Studies on mycorrhizal associations in Harvard Forest, Massachusetts

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An estimate was made of the abundance of different types of mycorrhizal associations in two plant communities of conifers and hardwoods in the Harvard Forest. Lists of plant species, the coverage of their foliage in the canopy and understorey layers, and the types of mycorrhizal associations for 45 species common in these communities are presented. Of the species examined, 91% were mycorrhizal, representing most of the known major types, viz. ectomycorrhiza, vesicular–arbuscular mycorrhiza (VAM), ericoid, and monotropoid mycorrhiza. Of the 45 species studied, 22% of the species showed ectomycorrhizal, and 71% VAM associations. A direct spore count was a more reliable method than the most probable number method for determining VAM occurrence in the soil. Spore numbers ranged from 4.4 to 11.8 spores/g oven-dried soil. In conifer stands, ectomycorrhizae were most common, although VAM were also observed in the conifer species. In hardwood stands, VAM were more frequent than in conifer stands, but mycorrhizae were heterogeneous and included a good proportion of the ericoid type. Ectomycorrhizae were more common in communities of low diversity; VAM occurred more frequently in communities of high plant species diversity.

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Les auteurs ont évalué l'abondance des différents types d'association mycorhizienne dans deux communautés végétales, forêt de conifères et forêt de feuillus, de la Forêt de Harvard. Ils présentent la liste des espèces végétales, la couverture de leur feuillage en étage supérieur et en sous-étages ainsi que les types d'association mycorhizienne chez les 45 espèces communes à ces deux communautés. Ils retrouvent des mycorhizes chez 91% de ces espèces, représentant la plupart des principaux types connus, soit les ectomycorhizes, les endomycorhizes à vésicules et arbuscules (VAM), les éricoïdes et les monotropoïdes. Sur les 45 espèces étudiées, 22% montrent des ectomycorhizes et 71% des VAM. Une numération directe des spores s'avère plus fiable que la méthode du nombre le plus probable de propagules pour déterminer la présence des VAM dans le sol. Les nombres de spore vont de 4,4 à 11,8 spores/g de sol séché au four. Dans le peuplement de conifères, les ectomycorhizes sont les plus communes, bien qu'on observe également des endomycorhizes chez certaines espèces coniférienes. Dans le peuplement d'arbres feuillus les VAM sont plus fréquentes que dans le peuplement de conifères, mais les mycorhizes sont hétérogènes et incluent une bonne proportion de mycorhizes éricoïdes. Les ectomycorhizes sont plus fréquentes dans les communautés de faible diversité; les VAM sont plus fréquentes dans les communautés montrant une large diversité d'espèces.

[Traduit par la revue]

Introduction

The role of mycorrhizal symbiosis in plant growth is now well established and its essential contribution to plant nutrition has been discussed at length (Harley and Smith 1983; St. John and Coleman 1983). Nevertheless, information on the distribution of mycorrhizal associations around the world is still incomplete and the factors that control or limit mycorrhizal abundance are poorly understood. In reviewing the distribution of ectomycorrhizae in native and man-made forests, Meyer (1973) presented a map of the predominant ectomycorrhizal forests that occupied the temperate zones of the world as well as the forests in tropical East Asia and in the high ranges of Central and South America. Since then, many studies have been published of mycorrhizal occurrence in the tropical, subtropical and temperate regions that place the earlier information in a new light (Bethlenfalvay *et al.* 1984; Brundrett and Kendrick 1988; Högberg 1982; Högberg and Piearce 1986; Hopkins 1987; Malloch and Malloch 1981, 1982; McGee 1986; Singer and Araujo 1979). Statements that ectomycorrhizal fungi can be found on about 90% of the trees in temperate forests (Le Tacon *et al.* 1987) need revision according to this new information. A revised view is also appropriate with respect to the tropical forests some of which have dominant ectomycorrhizal components unknown in the past (Högberg 1986). Many tree species appear to have more than one type of mycorrhizal association (Chilvers *et al.* 1987; Malloch and Malloch 1981; McGee 1986). Attempts to generalize about associations not well studied can lead to incorrect interpretations about the preference for certain habitats by ectomycorrhizal fungi compared with vesicular–arbuscular (VA) endomycorrhizal fungi in the different plant communities. Similarly, attempts to speculate on processes that lead to the dominance of certain symbiotic associations in specific regions, mainly in the tropics (Janos 1980), may be misleading or incorrect.

