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 DISPERSAL AND DISTRIBUTION

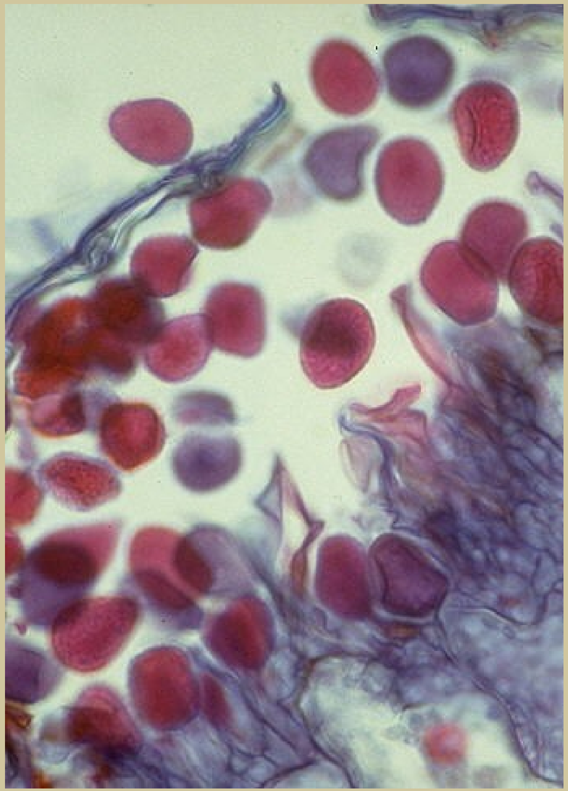
DISPERSAL OF FUNGI AND THEIR DIASPORES

Fungi are organisms represented in various terrestrial and some aquatic habitats, mainly in aerobic conditions. A number of spores (or fragments of mycelia), which can be found even in extreme conditions, are constantly spreading over the entire surface of the Earth.

The most common **ways of fungal dispersal** are through air, water, plants or animals.

The most common is dispersal through the air – **anemochory**. The dimensions (2–200 μm) and weight of fungal diaspores predispose them to overcome distances and obstacles which seed plant diaspores cannot overcome (up to 10,000 km has been detected for urediospores of *Puccinia graminis*).

Most spores occur up to 300 m above the ground, but they also soar even into the stratosphere – however, the atmosphere is not very „friendly“ environment for fungi and their spores, exposed to radiation and low humidity there. Spores with melanin (dark pigment) in the walls have an advantage, it protects them against UV radiation directly on the surface; even in the cell there may be other substances which absorb more radiation => its energy is usually converted into heat, which is subsequently „radiated“ from the spore.



Puccinia graminis, urediospores
http://www.dipbot.unict.it/sistematica/Puc_ure.html

In order to survive in the atmosphere, the spores must „balance on the edge“ between water loss and maintaining metabolic activity – in the cytoplasm, they have a high concentration of glycerol and other compounds which allow constant metabolism in conditions of limited water availability. Anyway, with this method of propagation (when they are exposed to drying, UV radiation or temperature fluctuations), a significant part of the spores lose their lifespan – that’s why anemochorous fungi produce a high amount of them.

Wind-dispersed spores are in many cases actively released from the fruitbodies – they are ballistospores of hymenomycetes (with the exception of species of the genus *Coprinus* and similar genera) or ascospores from unitunicate or bitunicate asci (in operculate *Pezizales*, all lids open and spores come out at the same time, while, on the contrary, in inoperculate fungi, spores are pushed out one by one by turgor). Spores are actively released from the fruitbody only at higher air humidity (e.g. fruitbodies of jelly fungi sporulate only when they are water soaked, but also spores of other mushrooms are no longer released from drying fruit-bodies). High metabolic activity in the hymenium can lead to heating of the air layer below the hymenophore => the released basidiospores are caught by the rising stream of warm air and carried upwards (up to above their „mother" fruitbody, which they can then re-dust).

Ganoderma applanatum,
fruitbody dusted with its own spores.

