Unit 7: Symbiotic associations (4 lectures)
Lichen – Occurrence; general characteristics; growth forms and range of thallus organization; nature of associations of algal and fungal partners; reproduction; mycorrhiza- ectomycorrhiza endomycorrhiza and their significance.

Symbiosis: (Sym=together,Bios=living, Symbiosis=living together)
Symbiosis is a close association between two or more organisms of different species.
There 3 types of symbiotic associations:
1.Mutualism – both species benefit
2.Commensalism – one species benefits and the other is neither harmed or benefitted
3.Parasitism – one organism benefits at the expense of another (predator/prey relationships are parasitic)
Depending on the interval of life spent together they can be divided into:
Oligatory, which means that one or both of the symbionts entirely depend on each other for survival, Facultative (optional) when they can generally live independently.

Symbiosis in plants can be divided into the following:
1. Lichens
2.Mycorrhiza
3.Root nodules: legumes and rhizobium

LICHEN:

A lichen is not a single organism. Rather, it is a symbiosis between different organisms - a fungus and an alga or cyanobacterium.

Nature of Association: Cyanobacteria are sometimes still referred to as 'blue-green algae', though they are quite distinct from the algae. The non-fungal partner contains chlorophyll and is called the **photobiont**. The fungal partner may be referred to as the **mycobiont**. While most lichen partnerships consist of one mycobiont and one photobiont, that's not universal for there are lichens with more than one photobiont partner. When looked at microscopically, the fungal partner is seen to be composed of filamentous cells and each such filament is called a **hypha**. These hyphae grow by extension and may branch but keep a constant diameter. Amongst the photobionts there are those that are also filamentous in structure while others are composed of chains or clusters of more-or-less globose cells.

Given that they contain chlorophyll, algae and cyanobacteria can manufacture carbohydrates with the help of light via the process of photosynthesis. By contrast, fungi do not make their own carbohydrates. Every fungus needs existing organic matter from which to obtain carbon. In a lichen some of the carbohydrate produced by the photobiont is of course used by the photobiont but some is 'harvested' by the mycobiont.

Occurance:Worldwide, over 20,000 lichens exist. Lichens can be found growing in almost all parts of the terrestrial world, from the ice-free polar areas to the tropics, from tropical rainforests to those desert areas free of mobile sand dunes. While generally terrestrial a few aquatic lichens are known. The surfaces (or **substrates**) on which lichens grow vary from the natural (such as soil, rock, wood, bone) to the man-made (bitumen, concrete, glass, canvas, metal - to give just a few examples).

Lichens possess structures not formed by either of the partners and produce chemicals usually absent when the fungus or the photobiont are cultivated separately and so lichens are more than a sum of their parts. In fact, lichens synthesize over 800 substances, many of them not found elsewhere in nature. Though the fungi that form lichens do not occur in nature as independent organisms, a number of the photobionts can be found in free-living forms. It is possible to separately culture the two partners in the laboratory but it is difficult to resynthesize the lichen. Success has been achieved when the fungus and photobiont are placed under stress (e.g. by reducing water and nutrient levels), suggesting that originally lichen partnerships formed to overcome adversity.

Classification and identification

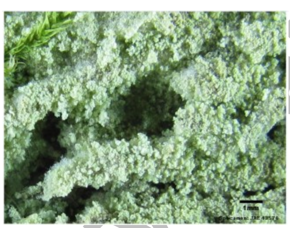
Lichens are classified with the fungi (being sometimes referred to as **lichenized fungi**). The fungi incorporated into lichens are largely ascomycetes, with very few basidiomycetes involved. Though a number of lichen species can be readily identified in the field the precise identification of many lichens demands examination of their macroscopic and microscopic structures (such as reproductive structures, spores and cellular features) as well as chemical tests. Chemical reagents can be applied to the lichen tissues and the presence or absence of a colour change noted but such 'spot' tests are crude and chromatographic methods yield more precise analyses. The usefulness of the chemical tests lies in the fact that the chemical substances are often species specific.