The goal of surveying a plant community, including the mycorrhizal associations, seems an impossible task when one considers the complicated, diversified, and heterogenous populations of microorganisms that most plants may carry in and on their root systems and that occur in the soil. In spite of the large number of observations that such a survey involves, there is no substitute for an approach based on observations of the entire plant community rather than selected species if one is to screen the distribution of mycorrhizal associations in a certain ecosystem and assess their interrelationships. In a forest stand this assessment involves an examination of the mycorrhizal associations in plants forming the canopy layer as well as in plants forming the understorey, because both root systems are interwoven to make a dense net-

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work of root matrix in the shallow forest soils. The underground network in most cases cannot be differentiated according to whether it belongs to the canopy or to the understorey vegetation.

The purpose of this study was to examine the presence of different types of mycorrhizae in stands of the temperate forests of Harvard Forest, Massachusetts. Although Harvard Forest has a long and detailed record of the history of the land use and of changes in the forest vegetation, very little information was available on the occurrence of mycorrhizal associations. Lyford and Wilson (1964) and Lyford (1980) reported observations of ectomycorrhizae on the fine roots of red maple and red oak. No broad study of the distribution of mycorrhizae in the temperate forests of New England is known to exist.

The two plant communities that were studied in and adjacent to Harvard Forest fit the general description of zone 3, i.e., transition hardwood – white pine – hemlock forest of New England (Westveld 1956). The ecological reasons for the presence of two different communities of conifers and hardwoods side by side relate to historical land use, since much of the studied area was aforested and reforested decades ago and the effects of man's interference in the native forests is still well marked (Griffith *et al.* 1930; Lyford *et al.* 1963).

Materials and methods

Two sites were studied in and adjacent to Harvard Forest, central Massachusetts, located about 400 m above sea level, 42°30'N, 72°11'W. The mean annual precipitation of 1050 mm is evenly distributed throughout the year. Granite, gneiss, and schist bedrock is overlaid with shallow, sandy loam, glacial till soils that are moderately to well drained (Stout 1952). The native forests are part of the transition hardwood – pine – hemlock vegetation zone (Westveld 1956). Sites were selected in the center of two plant communities that represented conifer forets (C) and hardwood forests (H), about 1 km from each other.

Names of plant species and the coverage provided by their foliage in mid-summer were recorded in 20 plant communities consisting of 400 m^2 per community according to a method modified from Braün-Blanquet (Danin *et al.* 1964). In the conifer site the coverage of foliage was estimated separately for the two distinct layers of canopy and understorey and the coverage of foliage of each layer was related to the surface area of the forest floor. In the hardwood community, where partition between canopy and understorey was not clear, coverage of the canopy layer included all plants taller than 3 m and in the understorey plants less than 3 m tall, including seedlings of species of the taller trees.

The different types of mycorrhizal associations were examined by digging up common plants in these communities, at least 10 specimens per species, in late spring with shoots attached to the root systems. In order to examine a whole root system of tree-forming species, plants not older than 3 years were selected. Whole root systems of five specimens per species were washed with tap water to remove soil and organic debris and the shoot was identified and kept in a local herbarium. The roots were cleared and stained (Phillips and Hayman 1970) and examined for the presence of mycorrhiza with ×16, ×100, and ×250 magnification. Any type of mycorrhiza was recorded as present or absent for each root system and no attempt was made to quantify the association. VA endomycorrhizal fungi were recorded only when arbuscules or intracellular coils were present, to avoid confusion with nonmycorrhizal fungi that could also have leading hyphae or vesicle-like structures. Ectomycorrhizae were recorded when both a mantle and Hartig net were observed. The other five specimens that were dug up were transplanted to 600-cm^3 plastic pots containing commercial sand grade 0, put under shade in the greenhouse, and left for 9 months with regular care for further growth. Their mycorrhizal status was reexamined at the end of the following winter, when buds turned green. VAM spores were recovered from pot cultures, if present.

