

remains the case that less than 1% of the known species of fungi have been found in aquatic habitats (see pp. 346-351 in Carlile *et al.*, 2001; Landy & Jones, 2006).

A Kingdom-specific characteristic of fungi is that they obtain their nutrients by **external digestion of substrates**. 'Wood' (that is, plant secondary cell wall) is the most widespread substrate on the planet. This is **lignocellulose**; an intimate mixture of lignin, hemicellulose and cellulose. About 95% of the Earth's terrestrial biomass is lignocellulose. Ability to degrade **lignin** is restricted to fungi. Basidiomycota and a few Ascomycota (see [Section 10.7](#)).

Wood degrading fungi are divided into those producing **white rots** and those causing **brown rots**. With a **white rot**, wood becomes markedly paler as the organism digests the (coloured) phenolics in lignin. This mainly affects hardwoods and in a white rot, hemicellulose, cellulose and lignin are degraded more or less simultaneously. *Trametes versicolor*, *Phanerochaete chrysosporium* and *Xylaria polymorpha* (an ascomycete) are examples.

With a **brown rot** fungus, wood becomes darker brown as the digestion proceeds. In this case hemicellulose and cellulose are preferentially removed, because the fungus does not degrade the lignin. This particularly affects softwoods. *Piptoporus betulinus*, *Serpula lacrymans*, and *Coniophora puteana* are examples.

Mycorrhiza is a symbiotic interaction between fungi and plant roots that developed very early in the process of colonisation of the terrestrial environment. Mycorrhizas originated over 450 million years ago. More than 6,000 fungi are capable of forming mycorrhizas and at least 95% of vascular plants of today have mycorrhizas associated with their roots. There are several types (see [Sections 16.8](#) to 16.17):

Endomycorrhizas. Here the fungal structure is almost entirely within the host root, so that the root looks normal. Arbuscular mycorrhizas (AM) are the commonest of all mycorrhizas, being associated with the roots of about 80% of plant species, including many crop plants. AM mycorrhizas have an ancient origin, fungi are assigned to subphylum Glomeromycotina (Section 3.6, above), e.g. *Glomus* spp. Enhanced growth of the plant host occurs mainly because the fungus improves phosphate availability to plant, but plant-to-plant transfer of nutrients can occur via the fungus.

Ericoid endomycorrhizas. These are mycorrhizas of heather (*Erica*), ling (*Calluna*) and bilberry (*Vaccinium*); plants of mountain moorland and lowland heaths. The fungi involved here belong to the Ascomycota, e.g. *Hymenoscyphus ericae*. These mycorrhizas improve nitrogen and phosphorus uptake by the plant; the nitrogen being derived from the fungus breaking down polypeptides in the soil. In extremely harsh conditions (e.g. winter in the Pennines) the mycorrhiza may support the host with carbon nutrients (again from polypeptide digestion). Normally, though, the fungus takes photosynthetically-produced carbohydrates FROM the plant host.

Orchidaceous endomycorrhizas. These are like ericoid mycorrhizas but have a carbon nutrition more dedicated to supporting the host. Orchids (family Orchidaceae) form the largest and most diverse group of flowering plants, with over 800 described genera and 25,000 to 30,000 species (with another 100,000+ hybrids and cultivars produced by horticulturists since the introduction of tropical species in the 19th century). Because of their intimate relationships with pollinators and their symbiosis with orchid mycorrhizal fungi, orchids are considered, along with the grasses, to exhibit the most advanced flowering plant evolution. The orchidaceous endomycorrhizal fungus utilises complex carbon sources in soil and the products of digestion are made available to the orchid. At the seedling stage the orchid is dependent on the fungus and can be interpreted as parasitising the fungus as a result. An example is the fungus *Rhizoctonia* (basidiomycetous, anamorphic fungus which is a widespread pathogen of non-orchidaceous crop plants).