Photo Josef Hlásek,
http://www.hlasek.com/ganoderma_lipsiense_a8473.html


R. Moore, W. D. Clark, K. R. Stern &
D. Vodopich: Botany.
Wm. C. Brown Publishing, 1995.

Spores of gasteroid fungi are passively broken off from the sterigmata and, after being released from the disintegrating fruiting bodies, are carried by wind. Some puffballs can become „steppe runners“: breaking off the fruiting body from the substrate => rolling in the wind => scattering spores.

Rainfall can also contribute to the spore dispersal: impact of a water drop leads to ejection of the spores (either from the fruitbody or spores which have already been released, lying on some substrate) into the air => further dispersal is ensured by air flow (in fact a combination of hydrochory and anemochory, mainly applicable for short distances).

Another case of combining anemochory with local hydrochory is applied, if some fungi that need a water drop of for germination of airborne spores.

Zoochory is mainly of two types – dispersal of spores attached to the body surface or passing through the digestive tract of animals.

Endozoochory: underground fungi spread through the digestive tract (the same mechanism is used by hypogeous fungi of different groups, *Elaphomyces*, *Tuber* or sequestrate basidiomycetes). They usually release aromatic substances as attractants – alcohols, ketones and esters (dimethyl sulphide), apparently they are not analogues of sex hormones; sometimes the mixture is more important than the individual compounds => it can be smelled out of the soil and attracts mammals => they dig up and eat the fruitbodies => the spores are then expelled with the droppings. Mammals are apparently very clever searchers (not only pigs and truffles) – spores of about 50 species of underground fungi were found in the feces, while many of them were not found at all in mycological field surveys.

Rodent *Glaucomys sabrinus* and its favourite food, *Elaphomyces granulatus*.

http://upload.wikimedia.org/wikipedia/commons/d/df/Glaucomys_sabrinus_2.jpeg

http://myco-nimbus.over-blog.fr/categorie-10021522.html

Endozoochory as a „byproduct of their aktivity“ is also ensured by a number of mycophagous animals – for example, small rodents (fruitbodies can make up to 100% of their diet during a certain period), but also bears („mushroom pickers“ in autumn around September, when fungi amount to 1–7% of their food; boletoid /*Suillus*/, russuloid /*Russula*/, puffballs /*Calvatia*/ or underground fruitbodies /*Rhizopogon*/) were found in their food.

Fungi are mostly only one of the components of their food, perhaps no mammal is obligatorily mycophagous (e.g. the rat-kangaroo *Bettongia gaimardi* is predominantly myco-phagous throughout the year; these species are especially threatened in tropical areas by rapid deforestation, which wipes „their“ fungi out of the ecosystem).

Fungi are a good source of some nutrients for mycophagous animals (higher concentration of N, P, K than in leaves or seeds, as well as vitamins, amino acids, steroids, polysaccharides, storage lipids, etc.); however, these animals must have adequate digestive tract equipment (enzymes, microbial mycobiota, especially in the small intestine).

Ceratocystis ulmi (the causative agent of elm graphiosis) is dispersed by bark beetles (they bear conidia on the body surface and in the digestive tract; *already mentioned in the chapter Fungal symbioses*). Also nematodes are quite often vectors of wood fungi.

http://faculty.unlv.edu/lstark/bio197lab/lab2.htm

Coprophilous fungi also dispersed with the help of animals, their spores are released (individually from asci or basidia, but e.g. *Pilobolus* /right photo/ actively shoots entire sporangia) towards the light (light means free space – a chance for greater „range“) => the spores stick to the surrounding grass after being released => it is grazed by herbivores => the spores (dormant until then) germinate after passing through the digestive tract. Sporangia of some zygomycetes and spores of some ascomycetes can be shot at 2–25 ms^{-1} with an acceleration of 20,000–180,000 g, allowing a range of up to 2.5 metres.