In each plant community, soils were sampled from two excavations made in July to recover spores of VA endomycorrhizal fungi. The two subsampled sites were located 1 m from the trunks of old hemlock trees in C and close to red oak, gray birch, and *Mitchella repens* in H. Soils were sampled from 5 to 40 cm under the raw humus layer and were stored in dark plastic bags at room temperature. The average pH was 4.5 and 3.9 for C and H, respectively, and in both sites soils were rich with organic matter. Soil pH determinations of water extracts were made using a glass-electrode pH meter.

Spores of VA endomycorrhizal fungi were recovered from soils within several days after the soils were brought from the field, and the two subsamples from a given site were mixed together, 100 replicates of 1 g each for each soil. Wet sieving was followed by centrifugation in 40% sucrose for 1 min (Daniels and Skipper 1982). The double separation procedure was helpful in removing organic debris. Spores then were rinsed in tap water and were counted under ×16 magnification. When counting, floating spores were distinguished from sinking spores per gram oven-dried soil; the first were considered dead and the latter alive.

Pot cultures of 1:3 mixture by volume of each soil with sand (15 replicates for each soil) were established in the greenhouse, using seedlings of *Trifolium subterraneum*, *Zea mays*, and *Sorghum bicolor* as bait plants. Fresh spores of VAM fungi in C and H soils were identified according to Schenck and Perez (1987).

Results

Composition of plant communities

The species list, total coverage, and relative coverage of foliage of canopy and understorey are given in Table 1 for C and in Table 2 for H. The canopy layers had 90 and 80% coverage and the understorey layers 10 and 45% in C and H, respectively. The dominance of *Tsuga canadensis* in C was evident and only a few other tree-forming species grew into the canopy. Out of 27 species that were listed in the understorey in C, three species, *Maianthemum canadense*, *Mitchella repens*, and *Vaccinium angustifolium*, contributed 80% of the relative coverage. Other species in the understorey contributed less than 3% each to the relative coverage (Table 1). In contrast to the community in C, where the thick foliage of hemlock blocked a large portion of the light from reaching the ground, in H the codominance of *Acer saccharum*, *Quercus coccinea*, and *Acer rubrum* allowed more light to reach the forest floor. This probably had a strong effect on the richness of species and coverage of foliage in the understorey, in which stratification was less marked compared with the hemlock stands. Out of 41 species that were recorded in the understorey in H, *Gaultheria procumbens* and *Vaccinium angustifolium* together made up 40% of the relative coverage and the rest had less than 3% relative coverage per species (Table 2).

Types of mycorrhizal associations

Data on mycorrhizal associations examined in late spring and the following winter in plants from Harvard Forest are presented in Table 3 with the list of their common hosts. Data collected in winter from pot cultures did not differ from data collected in the earlier spring except for *Brachyelytrum erectum*, in which the newly produced roots were still uninfected.

Forty-one (91%) out of 45 species examined had mycorrhizal associations. Thirty-two (71%) out of 45 species were found to be hosts of VA endomycorrhizal fungi. VA endomycorrhizae were present in 17 plant families out of 20 and included the Aceraceae, Araliaceae, Betulaceae, Caprifoliaceae, Cornaceae, Fabaceae, Fagaceae, Liliaceae, Lyco-

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TABLE 1. The composition of a plant community in a conifer forest in Harvard Forest

Canopy (total cover 90%)	Understorey (total cover 10%)		
Tsuga canadensis (85)	*Maianthemum canadense* (30)	*Cornus canadensis*	*Quercus coccinea* (s)
Acer saccharum (6)	*Mitchella repens* (30)	*Epigaea repens*	*Rubus hispidus*
Acer rubrum (3)	*Vaccinium angustifolium* (20)	*Fagus grandifolia* (s)	*Smilacina racemosa*
Betula papyrifera	*Acer rubrum* (s)	*Gaultheria procumbens*	*Thelypteris* sp.
Betula populifolia	*Acer saccharum* (s)	*Lycopodium clavatum*	*Trientalis borealis*
Fagus grandifolia	*Betula populifolia* (s)	*Lycopodium obscurum*	*Tsuga canadensis* (s)
Others	*Brachyelytrum erectum*	*Lysimachia quadrifolia*	*Vaccinium corymbosum*
	Castanea dentata (s)	*Medeola virginiana*	Others
	Clintonia borealis	*Monotropa uniflora*	
	Coptis groenlandica	*Pinus resinosa* (s)	