Growth forms

Lichens show a variety of growth forms and there are terms used to name these forms. The following are commonly seen

types:

1. **Leprose:**The thallus of a leprose lichen has a powdery appearance. Often *Lepraria* incana thalli are composed of tiny granules, with the mass of granules seated on a woolly layer of hyphae in some species. Each granule is composed of fungal hyphae and some photobiont cells and in many species the individual granules are fuzzy because fungal hyphae extend out from the surface of each granule.
2. **Crustose** lichens are markedly two dimensional and firmly attached to the substrate by their entire lower surfaces, making it impossible to see a crustose lichen's undersurface. A crustose lichen looks very much like a thin crust on the substrate.eg.*Graphis* sp,*Caloplaca sp(*bright orange *),Strigula,Dimerella* .
    - **a. Placodioid:** Some species are crustose centrally but somewhat foliose at the margins, such a lichen is called **placodioid** or **placoid** and *Placopsis perrugos,Lecanora.*
    - **b. Squamulose:** They are like an intermediate between crustose and foliose lichens. A colony of a squamulose lichen looks like a scattering of small flakes or scales on the substrate.There are numerous squamules on the soil but you can also see a number of the upright podetia with broader apices. Moreover, at the margins of some of the broader apices show additional podetia developing.Eg. *Psora*
3. **Foliose** lichens could be thought of as halfway between crustose and fruticose. Though obviously three dimensional they grow in a more-or-less sheet-like form, but often with a lobed appearance. They are not attached by their entire lower surfaces to their substrates. Indeed, some foliose lichens are just centrally attached to their substrates with the rest loose, so making it possible to see both the lower and upper surfaces very easily. eg.*Xanthoparmelia substrigosa ,Parmelia,Physcia,Collema,Peltigera.*
4. **Fruticose** lichens are erect or pendulous and markedly three-dimensional. The upright fruticose structures called **podetia** - sometimes with the appearance of fairly simple stalks, sometimes flared at the apex and so presenting a somewhat trumpet-like form. The genus *Usnea* sp., *Cladonia sp.Letharia and Bryoria are* examples.
    - **a. Byssoid/Filamentous** : A **byssoid** lichen has a somewhat wispy appearance, like cotton-wool teased out to some degree.eg.*Coenogoium,Ephebe,Racodium,Cystocoleus.*




Lepraria.sp *Caloplaca. sp* *Xanthoparmelia.sp* *Usnea* .sp



Placopsis perrugosa *Psora himalayana* *Coenogonium implexum*

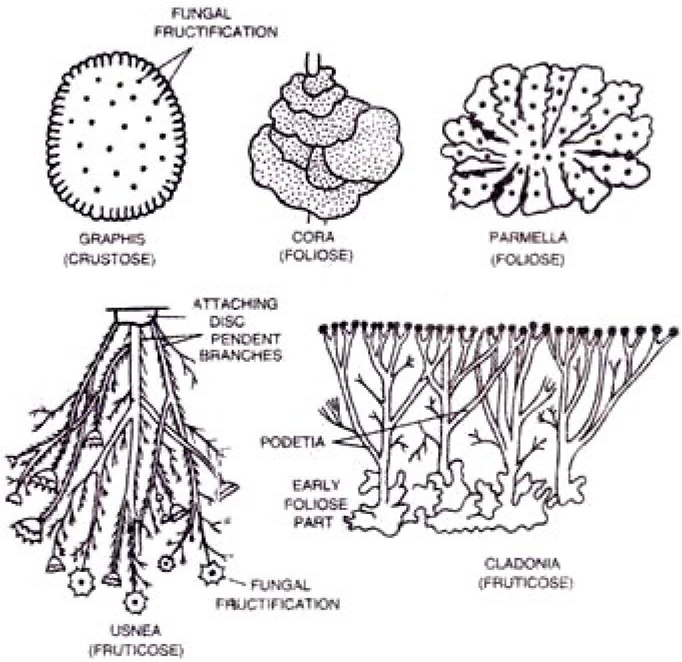
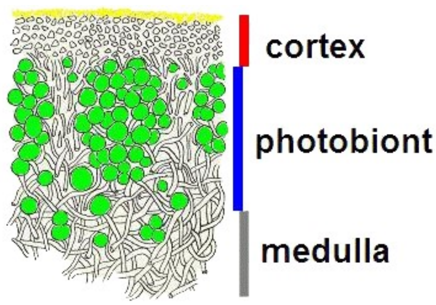
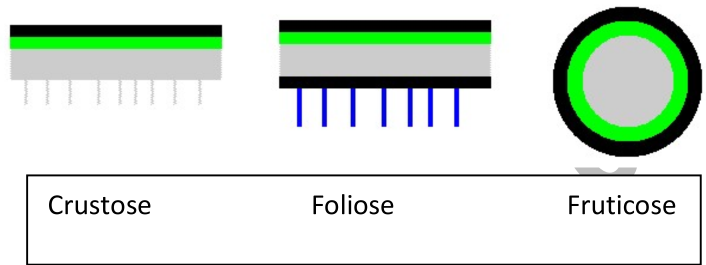


