

# Mycorrhizae

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## Introduction

The term ‘mycorrhiza’ describes the symbiosis between a plant root and fungal partner. In most cases mycorrhizae are mutualistic symbioses in which both partners benefit from the association. In general, the fungal partner benefits from a supply of photosynthetically fixed carbon from the host plant, whereas plants benefit mainly from greater acquisition of mineral nutrients via fungal structures. Plants may also enjoy several other benefits such as protection against root pathogens and improved water uptake. This article describes the importance of mycorrhizae in forests, the structure of different mycorrhizal types, fungi forming these types, and their global occurrence.

Mycorrhizae can be divided into seven structural types (Table 1). With the exceptions of monotropoid and orchid mycorrhizae, all other types can be found on woody plants and trees. Within a single mycorrhizal type there is considerable diversity in structure, development, and function. The identity of the symbionts can have a considerable influence on the structure of mycorrhizae formed. For example, the fungus *Hebeloma crustuliniforme* forms ectomycorrhizae with many species of *Picea* and *Pinus*, but arbutoid mycorrhizae with *Arbutus menziesii*. Similarly, fungi forming vesicular-arbuscular mycorrhizae may form mycorrhizae with extensive intracellular coils and few arbuscules in one plant species, and intercellular hyphae and many arbuscules in another plant species.

## Ectomycorrhizae

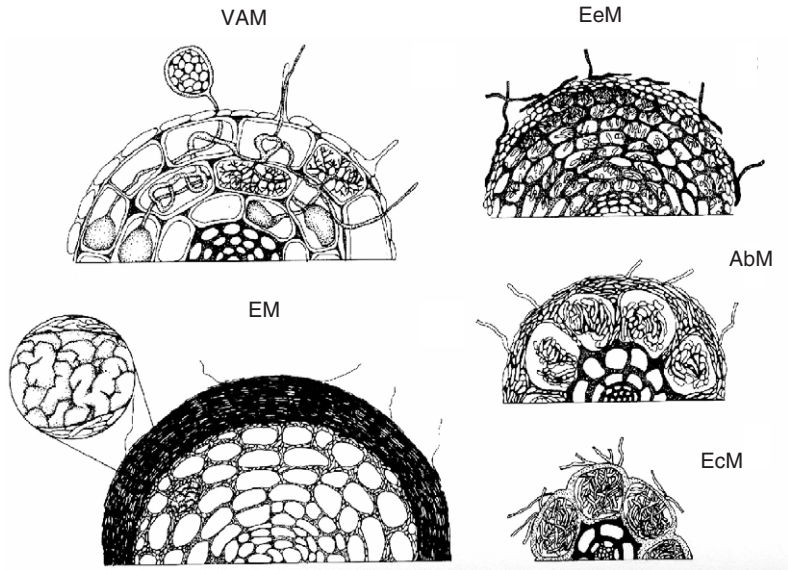
### Structure

Ectomycorrhizal roots are characterized by three structural components (Table 1, and Figure 1): (1) a

**Table 1** Characteristics of mycorrhizal types found on woody plants

	Type of mycorrhiza				
	Ecto	Vesicular-arbuscular	Ectoendo	Arbutoid	Ericoid
Intracellular colonization	—	+	+	+	+
Fungal mantle	+	—	+	+	—
Hartig net	+	—	+	+	—
Vesicles	—	+	—	—	—
Fungal taxa	Basidiomycete Ascomycete	Zygomycete	Basidiomycete	Basidiomycete	Ascomycete

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**Figure 1** Structures of different mycorrhizal associations. Shown are vesicular–arbuscular mycorrhiza (VAM), ectomycorrhiza (EM), ectendomycorrhiza (EeM), arbutoid mycorrhiza (AbM), and ericoid mycorrhiza (EcM). Redrawn with permission from Allen MF (ed.) (1992) *Mycorrhizal Functioning*. New York: Chapman & Hall.

