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)

FUNGI AND THEIR ENVIRONMENT

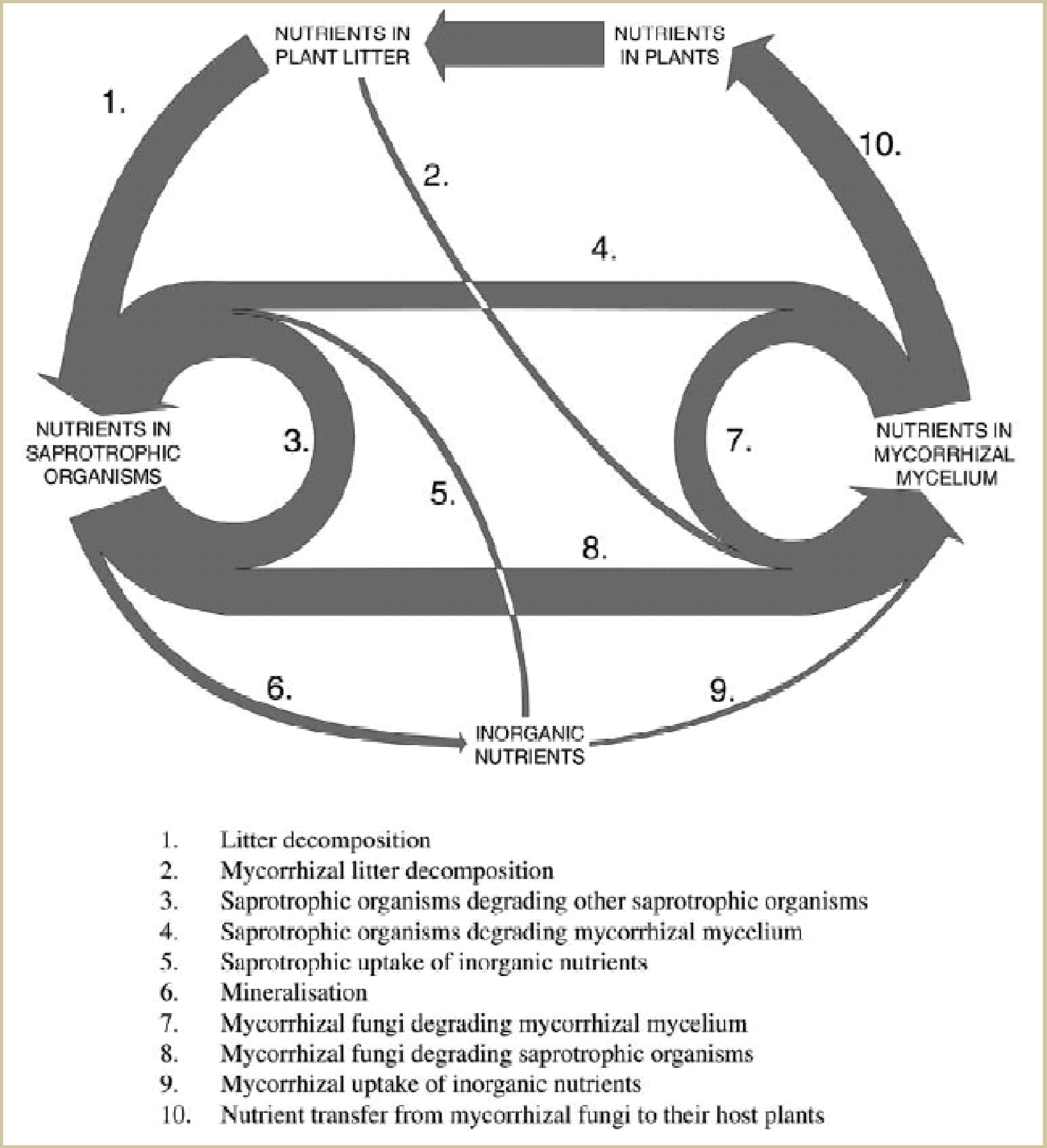
IMPORTANCE OF FUNGI IN NATURE, AUTECOLOGY AND SYNECOLOGY

The basic role of fungi in nature is **decomposition** of organic matter to inorganic compouds or particular elements (minerals, CO_2 – so-called **mineralisation** of organic matter), returning them back to soil and atmosphere, from which they are again used by primary producers. Different groups of fungi are involved in the detritus food chain, in which complex organic compounds are gradually degraded to simpler ones, always a bit less energy-rich.