NOTE: Plants are listed according to their presence in the canopy (>3.0 m) or in the understorey (<3.0 m), and estimations of their foliage cover are given in parentheses as a percentage. Other species are listed if present in less than 3% relative cover. Average of 20 separate records, each about 400 m². s, seedlings.

TABLE 2. The composition of a plant community in a hardwood forest in Harvard Forest

Canopy (total cover 80%)	Understorey (total cover 45%)		
Acer saccharum (30)	*Gaultheria procumbens* (20)	*Castanea dentata* (s)	*Prunus pensylvanica*
Quercus coccinea (30)	*Vaccinium angustifolium* (20)	*Clintonia borealis*	*Prunus serotina*
Acer rubrum (20)	*Acer pensylvanicum*	*Coptis groenlandica*	*Quercus alba* (s)
Betula populifolia (10)	*Acer rubrum* (s)	*Dennstaedtia punctilobula*	*Quercus coccinea* (s)
Quercus alba (4)	*Acer saccharum* (s)	*Epigaea repens*	*Quercus prinus* (s)
Betula papyrifera (4)	*Alnus incana* ssp. *rugosa*	*Kalmia angustifolia*	*Rubus allegheniensis*
Others	*Amelanchier canadensis*	*Lycopodium complanatum*	*Rubus hispidus*
	Amphicarpa monoica	*Maianthemum canadense*	*Smilacina racemosa*
	Aralia nudicaulis	*Malus sylvestris*	*Trientalis borealis*
	Aster divaricatum	*Mitchella repens*	*Ulmus americana* (s)
	Betula lenta	*Onoclea sensibilis*	*Vaccinium corymbosum*
	Betula lutea	*Pinus resinosa* (s)	*Viburnum acerifolium*
	Betula papyrifera (s)	*Populus grandidentata* (s)	*Viburnum dentatum*
	Betula populifolia (s)	*Potentilla canadensis*	Others

NOTE: Plants are listed according to their presence in the canopy (>3.0 m) or in the understorey (<3.0 m), and estimations of their foliage cover are given in parentheses as a percentage. Other species are listed if present in less than 3% relative cover. Averages of 20 separate records, each about 400 m². s, seedlings.

podiaceae, Pinaceae, Poaceae, Polypodiaceae, Primulaceae, Ranunculaceae, Rosaceae, and Rubiaceae. In two species from the Lycopodiaceae the presence of VA endomycorrhizae was not obvious because arbuscules were not clearly seen. In five species of the Betulaceae and Fagaceae, VA endomycorrhizae were infrequent and probably secondary to their common association with ectomycorrhizae. Whereas the ground hemlock, *Taxus canadensis* (Taxaceae), was heavily colonized by VA endomycorrhizae during the entire growth season, nearby trees of *Tsuga canadensis* (Pinaceae) were ectomycorrhizal.

VA endomycorrhizae were found in *Clintonia borealis* and in *Smilacina racemosa*. These differed from the common type of VA endomycorrhizae in that their arbuscular branches were coarse and thick. This type of arbuscule has been described for *Clintonia borealis* by Malloch and Malloch (1981). As reported also by those authors, the invading hyphae in *Clintonia borealis* in Harvard Forest produced several vesicles close to the initial penetration point. In *Smilacina racemosa* the invading hyphae had no vesicles like those seen in *Clintonia borealis*, but a few lateral hyphae emerged from about the same point on the invading hyphae, close to and below the appressorium-like structure. The inner infection of arbuscules resembled that of *Clintonia borealis* and developed from the invading hyphae within the deep inner layers of the cortex. Similar arbuscules in young roots of *Smilacina* were illustrated by Brundrett and Kendrick (1988).

Ectomycorrhizal associations were found in 10 (22%) species in the Betulaceae, Fagaceae, and Pinaceae. Most of the ectomycorrhizal fungi associated with these families had clamp connections.