hyphal sheath or mantle which encloses the root; (2) an inward growth of hyphae between the epidermal or cortical cells forming the Hartig net; and (3) an outward-growing mycelium of hyphae or rhizomorphs forming the extramatrical mycelium. The hyphal mantle constitutes between 20 and 40% of the root dry weight. The cellular structure of the hyphal mantle varies between fungal species and is used to identify species of ectomycorrhizae. The Hartig net forms the contact zone between the cells of the fungal symbiont and host plant. The Hartig net is formed by penetration of hyphae from the inner hyphal mantle. The depth of penetration differs in angiosperms and gymnosperms. In most species of angiosperms penetration is restricted to the outer cortical layer, forming a so-called epidermal Hartig net. Within the epidermal types two forms are found. In the paraepidermal type, the epidermal cells are only partially enclosed by hyphae. In the periepidermal type the epidermal cells are completely encircled by the fungal hyphae. Most species of gymnosperm form a cortical Hartig net, in which several layers of cortical cells extending to the endodermis are enclosed by hyphal layers. Penetration between the root cells is believed to involve fungal enzymes that disrupt the middle lamella, leading to complete fusion of plant and fungal cell walls to form the intercellular matrix or involving layer. Intercellular penetration induces prolific branching of fungal hyphae, producing a fanlike structure that moves across the radial plant cell walls. The prolific branching of hyphae and fusion of the plant and fungal cell walls produce a structure with a high surface area for exchange of mineral elements and metabolites.

The hyphae of the extramatrical mycelium extending from the surface of the hyphal mantle greatly increase the area of contact with the soil. In forest soils, ectomycorrhizal hyphae in the soils have been estimated to have a length of  $2000 \text{ km m}^{-2}$ , several orders of magnitude greater than the length of fine roots. The extramatrical mycelium provides the area of nutrient uptake in the soil and the transport pathway between the soil and the hyphal mantle. Extramatrical hyphae extend from the mantle both as single hyphae and as aggregates forming rhizomorphs. The degree of aggregation and the complexity of the rhizomorph structure vary greatly between fungal species. Six categories of rhizomorph are recognized, the simplest being loose aggregates of hyphae of similar diameter, the most complex having enlarged central hyphae in a highly organized structure. It is assumed that the structural differences in the rhizomorphs are associated with functional differences.

## Occurrence

Only about 3% of plant species form ectomycorrhizae but the species that form ectomycorrhizae dominate many ecosystems that occupy a large proportion of the land surface. The majority of economically important timber tree species in temperate regions form ectomycorrhizae. The Pinaceae, from which most species are ectomycorrhizal, dominate the boreal forests of the northern hemisphere. The dominants of the northern temperate forests, Fagaceae, and the southern temperate and subtropical forests, Myrtaceae, are both families of mainly ectomycorrhizal species. Ectomycorrhizal species are also found in the tropics; the Dipterocarpaceae, the most important family in moist and monsoon forests of Southeast Asia, is composed of mainly ectomycorrhiza-forming species.

A number of leguminous tree genera from both the moist tropics and dry miombo woodlands, including *Azelia*, *Eperua*, and *Intsia*, and *Brachystegia* with *Julbernaldia* respectively, are also known to form ectomycorrhizal associations. However, many of the tree species forming ectomycorrhizae also form vesicular-arbuscular (VA) mycorrhizae. The formation of ectomycorrhizae is linked to accumulation of an organic litter layer in soils.

## Fungi forming ectomycorrhizae

A large number of fungi form ectomycorrhizae, the majority being basidiomycetes. Ectomycorrhizae are also formed by a number of ascomycetes and a few species of zygomycetes. It is estimated that between 5000 and 6000 species of fungi form ectomycorrhizae. About 75% of ectomycorrhizae are epigeous, and *c.* 25% hypogeous, including a large number of ascomycetes. Ectomycorrhizal fungi differ in the degree of host specificity. The majority of species have a broad host range colonizing a large number of tree species. However, a number of species have a more restricted range and there are an estimated 250 species that are genus-specific. The root system of an individual tree will normally be colonized by a range of ectomycorrhizal fungal species. The number of fungal species colonizing roots of a tree depends upon both tree species and environmental conditions.

## Vesicular-Arbuscular Mycorrhizae

In forestry, VA mycorrhizae are poorly neglected in favor of ectomycorrhizae, yet VA mycorrhizae are found on a large number of temperate tree species and the majority of tropical species.

## Structure

The fungal structure of VA mycorrhizae is an internal mycelium growing within the root, intracellular

vesicles and arbuscules, and an extraradical mycelium extending into the soil. Whereas all VA mycorrhizae form arbuscules, *Gigaspora* and *Scutellospora* do not form vesicles.