Fig. 2.54. Forms of Lichens.

Thallus Structure:

The following very simplistic cross-sectional diagrams show the broad internal compositions of many of the crustose, foliose and fruticose lichens:





Leftmost is a crustose species. Black indicates the **cortex**, a band of compacted fungal hyphae that serves as a protective skin. Below the cortex, in green, is a layer of photobiont cells. If the upper cortex is carefully scraped away, the photobiont layer(green if it's algal and blue-green if its cyanobacterial) is exposed . Below the photobiont layer is the **medulla**,which is a loose weave of fungal hyphae, and shown here in grey. You can also see some grey hyphae growing down from the medulla and these hyphae penetrate the substrate and so anchor the thallus very tightly.

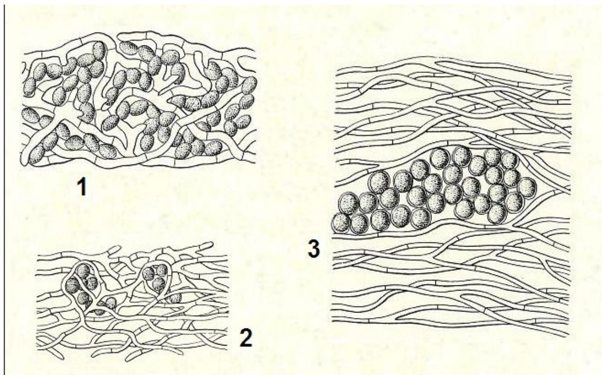
The middle diagram shows a foliose lichen. An immediate difference from the crustose lichen diagram is that the foliose thallus shown here has two cortices - an upper cortex and a lower cortex beneath the medulla. The foliose diagram has an additional colour. The blue lines indicate **rhizines**, which are bundles of hyphae. These penetrate the substrate and anchor the thallus.

Fruticose lichens are typically highly branched with the branches often more or less circular in cross section. The final diagram shows a cross section of the branch of a fruticose lichen. There is a single cortex which constitutes the outermost band, within which there is a concentric photobiont band and the medulla occupies the central portion of the branch.

Though a crustose thallus has distinct upper and lower surfaces, the tight binding to the substrate results in the lower surface not being visible. Rhizines on a foliose thallus may be dense or sparse and there are foliose species without rhizines. A lichen with rhizines is termed **rhizinate** and an **erhizinate** one lacks rhizines. When rhizines are present (and regardless of whether they are dense or sparse) they may be found anywhere under the thallus in some species while in other species the rhizines are confined to certain areas. This variation in rhizine density and placement means that some foliose thalli are fairly loosely attached to their substrates while others are very firmly attached. In some foliose species the thallus is attached only centrally , leaving the rest of the thallus free of the substrate and so allowing the underside to be seen easily. Other foliose species have thalli so well attached over much of their under-surface that they might initially be mistaken for crustose species. There is also variety in rhizine shape between species. Rhizines may be just simple linear bundles as shown in the diagram above, However they may also be anything from sparsely to richly branched. In some species the rhizines fork and may do so repeatedly. In others each rhizine has a main axis but with short lateral branches coming off the main axis and yet others resemble well-worn paint brushes that have bristles going off in all directions. As already mentioned some foliose species have no rhizines and *Xanthoparmelia semiviridis* is a striking example. The thalli sit loosely on the soil, curled up when dry but flat and with a darker colour when moist .