Four species from the Ericaceae had ericoid mycorrhizal associations. The symbiotic fungus, which appeared to be the same in all cases, lacked clamp connections and was difficult to stain. The nonphotosynthetic saprophytic plant *Monotropa uniflora* had monotropoid mycorrhiza and was found often in close proximity to *Vaccinium* spp. or *Pinus strobus*.

Two species from the Myricaceae, one species from the Lycopodiaceae, and one species from the Polypodiaceae were not found to be mycorrhizal (Table 3).

Spore counts and spore identification

Numbers of spores that were counted in soils from C and H are presented in Table 4. Although there was a significant difference between means for total number of spores in these sites, with the higher number found in the hardwood soil,

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TABLE 3. Summary of the occurrence of different types of mycorrhizae in wild plants in Harvard Forest, arranged by plant family

Host species	Type of fungal association			
	Ectomycorrhizal	VAM	Ericoid mycorrhizal	Other
Aceraceae				
Acer pensylvanicum		+		
Acer rubrum		+		
Acer saccharum		+		
Araliaceae				
Aralia nudicaulis		+		
Betulaceae				
Alnus incana ssp. *rugosa*	+	*		
Betula papyrifera	+	*		
Betula populifolia	+	*		
Caprifoliaceae				
Viburnum acerifolium		+		
Viburnum dentatum		+		
Cornaceae				
Cornus canadensis		+		
Ericaceae				
Epigaea repens			+	
Gaultheria procumbens			+	
Kalmia angustifolia			+	
Vaccinium angustifolium			+	
Fabaceae				
Amphicarpa monoica		+		
Fagaceae				
Fagus grandifolia	+			
Quercus alba	+	*		
Quercus borealis	+			
Quercus coccinea	+	*		
Quercus velutina	+			
Liliaceae				
Clintonia borealis		+		
Maianthemum canadense		+		
Smilacina racemosa		+		
Lycopodiaceae				
Lycopodium clavatum		*?		
Lycopodium complanatum		*?		
Lycopodium obscurum		—		
Monotropaceae				
Monotropa uniflora				monotropoid
Myricaceae				
Comptonia peregrina		—		
Myrica gale		—		
Pinaceae				
Pinus strobus	+			
Tsuga canadensis	+			
Poaceae				
Brachyelytrum erectum		+		
Polypodiaceae				
Dennstaedtia punctilobula		+		
Onoclea sensibilis		+		
Thelypteris sp.		—		
Primulaceae				
Lysimachia quadrifolia		+		
Trientalis borealis		+		
Ranunculaceae				
Coptis groenlandica		+		
Rosaceae				
Amelanchier canadensis		+		
Potentilla canadensis		+		
Prunus pensylvanica		+		
Rubus hispidus		+		
Rubus idaeus		+		

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TABLE 3 (*concluded*)

Host species	Type of fungal association: Ectomycorrhizal	VAM	Ericoid mycorrhizal	Other
Rubiaceae				
Mitchella repens			+	
Taxaceae				
Taxus canadensis		+		

NOTE: Data are from plants that were collected in the forest and examined immediately, as well as from plants that were transplanted from the forest to sand culture and examined 9 months later. +, present; —, absent; *, infrequent; ?, it is not clear whether the endosymbiont is a mycorrhizal fungus.

TABLE 4. Numbers of VAM fungal spores that were recovered from hardwood soil (H) and conifer soil (C) in Harvard Forest, using centrifugation in sucrose following wet sieving

	H	C	
Sinking (healthy) spores	3.9±0.9	2.9±0.6	ns
Floating (dead) spores	7.9±1.7	1.5±0.5	*
Total	11.8±2.0	4.4±0	*

NOTE: Each datum represents a mean of 100 samples. The number of spores is given per gram oven-dried soil. *, significant difference between soils at $p < 0.05$.

there was no significant difference between the means of numbers of viable spores. The dead (floating) spores made up 32 and 67% of the total number of spores in C and H, respectively.

