Plant-fungal interactions

Ecology of Fungi

Fungi play a crucial role in the balance of ecosystems. They colonize most habitats on Earth, preferring dark, moist conditions. They can thrive in seemingly hostile environments, such as the tundra, thanks to a most successful symbiosis with photosynthetic organisms like algae to produce lichens. Fungi are not obvious in the way large animals or tall trees appear. Yet, like bacteria, they are the major decomposers of nature. With their versatile metabolism, fungi break down organic matter, which would not otherwise be recycled.

Fungi play pivotal roles in all terrestrial environments. They are a major component of global biodiversity and control the rates of key ecosystem processes. Fungi are perhaps best known for their role as decomposers, dominating the decomposition of plant parts, and particularly of lignified cellulose. They produce a wide range of extracellular enzymes that break down complex organic polymers into simpler forms that can be taken up by the fungi or by other organisms. This process is an essential step in the carbon cycle; without it, plant detritus would quickly tie up available carbon and mineral nutrients. It is not surprising, therefore, that eliminating fungi results in a significant reduction in both carbon and nitrogen depletion from litter. In fact, fungal hyphae often account for the greatest fraction of soil biomass and can reach lengths of hundreds to thousands of meters per gram of soil.

In addition to their central roles in carbon and nutrient cycling, fungi are also a major component of terrestrial food webs. Fungal mycelia serve as the primary carbon source in a number of soil food webs, and fungal fruiting bodies can serve as a significant food source for large vertebrates, including humans. Some fungi can also act as predators: Perhaps the best-known examples are nematode-trapping fungi, but fungi also trap, poison, or parasitize and feed on other groups of soil invertebrates, including tartegrades, collembola, copepods, and rotifers. Interestingly, fungi express these behaviors in nitrogen-poor environments, suggesting that they seek nitrogen rather than carbon from their predation.

Habitats of fungi

Although fungi are primarily associated with humid and cool environments that provide a supply of organic matter, they colonize a surprising diversity of habitats, from seawater to human skin and mucous membranes. Chytrids are found primarily in aquatic environments. Other fungi, such as *Coccidioides immitis*, which causes pneumonia when its spores are inhaled, thrive in the dry and sandy soil of the southwestern United States. Fungi that parasitize coral reefs live in the ocean. However, most members of the Kingdom Fungi grow on the forest floor, where the dark and damp environment is rich in decaying debris from plants and animals. In these environments, fungi play a major role as decomposers and recyclers, making it possible for members of the other kingdoms to be supplied with nutrients and live.

Fungi as Decomposers and recyclers

The food web would be incomplete without organisms that decompose organic matter. Some elements—such as nitrogen and phosphorus—are required in large quantities by biological systems, and yet are not abundant in the environment. The action of fungi releases these elements from decaying matter, making them available to other living organisms. Trace elements present in low amounts in many habitats are essential for growth, and would remain tied up in rotting organic matter if fungi and bacteria did not return them to the environment via their metabolic activity.

The ability of fungi to degrade many large and insoluble molecules is due to their mode of nutrition. As seen earlier, digestion precedes ingestion. Fungi produce a variety of exoenzymes to digest nutrients. The enzymes are either released into the substrate or remain bound to the outside of the fungal cell wall. Large molecules are broken down into small molecules, which are transported into the cell by a system of protein carriers embedded in the cell membrane. Because the movement of small molecules and enzymes is dependent on the presence of water, active growth depends on a relatively high percentage of moisture in the environment.

As saprobes, fungi help maintain a sustainable ecosystem for the animals and plants that share the same habitat. In addition to replenishing (reloading) the environment with nutrients, fungi interact directly with other organisms in beneficial, and sometimes damaging, ways.

Mutualistic Relationships

Symbiosis is the ecological interaction between two organisms that live together. The definition does not describe the quality of the interaction. When both members of the association benefit, the symbiotic relationship is called mutualistic. Fungi form mutualistic associations with many types of organisms, including cyanobacteria, algae, plants, and animals.

