MASARYK UNIVERSITY, FACULTY OF SCIENCE

DEPARTMENT OF BOTANY AND ZOOLOGY

FUNGAL ECOLOGY

(sometimes with special regard to macromycetes)

Fungi and their environment • Life strategies and interactions of fungi • Ecological groups of fungi, saprotrophs (terrestrial fungi, litter and plant debris, wood substrate, etc.) • Fungal symbioses (ectomycorrhiza, endomycorrhiza, endophytism, lichenism, bacteria, animal relationships) • Parasitism (parasites of animals and fungi, phytopathogenic fungi, types of parasitic relations) • Fungi in various habitats (coniferous forests, broadleaf forests, birch stands and non-forest habitats, fungal communities) • Fungal dispersal and distribution • Threat and protection of fungi

(the study material has not been corrected by native speaker)

FUNGAL COMMUNITIES

The just-completed overview introduced us to some species of macromycetes which can be found in various habitats of the Czech Republic.
In addition to this overview, let us say a few words not from the point of view of inhabited habitats, but about fungal communities on/in various substrates and environments, this time also with regard to microscopic fungi.

Historical development, bound to habitat conditions, leads to formation of **communities of organisms** (it is difficult to talk about fungal communities only, although these words are used here for simplicity – there are interactions with other living organisms too in all habitats). Different communities develop on different types of substrates and different ones are also formed in different successional stages. Compared to communities of higher plants, cryptogams colonise their substrates more easily and quickly (e.g. after disturbance); on the other hand, a well-established community can hardly be displaced by another one.

Autotrophic organisms are usually included in the phytosociological system of community classification – in addition to vascular plants, bryophytes and lichens are also included.
Some authors also apply an approach using the coenological properties of fungi and describe **mycocoenoses** equally to phytocoenoses and zoocoenoses => together it is possible to define a biocoenosis or, as a whole, a biogeocoenosis.

Fungi are often affecting phytocoenoses, especially if soil micromycetes or mycorrhizal fungi are also taken into account. (From this point of view, analysis of the soil horizon A is of the greatest importance.) There are species, which are frequent edifiers in communities, but the communities cannot be based on them due to their wide ecological amplitude – even here, diagnostic species with high fidelity and constancy are decisive. (For example, rusts have a significant indicator ability, especially dioecious species that alternate hosts, which must therefore occur together in the same community or in neighbouring communities.) But what applies to mycocoenology as well as to phytocoenology: the vegetation must be homogeneous, excluding transitional stands and ecotones.

It is difficult to study all fungi in the locality, a survey is mostly limited to study of macromycetes. A certain disadvantage is that it is not possible to monitor the vegetative component in the field (although in principle it is the most important), but only occurrence of fruitbodies, the formation of which strongly depends on weather (e.g. summer fructification in one year, while autumn in the next one). For fungi, coverage is not determined – the number of fruitbodies and their sociability (individual or clustered) is taken into account.

Should fungi growing topically in the same place, but on different substrates, be included in the same community? The answer is yes – in the case of higher plants, we also do not exclude species with a different nutrition (mycorrhizal or parasitic) from the relevé. Different fungal species use a specific space for their growth – here, too, stratification into particular layers can be applied, where communities of fungi belong to certain synusia.

Lignicolous fungi

Wood is a good source of carbon, but not a sufficient source of nitrogen and phosphorus – fungi for which wood is a „home“ substrate help themselves by forming mycorrhizae, parasitism and even „hunting“ nematodes.

Considering that wood is usually not a „continuous“ substrate in nature, there is a need for wood fungi to move from one place, where they have already exhausted nutrients, to another place through a „barren“ part of the substrate. For this purpose, mycelial cords or rhizomorphs are formed.

There are many representatives of this group in our country; parasitic (*Armillaria*, some polypores) or saprotrophic basidiomycetes (various, even „domesticated“ species – e.g. *Serpula lacrymans*), forming fruitbodies on the wood surface, have already been mentioned. Other fungi live completely inside the wood mass, not growing on the surface even for the purpose of creating reproductive structures – e.g. *Ceratocystis*, endophytic fungi.