Most of the fresh spores that were recovered from pot cultures of local soils mixed with sand and grown with subclover, sweet corn, and sorghum were identified as *Acaulospora* sp. and a few belonged to the genus *Glomus*. *Acaulospora* sp. was dominant in both soil mixtures and in 15 pots with the three bait species.

Spore production in pot cultures with native plants

Increased numbers of VA endomycorrhizal spores were observed in the following species growing in sand culture for 9 months after they had been transplanted from the field: *Amphicarpa monoica*, *Aralia nudicaulis*, *Clintonia borealis*, *Dennstaedtia punctilobula*, *Mitchella repens*, *Onoclea sensibilis*, *Potentilla canadensis*, *Rubus idaeus*, and *Taxus canadensis*. In all of these associations, spores remained in the old or newly formed roots but in *Amphicarpa monoica*, spores were also attached to the root surface by long hyphae. In *Taxus canadensis*, spores were also released into the sand. Several thousand spores per root system were estimated for *Amphicarpa monoica*, hundreds per root system for *Mitchella repens*, *Potentilla canadensis*, and *Taxus canadensis*, and all the other species had from a single spore up to tens of spores. The diameters of these spores were usually less than 100 μm, but ranged up to 150 μm.

Discussion

Although the recorded species in Tables 1 and 2 do not comprise a full list of floral richness of these communities, they include the most common native plants. They also have species in common with those occurring in the deciduous forest of the University Woods in Champaign County, Illinois (McDougall 1922) and in the boreal region in Timiskaming District, Ontario, studied by Malloch and Malloch (1981).

The dominance of maple trees (*Acer saccharum*, *A. rubrum*) in the hardwood community around Harvard Forest was also characteristic of the University Woods in the midwest U.S.A. (McDougall 1922). However, the pH of the soil in the hardwood plant community in Harvard Forest, where maples contributed about half of the coverage of foliage in the canopy layer, was 3.9 compared with pH 5 that was reported as optimal for maple growth (Le Tacon *et al.* 1987). Most of the understorey layer in both plant communities consisted of monotypic patches such as *Maianthemum canadense*, *Mitchella repens*, *Vaccinium angustifolium*, *Lycopodium* spp., and ferns.

Forty-one (91%) species out of 45 that were examined had mycorrhizal associations. This is a high rate compared with 64% that was observed in University Woods (McDougall and Liebtag 1928), but at that time it was noted that more extensive observations would probably decrease the percentage of negative results. The mycorrhizal types observed in Harvard Forest included VA endomycorrhizal, ectomycorrhizal, ericoid, and monotropoid mycorrhizal associations.

Ten (22%) species of trees were found to have ectomycorrhizal associations in Harvard Forest and this is a high rate compared with 8 (6%) species out of 145 species of trees that were studied in the deciduous forest of University Woods (McDougall and Liebtag 1928). These data, although from forests of the temperate zone in North America and related to the total number of species recorded in a plant community, do not support the view of Le Tacon *et al.* (1987) who suggested that temperate forests are dominated by ectomycorrhizal associations. This view probably does not take into account all the tree species that grow in the deciduous forests of North America, many of which associate with VA endomycorrhizal fungi.

VA endomycorrhizae were found in 71% of the plant species that were studied in Harvard Forest, and endotrophic mycorrhizae were reported in 59% of the 144 species studied in University Woods, with ericoid and orchid types not included (McDougall and Liebtag 1928). These data fit the general view that VA endomycorrhizae are the most common type of mycorrhizal association in the plant kingdom.

Examination of mycorrhizal symbioses in species that were studied in Harvard Forest confirm most of the earlier observations described by Malloch and Malloch (1981, 1982) in the boreal region, and only a few further comments need to be added: (*i*) *Alnus incana* ssp. *rugosa* and *Betula papyrifera*, which exhibited at least some mycorrhizae of the *Cenococcum*

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type in the boreal region, did not carry that fungus in our samples. (*ii*) *Epigaea repens*, *Gaultheria procumbens*, and *Kalmia angustifolia* were always found to have ericoid mycorrhizae. None of them was observed to be ectomycorrhizal. (*iii*) A detailed study of *Comptonia peregrina* (Berliner and Torrey 1989) confirms that this species does not form a mycorrhizal association of any type. (*iv*) *Prunus pensylvanica* in Harvard Forest had VA endomycorrhizal associations in all the samples, none of which were ectomycorrhizal. (*v*) VA ectomycorrhiza in *Clintonia borealis* in Harvard Forest was similar to that in the boreal region. However, there is some doubt whether this type of infection is induced by a very characteristic fungus, as was suggested by Malloch and Malloch (1981), since it was shown that the host rather than the endosymbiont has an influence on the morphology of the VA ectomycorrhizal fungus inside the root (Lackie *et al.* 1987).