Fungus/Plant Mutualism

One of the most remarkable associations between fungi and plants is the establishment of mycorrhizae. Mycorrhiza, which comes from the Greek words myco meaning fungus and rhizo meaning root, refers to the association between vascular plant roots and their symbiotic fungi. Somewhere between 80 and 90 percent of all plant species have mycorrhizal partners. In a mycorrhizal association, the fungal mycelia use their extensive network of hyphae and large surface area in contact with the soil to channel water and minerals from the soil into the plant. In exchange, the plant supplies the products of photosynthesis to fuel the metabolism of the fungus.

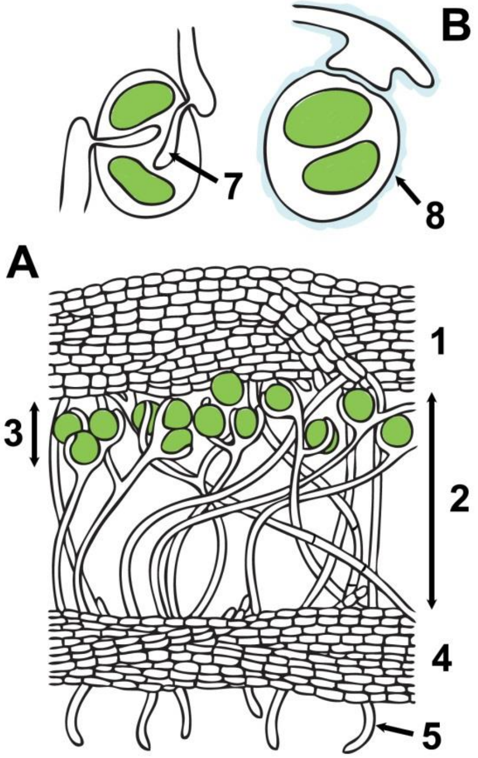
There are a number of types of mycorrhizae. Ectomycorrhizae ("outside" mycorrhiza) depend on fungi enveloping the roots in a sheath (called a mantle) and a Hartig net of hyphae that extends into the roots between cells. The fungal partner can belong to the Ascomycota, Basidiomycota or Zygomycota. In a second type, the Glomeromycete fungi form vesicular–arbuscular interactions with arbuscular mycorrhiza (sometimes called endomycorrhizae). In these mycorrhiza, the fungi form arbuscules that penetrate root cells and are the site of the metabolic exchanges between the fungus and the host plant. The arbuscules (from the Latin for little trees) have a shrub-like appearance.

Orchids rely on a third type of mycorrhiza. Orchids are epiphytes that form small seeds without much storage to sustain germination and growth. Their seeds will not germinate without a mycorrhizal partner (usually a Basidiomycete). After nutrients in the seed are depleted, fungal symbionts support the growth of the orchid by providing necessary carbohydrates and minerals. Some orchids continue to be mycorrhizal throughout their lifecycle.

If symbiotic fungi are absent from the soil, what impact do you think this would have on plant growth? Without mycorrhiza, plants cannot absorb adequate nutrients, which stunts their growth. Addition of fungal spores to sterile soil can alleviate this problem.

Lichens

The lichen is special association of a mycobiont (fungus) and a photobiont (alga or cyanobacterium) forming a stable self-sustaining thallus. It should be emphasized that lichens are rarely formed by a single mycobiont and a single photobiont species. The biomass of lichens is dominated by the mycobiont and lichens are identified and named according to the fungal partner. The photobiont is almost a slave of the mycobiont, it cannot reproduce sexually or spread on its own and even its cell cycle is completely controlled by the mycobiont. The photobiont can be isolated and maintained alone while the mycobiont generally cannot be kept in pure isolate. There are approximately 100 photobiont species, the majority is green algae (85%) the others are cyanobacteria (15%). On the other hand there are 14 000 – 15 000 lichen forming fungal species, almost all belonging to Ascomycota (Pezizomycotina), while there are approximately 20 lichen forming basidiomycetes. The mycobionts can reproduce sexually and spread on their own but when such reproduction happens, only the fungal partners disperse.