In a number of species hyphae may grow out from a cortex to give the cortex a hairy appearance. Amongst the hairy species there are those in which the hairs are sparse and at the other extreme those in which the hairs are dense. There is also variation in the structure and arrangement of such hairs and there are technical descriptive terms for all these variations, but there is no point in going into that sort of detail on this website.

Cortices vary considerably in their structure and there are cortex-less lichens, such as various byssoid lichens.
A **byssoid** thallus has a somewhat wispy appearance, like cotton-wool teased out to some degree, and is composed of loosely interwoven hyphae and photobiont cells. When present, cortices vary from thin to relatively thick depending on the species. Schneider provided drawings of FLIMSY thalli as well as of a VARIETY of more robust thalli.



1. *Biatorina pineti*

2. *Arthonia radiata*

3. *Xylographa parallela* (A wood-inhabiting species with the thallus often growing within the wood.)

In each of the simple diagrams above, the photobiont cells are shown as being confined to a well-defined band immediately below a cortex and distinct from the medulla. That is the case in a great many lichens (and such lichens are described as **heteromerous**) but there are a few genera in which the photobiont cells are distributed randomly through the thallus and Schneider included drawings of a such species, described as **homoiomerous**..

Reproduction:

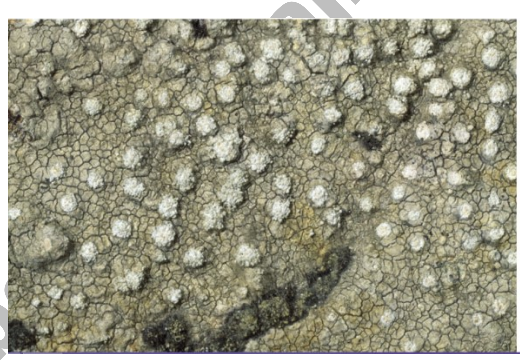
Lichens may reproduce both asexually (or vegetatively) or sexually by several methods.

Vegetative Methods:

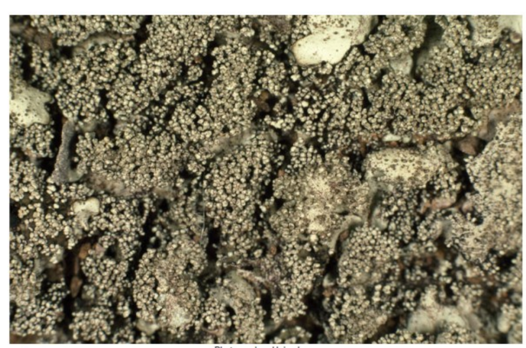
A fragment broken off from a lichen thallus may grow into a new thallus. This is a means of vegetative propagation, the new thallus being genetically identical to the thallus from which the fragment came. Many lichens are brittle when dry and are therefore easily fragmented, for example by some animal stepping on a dry thallus. Obviously fragmentation is especially easy with the foliose and crustose species. Fragmentation could be described as 'accidental' vegetative reproduction.

Soridia: There are more specialized, means of vegetative reproduction. The surface of a thallus may show minute, powdery granules (called **soredia**), each soredium consisting of a few photobiont cells surrounded by fungal filaments.

Isidia: The thallus may sometimes produce tiny, simple or branched spiny outgrowths (called **isidia**), again a mixture of fungal and photobiont cells. The isidia are easily broken and both they and the soredia are easily dispersed and contain everything needed to produce new thalli. There are species which produce neither soredia nor isidia, others produce both and yet others will produce only one of the two.



Soridia(***Pertusaria subventosa***)



Isidia(***Xanthoparmelia ewersii***)

Sexual Methods

Only the fungal partner reproduces sexually.