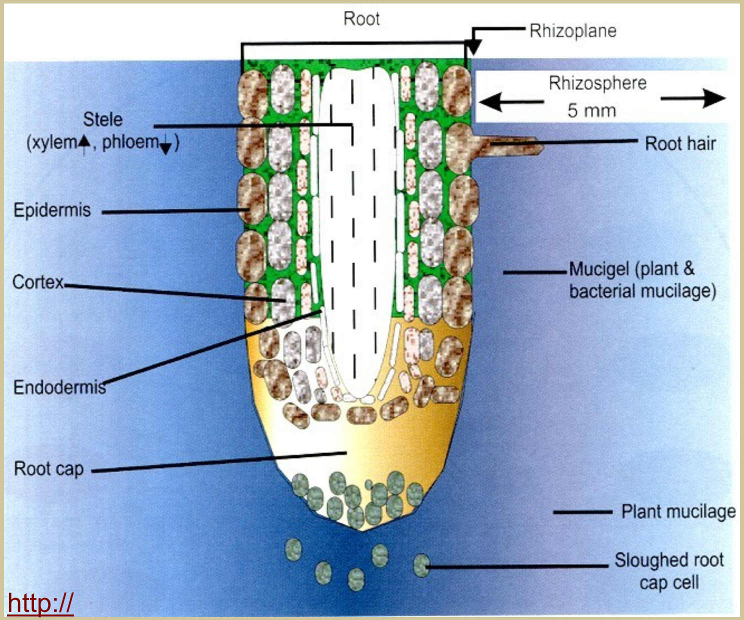
/*Since lignicolous fungi have already been discussed in detail in the chapters on saprotrophic and parasitic fungi, they will not be discussed further here.*/

Soil fungi

The soil environment is quite stable in terms of temperature and humidity; practically all known groups of fungi and fungus-like organisms grow here: *Basidiomycota* as mycelium, *Ascomycota* (*Chaetomium*), *Deuteromycota* (*Aspergillus, Trichoderma*), *Glomeromycota*, *Mucoromycota* (*Zygorhynchus, Absidia*), to a lesser extent *Chytridiomycota*, *Oomycota* and *Myxomycota*.

According to the life strategy, we can distinguish three groups of soil fungi:
– „R“ strategists growing rapidly in wet conditions using rain-flushed nutrients from above-ground biomass (leaf exudates, remnants of organisms); this group includes the mentioned *Mucoromycota, Ascomycota* and their anamorphs (*Deuteromycota*), we mostly find these fungi by flushing the soil;
– mykorrhizal fungi (mostly *Glomeromycota*) have a stable carbon source in the partner plant; they can also excrete simple organic compounds => source of carbon for other microorganisms;
– the third group is represented by fungi which survive for a long time in hyphal form (e.g. *Rhizoctonia*), some not sporulating (their occurrence in the soil is thus difficult to detect); they usually grow slowly, gradually degrading organic remnants.

The soil is also a reservoir of persistent stages – in addition to spores, we also find sclerotia here. Soil fungi often live most of their lives in the form of these stages, and the development and growth of mycelia only appears under suitable conditions – sufficient water and nutrients.



http://biology.kenyon.edu/courses/biol272/agriculture/agriculture.htm

The soil itself is a very oligotrophic substrate, in which remnants of organisms are the sources of organic nutrition.

Most nutrients are primarily found in the **rhizoplane** (space immediately at the root surface) or **rhizosphere** (the area around the root where organisms are affected by the root activity), enriched with root exudates; here the humidity is optimal too.

The cells of the growing root (root tip, root hairs) release polysaccharides and other compounds (proteins, organic acids) into the environment, forming a so-called mucigel (apparently it plays the role of a lubricant when the root makes its way through the soil). These exudates are a source of nutrients for many organisms (fungi, bacteria and animals); however, they can act as growth inhibitors on some species and on the contrary stimulate others (*Sclerotinia cepivora*, an onion parasite, has dormant sclerotia until they are affected by bulb root exudates).