Fungi are of fundamental importance in the carbon cycle; they obtain carbon mainly by dedradation of polysaccharides (cellulose, etc.), lignin, but also lipids and other substances – their degradation finally leads to release of CO_2.
By degradation of proteins, fungi obtain nitrogen, which, however, they degrade „only“ to NH_3 => after release into the soil, ammonia is oxidised to NO_2^- or NO_3^-, or converted to N_2 by denitrifying bacteria. From these organic macromolecules fungi obtain the energy needed for life.

In addition to mineralisation, fungi also participate in **humification** – humic substances are synthesised from organic compounds degraded only to a certain degree; higher content of these substances increases the soil fertility in the habitat.

In some ecosystems, rapid decomposition of litter and release of simple nutrients leads to strong mineralisation (tropical and temperate forests, meadows). Conversely, there are ecosystems where C and N remain bound in biomass (for example boreal forest, see diagram) and final mineralisation is reached only minimally, in the case of disturbances and losses (dead mycelium is a substrate for other fungi and bacteria).



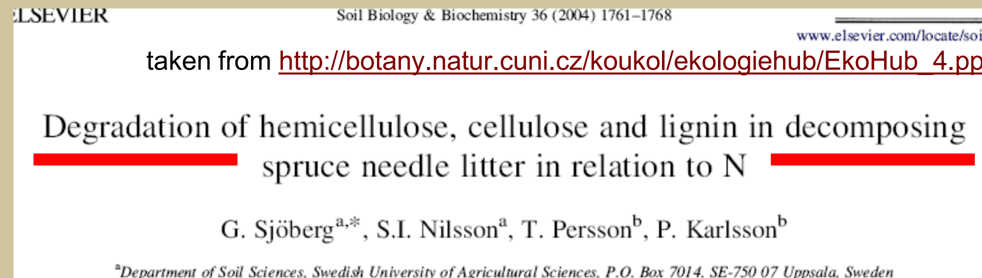
Nutrient cycle
in boreal forest ecosystem

Source: Lindahl et al. 2002,
taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

To clarify the terminology:

• **decomposition, decay** – superior term for all processes associated with mechanical, biological and chemical changes in dead organic matter, e.g. plant debris and litter;

• **degradation** – disintegration of particular compounds, with emphasis on their composition and chemical features;


ELSEVIER Soil Biology & Biochemistry 36 (2004) 1761–1768

www.elsevier.com/locate/soilb

taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

Degradation of hemicellulose, cellulose and lignin in decomposing spruce needle litter in relation to N

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– **biodegradation** – microbial degradation of specific chemical compounds, often of human origin, mostly toxic, difficult to degrade, contaminating, …; this term is usually applied in biotechnology;

• **immobilisation** – a process by which inorganic elements, ions and chemical groups are bound (or even **accumulated**) in organic matter; thus they cannot be leached out, are not released from the environment and are not directly accessible to plants;

• **mineralisation** – the opposite of immobilisation, a process in which particular ions, elements and chemical groups are released from complex organic compounds;

• **humification, sequestration** – long-term deposition of organic matter in soil, making it relatively inaccessible to most organisms.

Fungi together with bacteria are involved in decomposition of organic matter; fungi have some advantages over bacteria:
– apical growth of hyphae, which are firmly anchored in the substrate => they can exert effective pressure, allowing penetration into the tissue (especially *Ascomycota* and *Basidiomycota* form mycelial cords, rhizomorphs and similar structures allowing long-term contact of the fungus with the tissue);
– richer enzymatic equipment, more efficient metabolism.