Roots become colonized from hyphae originating from the hyphal mycelium in the soil, spores or old colonized root fragments. The hyphae of the internal mycelium spread from an entry point to form two recognized types of the internal mycelium colonization, the Arum and Paris types. In the Arum type, hyphae proliferate in the cortex by growing longitudinally between host cells. Hyphae grow through longitudinal intercellular air spaces. This type is regarded as the typical VA mycorrhizal type. In the Paris type, hyphae develop intracellular coils and the hyphae spread directly from cell to cell. Arbuscules are formed by repeated dichotomous branching. The width of hyphae decreases from an initial trunk hypha 5–10 µm in diameter to fine branch hyphae less than 1 µm in diameter. In the Arum type arbuscules form from dichotomously branched hyphae that penetrate the cortex cells, whereas in the Paris type arbuscules grow from the intracellular coils. The fungus is always located outside the cytoplasm in an apoplastic compartment. The periarbuscular membrane surrounding the arbuscule is modified functionally. Together with the fungal membrane of the arbuscule, the periarbuscular membrane forms an interfacial zone, important for the transfer of nutrients between the symbionts. Arbuscules are considered the major site of exchange between the fungus and host. Arbuscules start to form approximately 2 days after root penetration, and in fast-growing species arbuscular turnover is about 7 days. However, in slow-growing woodland plants arbuscules are longer-lived and more robustly branched. Compared with the arbuscules the hyphae of the internal mycelium are long-lived and can remain in roots for months.

Vesicles develop to accumulate storage products in many VA mycorrhizal associations. Vesicles are thick-walled hyphal swellings in the root cortex that contain lipids and numerous nuclei. Vesicles vary in shape from ovoid, irregular-lobed to box-like, depending on the fungal species. They are likely to act both as storage organs and as propagules. However little is known about the biology of these structures.

Similar to the extramatrical mycelium of ectomycorrhizal roots, the extraradical mycelium of VA mycorrhizae increases the area of contact with the soil and transport pathway between the soil and the root. The hyphae of the extraradical mycelium are highly branched with species-specific branching patterns.

## Occurrence

Most herbaceous plants are colonized by VA mycorrhizae. However, VA mycorrhizae are not restricted to herbaceous plants and are found on a large number of temperate tree species and most tropical trees. The only family of tropical trees that are not typically VA mycorrhizal is the Dipterocarpaceae. Trees of savanna grasslands and semiarid bushlands are also dominated by VA mycorrhiza-forming species. Although, in temperate regions, VA mycorrhiza-forming species are less important in geographical area than ectomycorrhiza-forming species, the majority of temperate tree species form VA mycorrhizae. Whereas the Pinaceae (*Abies*, *Larix*, *Picea*, *Pinus*, and *Pseudotsuga*) are ectomycorrhizal, most other gymnosperms form VA mycorrhizae. This includes the Cupressaceae, Taxaceae, and Taxodiaceae. A number of families of angiosperms also commonly contain VA mycorrhizal-forming species, including the Rosaceae (*Malus* and *Prunus*), Leguminosae, Oleaceae, and Tiliaceae. VA mycorrhizae are reported to be the ecologically most important type in New Zealand forests. However, a large number of species also form both VA mycorrhizae and ectomycorrhizae. The formation of both VA mycorrhizae and ectomycorrhizae is particularly well described on *Eucalyptus*, *Populus*, and *Salix*. In most cases, VA mycorrhizae develop at earlier successional stages than ectomycorrhizae. VA mycorrhizae are more frequent on plants growing on mineral soils.

## Fungi Forming Vesicular Arbuscular Mycorrhizae

The fungi of the order Glomales, which form VA mycorrhizae, have been classified into three families containing five genera, *Acaulospora*, *Entrophospora*, *Gigaspora*, *Glomus*, and *Scutellospora*. About 150 species have been described. Due to the difficulties involved to identify species colonizing roots, the number of species associated with roots of a single plant in the field is uncertain.

## Ectendomycorrhizae

Ectendomycorrhizae are a distinct form of mycorrhiza formed on *Picea* and *Pinus*, mainly on juvenile trees and often in disturbed soils or nurseries.