Schematic structure of a lichen thallus. A: Cross section of the thallus. B: Main types of the algal-fungal interaction. 1: upper cortex; 2: medulla; 3: layer of algae; 4: lower cortex; 5: rhizina; 6: algal cell; 7: haustorium; 8: hydrophobic sheath.

Lichens display a range of colors and textures and can survive in the most unusual and hostile habitats. They cover rocks, gravestones, tree bark, and the ground in the tundra where plant roots cannot penetrate. Lichens can survive extended periods of drought, when they become completely desiccated, and then rapidly become active once water is available again.

Lichens are not a single organism, but rather an example of a mutualism, in which a fungus (usually a member of the Ascomycota or Basidiomycota phyla) lives in close contact with a photosynthetic organism (a eukaryotic alga or a prokaryotic cyanobacterium). Generally, neither the fungus nor the photosynthetic organism can survive alone outside of the symbiotic relationship. The body of a lichen, referred to as a thallus, is formed of hyphae wrapped around the photosynthetic partner. The photosynthetic organism provides carbon and energy in the form of carbohydrates. Some cyanobacteria fix nitrogen from the atmosphere, contributing nitrogenous compounds to the association. In return, the fungus supplies minerals and protection from dryness and excessive light by encasing the algae in its mycelium. The fungus also attaches the symbiotic organism to the substrate.

The thallus of lichens grows very slowly, expanding its diameter a few millimeters per year. Both the fungus and the alga participate in the formation of dispersal units for reproduction. Lichens produce soredia, clusters of algal cells surrounded by mycelia. Soredia are dispersed by wind and water and form new lichens.

Lichens are extremely sensitive to air pollution, especially to abnormal levels of nitrogen and sulfur. The U.S. Forest Service and National Park Service can monitor air quality by measuring the relative abundance and health of the lichen population in an area. Lichens fulfill many ecological roles. Caribou and reindeer eat lichens, and they provide cover for small invertebrates that hide in the mycelium. In the production of textiles, weavers used lichens to dye wool for many centuries until the advent of synthetic dyes.

Fungus/Animal Mutualism

Fungi have evolved mutualisms with numerous insects in Phylum Arthropoda: jointed, legged invertebrates. Arthropods depend on the fungus for protection from predators and pathogens, while the fungus obtains nutrients and a way to disseminate spores into new environments. The association between species of Basidiomycota and scale insects is one example. The fungal mycelium covers and protects the insect colonies. The scale insects foster a flow of nutrients from the parasitized plant to the fungus. In a second example, leaf-cutting ants of Central and South America literally farm fungi. They cut disks of leaves from plants and pile them up in gardens. Fungi are cultivated in these disk gardens, digesting the cellulose in the leaves that the ants cannot break down. Once smaller sugar molecules are produced and consumed by the fungi, the fungi in turn become a meal for the ants. The insects also patrol their garden, preying on competing fungi. Both ants and fungi benefit from the association. The fungus receives a steady supply of leaves and freedom from competition, while the ants feed on the fungi they cultivate.

Fungivores

Animal dispersal is important for some fungi because an animal may carry spores considerable distances from the source. Fungal spores are rarely completely degraded in the gastrointestinal tract of an animal, and many are able to germinate when they are passed in the feces. Some dung fungi actually require passage through the digestive system of herbivores to complete their lifecycle. The black truffle—a prized gourmet delicacy—is the fruiting body of an underground mushroom. Almost all truffles are ectomycorrhizal, and are usually found in close association with trees. Animals eat truffles and disperse the spores. In Italy and France, truffle hunters use female pigs to sniff out truffles. Female pigs are attracted to truffles because the fungus releases a volatile compound closely related to a pheromone produced by male pigs.