Let's clarify several terms, defining the occurrence of fungi in the ecosystem:

• **habitat** [from Latin habitatio] is defined by properties of substrate and environment, colonised by given population of a particular fungal species, i.e. habitats of different populations of one species may differ;
it may be synonymised with the word biotope, but the term habitat is more commonly used in English-speaking countries;
– microhabitat represents more detailed habitat (on small scale);

• **substrate** can have two meanings: organic or mineral matter colonised by the fungus, or specific chemical component that the fungus is able to utilise;

• **niche** expresses a set of abiotic and biotic traits of the environment.

Interesting fact: How many species can inhabit the same habitat? In Scandinavia, wood colonising species (approximately 2,500 species) were counted and compared with the number of possible niches on which they can specialise:

Tree species *Picea, Abies, Fagus, …*	> 10
Substrate *trunk, branch, twig, ...*	> 3
Trunk / log *standing, fallen*	2
Age *Month, year, dozens of years, …*	> 5
Wood part *bark, sapwood, heartwood, ...*	> 3
Cause of tree death *natural (old age), bark beetles, game biting, fire, …*	> 5
Physical factors *moisture, sun exposure, …*	> 5
Others *interactions with organisms, …*	> 5
Total number of possible niches	> 100.000

Source: Stenlid et al. 2008, taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_1.ppt

Autecology investigates ecological relationships of individual organisms; in the case of fungi it concerns:
– habitat specificity;
– geographical distribution;
– physiological characteristics;
– interactions with other organisms;
– „species behaviour“ (growth, reproduction, adaptations);
– includes laboratory experiments or fieldwork and observations in situ;
– all classical mycologists are and were dealing with autecology.

Output of the autecological study is a thorough knowledge of physiological features, habitat requirements and growth parameters of particular fungi (or their selected strains), often under simplified and optimal laboratory conditions.

On the other hand, **synecology** investigates:
– interrelations between communities of living organisms and their environment;
– total numbers of species in the selected synusium;
– relative frequency of the species;
– density (abundance) of the species;
– includes field collections, isolations, and multivariate analyses.

Results of the synecological study provide knowledge of the community, spectrum of species, succession, abundance of selected species.

One without the other is usually not possible – it is necessary to know, for example, enzymatic equipment and other traits of individual species or strains, together with their relationships with other "inhabitants" of the habitat.

ENVIRONMENTAL FACTORS AFFECTING FUNGAL COMMUNITIES

Ecological factors, to which fungi are exposed and which affect their occurrence and growth in different habitats, can be classified in several basic groups:
– **climatic**: precipitation and humidity, temperature, air and its movement, light;
– **edaphic**: composition of the substrate, its physical and chemical properties;
– **topographic**: location of the site – altitude, terrain relief, slope exposure;
– **biotic**: interactions of living organisms within the habitat.
The previous points can also include human activity (sometimes referred to as anthropogenic factors), direct or indirect.

Climatic conditions – occurrence of fungi is influenced not only by macroclimate of the area, but also by mesoclimate of the habitat and microclimate directly at the place of growth.

Mesoclimate can be, for example, a stably humid mesoclimate of continuous cover forest, or dry mesoclimate of open sunny habitats or wind-dried habitats.

From the microclimate point of view, humidity of the given habitat/substrate is the most important – moist shaded versus dry sun-exposed sites, wood buried in soil / lying on soil surface, inner or outer side of hollow stump, etc.

Fungi react sensitively to changes in the mesoclimate and microclimate – in general, values of environmental factors exceeding the optimal range represent stress for fungi, and if particular species are unable to cope with changed conditions, it may result in changes of species composition at the given locality.

For some fungi, **water** represents the environment in which they live (*Chytridiomycota* or aquatic *Hyphomycetes*) or spread their zoospores (soil water, water on plant surface).