## Structure

Ectendomycorrhizae have some of the structural characteristics of both ectomycorrhizae, and endomycorrhizae. The development of ectendomycorrhizae is similar to that of ectomycorrhizae, resulting in a thin or hyaline hyphal mantle that does not cover the root tip, and a Hartig net that can extend to the

inner cortex. However, unlike ectomycorrhizae, ectendomycorrhizae also have intracellular penetrations of hyphae which branch repeatedly once inside the cell.

### Occurrence

Ectendomycorrhizae occur primarily on *Picea* and *Pinus*, and are commonly found in pot cultures or nursery trees of several years of age. They occur on a wide range of soil types, but are common on disturbed soils or soils of agricultural origin.

### Fungi forming ectendomycorrhizae

Ectendomycorrhizae are formed by a number of fungi but most can be referred to as *Wilcoxina* and assigned to two taxa, *W. mikolae* and *W. rehmsii*. *Wilcoxina mikolae* produces chlamydospores and occurs in disturbed mineral soils; *W. rehmsii* does not produce chlamydospores and occurs on peaty soils.

### Mycorrhizae in the Ericales

Two types of mycorrhizae are formed with woody plants in the Ericales that are important in forest, namely arbutoid and ericoid mycorrhizae.

Arbutoid mycorrhizae are formed on woody plants in the genera *Arbutus* and *Arctostaphylos*, and in genera of the Pyrolaceae including *Chimaphila*, *Moneses*, *Pyrola*, and *Orthilia*. Arbutoid mycorrhizae are characterized by a hyphal mantel and Hartig net similar to that of ectomycorrhizae, but also an intercellular proliferation of mycelia to form dense hyphal complexes. These hyphal complexes can only be revealed by anatomical investigation. The fungi-forming arbutoid mycorrhizae are mainly basidiomycetes that commonly form ectomycorrhizae in other tree species. These include genera of basidiomycetes such as *Laccaria*, *Piloderma*, and *Rhizopogon*, and ascomycetes such as *Cenococcum*.

Ericoid mycorrhizae are formed by most of the genera of plants in the Ericales; these include genera forming important midstory and understory plants such as *Rhododendron* and *Vaccinium*, as well as tree species within the genus *Erica*. The ericoid mycorrhizal root is a delicate structure of only two cortical layers, an outer hypodermis and an inner endodermis, surrounding a stele consisting of only one or two tracheids, a sieve element and a companion cell. Mycorrhizal colonization of the root is restricted to expanded epidermal cells, in which fungal hyphae penetrate the cell walls and form a dense hyphal profusion, fully filling the colonized cell. Examples of fungi-forming ericoid mycorrhizae have been identified as members of the genera *Hymenoscyphus* and *Oidiodendron*. Soils

that support ericaceous vegetation are characteristically nutrient-poor.

### Species Assemblages Colonizing Trees

Individual trees may be colonized by a large number of species of mycorrhizal fungi. Ectomycorrhizal fungi are divided into broad, intermediate, and narrow-range fungi, reflecting the number of potential host tree species that they colonize. Ectomycorrhizal species are also categorized into early and late successional species, reflecting the appearance of fruiting bodies of the species in developing tree stands. However, species categorized as early successional are also found in mature trees stands, and late successional species often colonize young or juvenile trees growing in mature stands. Little is known about species assemblages in VA colonization of tree species; however, most VA species are believed to be broad-range species. Current knowledge of species assemblages of VA is restricted by problems of *in planta* identification. Species assemblages of trees are influenced by environmental conditions, including, among others, soil fertility, especially nitrogen and soil acidity, elevated atmospheric carbon dioxide, and toxic levels of ozone. The influence of elevated atmospheric carbon dioxide and ozone is thought to be mediated by changes in rates of photosynthesis and hence carbon flow to the mycorrhizae.

### Identification of Mycorrhizae

The population structure of arbuscular and ectomycorrhizae can be estimated using fruiting bodies (mushrooms) for ectomycorrhizae or soil spores for arbuscular mycorrhizae. For ectomycorrhizae, fruiting bodies within an area can be collected, identified, and their abundance estimated. However, this depends upon the ectomycorrhizal fungus-forming epigeous fruiting bodies. Fruiting body production often correlates poorly with the below-ground abundance. The spores of arbuscular mycorrhizae must be isolated from the soil and can be identified to genus or species using morphological characteristics.