Ectomycorrhizas. These are the most advanced symbiotic association between higher plants and fungi. The root system is surrounded by a sheath of fungal tissue up to several mm thick from which hyphae penetrate between the outermost cell layers of the root and from which a network of hyphal elements (hyphae, strands and rhizomorphs) extend out to explore the soil. About 3% of seed plants including the majority of forest trees (temperate and tropical) have ectomycorrhizas. Fungi involved are mostly Basidiomycota (also some Ascomycota). Basidiomycota include most of the common woodland mushrooms; e.g. *Amanita* spp, *Boletus* spp., *Tricholoma* spp. There are both highly specific (*Boletus elegans* and larch) and non-specific associations (*Amanita muscaria* with 20 or more trees). In the other ‘specificity direction’, forty fungal species are capable of forming mycorrhizas with pine. Ectomycorrhizal fungi depend on the host for the bulk of their carbon. Only a few of them can utilise cellulose and lignin as saprotrophs. The fungus provides enhanced mineral ion uptake to the plant, particularly phosphate and ammonium ions. Fungi efficiently utilise organic compounds in the soil containing nitrogen (polypeptides) and phosphate (nucleic acids); the plant can't do this for itself. Most plants, pines especially, fail to grow or grow only poorly when they lack their ectomycorrhizas.

Lichens. These are usually associations between a fungus and a green alga, although the fungus can survive independently in nature (see Section 13.18). Some lichens contain both a cyanobacterium and a green alga (so they are tripartite associations), and other bacteria may also contribute to the community. There are about 13,500 species of fungi involved in lichens, representing about 20% of all known fungi. They are mainly Ascomycota with a few Basidiomycota. Lichens are extremely resistant to environmental extremes and are pioneer colonisers on rock faces, tree bark, stone walls, roofing tiles, etc., as well as early colonisers of terrestrial habitats (there are fossils from the Triassic Period).

Endophytes. Aside from pathogens or mycorrhizas some, maybe many, plants harbour other fungi that can affect their growth. These fungi are called ‘endophytes’ because they exist within plants (see [Section 13.19](#)). Endophytes are at least harmless and may be beneficial. A wide range of plants have now been examined and endophytes have been found in most of them, including aquatic plants, and red and brown algae; indeed, it has been said that:

“...All we know for certain is that endophytes are present in any healthy plant tissue!” (Sieber, 2007).

Many different fungi can be isolated from plants growing in their native habitat, representing all taxonomic groups of fungi. They can be present in most plant parts, but especially the leaves, which may be fully colonised by a variety of fungi within a few weeks of emergence.

Endophytes remain within the plant tissue, except that fruiting structures may emerge through the surface of the plant. Most endophytes are transmitted horizontally; that is, each plant is colonised by fungal propagules that arrive from the environment. The source of transmission has been determined in only a few cases. Propagules of endophytes have been found in the body of insect pests of the plant host, and at least two insect pathogens have been identified as endophytes, so insects may disperse some fungi from plant to plant.

Endophytes became a hot research topic when it was found that some which live entirely within grasses are responsible for the toxicity of some grasses to livestock. It's become evident that there are numerous endophytic fungi. A functional relation to the host is not always obvious.

Some may be simple passengers; living in the inner spaces of the plant in much the same way as they would live in any other moist, secluded place. But there are some intriguing stories, like the endophyte in oak leaves that remains dormant until an insect activates it by chewing on the leaf. The fungus responds to the insect attack by becoming a pathogen, killing a zone of the leaf surrounding the insect so the insect dies for lack of live leaf tissue to feed on. With the insect

pest dead, the fungus returns to being harmless and the oak's leaves can photosynthesise in peace!

Epiphytes. Fungi that live on the surfaces of plants are called epiphytes (see [Section 13.20](#)). Some show special adaptations to the plant surface, which is a challenging environment, being dry, waxy and exposed to direct sunlight. So, epiphytes are often coloured (particularly melanised) to protect them from UV radiation, and some can digest lipids sufficiently to use the waxy layer covering the leaf epidermis. The yeast form usually has a short life cycle, which enables yeast epiphytes to multiply even if favourable conditions last only a short time.

