MiSACbriefings 4c
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# Fungi at work 3: Making plant roots work

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Nearly all the plants in your garden, the crops in our fields & pastures and the trees in our forests depend on fungal associates in their roots to help them grow.

Plants obtain their nutrients by absorbing minerals and water from the soil using their roots. But they are also offered quite a lot of help from certain species of fungi. The relationship appears to have started because a plant's roots alone are not able to supply the plant with all the nutrients it needs. The fungi associated with plant roots are called **mycorrhizas**; a mycorrhiza is a mutualistic (or symbiotic) interaction between a fungus and the roots of a plant.

## Introducing mycorrhizas

In this relationship, the roots of the plant are infected by a fungus, but the rest of the fungal mycelium continues to grow through the soil, digesting and absorbing nutrients and taking up water, to share with its plant host (Fig. 1). The plant benefits from increased nutrient uptake via the fungal mycelium, while the fungus is supplied with photosynthetic sugars by its host.

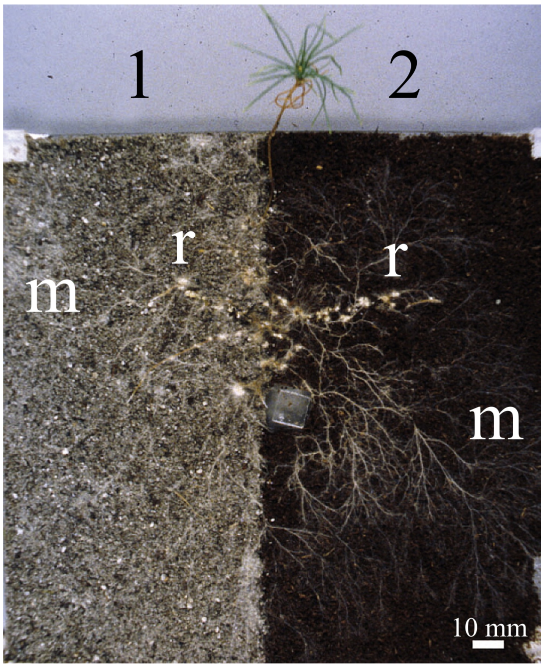


**Fig. 1.** A pine seedling grown in an experimental microcosm with the ectomycorrhizal fungus *Suillus bovinus*. The seedling is growing in two soils: 1 is a podzol (the typical soil of northern forests) and 2 is a loamy organic soil. Fungal mycelia (m; evident mainly as hyphal strands) extend from the colonised root tips (r) into both soils and are far more extensive than the roots.

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The mycorrhizal association seems to have evolved as soon as plants first colonised the land 450 to 600 million years ago. Today, 95% of vascular plants have mycorrhizas associated with their roots, in all habitats. These include deserts, lowland tropical rainforests, aquatic ecosystems and at high latitudes and altitudes.

Mycorrhizas were traditionally classified into two types: **endomycorrhizas** in which the fungal structure is almost entirely within the host root (Fig. 2A), and (the more-advanced arrangement) **ectomycorrhizas** in which the plant root system is completely surrounded by a sheath of fungal tissue with the hyphae penetrating between the outermost cell layers of the root (Fig. 2B).

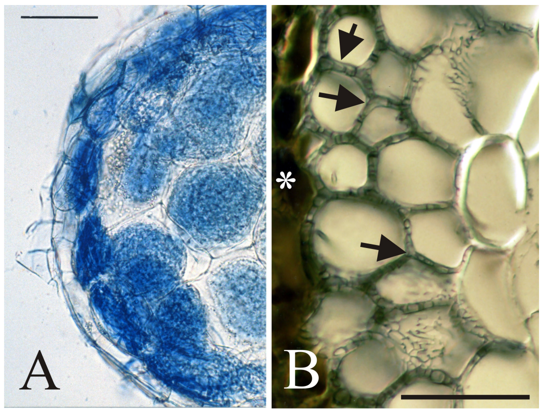


**Fig. 2.** Light micrographs of sectioned roots showing infections with mycorrhizas. A, the fungus *Rhizoctonia cerealis* forming endomycorrhizas with seeds of the heath spotted orchid (*Dactylorhiza maculata*). B, hyphae of an ectomycorrhiza penetrating between cortical cells of the root of *Tsuga canadensis* (Hemlock) (shown by the arrows). Tannin-filled epidermal cells are identified by an asterisk. Scale bars = 100 µm.

*Image A* © R.W.S. Weber & J. Webster; *Image B* © Mark Brundrett, both reproduced with permission from the textbook *21st Century Guidebook to Fungi* (Cambridge University Press, 2020)

The numerous hyphae of the fungi greatly increase the surface area available for absorbing nutrients into the partnership. The hyphae can also 'go looking for food', by growing into areas of fresh nutrients. Uptake of nutrients by plant roots can create zones of nutrient deficiency. Hyphae can grow rapidly past these depletion zones and, by so doing, enhance the absorption of nutrients shared with the root. For the plant, nourishing a fungus so that it continues to extend its hyphae is quicker and more economical than extending its own roots.

Movement of nutrients through soil depends on their chemistry and the chemistry of the soil. Phosphorus, as phosphate ($PO_4^{3-}$) ions, has low mobility in soil because the phosphates of the most-common divalent metals are insoluble. So, phosphorus tends to be the limiting macronutrient in most ecosystems.