Ectomycorrhizal fungi colonizing roots can be identified using morphological and molecular biological methods. Morphological identification uses both structural features of the mycorrhizal root tip such as color and ramification, and the cellular patterns of the hyphal mantel. This permits identification to genus or species level. Morphological methods can also be used to identify some arbuscular mycorrhizae. Morphological features that are important include variations in the size, shape, wall thickness, position, and abundance of vesicles,

branching patterns, the diameter and structure of hyphae, and the staining intensity of hyphae. However, this method is of limited potential as a single mycorrhizal species may have a different morphology between plant host species. Both ectomycorrhizae and VA mycorrhizae can be identified *in planta* using molecular biological techniques. Ectomycorrhizae are commonly identified by using polymerase chain reaction (PCR) amplification of DNA followed by restriction fragment length polymorphism (RFLP). Target DNA for amplification is often the internal transcribed spacer (ITS) region rDNA. VA mycorrhizae are commonly identified using short arbitrary primers in random amplified polymorphic DNA (RAPD-PCR) techniques. Target regions are often the small subunit (18S) or large subunit (25S) ribosomal gene. These techniques are often used with subsequent RFLP analysis. Family-specific primers allow identification of the major families of VA mycorrhizae.

## Tree Benefits of Mycorrhization

### Mineral Nutrient Acquisition

The improved mineral nutrition of mycorrhizal plants is well documented, in particular, a role in the uptake of P by ectomycorrhizae or arbuscular mycorrhizae, and N uptake by ectomycorrhizae and to a lesser extent arbuscular mycorrhizae. In *Eucalyptus grandis* and *E. maculata*, inoculation with the ectomycorrhizal fungus *Pisolithus* spp. enabled the seedlings to utilize amino acids as organic N sources, which could not be utilized by nonmycorrhizal seedlings. Ectomycorrhizal colonization facilitates utilization of many organic sources of N, including amino acids, proteins, and leaf litter. *Pinus sylvestris* seedlings colonized with *Suillus bovinus* were able to utilize N from the litter fermentation layer of a forest soil. In addition to the elements P and N, mycorrhizae have been shown to facilitate plant acquisition of Mg, Cu, Zn, and Mn.

Much of the benefit of mycorrhizae in mineral nutrient acquisition is a consequence of the extramatrical or extraradical mycelium. Both ectomycorrhizae and arbuscular mycorrhizae can greatly increase the volume of soil exploited due to the extent and high surface area of the extramatrical mycelium. It has been shown in a number of investigations that the external hyphae of mycorrhizae can absorb P from outside the root depletion zone and transport P to the host plant. In an investigation with Norway spruce (*Picea abies*) and the ectomycorrhizal fungus *Paxillus involutus*, translocation of P by the extramatrical mycelium over a distance of 5 cm was demonstrated. In *Pinus*

*sylvestris* mycorrhizal with *Suillus bovinus*, P was translocated over 30 cm, mainly in rhizomorphs.

The high effectivity of the hyphae of both ectomycorrhizae and arbuscular mycorrhizae in P uptake may also be due to the accumulation of polyphosphates in vacuoles, where they act as both a storage form of P and function in an alternative form of energy storage. In addition to the increase in surface area provided by the extramatrical mycelium, ectomycorrhizae have also been shown to exude organic acids and mobilize sparingly soluble P mineral sources. The ectomycorrhizal fungus *Paxillus involutus* has been shown to exude high amounts of malate and oxalate. *Pinus rigida* ectomycorrhizal with *Pisolithus tinctorius* was able to extract P from insoluble aluminum phosphate. The exudation of organic acids may be a primary factor in the weathering of minerals.

Both ectomycorrhizae and arbuscular mycorrhizae have high levels of phosphatase activity, which are important in the utilization of organic P sources. In forest soils the majority of P in the rooting layer is in the form of organic P. The levels of phosphatase in mycorrhizae are often similar to those of tree fine roots. As an example, in Norway spruce ectomycorrhizal with a number of fungi, similar levels of acid phosphatase were found in mycorrhizal and nonmycorrhizal roots. However, there are differences in the levels of phosphatase activity between different ectomycorrhizal species. In Norway spruce mycorrhizal with *Thelephora terrestris*, a higher phosphomonoesterase activity was found in mycorrhizal roots and rhizomorphs than nonmycorrhizal roots. However, independent of the levels of acid phosphatase activity between mycorrhizae and nonmycorrhizal roots, the large surface area of the extramatrical mycelium will greatly increase the potential to mobilize organic P.