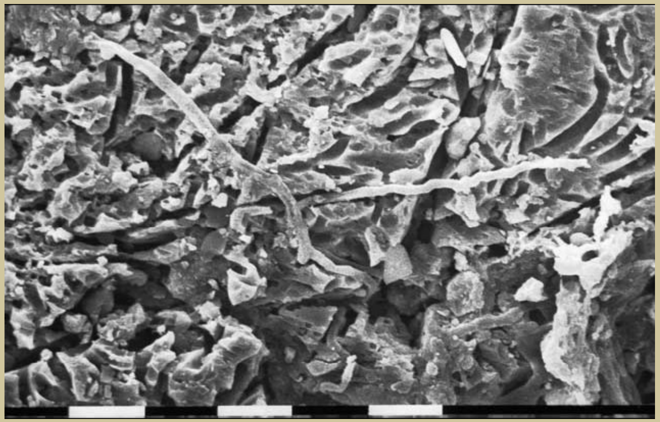
The phenomenon of mycostasis is applied – inhibition of spore germination, which appears in soils poor in nutrients or heavily flushshed with water (which entails rapid leaching of substances). Mycostasis can also be caused by the action of certain microorganisms (production of antibiotics, but also other compounds inhibiting the growth of fungi – CO_2, ethylene, ammonia).

In addition to decomposition of organic substances, which mainly returns carbon, nitrogen, phosphorus to the nutrient cycle in soil, fungi also participate in bedrock **weathering**, during which they release mineral elements, calcium, magnesium, potassium or trace elements into the soil – this process is of fundamental importance for the soil colonisation by plants. The most susceptible to weathering are sandstone, limestone, marble or feldspar; a big unknown is possible influence of human pollution.

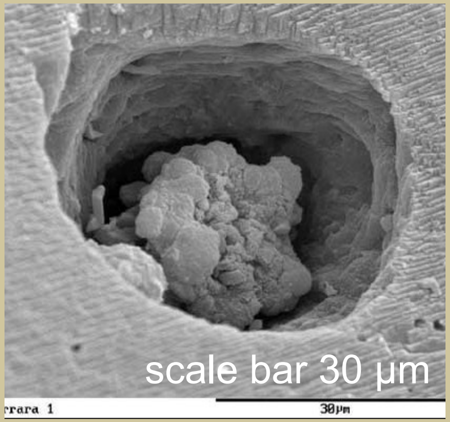
Pinus sylvestris seedling colonised by *Hebeloma crustuliniforme*; feld-spar is more colonised than quartz.

Mineral particles from the bedrock in the soil are mainly colonised by the mycelium of mycorrhizal fungi, to a much lesser extent by soil saprotrophs (only if they have enough carbon, this is an energy-intensive process) and wood-decaying fungi (they excrete a large amount of substances potentially suitable for weathering, but little comes into contact with rock or mineral particles). Although these are extremely slow processes, the impact of which must be assessed within geological history (AM fungi appeared before lichens, but lichens are more influential when they inhabit rock surfaces directly), mycorrhizal fungi are currently estimated to be responsible for 2% of weathering ("tunneling" :o) and proportion of lichens and fungi on the rocks (mainly dark yeast-like and microcolonial fungi) is unknown...

The weathering mechanism is, first of all, mechanical – hyphal growth in fissures, pores, cracks (thigmotropic growth), where the mycelium dries/moistens and melting/freezing applies (only the fungi cannot do it, but they accelerate the weathering initiated by physical factors).



Feldspar crystal with grooves probably of fungal origin + 2 hyphae (bar 10 µm).



Fungal colony in a hole it etched into the marble.

Hoffland et al. 2004; http://home.hiroshima-u.ac.jp/er/ZR5_SH_08.html

Another mechanism is chemical – mainly the hyphal tips intensively excrete low-molar organic acids (oxalic, malic, citric), siderophores (peptides containing iron), anions, HCO_3^- or lichen acids (on the other hand, the lichen thallus can protect the substrate from temperature fluctuations, damage by wind, humidity /surface „patina“/, it always depends on the community of organisms, inorganic material or atmospheric conditions).