3.12 Chapter 3 References and further reading

- Aime, M.C., Matheny, P.B., Henk, D.A., Frieders, E.M., Nilsson, R.H., Piepenbring, M., McLaughlin, D.J., Szabo, L.J., Begerow, D., Sampaio, J.P., Bauer, R., Weiss, M., Oberwinkler, F. & Hibbett, D. (2006). An overview of the higher level classification of Pucciniomycotina based on combined analyses of nuclear large and small subunit rDNA sequences. *Mycologia*, **98**: 896-905. DOI: <https://doi.org/10.3852/mycologia.98.6.896>.
- Aime, M.C., Toome, M. & McLaughlin, D.J. (2014). Pucciniomycotina. In: *The Mycota Systematics and Evolution, VII part A*: (2nd ed.), (eds D.J. McLaughlin & J.W. Spatafora), pp. 271-294. Berlin, Heidelberg: Springer-Verlag. ISBN 978-3-642-55317-2. DOI: https://doi.org/10.1007/978-3-642-55318-9_10. [VIEW on Amazon](#).
- Anslan, S., Nilsson, R.H., Wurzbacher, C., Baldrian, P., Tedersoo, L. & Bahram, M. (2018) Great differences in performance and outcome of high-throughput sequencing data analysis platforms for fungal metabarcoding. *PeerJ Preprints* **6**: article e27019v2. DOI: <https://doi.org/10.7287/peerj.preprints.27019v2>.
- Badotti, F., de Oliveira, F.S., Garcia, C.F., Vaz, A.B.M., Fonseca, P.L.C., Nahum, L.A., Oliveira, G. & Góes-Neto, A. (2017). Effectiveness of ITS and sub-regions as DNA barcode markers for the identification of Basidiomycota (Fungi). *BMC Microbiology*, **17**: 42 (12 pages). DOI: <https://doi.org/10.1186/s12866-017-0958-x>.
- Beakes, G.W., Honda, D. & Thines, M. (2014). Systematics of the Straminipila: Labyrinthulomycota, Hyphochytriomycota, and Oomycota. In: *The Mycota Systematics and Evolution, VII part A*: (2nd ed.), (eds D.J. McLaughlin & J.W. Spatafora), pp 39-97. Berlin, Heidelberg: Springer-Verlag. ISBN 978-3-642-55317-2. DOI: https://doi.org/10.1007/978-3-642-55318-9_3. [VIEW on Amazon](#).
- Begerow, D., Schäfer, A.M., Kellner, R., Yurkov, A., Kemler, M., Oberwinkler, F. & Bauer, R. (2014). Ustilaginomycotina. In: *The Mycota Systematics and Evolution, VII part A*: (2nd ed.), (eds D.J. McLaughlin & J.W. Spatafora), pp. 295-329. Berlin, Heidelberg: Springer-Verlag. ISBN 978-3-642-55317-2. DOI: https://doi.org/10.1007/978-3-642-55318-9_11. [VIEW on Amazon](#).
- Begerow, D., Stoll, M. & Bauer, R. (2006). A phylogenetic hypothesis of Ustilaginomycotina based on multiple gene analyses and morphological data. *Mycologia*, **98**: 906-916. DOI: <https://doi.org/10.3852/mycologia.98.6.906>.
- Beimforde, C., Feldberg, K., Nylinder, S., Rikkinen, J., Tuovila, H., Dörfelt, H., Gube, M., Jackson, D.J., Reitner, J., Seyfullah, L.J. & Schmidt, A.R. (2014). Estimating the Phanerozoic history of the Ascomycota lineages: combining fossil and molecular data. *Molecular Phylogenetics and Evolution*, **78**: 386-398. DOI: <https://doi.org/10.1016/j.ympev.2014.04.024>.
- Benny, G.L., Humber, R.A. & Voigt, K. (2014). Zygomycetous fungi: phylum Entomophthoromycota and subphyla Kickxellomycotina, Mortierellomycotina, Mucoromycotina, and Zoopagomycotina. In: *The Mycota Systematics and Evolution, VII part A*: (2nd ed.), (eds D.J. McLaughlin & J.W. Spatafora), pp. 209-250. Berlin, Heidelberg: Springer-Verlag. ISBN 978-3-642-55317-2. DOI: https://doi.org/10.1007/978-3-642-55318-9_8. [VIEW on Amazon](#).
- Binder, M. & Hibbett, D.S. (2006). Molecular systematics and biological diversification of Boletales. *Mycologia*, **98**: 971-981. DOI: <https://doi.org/10.3852/mycologia.98.6.971>.
- Blackwell, M., Hibbett, D.S., Taylor, J.W. & Spatafora, J.W. (2006). Research Coordination Networks: a phylogeny for kingdom Fungi (Deep Hypha). *Mycologia*, **98**: 829-837. DOI: <https://doi.org/10.3852/mycologia.98.6.829>.