Separating and counting VAM spores from soil of the forest floor and separating them into two groups of sinking (healthy) and floating (dead) spores was found to be a more reliable method for evaluation of the VA endomycorrhizal spores in the soil than the use of the most probable number method (Porter 1979). Estimates based on two samples at each site are probably not fully representative of the whole area but it is worth noting that the values of 4.4 and 11.8 spores/g oven-dried soil, that were determined for C and H respectively, are high compared with 0.2 and 0.07 spores/g dry weight soil reported in prairie soil and wheat field soil in Kansas (Hetrick and Bloom 1983) and 1.95 and 10.0 spores/g dry soil in two cultivated paddocks (Porter 1979). The number of spores of VA endomycorrhizal fungi in the soil may reflect the presence of spore-producing plants in that site some time in the past because such spores are soil-borne (Alexopoulos and Mims 1979). It was shown that several plants in the understorey layer (e.g., *Mitchella repens* and *Potentilla canadensis*), transplanted into pot culture with sand, produced up to several thousand VAM spores per root system in not more than one cycle of plant growth.

As a large proportion of spores in forest soils were found to be dead or misshapen, mainly in H, no attempt was made to identify the fungal species from that material. Instead, spores were identified from a fresh crop produced in pot culture that originated from spores in samples from C and H. The dominance of an *Acaulospora* sp. in pot culture does not necessarily reflect its abundance in the soil.

Using the data collected in this study, we may attempt to estimate the abundance of the different types of mycorrhizae in the two plant communities studied at the Harvard Forest. Assuming that root spread in the soil is proportional to the crowns above the ground (Stout 1956), the dominance of *Tsuga canadensis* above the ground in C leads to the speculation that ectomycorrhizal associations are probably most common in the soil of this plant community. Nevertheless, VA endomycorrhizal hosts are abundant in the understorey vegetation together with ericoid endomycorrhizal hosts that contribute a large portion of different types of mycorrhizal association to the soil in this stand. Thus, the number of VA endomycorrhizal spores found in C soil may be considered moderate to high. In H soil the composition is more heterogeneous. The coverage of foliage contributed by VA endomycorrhizal hosts is higher, when canopy and understorey layers are combined, than that of ectomycorrhizal hosts. Ericoid mycorrhizae may also play a large part in the mycorrhizal associations of the soil as hosts from the Eriacaceae are very common in the understorey. Despite the patchy composition of the understorey in these plant communities, it is reasonable to speculate that VA endomycorrhizal associations are the most common in the hardwood forest, while ectomycorrhizal associations are the most common in the conifer forest, and that these two major types of mycorrhizal symbioses coexist and do not exclude other mycorrhizal types.

The hardwood stand examined in this study differed substantially in species occurrence from that studied by Brundrett and Kendrick (1988). Of the eight species that were reported in common in our study and their Table 1, six were VA mycorrhizal, including *Acer saccharum* and five herbaceous species, and two were woody species, *Pinus strobus* and *Fagus grandifolia*, which were ectomycorrhizal. In both populations, characterized by high species diversity, VA mycorrhizae were dominant.

The conclusion that comes from this study is that forest communities like those in Harvard Forest can support a heterogeneous occurrence of different types of mycorrhizal associations, without a clear-cut dominance for any one of them. Exceptions occur in the case of a monotypic plant community comprised of ectomycorrhizal host plants. This conclusion supports the view of Malloch *et al.* (1980) for the forests of the temperate zone, where ectomycorrhizae predominate in plant communities of low species diversity and VA endomycorrhizae are the most common type in plant communities with high species diversity.

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