It is still not entirely clear what leads fungi to disrupt mineral substrates. It can only be a side effect of excreting the mentioned substances (when the fungi do not need a lot of inorganic elements, it can be assumed that they could only obtain phosphorus in this way); on the other hand, in the case of mycorrhizal fungi, the release of elements favours the nutrition of partner plants (which, for example, when potassium is lacking, release less carbon for their mycobionts).

Aquatic fungi

Aquatic biotopes in the broadest sense include not only the seas, freshwater reservoirs and running water, but also wetlands, swamps, springs (normal or thermal) or puddles after rain. We find a lot of fungi here, but some are not indigenous (e.g. imperfect fungi as *Cladosporium* or *Alternaria*).

Only zoosporic fungi live their entire life cycle in water; the other groups spend only part of their lives in water and probably got into the water secondarily during the phylogeny.

Fungi can be found in various aquatic biotopes, they are saprotrophs or parasites on other organisms (plants, algae, animals and other fungi).

Aquatic fungi do not form any large structures, the largest being the apothecia of some marine ascomycetes, several millimetres in size.

Mainly **zoosporic fungi** (*Chytridiom.*, *Blastocladiom.* and *Oomycota* in general) live in **fresh water** – these are truly aquatic organisms (sensu stricto), usually unable to spread outside the aquatic environment, even in soil they need water.

Different oomycete or fungal species are found in different areas of the aquatic habitats, but in general more of them occur near the bank than in deep water – apparently there is more plant and animal debris as nutrition source.

Frequency of occurrence usually varies throughout the season, depending on weather and nutrient availability – this is especially evident in parasitic species, whose peaks of occurrence often directly follow the peaks of host occurrence.

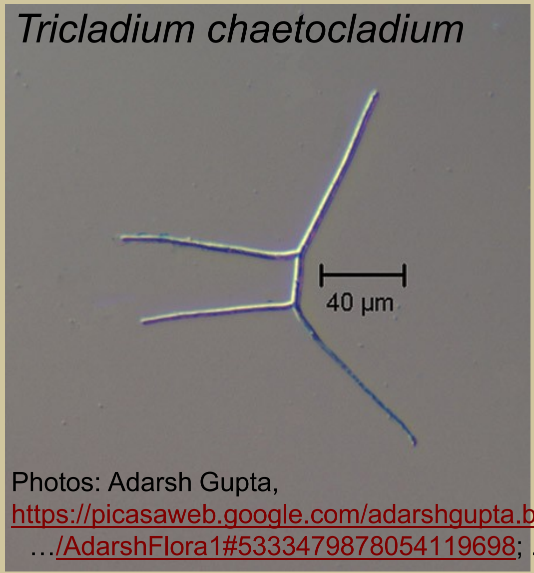
Chytridiomycota can play an important role in reducing the plankton in reservoirs (in addition to saprotrophs, there are many parasites, for example *Rhizophydium* species on algae and pollen grains) – thus they contribute to maintaining the biological balance, they can also indicate eutrophication.

Freshwater *Oomycota* are also saprotrophs (e.g. *Leptomitus lacteus* forms large colonies in water polluted by organic compounds) and parasites (*Aphanomyces astaci*). Some oomycetes tolerate a low level of oxygen in water (*Aqualinderella fermentans* turns to fermentative metabolism in the case of oxygen shortage, *Leptomitus* obtains carbon not from glucose but from fatty acids).