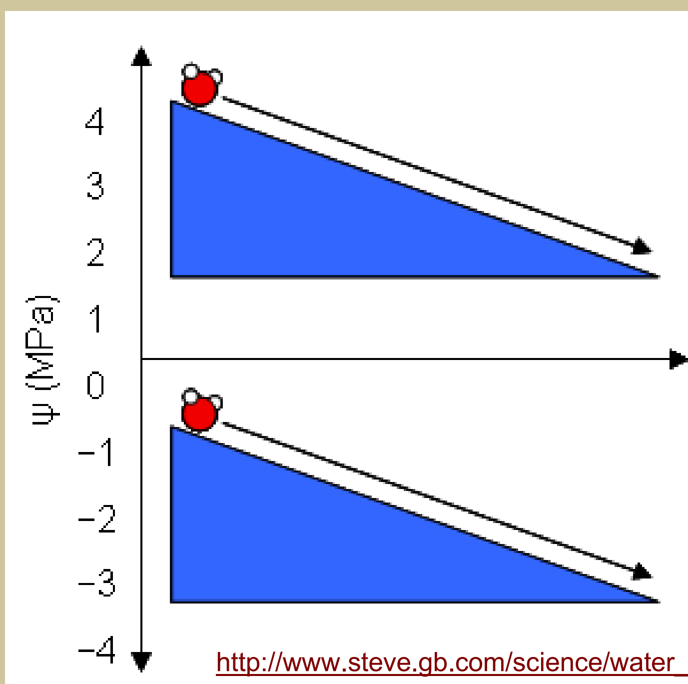
Terrestrial fungi need water not only in the substrate (soil, wood, etc.), but also a certain relative humidity (the ratio of actual humidity to the maximum possible humidity at a given temperature).

Photo Jaroslav Malý, http://www.nahuby.sk/obrazok_detail.php?obrazok_id=34070

According to their water requirements, we distinguish xerophilic / osmophilic fungi (exactly xero- or osmophilic fungi are rare, they are mostly xerotolerant / osmotolerant species, able to grow in dry conditions or at sites with concentrated solutions of some compounds), mesophilic and hygrophilic fungi – extreme case (except directly water fungi) is represented by species growing and fructifying on substrate (detritus, wood) submerged in water (e.g. *Mitrula paludosa*, see photo).

Specific situation is at parasitic fungi, which are not directly dependent on the external water supply, but on the water regime of their host (substrate). However, success of their infection may depend on humidity in the environment, some fungi need a water drop for zoospore movement, hence horizontal precipitation (dew) is enough for them; however, once they penetrate the tissue, they are no longer dependent on external water, but on the host’s water regime.

Compared with growth of vegetative mycelium, the formation of fruitbodies requires higher supply of water and nutrients; precipitation is a crucial condition for fructification even in the case of xerophilic fungi in dry habitats. (On the other hand, extreme humidity associated with low evaporation rate can lead to abnormalities in the fruitbody formation – elongated stipes and reduced pilei have been observed in *Polyporus brumalis*.)
The water supply has a different effect on the formation of different types of fruitbodies – some perennial fungi have a continuous growth, holothecia and crustothecia of terrestrial and lignicolous fungi grow after rain, pilothecia usually after the second rain. The presence of a water drop is needed to release spores or sporangia (*more in the chapter Fungal spores*).



http://www.steve.gb.com/science/water_potential.html

Transfer of water from the environment to the cell or vice versa is determined by the difference between **water potentials** of the cell and the environment (the substrate or environment where the fungus grows may not be homogeneous – for example, litter contains different components with different potentials); fungal cells receive water if they have a lower potential than the surrounding environment (the values are usually negative, in such case a lower potential has higher absolute value!).

Table 3.9 Water availability in different environments and approximate lower limits for growth of some fungi

Water activity	Water potential (MPa)	Examples
1.0	0	Pure water
0.996	–0.5	*Phytophthora cactorum*, lower limit
0.995	–0.7	Typical mycological media
0.98	–2.8	Sea water
0.97	–4	Most wood-destroying fungi, lower limit
0.95	–7	Bread. Leaf-litter Basidiomycetes, lower limit
0.90	–14	Ham. *Neurospora crassa*, lower limit
0.85	–22	Salami. *Saccharomyces rouxii* in NaCl solution, lower limit
0.80	–30	*Aspergillus nidulans* and *Penicillium martensii*, lower limits
0.75	–40	Saturated NaCl solution, *Aspergillus candidus*, lower limit
0.65	–60	22 molal glycerol
0.60	–69	Limit for cell growth – *Zygosaccharomyces rouxii* in sugar solutions and the mould *Monascus* (*Xeromyces*) *bisporus*
0.58	–75	Spores of some *Eurotium*, *Aspergillus* and *Penicillium* species are able to survive for several years
0.55	–80	Saturated glucose solution. DNA denatured
0.48	–90	Antarctic dry valleys