Plant-fungal interactions

Mycorrhizae

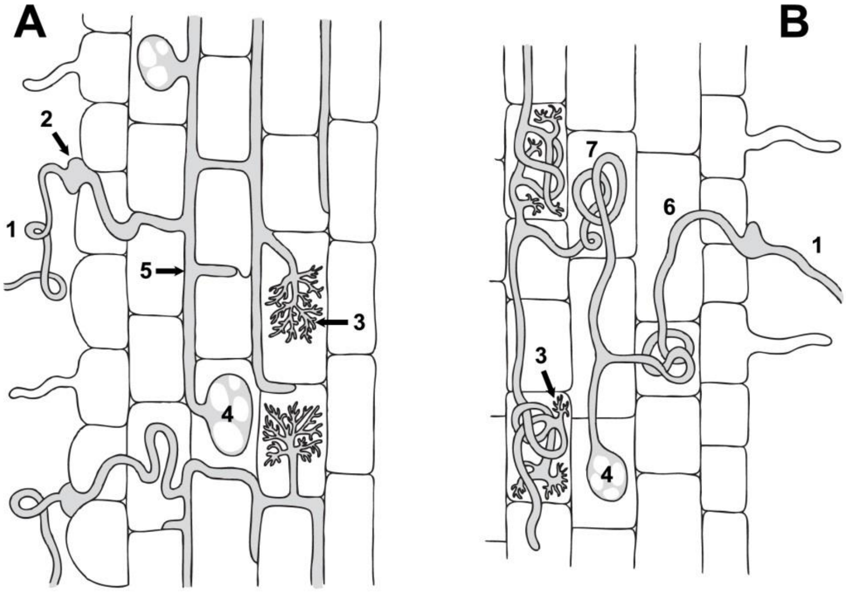
Most land plants live in mutualistic symbiosis with fungi in their roots: this structural, functional unit is called mycorrhiza. Mycorrhizae are “dual organs of absorption formed when symbiotic fungi inhabit healthy absorbing organs (roots, rhizomes or thalli) of most terrestrial plants and many aquatics and epiphytes.” (Trappe). Different types of mycorrhizae can be distinguished according to the plant and fungal partners and structural characteristics. Important distinctions are whether the hyphae colonizing the plant grow intracellularly (endomycorrhizae) or only intercellularly in the plant tissue (ectomycorrhizae) or both (ectendomycorrhizae). The most common types are arbuscular mycorrhizae (AM) and ectomycorrhizae (ECM).

ECM are formed with fungi belonging to Asco- and Basidiomycota or a few zygomycetes, many of which produce macroscopic sporocarps. ECM plants are mostly woody plants, trees and shrubs. ECM have three main functional-anatomical parts: (i) special intraradical hyphal structures termed the Hartig-net formed in the intercellular spaces, (ii) the fungal mantle covering the root surface and (iii) the hyphal structures emanating (arising) from the mantle surface (e.g. cystidia, hyphae, rhizomorphs).

The most prevalent mycorrhiza type is the arbuscular mycorrhiza (AM). There are AM forming plants in all main terrestrial plant groups, on the other hand, all AM fungi exclusively belong to the phylum Glomeromycota. These fungi are obligate biotrophic endocellular symbionts. Their name refers to the special, multi-branched intracellular structure, the arbusculum resembling a small tree. Because of the high density of fine branches on the arbuscules, the surface of the plant cell membrane is multiplied, owing to a special membrane (periarbuscular membrane, PAM) that surrounds the arbuscules and contains special transporters and aquaporins etc. Arbuscules are ephemeral (transient) structures, they function for a couple of days, collapse and new arbuscules arise.

Prior to the colonization of the roots, the plant and fungal partners stimulate each other and their mutual recognition plays a crucial role in the success of the establishment of the interaction. The roots excrete strigolactons which stimulate the growth and branching of AMF hyphae and also the germination of AMF chlamydospores. The fungi produce “myc-factors” (lipochitooligosaccharides) which initiate processes necessary for the successful colonization in the plants. The hyphae run on the surface of the roots and develop a swollen structure (appressorium or hyphopodium) from which a hypha grows into the root. The plant cells undergo a complete reorganization when the AMF hypha enters and grows through the cell, this special organization is called the pre-penetration apparatus (PPA). The endoplasmic reticulum (ER) forms a tube like structure which assigns the direction of the hyphal growth. The plant cell nucleus also moves to the penetration site and migrates in front of the growing hyphae through the cell. The intracellular growth of the hyphae needs continuous membrane development, so there is an intensive production of vesicules fusing into the plant cell membrane surrounding the hyphae. This process is controlled by the exocytosis regulation.