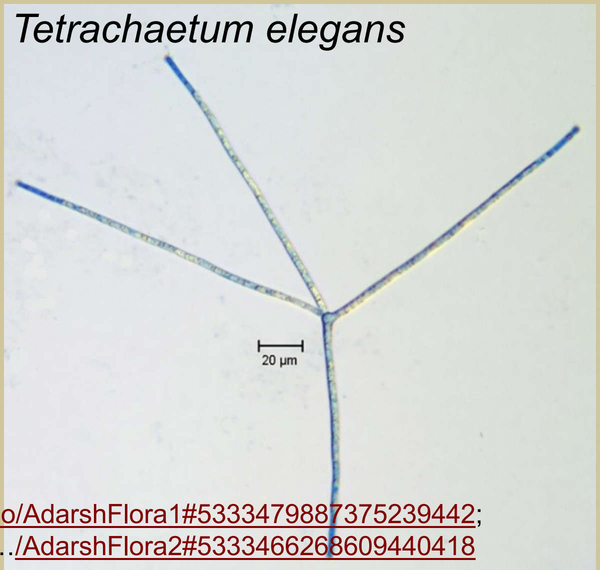
Photo: *Leptomitus lacteus* Photo Dirk Klos, http://protist.i.hosei.ac.jp/PDB/Galleries/Klos/Bavaria/Leptomitus_1.html

Higher fungi in water are mainly *Deuteromycota* (especially *Hyphomycetes*); if teleomorphs were found, they mainly belong to *Ascomycota* (forming fruitbodies); some are assumed to be *Basidiomycota* (if dolipores or clamps were observed).

The shape of the conidia extending into space turned out to be an evolutionary advantage for dispersal by the water stream – this secondary adaptation is typical for the so-called Ingoldian fungi (named after the British mycologist C.T. Ingold), aquatic hyphomycetes with large four-pointed or elongated spores or conidia. These fungi (worldwide distribution, about 300 species) live mostly saprotrophically on organic substrates in clean streams; they often represent anamorphic stages of ascomycetes, but some basidiomycetes also have similar star-shaped basidiospores.



Tricladium chaetocladium



Tetrachaetum elegans

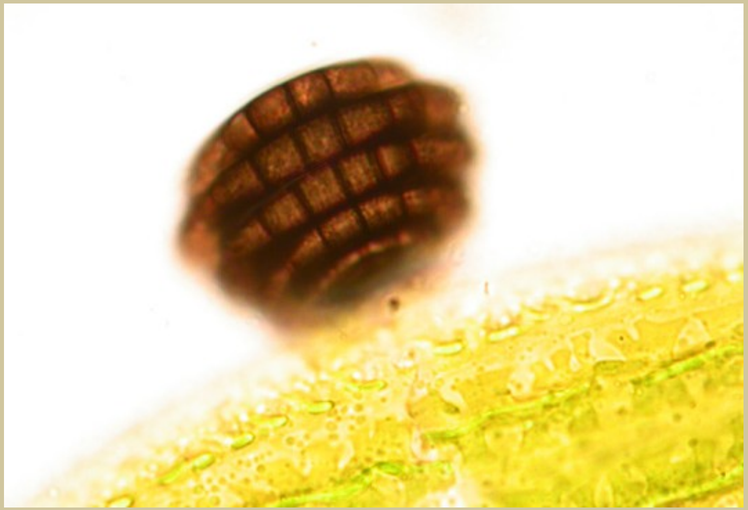
Canalisporium pulchrum

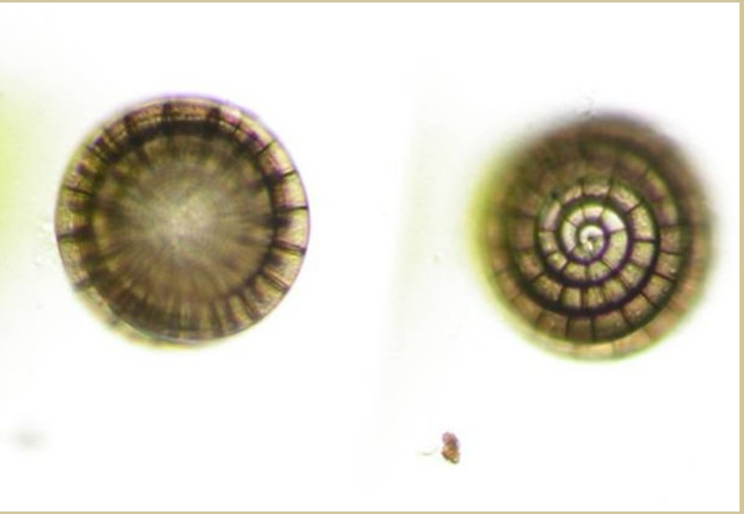

Photos: Adarsh Gupta,
https://picasaweb.google.com/adarshgupta.bio/AdarshFlora1#5333479887375239442;
…/AdarshFlora1#5333479878054119698; …/AdarshFlora2#5333466268609440418

http://fungi.life.illinois.edu/about/mitosporic_fungi;
převzato z http://botany.natur.cuni.cz
/koukol/ekologiehub/EkoHub_10.ppt