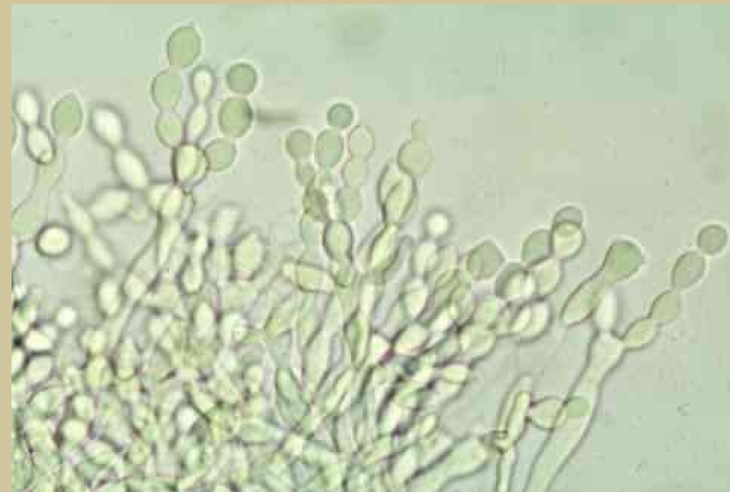
Active ejection of spores or sporangia basically represents autochory, which in these cases is combined with zoochory or anemochory in the further course of dispersal.

On the same level as endozoochory of hypogeous fungi is **epizoochory** in the case of powdery mildew fruitbodies with branched appendages, which can attach to the bodies of forest animals; it is not as essential relationship as in the case of ambrosia fungi, but it is still a significant contribution to the spore dispersal.

While powdery mildew uses „mechanical aids“ to attach spores, other fungi spread spores on the surface of animal bodies (most often insects or slugs), secreting mucus covering the spores or substances which attract insects by their smell – well-known are chlamydospores of the *Asterophora* species (flies are attracted by the smell of decaying *Russula* or *Lactarius*), gleba surface of the genus *Phallus*, ...

Asterophora lycoperdoides and its chlamydospores, *Phallus impudicus* and detail of its gleba.

... conidia of the genera *Monilia* or *Claviceps* (excretion of honeydew, smelly seeds of infected grasses), spores of some rusts – these are also entomogamous, using insects to transfer spermatia to receptive hyphae.



http://www.biology.ed.ac.uk/research/groups/jdeacon/microbes/applerot.htm

Woodpeckers are also unintentional vectors of wood fungi – they transfer fungi, which enter the tree through worm paths, to other trees where there are also insects, but the fungus has not yet been there (this form of dispersal is significant for tracheomycosis fungi, which rarely fructify and do not even form many conidia).

Photo Michaela Sedlářová, http://botany.upol.cz/atlasy/system/nazvy/claviceps-microcephala.html

Dung beetles can help ectomycorrhizal fungi by their activity, when they roll „their ball“, wrapping the spores on it, and then bury it in the ground => closer to the roots.

Monilia fructigena and its conidia, detail of *Claviceps microcephala* pseudosclerotium in the spike of *Molinia* sp.

Other forms of dispersal are rarer.

Phytochory is most common in parasitic fungi, diaspores are dispersed by seeds or fruits of the host plant (e.g. mycelium of *Ustilaginales* in embryo).

Parasitic fungi can also spread from one plant to another at the point of contact or fusion of roots; e.g. honey fungi do not even need direct contact with host trees, they overcome distances of the order of metres by rhizomorphs.

http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/prm7770

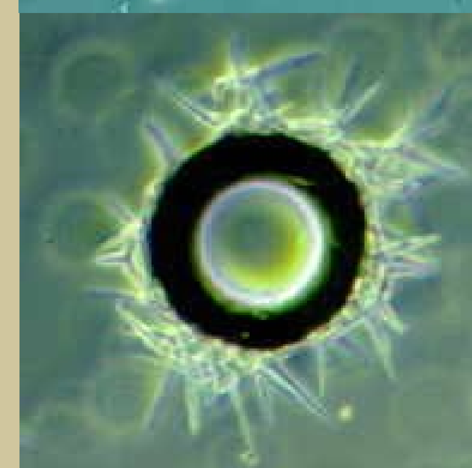
http://picasaweb.google.com/lh/photo/zUk72cTK3B5RQvYyE4IqBg

Left: mycelium of *Ustilago nuda* in barley embryo (right photo); right: rhizomorphs of *Armillaria* sp.