The arbuscules, albeit different, show several similarities with the intracellular haustoria of endocellular biotrophic pathogens. The AMF could also develop structures named vesicles in the roots, mainly in the intercellular spaces. The main function of these vesicles is storage. Their appearance could be seasonal and some AMF species do not form vesicles at all. Two main types of AM anatomy can be distinguished, of course, with several intermediate forms as well (figure).



Two main types of root colonization in arbuscular mycorrhizae (AM). A: Arum-type B: Paris-type. 1: extraradical hyphae; 2: appressorium/hyphopodium; 3: arbusculum; 4: vesiculum; 5: intercellular hyphae; 6: intracellular hyphae; 7: hyphal coils.

In the Arum-type the fungal hyphae grow intercellularly and well-developed arbuscules are formed on branches entering the neighboring cells. In the Paris-type the hyphae grow intracellularly, develop hyphal coils in some cortical cells and smaller arbuscules develop on these coils. Both the fungal and the plant partner influence the type developed.

Endophytic fungi

Endophytic fungi spend at least one phase of their life cycle colonizing plant tissues inter- or intracellularly causing no symptoms of tissue damage. This definition is not a phylogenetic term, endophytic fungi can thus be found in several fungal groups. The best known endophytes (C-endophytes) belong to the family Clavicipitaceae (ergot family, Pezizomycotina, Ascomycota) and colonize aboveground tissues of grasses. The rare intercalary (emergent) growing of hyphae was found in these endophytes. Fungal endophytes can be grouped according to several aspects, e.g. plant tissues colonized, systemic, non-systemic spread in plant. A form-group of root-colonizing endophytic fungi is the so called dark septate endophytes (DSE) that belong to a few orders of the phylum Ascomycota. DSE fungi are septate and generally have melanized hyphae that colonize the cortical cells and intercellular regions of roots and form a densely septated intracellular structure called microsclerotia. Although C-endophytes have been intensively studied, our general knowledge on the function and diversity of endophytes is limited especially if compared to some types of mycorrhizae.

See more in: https://cals.arizona.edu/mycoherb/arnoldlab/Rodriguez.pdf

Plant pathogenic fungi

Plant pathogenic fungi are spread through all fungal groups and their interaction with plants is diverse, with few common structural characteristics. Biotrophic pathogens need living host cells/tissues to exhaust while nectrotrophic pathogens first kill the host tissues to be able to take the nutrients from the host. Accordingly, there are fundamental differences between the molecular mechanisms, possible defense reactions of those two types. E.g. programmed cell death (PCD), which helps necrotrophic fungi, could protect the spread of biotrophic pathogens.

The fungal binding on the host surface is a fundamental step of the successful infection. The chemical and physical characteristics of this surface have fundamental effects on the adhesion and germination of fungal propagules on the plant, e.g. hydrophobic surfaces, like the outermost cuticle layer of the plants, could induce spore germination. Similarly to AMF, several plant pathogenic fungi develop appressoria at the entry points. Plant pathogenic fungi can have different mechanisms to enter the plant. Pressure is the main driving force of the entry of the rice pathogen *Magnaporthe grisea*. The changes of the wall and chemical content of the appressorium of the fungus induce osmotic water influx which produces enormous pressure pushing the hypha across the plant cell wall. Other pathogens use enzymes or enzymes and pressure together to enter the host plants. In stem rust, the hyphae grow on the leaf surface till they reach a guard cell of a stoma and the growing on the guard cell induces the turning downwards of the hyphae which therefore grows through the stoma and colonize the plant. Biotrophic endocellular parasites can develop special intracellular structures called haustoria through which they take the nutrients up from host cells.

References:

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