Some fungi form an aquatic anamorph and a terrestrial teleomorph with airborne ascospores – this is suitable for dispersal, while conidia released into the water are only carried downstream, sexual spores can be carried upstream or possibly into another stream.

Another examples of „amphibiousness“ are the so-called aero-aquatic hyphomycetes, growing at the edges of flowing water or stagnant water bodies. Their mycelium grows submerged, but conidia are formed only in air; these „aerial“ conidia are round, hydrophobic and float on the water surface – they are spread further when flooded, while they can persist on the mud surface when the water dries up. Such an „amphibious“ way of life is an advantage in the case of seasonal changes in the environment.

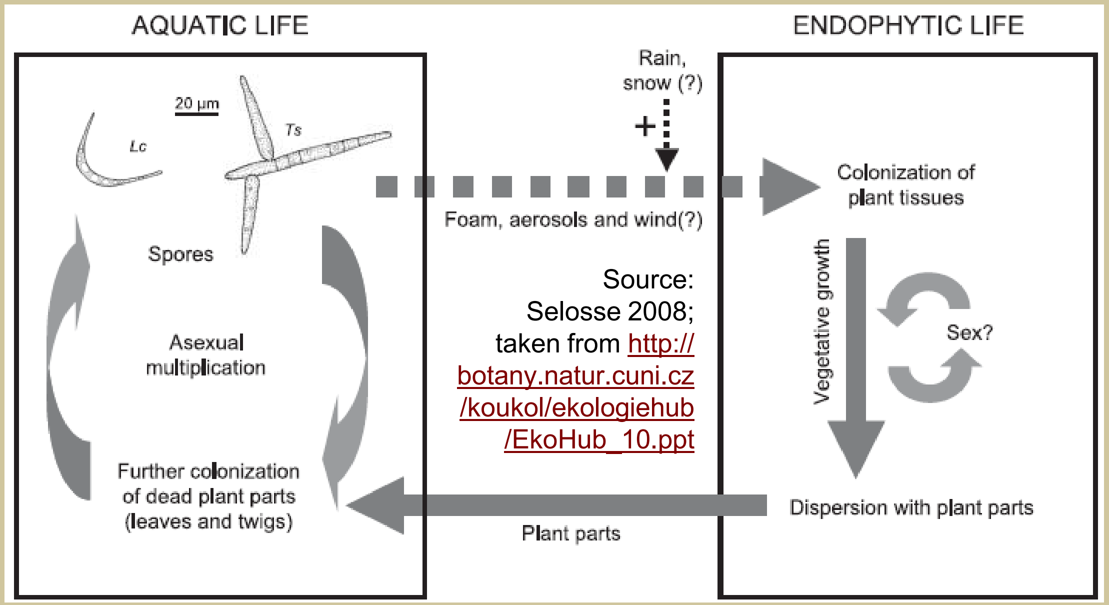




Top: conidium of *Helicoon* sp.; bottom: conidia of *Helicodendron* sp.; helicoidal shape allows them to rise in the water column.

Photos: André Advocat, http://forum.mikroscopia.com/index.php?showtopic=811, http://forum.mikroscopia.com/uploads/post-32-1087101102.jpg; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_10.ppt

The most common substrate is leaves fallen into the water (esp. in clean flowing waters, where other nutrient sources are limited) – this is related to growth peak of these fungi (distinct in temperate zones, where leaf fall is a seasonal matter): the greatest development in autumn, followed by leaf decomposition and conidia production in winter (the „amphibious" fungi have an advantage – falling leaf can already be „inoculated“ by airborne spores; otherwise the succession is similar to terrestrial fungi /*see chapter Saprotrophs*/). In addition to colonising leaf litter and sub-merged plant parts, some of these hyphomycetes live as endophytes in the tissues of woody plants (willows and alders, but also other trees).