In the case of **hydrochory**, mainly zoospores are dispersed, not only directly in water by aquatic fungi, but also, for example, in soil water (oomycetes and especially chytridiomycetes, which can also be vectors of viruses). The movement of zoospores is either passive in the encysted state or active – for example, in parasitic oomycetes, positive chemotaxis induced by root exudates is applied. In the case of active spreading of motile cells, this is also a form of **autochory**.

Another case of hydrochory is the transfer of conidia of aquatic hyphomycetes – so-called Ingoldian water fungi, whose conidia swim in the plankton of clean waters (*see also Aquatic fungi*). In the course of evolution, these fungi (anamorphs of mainly ascomycetes, less basidiomycetes) entered the water secondarily and the spores are shaped to be carried by water current (protrusions in different directions, as large a surface as possible, see here).

In the case of terrestrial fungi, it is rather a passive transfer of spores by flowing water (if they fall into water) or through precipitation (sprinkling of drops during rain, see above).



Conidia of *Lemonniera* sp., attached on air bubble in the bottom photo – therefore, water foam is an environment rich in carried spores.

Anthropochory has a special position, the spread due to human activity – especially with transport, but also with waste.

A typical example is *Clathrus archeri* imported from Australia (=> further spread in Europe by zoochory), but also epiphytoties of *Plasmopara viticola*, *Phytophthora infestans* (introduced from America to Europe) or *Ophiostoma novo-ulmi* (on the contrary from Europe to North America).

Photo: *Clathrus archeri*

Actually, the mycorrhizal fungi of larch forests (today commonly considered „domestic“ in our country) were only introduced to Bohemia and Moravia with the planting of larches (original in the Alps or the Carpathians) in the 18th century.

Also „domesticated“ fungi, which in conditions of our nature have slowly lost the ability to survive outdoors (*Serpula lacrymans*), are anthropochorous.

DISTRIBUTION RANGES OF FUNGI

On a global scale, it can generally be said that fungi have much wider ranges compared to vascular plants. This is, of course, due to easy transfer of small spores, but on the other hand, the transfer itself may not be enough to „settle“ in a new place – application of ecological limits is similarly obvious, the spore must find suitable conditions not only to germinate, but also to enable the germinating hypha to grow further successfully.

The limiting factor is especially the substrate (e.g. calcareous species need calcareous soil, mycorrhizal species need their symbiont, coprophilous species need dung of a particular animal); in the case of parasites, a certain amount of fungus needs to be accumulated for successful infection („infection density“).

Heterothalism plays a very important role – even if the fungus germinates in a new area, it must find a „partner“ of the complementary mating type in order to continue the reproduction.

It is good to know not only the total distribution range, but also various dispersities; it is also important to distinguish whether the species is permanently present in some area or if it has only temporarily occured there, but will not survive there in a long-term perspective.

Rust fungi and powdery mildews (phylogenetically the oldest?) have the largest distribution ranges; the ranges of parasites also depend on the occurrence of host plants. However, occurrence of the host plant does not necessarily mean occurrence of the parasite – the plant could have spread to areas where some other condition no longer suits the parasite, and therefore it is not present there. The distribution range of a fungus which is identical to range of its host is referred to as homotopic; conversely, a heterotopic range is if the distribution of the fungus does not overlap the distribution range of the host.

Saprotrophic fungi usually have a wide ecological amplitude due to a considerable range of tolerance to the ecological factors of their habitats – many of them are ubiquitous, their distribution is close to cosmopolitan (be careful with use of the word cosmopolitan – this means not only occurrence on all continents /excluding Antarctica/, but also in all climate zones – and that’s not even common for fungi!).

Common species with such wide distribution are e.g. *Schizophyllum commune*, *Laetiporus sulphureus*, *Mycena pura*, *Coprinus comatus*, *Phallus impudicus*, *Scleroderma verrucosum*.





Top left *Schizophyllum commune*, centre *Mycena pura*, right *Phallus impudicus*,
bottom left *Laetiporus sulphureus*, centre *Coprinus comatus*, right *Scleroderma verrucosum*.

The distribution of fungi can point to the climatic conditions of different areas (to show mountain ranges, warm areas, etc.), however, the differences in species composition between different climate zones are not as pronounced as in vascular plants.