Apothecium:Here the spores often produced in a long-lived saucer-like structure called an **apothecium**, which is easily visible to the naked eye in many species.

Perithecium:Instead of apothecia various lichens produce their fungal spores in perithecia.A **perithecium** is a small, and typically black, hemispherical pustule within which the asci are produced.

Graphid/lirellae: A group of lichens with striking spore producing structures are the so-called **graphid** lichens, which produce their fungal spores in apothecia that are elongated and narrow and are called **lirellae** . Lirellae look like short scribbles on the thallus and the term graphid is derived from the classical Greek word for 'writing'.

Apothecium(Usnea)

Perithesium (***Strigula)***

Graphid (***Graphis)***

- **Beard Moss** - *Usnea barbata*
- **Canary moss** - *Parmotrema perlatum*
- **Chalice Moss** - *Cladonia pyxidata*
- **Iceland Moss** - *Cetraria islandica*
- **Jaffna Moss** - *Alectoria sarmentosa*
- **Reindeer Moss** - *Cladina rangifera,* eaten by reindeer and caribou during winter
- **Velvet Moss** - *Umbilicaria grisea*, once known by the name *Gyrophora murina*
- **White Moss** - a term that has been used for a number of lichen species

MYCORRHIZAS

Mycorrhizas are symbiotic relationships between fungi and plant roots (the term means literally 'fungus root'). Perhaps more than 80% of the species of higher plants have these relationships, and so do many pteridophytes (ferns and their allies) and some mosses (especially liverworts). They are as common on crop plants (cereals, peas, tomatoes, onions, apples, strawberry, etc) as in wild plant communities, and in several cases they have been shown to be important or even essential for plant performance. As the American plant pathologist, Stephen Wilhelm, said: '...in agricultural field conditions, plants do not, strictly speaking, have roots, they have mycorrhizas'.

To a large degree, mycorrhizas seem to be symbiotic (mutualistic) relationships, in which the fungus obtains at least some of its sugars from the plant, while the plant benefits from the efficient uptake of mineral nutrients (or water) by the fungal hyphae. However, there can be circumstances in which the fungus is mildly detrimental, and others in which the plant feeds from the fungus.

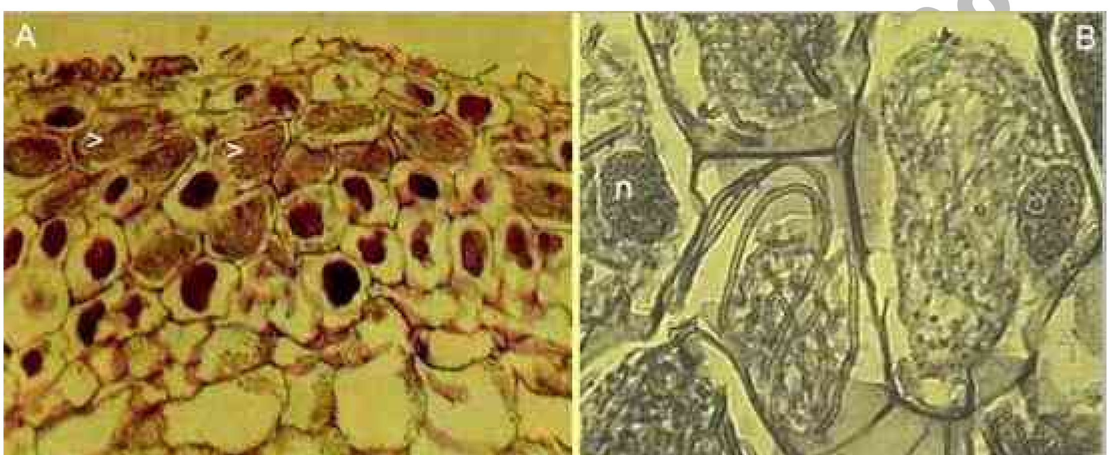
The three of the commonest types of mycorrhiza. Each of them represents a distinctive type of association.