Life cycle of an „amphibious“ aquatic/endophytic fungus.

Aquatic fungi also play a beneficial role in the development of invertebrate populations – litter „pre-chewed“ by fungi provides them more available nutrients; moreover, this action increases the content of proteins and phosphorus, thereby improving the litter quality and taste. Thus the animals accelerate decomposition of plant remnants, and their „grazing“ can finally reduce the fungal populations.

Marine fungi must be adapted to high concentration of ions in the environment and its possible fluctuations => thus also changes in the water potential (they are compensated by accumulation of ions in the cells). Of the abiotic factors, their occurrence is mainly influenced by salt content (they also occur in the Dead Sea), pH (7.5-8.5), temperature and amount of available oxygen. Some fungi live at a depth of up to 4000 m – they can withstand pressure, darkness and low temperature (but not anaerobic environment, only bacteria can be found there).

Only ca 500 species are known from the seas (a huge difference if we compare the area of land and the number of terrestrial species). Of the higher fungi, esp. yeasts and other ascomycetes occur in seas; in order to slow down descent in the water column, they produce sigmoid-shaped conidia or with projections. Of the zoosporic groups, mainly *Thraustochytriales*, *Labyrinthulales* and chytrids are represented; 90% of marine fungi are obligately marine.

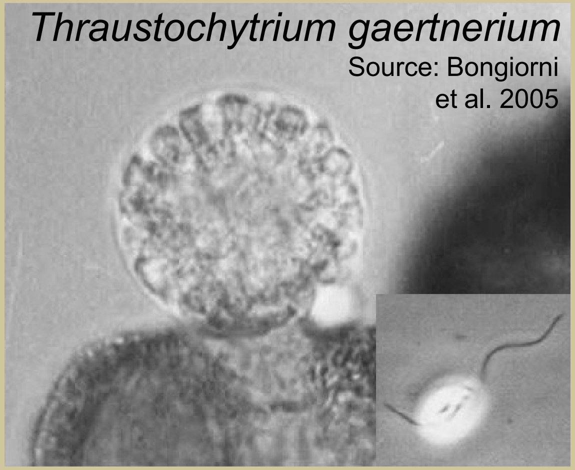
taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_2.ppt

Remispora stellata

Corollospora maritima

Marinospora calyptrata

http://cryo.naro.affrc.go.jp/sougou/joho; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_10.ppt



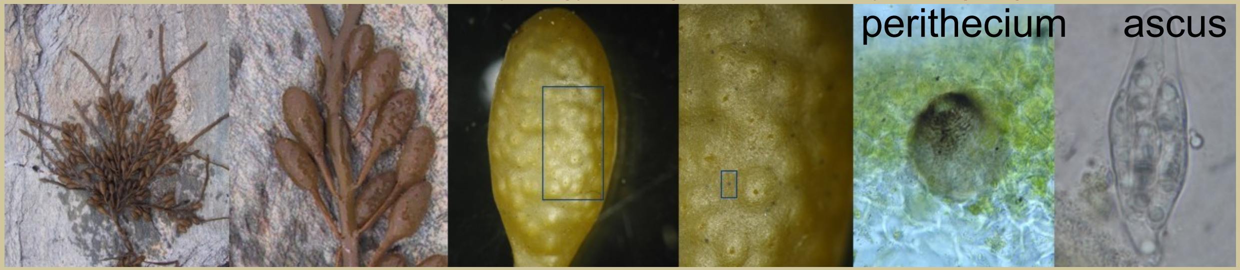
Thraustochytrium gaertnerium

Source: Bongiorni et al. 2005

Like freshwater fungi, marine fungi are mostly limited by substrate availability. Many species are lignicolous (ascomycetes and anamorphic fungi, as well as a few basidiomycetes – these groups are represented in the sea by a total of ca 300 species); wood is a surprisingly common substrate in the sea (submerged structures, ship remains, „drift wood“ carried by water) and its decay resembles soft rot. Other species are decomposers of leaves fallen from the shore, dead algae or aquatic animals. In addition to decomposers of dead bodies, there are also a lot of parasites (necrotrophs on macroalgae, but also parasites of other organisms).

