**Morphology**

Within the fungus kingdom, macrofungi are a group that form visible, often coloured, cup- or cap-like structures (scientifically known as 'fruiting bodies' or 'sporophores') that emerge from the soil. These fruiting bodies are where the spores are formed. The spores are small (1 - 100 µm), usually single-celled, reproductive structures able to tolerate unfavourable growing conditions (e.g. drought). Below the fruiting bodies, each fungus has a mass of hyphae, the typical branching thread-like filaments produced by most fungi. The mycelium is made up of the mass of these hyphae and is responsible for its growth. In the case of soil macrofungi, a large portion of the mycelium is hidden since it grows belowground. When environmental conditions become favourable, the fungus develops the fruiting body and spores that, once released, disperse through the air, or are carried by insects or water. [35, 36]

**Taxonomy**

Macrofungi, taxonomically belonging to the subkingdom Dikarya, are classified into two main phyla: Ascomycota and Basidiomycota. The Ascomycota, the largest group of macrofungi with more than 64,000 described species, are usually characterised by a cup-like or disc-like fruiting body (technically known as ascoma), where spores are formed within a typical structure, named the ‘ascus’. The Basidiomycota (more than 33,000 described species) mostly have a fruiting body (called basidioma) with an umbrella-shaped cap (known as pileus) borne on a stalk (known as a stipe) where the spores are produced. Other phyla that include soil fungi are Glomeromycota, Zygomycota, Chytridiomycota and Blastocladiomycota (see pages 40-41).

**Microhabitat**

Macrofungi are found in most terrestrial habitats, from woodlands to grasslands, but they are probably most diverse in forests. They need the right climatic conditions to form fruiting bodies; in particular, moisture to allow their spores to develop. Depending on their functions, they can be defined as saprotrophic, parasitic or mycorrhizal. The saprotrophic species play a key role in the degradation of decaying organic matter (i.e. soil, leaf litter and dead wood). The parasitic (see box on page 33) fungi are responsible for several diseases in plants (see box, next page), animals (mostly invertebrates) and other fungi. The mycorrhizal fungus form symbioses with plant roots, a mutualistic association that is beneficial to both partners (see box, page 33).

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**Fungi: edible, poisonous, bioluminescent and giant**

- There are several edible Basidiomycota and Ascomycota. Mushrooms, such as Boletus edulius and truffles (Tuber spp., see box on page 40), are consumed in many countries.
- Some Basidiomycota produce deadly toxins, such as amatoxin produced by Amanita phalloides. Thirty grammes of this fungus may kill a person; others, such as ganoderic acid and ganoderic acid, are considered medicinal fungi.
- Some Basidiomycota (e.g. species belonging to the genus Mycenoid) are bioluminescent.
- In Hainan Island (southern China) a giant specimen of Fomitiporia ellipsoidea (belonging to the group of bracket fungi, also included in Basidiomycota) was found to be 20 years old with an estimated volume of 409,000 - 525,000 cm³ and a weight of 400 - 500 kg. This represents the largest fungal fruiting body (both in volume and in weight) ever found.

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Diversity, abundance and biomass

Fungi are extremely abundant. Millions of species have been estimated, but only about 150 000 have been described. Macrofungi have about 90 000 known species. Together with bacteria, fungal hyphae constitute the largest portion of the microbial biomass of soil. Generally, fungal biomass is found to be greater than bacterial biomass in forest soils.

How a fungus is made

- A hypha is a long, branching filamentous structure. In most fungi, hyphae are the main mode of growth, and collectively form the mycelium.
- Hyphae grow at their tips. They can branch through the bifurcation of a growing tip, or through the emergence of a new tip from an established hypha.
- There are different types of hyphae:
  - septate, which have cross walls (called septa) at fairly regular intervals;
  - aspitate or coenocytic, which do not have septa.
- Hyphae can fuse to one another. This process is known as anastomosis.
- Yeasts are fungi that do not have hyphal structures. They are the only unicellular fungi.

Fungal hyphae have a branching structure that resembles plant roots. They allow the fungus to obtain nutrients from the soil (SA).