1. Orchid mycorrhizas

Some types of orchid are non-photosynthetic; others only produce chlorophyll when they have grown past the seedling stage. In all cases, the plant depends on sugars derived from a fungal partner for at least part of its life. The minute orchid seeds, with negligible nutrient reserves, will not germinate unless a fungus infects them, although the seeds can germinate aseptically if supplied with the 'fungal sugar' **trehalose**.

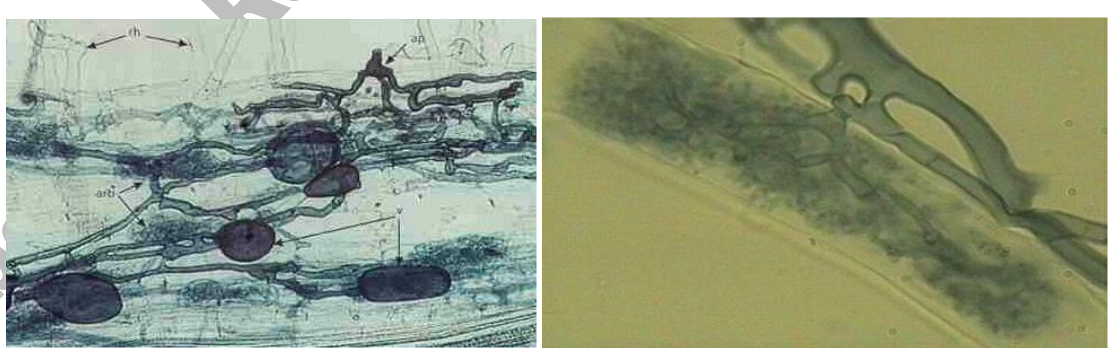
These mycorrhizas are unusual because, in effect, the plant parasitises the fungus that invades it. The fungi in these associations resemble the common plant pathogen *Rhizoctonia solani*, but recent taxonomic studies have assigned them to several related genera. They are mainly **saprotrophic** - they grow by degrading organic matter in soil - but they might obtain trace elements or some other factor from the plant.

An interesting variation on this theme is shown by some orchids and other non-photosynthetic plants (*Monotropa* species) that have wood-rotting species of *Armillaria* as their mycorrhizal symbionts. In some of these cases the fungus can even be a pathogen of tree roots, so that the non-photosynthetic plant gains its nutrients by indirect parasitism of a living tree



2. Arbuscular mycorrhizas

Arbuscular mycorrhizas are found on the vast majority of wild and crop plants, with an important role in mineral nutrient uptake and sometimes in protecting against drought or pathogenic attack. Structures resembling those of the present-day AM fungi have been found in fossils of primitive pteridophytes of the Devonian period. It is thought that these fungi colonised the earliest land plants and that mycorrhizal associations could have been essential for development of the land flora.



The fungi involved are members of the zygomycota (related to Mucor). They are classified currently in six genera (Acaulospora, Entrophospora, Gigaspora, Glomus, Sclerocystis and Scutellospora) and they seem to be obligate symbionts: none of them can be grown in axenic culture, i.e. in the absence of their hosts.

The image above shows part of a clover root from the Pentland Hills near Edinburgh, naturally infected by an AM fungus. There was no evidence of fungal infection until the root tissues were cleared with strong alkali and then stained with trypan blue to reveal the fungus. The site of penetration is shown at top right, where the fungus produced a pre-penetration swelling (appressorium, ap), then it grew between the root cells and formed finely branched arbuscules (arb) and swollen vesicles (v). The arbuscules are thought to be sites of nutrient exchange - the fungus obtains sugars from the plant, and the plant obtains mineral nutrients (e.g. phosphorus) that the fungus absorbs from the soil. Vesicles are thought to be used for storage. Root hairs (rh) are also labelled.

The image below shows a single arbuscule with its repeated dichotomous branching inside a root cell. The plant cell remains alive, because its membrane extends to encase all the branches of the fungus. Strictly speaking, therefore, the fungus is always outside of the cell, surrounded by the cell membrane. Feeding relationships of this type, in which a fungus produces special nutrient-absorbing structures within the host cells, are termed biotrophic. For further details see Biotrophic plant pathogens.