http://oregonphotoblog.org/gallery/albums/Carters-Photos/drift_wood_001.jpg

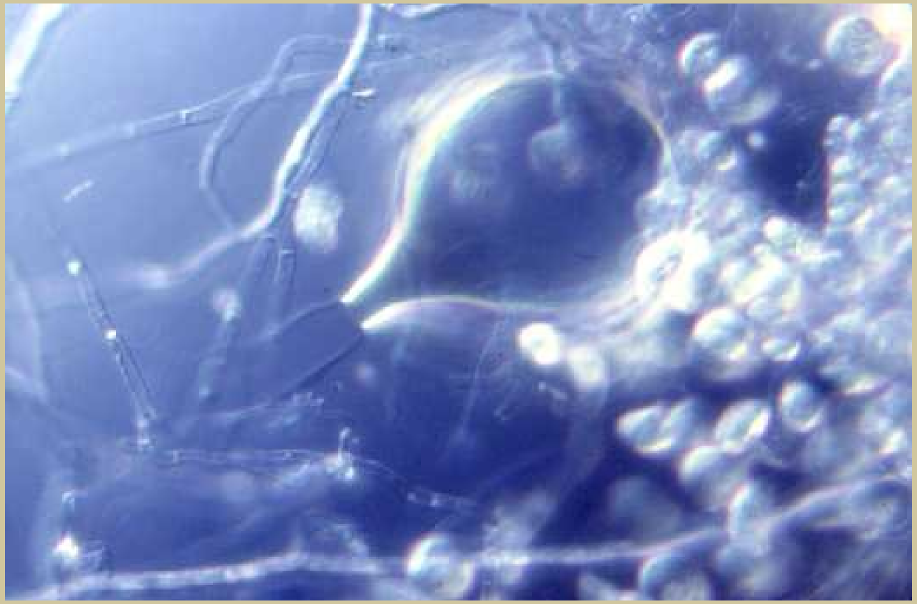
http://website.nbm-mnb.ca/mycologywebpages/NaturalHistoryOfFungi/AlgalMutualisms.html



About a third of marine fungi create so-called mycophycobiosis on algae – a mutualistic symbiotic relationship, in which the fungus obtains more nutrients from the alga and in return the mycelium can serve as a conductive path (this help is used e.g. by brown algae). An example is *Mycophycias ascophylli* (*Capnodiales*, see photo), growing in the tissues of *Ascophyllum nodosum* and forming fruitbodies in its receptacles.

„Marine“ lichens have been found only in the coastal zone (on rocks etc.).

Specific case is represented by **mangrove fungi**, although only ca 42 sapro-trophic species are known (ascomycetes, basidiomycetes, but also oomycetes). Mangroves are the source of a large amount of litter (leaves, branches, ...) and at low tide a considerable mass of organic matter floats into the sea.



Halophytophthora masteri (Peronosporales)

http://newell.myweb.uga.edu/images/hmasteri.jpg

Salt marsh fungi inhabit coastal ecosystems dominated by grasses of the genus *Spartina* – here they are crucial for the decomposition of organic matter and as food for invertebrates.

Even in terrestrial ecosystems, salt marsh fungi can be found in habitats with a high salt content, such as soil near mineral springs; halophilic species are common here (e.g. Soos National Nature Reserve in the Czech Republic).

Top: coastal salt marsh with *Spartina anglica*

Photo Ian & Tonya West, http://www.soton.ac.uk/~imw/jpg-Hurst/6HS-Spartina.jpg

Bottom left: *Lulwoana* sp., occurring at Soos NNR.

Photo Martina Hujslová; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_10.ppt

Right: *Lulworthia* sp.

http://cryo.naro.affrc.go.jp/sougou/joho