Estimates of the contribution of inorganic P uptake to the total uptake by trees suggest that the contribution may be significant. In Norway spruce ectomycorrhizal with *Paxillus involutus*, 52% of the total P uptake was shown to be via the extramatrical hyphae. It is possible that experimental systems may overestimate the mycorrhizal contribution to P acquisition. However, as the mycorrhizal contribution is so high, it is very likely that under field conditions mycorrhizae play a significant role in P acquisition.

### Water relations

Both ectomycorrhizae and arbuscular mycorrhizae can improve the water relations of plants. For example, in two species of *Acacia*, mycorrhizal plants had a higher number of open stomates under

drought conditions. However, the mechanisms involved are still controversial. A number of mechanisms of increased host drought tolerance have been suggested, such as increased root hydraulic conductivity, alteration of stomatal regulation due to hormone signals, osmotic adjustment, hyphal water transport, and improved P nutrition. Improved water status has often been associated with improved host P nutrition. That mycorrhization nearly always results in an improved P nutrition of the host plant and/or larger plants often makes interpretation of the mechanisms involved in improved water relationships difficult. However, the rhizomorphs of ectomycorrhizae provide possible conduits for the transport of water. In *Pinus pinaster* inoculated with a number of strains of *Pisolithus tinctorius*, a significant correlation between plant water potential and the extension growth and rhizomorph diameters of the different strains could be shown.

### Plant-Pathogen Interactions

Apart from beneficial effects on the nutrition and water supply of host trees, mycorrhizae have been proven to increase the resistance of trees to infection by pathogens of the fine roots. Different species of mycorrhizal fungi vary in their efficiency at preventing root infections, although the mechanisms involved in this process are rather poorly understood. Possible modes of action include the production of antibiotics by the mycorrhizal fungi, stimulation of host defense mechanisms, and the physical barrier presented by the Hartig net in ectomycorrhizae. In casuarina (*Casuarina equisetifolia*) arbuscular mycorrhizal fungi increased the resistance to the root pathogen *Fusarium vesicubesum*. Both ectomycorrhizal and arbuscular mycorrhizal fungi have been shown to produce antibiotics. In addition, ectomycorrhizal fungi produce phenolic substances and oxalic acid that suppress root pathogens.

### Amelioration of Metal Toxicity

Ectomycorrhizal fungi have been demonstrated to alleviate growth depressions of tree seedlings due to toxic effects of Al, Ni, Zn, and Cd. For other important heavy metals, for example Hg and Pb, direct evidence of amelioration by ectomycorrhizal fungi is still lacking. Metal tolerance of higher plants may be due to a range of potential processes. These may include: (1) a reduction of metal exposure by excretion of chelating substances; (2) extracellular sequestration (e.g., by mucilage, pH gradients in the rhizosphere); (3) modified uptake systems at the plasmalemma; or (4) intracellular detoxification. Mycorrhizal fungi may also alter metal sensitivity

of their hosts by any of the mechanisms outlined. A number of possible mechanisms have been suggested, including: (1) filtering of toxic metals in the hyphal sheath or Hartig net; (2) reduced transfer of metal to the shoot; (3) metal sorption on the extramatrical mycelium; and (4) chelation by organic acids and other substances released by mycorrhizal fungi.

## The Costs of Mycorrhization

Production and maintenance of mycorrhizae impose a carbon cost on the host plant in excess of 30% of total photosynthesis. In seedlings growing at adequate nutritional levels, the carbon requirements of the mycorrhizal fungi may result in reduced growth rates of the host plants.

## Mycorrhizae in Ecosystems

### Boreal and Temperate Forests

In boreal and temperate forests there is good evidence to suggest that ectomycorrhizae play an important role in N recycling and acquisition. Ectomycorrhizal fungi release enzymes such as peroxidase and phenol oxidase that allow them to contribute to decomposer activity. In Ca-deficient forests, ectomycorrhizae have been shown to be involved in the uptake of Ca from mineral weathering. This may be due to the release of organic acids. High release of organic acids, especially oxalate, has also been shown in ectomycorrhizal fungi forming hyphal mats, resulting in bleaching of soil horizons.