Soil-borne plant pathogenic fungi

- Soil-borne plant pathogenic fungi (SPPF) comprise organisms that are included in the Fungi kingdom and in the group of fungal-like organisms currently assigned to the Stramenopiles (see page 37). As pathogens, they are responsible for several plant diseases [37].
- Among fungi, both Ascomycota and Basidiomycota are represented. The major species belong to the genera Fusarium, Phoma, Sclerotinia and Verticillium within Ascomycota, and to Armillaria and Rhizoctonia within Basidiomycota.
- SPPF produce survival structures that may be as simple as cells, called chlamydospores, with a thick wall, or may be more complex like the sclerotia, typical of some fungi (e.g. Sclerotium, Sclerotinia and Botrytis).
- In addition to the survival function, aggregation of hyphae, called rhizomorphs since they resemble plant roots, is typical of species belonging to the fungal genus Armillaria and may play a crucial role in fungal spread through the soil, host infection and disease transmission.
- Soil type, pH, water content and temperature of the soil are among the major factors affecting the presence of the soil-borne plant pathogenic fungi.
- Fusarium species and Rhizoctonia solani, although commonly present in moist soils, tolerate lower water content levels. They also prefer warmer soils (25 - 35 °C).
- SPPF are grouped into two functional categories: soil inhabitants and soil invaders. The first category generally includes un specialised microbes that infect seedlings and young roots, while the second are disease agents that show a degree of host specificity. Seed decay, damping-off and root rot of seedlings are the most common diseases caused by soil-borne fungi.
- Soil-borne plant pathogenic fungi are reported worldwide in agricultural and forests soils.
- The number of plant pathogenic fungal species on Earth has been estimated to be as high as 270 000; however, the number of SPPF is largely unknown.
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- The number of plant pathogenic fungal species on Earth has been estimated to be as high as 270 000; however, the number of SPPF is largely unknown.
- The abundance of SPPF is generally measured as ‘inoculum density’, which is expressed as the mass, or the number, of spores per gramme of soil. Inoculum density has been reported as ranging from 100 to 100 000 spores per gramme of soil, depending on the species.
fungi are found in all terrestrial biomes and in association with most plant families. They are found with trees, shrubs, forbs, grasses and agricultural crops. Arbuscular mycorrhizas are abundant in tropical forests, grasslands, savannas, deserts and arable lands, and ectomycorrhizas dominate temperate and boreal forests. Ericaceous mycorrhizas are common in boreal forests and heathlands. Orchid mycorrhizas are essential to the survival of orchids throughout the world.

**Morphology**

Mycorrhizas are literally ‘fungus-roots’ created by symbiotic associations (see box, page 33) between plant roots and fungi. Mycorrhizal fungi form structures outside and inside plant roots. All types form extensive networks of microscopic hyphae that extend outwards from plant roots into the surrounding soil or leaf litter. Arbuscular mycorrhizas (AM), ericaceous mycorrhizas and orchid mycorrhizas are sometimes called ‘endomycorrhizas’ because the fungi form distinctive structures between and inside the cortical cells of plant roots, but do not generally cause obvious changes in root morphology. By contrast, ectomycorrhizas (EcM) often cause distinct changes to roots that can be observed without a microscope. Reproductive structures also differ among mycorrhizal types. Arbuscular mycorrhizal fungi reproduce with microscopic vesicles and arbuscules. This phylum contains 17 genera and 240 species distributed in nine families and four orders. Common genera include Glomus, Rhizophaghus, Scierocyistis, Gigaspora, Scutellillospora, Cetraspora and Acaulospora. Glomeromycota produce abundant hyphae and spores in soils. In grasslands and agricultural lands, these fungi comprise an estimated 20–30% of soil microbial biomass, making arbuscular mycorrhizal fungi among the most abundant organisms in many soils.

**Glomeromycota**

Fungi in the phylum Glomeromycota form arbuscular mycorrhizal symbioses with the majority of plant species, by colonising the root cortex (see box, page 43) and forming an extensive mycelium, vesicles and arbuscules. This phylum contains 17 genera and 240 species distributed in nine families and four orders. Common genera include Glomus, Rhizophaghus, Scierocyistis, Gigaspora, Scutellillospora, Cetraspora and Acaulospora. Glomeromycota produce abundant hyphae and spores in soils. In grasslands and agricultural lands, these fungi comprise an estimated 20–30% of soil microbial biomass, making arbuscular mycorrhizal fungi among the most abundant organisms in many soils.

**Ectomycorrhizas**

Approximately 6000 fungal species establish ectomycorrhizal associations with many species of trees and woody plants. At least 20 families of Basidiomycota (e.g. Amanitaceae, Russulaceae, Boletaceae) and seven families of Ascomycota (e.g. Pezizaceae, Tuberaeaceae) are known to establish ectomycorrhizas. The biomass of ectomycorrhizal fungi mycelia has been estimated to range from 700 to 900 kg per hectare, and 20–40% of an ectomycorrhizal root weight is due to the fungus. Sclerocystis coremioides. (SLS, MBR)

**Diamonds of cuisine**

- Mycorrhizas are among the most widespread symbionts in the world. They are found in more than 80% of all plant species and 92% of all plant families.
- Mycorrhizas can be managed as biofertilisers as they increase plant nutrient uptake (see pages 98–99).

