*-type AM has been shown to be slower than that of *Arum*-type AM (Brundrett and Kendrick 1990a, 1990b; Cavagnaro et al. 2001b). Brundrett and Kendrick (1990a, 1990b) inferred that slower colonization of *Paris*-type AM may be beneficial for the host plants by keeping the energy supply to the fungi low, which may be desirable for plants growing slowly in a woodland environment. Although the factors influencing AM morphology remain unclear, the results of this study show that the identity of the plant plays a very important role.

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