The centre of their distribution in the tropics and subtropics have, for example, *Marasmius* or *Lentinus* species; on the other hand, the greatest species richness in temperate zones have, for example, *Amanita*, *Russula*, *Lactarius*, *Lycoperdon* or some polyporoid fungi.

Different populations of the same species or closely related, but different species can grow on different continents – here the assessment based on compatibility tests can play an important role.

Similar to vascular plants, the differences between the mycobiota of Europe and North America can be described. The North American mycobiota is richer – after all, North America covers more climatic zones and its biota was not so decimated by the ice ages, which is also reflected in the spectrum of fungi; there is also a clear connection to breadth of the plant species spectrum, especially in the case of parasitic and symbiotic fungi.

Fungi which occur naturally in a given area are **autochthonous** (native), on the other hand, any species are **allochthonous** (non-native) in places of occurrence outside their natural area. The mentioned distinction can be applied not only to distribution on a „large scale“, it is also possible to distinguish native and non-native species even locally at the level of a specific habitat (substrate) – for example, autochthonous species of „water moulds“ *Saprolegnia* or *Achlya* occur on leaf litter in streams, while terrestrial hyphomycetes as *Penicillium*, *Aspergillus*, *Alternaria* or *Cladosporium* are allochthonous there.

Many allochthonous species have reached their places of non-native occurrence due to human activity – in this case we call them **introduced** species. Sometimes it can be a targeted transfer, for example planting of mycorrhizal plants with their partner fungi – e.g. ecto-mycorrhizal fungus *Hydnangium carneum* with seedlings of the *Eucalyptus* trees (introduced from Australia during planting in Spain) or arbuscular mycorrhiza on spoil tips, during the recultivation of eroded areas (*Glomus claroideum*).

Hydnangium carneum

http://forum.funghiitaliani.it/index.php?showtopic=17141

In most cases, the introduction is unintentional – a well-known example is the already mentioned *Clathrus archeri*, an Australian species which spread throughout Europe during the 20th century. Currently important is introduction of *Favolaschia calocera* from Madagascar, invasively spreading in New Zealand, where it threatens to displace native lignicolous fungi; this species has already been discovered in Europe (Italy). On the contrary, examples of European „export“ are *Amanita muscaria* in New Zealand (where it forms a mycorrhiza with *Nothofagus* species) or *Amanita phalloides*, introduced to the east coast of North America, to South America, Australia and also to New Zealand.

Favolaschia calocera

Amanita muscaria

http://www.treesforlife.org.uk/forest/photo/fantastic_fungi.html

Amanita phallloides

http://www.kuleuven-kortrijk.be/facult/wet/biologie/pb/kulakbiocampus/paddestoelen/groene%20knolamaniet.htm

A specific case is invasive phytopathogenic fungi *(more in Economic damages caused by fungi)*.

Finally, let's take a brief look at **fungi of the Czech Republic**.
In addition to species with a wide distribution range covering various climatic regions, the core of the Czech mycobiota is represented by Central European species (this term refers to species with a distribution centre in the Central European region, as there are very few species found only here); in addition to them, species from warmer or colder regions also occur in Czech territory.

• Psychrotolerant species occur in mountainous locations (ranging from montane to alpine) or in inverse locations of lower elevations (deep, narrow valleys, gorges):
– among them, strictly mountainous species, bound to mountain vegetation (natural spruce forests, mountain pine stands, vegetation above the forest line, raised bogs) should be distinguished;
– the Carpathian-Alpine species enter into the mountain forests (*Hygrophorus marzuolus*, *Albatrellus pes-caprae*).

Left: *Albatrellus pes-caprae*; right: *Hygrophorus marzuolus.*

• Thermophilic species occur in warm forests or in sunny steppe habitats:

– Mediterranean species, which have the northern limit of their distribution here, occur in warm areas of our country (*Omphalotus olearius*, *Amanita vittadinii*, *Pleurotus eryngii*);

– there are only few strictly lowland fungi, mainly species bound to riparian forests;

– thermophilic species can also occur on sunny slopes in mountain areas where temperature inversion is applied.

Top: *Amanita vittadinii*; bottom left: *Pleurotus eryngii*; right: *Omphalotus olearius*.