- Many species of ectomycorrhizal fungi are important culinary mushrooms and truffles.
- Arbuscular mycorrhizal fungi reproduce through spores that can have various dimensions and colours: (a) a broken spore of Cetraspora pellucida, (b) the tiny spores of Gigasporae rosea, and (c) structures producing spores (sporocarps) of the fungus Sclerocystis coremioides associated with mosses. (SLS, MBR)

- Some of the fungi that are found in woodlands are ectomycorrhizal: (a) Boletus bicolour, and (b) Scleroderma aurantium. (MW)

- Short lateral roots of a beech tree colonised by a white layer of hyphae of the ectomycorrhizal fungus Xeromastum pruinatum. (MB)

- Orchid mycorrhizas are important culinary mushrooms and truffles. Tuber magnatum (Tuberaceae), known as the diamond of cuisine, is a prized ingredient for cooking. (AO)

- Plants belonging to Ericaceae, like heather (Calluna vulgaris) and orchidaceae, may form specific fungal symbioses called ericaceous and orchid mycorrhizas, respectively. (RH)
Fungi – Other fungi

Zygomycota

A unique feature of the Zygomycota is the zygospore, which is formed within a structure called the zygosporangium after the fusion of specialised hyphae called gametangia during sexual reproduction [35, 36]. The mature zygospore is often thick-walled and undergoes a dormant period before germination. Nevertheless, asexual reproduction occurs much more frequently than sexual reproduction in the zygomycetes. During asexual reproduction, hyphae grow over the surface of the material on which the fungus feeds and produce clumps of erect stalks, called sporangiophores. The tips of the sporangiophores form spore-producing structures, the sporangia. Thin-walled spores are produced within the sporangia and are thus shed above the substrate, in a position where they may be dispersed by wind or water, allowing the fungus to spread and colonise new substrates quickly and efficiently. The Zygomycota include two main classes: Zygomycetes (that comprise Mucorales, the most studied order) and Trichomycetes. More than 1,000 species have been described so far. Zygomycetes are commonly decomposers, symbiots or parasites (see box, page 33) in terrestrial habitats. For example, members of the Mucorales are easily isolated from soil, humus and dung. Furthermore, some Mucorales are used to ferment foods and produce important industrial products, such as lactic acid and rennin (used to make cheese). Conversely, some species have a negative economic impact by causing storage rot in fruits. Trichomycetes are obligate associates of arthropods, including insects and millipedes. The host may be an adult or larva, in terrestrial or aquatic habitats. The fungi are usually found attached to the gut lining of the host. The precise relationship is difficult to determine in most cases; however, they often seem to be commensals, doing little or no harm to their hosts, with the fungus gaining nutrients from the gut of the host. Some zygomycota can also be pathogens of animals, plants, amoebae and, especially, other fungi. Of the more than 1,000 species of described Zygomycota, the majority are found in soil, with some genera (Mucor, Mortierella and Rhizopus) that are extremely common and reported in almost all surveys of soil fungi.

Chytridiomycota

Chytridiomycota (chytrids) are characterised by their asexual state, a motile (capable of moving) zoospore with a single whiplash flagellum oriented and located posteriorly [35, 36]. Zoospores are released through an opening in the wall, and vectors of plant viruses such as Chytridiomycota are the only fungi producing this type of spore. (GB)

The hat thrower

- A unique spore dispersal strategy for the Zygomyctota of the order Mucorales is exhibited by the dung fungus of the genus Pilobolus.
- Its name literally means ‘the hat thrower’. When spores are ready, the turgor pressure within the vesicle beyond the sporangium (spore-producing structure) builds to a sufficient level that allows the sporangium to be launched. The entire black sporangium is explosively shot off up to distances of several metres.
- For an organism less than 1 cm tall, this involves acceleration from 0 to 20 km/h in only 2 µs, equivalent to a human being launched at 100 times the speed of sound (more than 120,000 km/h).

Blastocladiomycota

The Blastocladiomycota (blastoclads) are one of the currently recognised phyla within the Fungi kingdom. Blastoclads were originally the order Blastocladiales within the phylum Chytridiomycota, until molecular and zoospore structural characters were used to demonstrate that it was a group separated from chytrids. Similar to Chytridiomycota, Blastocladiomycota produce zoospores to colonise new substrates. Furthermore, members of Blastocladiomycota are capable of decomposing complex materials, such as cellulose and chitin. Of economic importance is Physochrysis mydya, a parasite of maize and the causal agent of brown spot disease. There is a blastoclad, Sorochrysis milnesiosphora, that is a tadpole parasite (see page 44). However, the best known species, belonging to the genus Colomyxoa, are nematode parasites. As they are mainly known to be aquatic fungi, a reliable evaluation of their abundance in soil is not available.

Chytridiomycota and Blastocladiomycota are responsible for some plant diseases: (a) potato wart disease caused by the chytrid Synchytrium endobioticum and (b) brown spot disease brought by the blastoclad Physochrysis mydya on maize (SK, mm, SPR).