The hyphae of AM fungi extend into soil, where their large surface area and efficient absorption enable them to obtain mineral nutrients, even if these are in short supply or are relatively immobile. AM fungi seem to be particularly important for absorption of phosphorus, a poorly mobile element, and a proportion of the phosphate that they absorb has been shown to be passed to the plant.

3. Ectomycorrhizas

Ectomycorrhizas (sometimes termed ectotrophic mycorrhizas) are characteristic of many trees in the cooler parts of the world - for example pines, spruces, firs, oaks, birches in the Northern Hemisphere and eucalypts in Australia. However, some trees (e.g. willows) can have both ectomycorrhizas and arbuscular mycorrhizas, and most tropical trees have only arbuscular mycorrhizas.

The fungi involved are mainly Ascomycota and Basidiomycota, including many that produce the characteristic toadstools of the forest floor (Figures A-C below). Most of these fungi can be grown in laboratory culture but, unlike the wood-rotting fungi, they are poor degraders of cellulose and other plant wall materials. So they gain most of their sugars from the living plant roots in natural conditions.

A. Rings of toadstools of mycorrhizal fungi (Hebeloma and Lactarius species) around the base of a birch tree.
B. Fruitbody of Lactarius. The gills of this toadstool were cut to show that the fungus exudes a milky fluid when the tissues are damaged - hence the name 'Lactarius'.
C. Fruitbody of Amanita muscaria (the 'fly agaric') which is a typical mycorrhizal fungus of birches but also can be found on some other trees.

D, E. Mycorrhizal roots. In ectomycorrhizas the terminal branches of the root system are highly modified - the roots are short and stumpy, covered with a mantle (sheath) of fungal tissue (the creamy-white root surface in D), and there are few or no root hairs. The fungus takes over the normal nutrient-absorbing role of the root hairs. In E the fungal mantle is less conspicuous, but the fuzzy appearance of the roots is due to many fungal hyphae growing from the mantle into the soil. Such roots are seen easily if the undecomposed, surface litter is scaped away from the forest floor to reveal the decomposing litter containing a mass of mycorrhizas and their fungal networks.

F. Cross-section of a pine mycorrhiza, showing the substantial fungal sheath that encases the root (labelled 's')..

G. Higher magnification of the sheath (left side) composed of a tightly packed fungal 'tissue'. From the inner side of the sheath, the fungus grows between the root cortical cells, forming a network termed the Hartig net (Hn). The sections in F and G were stained to show phenolic compounds (red) that often are formed in pine roots in response to mycorrhizal infection. They might have a role in limiting the fungal invasion of the tissues.

Functioning of ectomycorrhizas

Experiments with radioactive tracers have shown that when labelled CO_2 is applied to leaves of tree seedlings, the label is found in plant sugars (sucrose, etc.) which move to the roots; then the label enters the fungal sheath where it occurs in the form of typical 'fungal carbohydrates' such as **mannitol** and **trehalose**. Most plants and plant tissues cannot metabolise these compounds, so there is, in effect, a one-way flow of carbohydrate to the fungus. The cost of this to the plant may be considerable. However, the plant also can benefit from the association, because the fungal hyphae that ramify into soil are very efficient in capturing mineral nutrients; these accumulate in the sheath but at least some minerals are transferred to the plant, presumably from the Hartig net.

Recent work has shown that several ectomycorrhizal fungi can degrade proteins (they release **protease** enzymes) and thus can obtain nitrogen from the decomposing leaf litter. This could be highly significant in temperate and sub-boreal forests, where the rates of mineral nutrient recycling are low because of the low microbial activity in cool, acidic conditions. Ectomycorrhizal fungi might thus play a key role in the nitrogen nutrition of trees.

It has also been shown that young seedlings growing in the shade of 'mother' trees can be attached to the 'parent' by a common network of mycorrhizal hyphae in the soil. In these conditions, at least some movement of labelled carbohydrates has been shown to occur from the roots of the parent to the younger trees, perhaps helping to nurture the seedlings.