The formation of a common hyphal mycelium between different tree species colonized by the same ectomycorrhizal fungus is thought to be involved in the transfer of carbon between species. This has been shown experimentally in a carbon transfer between *Betula papyrifera* and *Pseudotsuga menziesii* sufficient to improve growth. It is believed such carbon transfer may be important for tree seedlings growing in deep shade.

### Subtropical and Tropical Forests

In an investigation of the distribution of arbuscular and ectomycorrhizal tree species in savannas, it was shown that ectomycorrhizal trees dominate soils with low levels of N and P, whereas arbuscular mycorrhizal species dominate soil low in P but relatively rich in N. This suggests that ectomycorrhizal trees may have a greater advantage for N acquisition than VA mycorrhizal species. However, in the humid tropics of French Guyana, ectomycorrhizal tree species were found not to dominate the poorest soils. In the moist tropics most tree species are VA mycorrhizal. Many of the soils are acidic and highly

leached, with a consequence that the soils have low available P levels due to Al fixation of P. Under these conditions VA mycorrhizae may be important in the rapid cycling and uptake of inorganic P.

### Ectomycorrhizal Fungal Fruiting Bodies as Nontimber Forest Products

Fruiting bodies of ectomycorrhizae are commonly collected and sold. In some forest areas the value of the mycorrhizal fungal fruiting body harvest exceeds the value of wood production. Harvesting is mainly restricted to a small number of valuable species such as *Boletus edulis*, *Cantharellus cibarius* (chanterelles), *Tuber magnatum* (white truffles), and *T. melanosporum* (black truffles).

*See also:* **Health and Protection:** Biochemical and Physiological Aspects. **Tree Physiology:** A Whole Tree Perspective; Nutritional Physiology of Trees; Root System Physiology.

### Further Reading

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## Physiology of Sexual Reproduction in Trees

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### Introduction

The physiology of sexual reproduction in forest trees has progressed substantially over the past 20 years. Three previous symposia of the International Union of Forestry Research Organizations (IUFRO) not only summarized current knowledge but also laid out

the ground work for future studies. Many of these questions are still valid today but substantial progress has been made in early maturation, flower induction, and pollination biology. Many questions still exist (mechanism of flowering) and new questions are being asked (environmental effects on progeny performance).

New technology, principally molecular techniques, is now available and offers exciting new possibilities for future flowering, pollination, and seed production studies. However, there has been a substantial shift in flowering research. Considerably fewer studies are being published on the mechanism of flowering in conifers but, equally so, the volume of work dealing with hardwoods, especially tropical hardwoods, is growing.

The perspective of this contribution in forest tree seed production has a definite commercial bias. Procuring seed as a mechanism for delivery of tree improvement programs as well as plantation forestry has been the incentive for pursuing both fundamental research and program development. Much of the emphasis has been with seed orchard development simply because it is the most cost-effective tool for delivery of genetic gain.

Developmental biologists may object to my use of the word 'flowering' when referring to conifers. Certainly the use of 'sporangiate strobili' would be more precise but also more awkward. Here 'flowering' is restricted to the general process of sexual reproduction in conifers. The terms 'seed' and 'pollen cones' refer to the mega- and microsporangiate cones, respectively.

### Plantation Forestry

According to statistics provided by the Food and Agriculture Organization, global forest plantations have grown from about 18 million hectares in 1980 to 187 million hectares in 2000 (both hardwoods and conifers). This represents about 5% of the total global forest cover. Asia accounts for about 62% of the current plantation area, followed by Europe (17%), North and Central America (9%), South America (6%), Africa (4%), and Oceania (2%). Globally, broadleaved trees make up 40% of the total, of which *Eucalyptus* is the principal genus and conifers make up 31%, of which *Pinus* is the principal genus. Over the past decade, the percentage of these plantations destined for industrial use has increased from 36% to 48%. Tree improvement, as part of plantation forestry, has been a principal driver of flowering research, especially for temperate conifers.

Critical to the success of these programs is a sustainable supply of not only the species but also