In contrast, ammonium ($NH_4^+$) ions are about ten times more mobile than phosphate, and are most abundant in acidic soils, such as those of forests and heathland. In most other soils, nitrate ($NO_3^-$) ions are the main immediately-available source of nitrogen for the root. However, the more-soluble and more-mobile nutrients are also the ones most likely to be washed out of the soil by rain.

## Making nutrients available

What the fungal component of the mycorrhizal association does is change the meaning of the word “available”. When horticulturalists talk about ‘available nitrogen and phosphorus’ they are referring to soluble salts in the soil water. If the salt is not soluble, it is not available to plants.

The fungi produce organic acids, such as citrate and oxalate, and secrete enzymes (particularly acid phosphatases) that release phosphate from soil complexes so it can be taken into the hyphae.

Fungi store and translocate phosphorus in the hyphae in the form of organic polyphosphates. This maintains a low inorganic phosphate concentration in the hypha and enhances uptake of any external phosphate that might be nearby. In many mycorrhizal plants, up to 80% of the plant’s phosphorus comes to it through the hyphal network.

Similar considerations apply to the nutrient nitrogen. Plant roots without mycorrhizas may have limited availability of $NH_4^+$ and $NO_3^-$ ions. Mycorrhizal fungi are particularly efficient at assimilating ammonium through high-affinity transporters. Their main contribution, however, is their ability to use organic nitrogen sources, through the production of proteases and peptidases, which allow them to access nitrogen sources that are not available to non-mycorrhizal plant roots.

Mycorrhizas also offer other benefits to their plant partner. Metal ions such as potassium, calcium, copper, zinc and iron are all assimilated more quickly and in greater amounts by mycorrhizal plants, again through the ability of the fungal hyphae to absorb, translocate and release minerals quickly and efficiently.

Also, some mycorrhizal fungi can immobilise and accumulate heavy metals, such as cadmium and arsenic, so the host plant remains undamaged when growing in soils with high concentrations of heavy-metal pollutants.

Mycorrhizal fungi can also help their plant partners by increasing their tolerance to other adverse conditions. The weft of hyphae that surrounds mycorrhizal roots not only acquires nutrients from the soil but also protects the host plant against root pathogens. Probably the most crucial fact, though, is that mycorrhizal plants can grow in conditions of high water stress. The extended mycelia of mycorrhizal fungi find reserves of water from deeper and further in the soil than the host plant roots themselves can reach.

Soil contains more carbon than is present in the atmosphere and above-ground vegetation combined, and soil fungi (saprotrophs and mycorrhizas together) regulate carbon, nitrogen and other mineral nutrient cycles in terrestrial ecosystems; (it’s called ‘ecosystem multifunctionality’).

In recent years it has become clear that mycorrhizas form a network that may link together different plants of different species in a habitat. This, called the ‘wood wide web’, allows nutrients and chemical signals to flow between plants through their shared fungi. Disadvantaged plants and seedlings (shaded, water stressed, in poor soil etc.) have their nutrition supplemented by resources from neighbouring plants translocated through the mycelial network. A consequence of this activity is that mycorrhizas improve survival of plant offspring and can increase population size and species distributions in habitats.

Very recently, it has been suggested that the mycelia in soil provide even more value with ‘logistics networks’ for transport of materials through soil ecosystems. Here, ‘logistics’ is used in its general business sense of the flow of things between points of origin and use; like the ‘flow’ of cornflakes between factory and breakfast table. The idea being that the hyphae are not only responsible for ***internal*** translocation but also the ***external*** fluid layers formed around the hyphae creating a ‘mycosphere’ of structured biofilms within which materials and microbes (motile bacteria, for example) can travel in all directions through the soil.

## Mycorrhizal communities

Mycorrhizal networks not only promote and support plant life above the soil, they make important contributions to the chemistry, structure and function of the soil itself. They also provide nutrition for enormous numbers of small and more-minute animals in the soil.

Most of the mushrooms and other fruit bodies you see in woodland are produced by mycorrhizal fungi (Fig. 3). When the mycelium makes such fruit bodies their primary purpose is to produce and distribute spores, but they also become vital food sources for many animals, from large arthropods and molluscs, to small mammals and humans.

**Fig. 3**. Fly agaric mushrooms (*Amanita muscaria*) In a local woodland. This fungus can form mycorrhizal associations with the roots of 20 or more tree species (as varied as birch, eucalyptus, spruce and Douglas fir). Most of the mushrooms and toadstools seen in autumn in the UK are the fruit bodies of mycorrhizal fungi.

Image © David Moore.

Microarthropods known as collembola or springtails are common members of the soil community. They feed on many organisms including bacteria, lichens and decomposing materials but they prefer fungal hyphae over all other food sources. They are primitive wingless insects that range in size from 0.2 mm to 9 mm. Their population densities easily reach $10^4$ $m^{-2}$ so hyphal grazing by these invertebrates can result in dramatic changes to mycelial morphology. They express intriguing food preferences; some graze hyphal tips and fine mycelia, others choose to feed on conidial fungi rather than mycorrhizal fungi.

Many species of mites and nematodes occur in habitats rich in decaying organic matter and many are fungal feeders (mycophagous). Then there are the larvae (or maggots) of many small dipteran flies. It is rare to find a mushroom in the field that is completely free of maggots. The larvae eat their way throughout the fungal tissue, causing enormous damage. Again, they show feeding preferences; some prefer the mushroom stems, some the mushroom caps, others the mushroom’s gills.