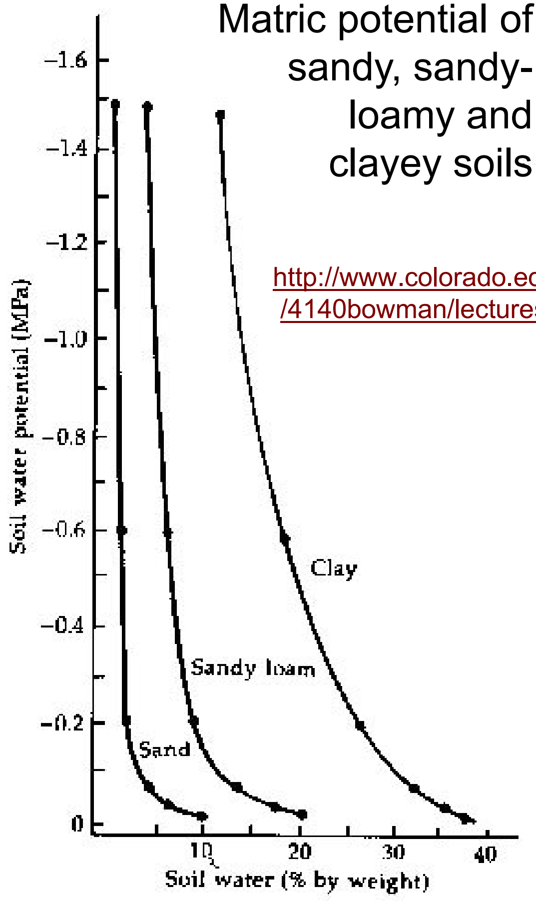
Data from various sources. Molality (molecular weight in grams per 1000 grams solute) and not molarity (MW in g per final volume of 1000 ml) is used in dealing with osmotic potentials. The lower limits of growth are those obtained at optimal temperature and nutrition; when these factors are sub-optimal the limits are not so low. As indicated with *Saccharomyces rouxii*, organisms are usually more tolerant of high sugar than high salt concentrations.

Water potential (given in pressure units) depends on osmotic potential + matric potential + turgor: $\psi = \psi_\pi + \psi_m + \psi_p$.

Table: values of water potentials of selected substrates in comparison with tolerance limits of some fungi.

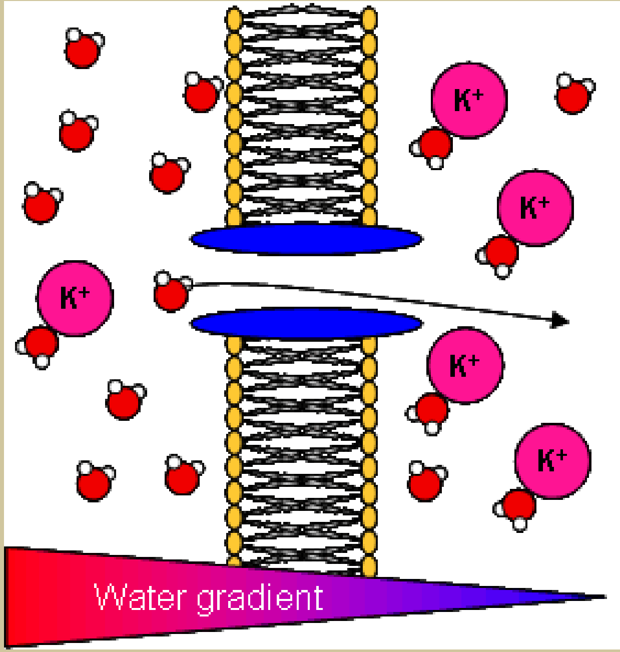
Source: M. J. Carlile & S. C. Watkinson: The Fungi, Academic Press, London, 1994

• Osmotic potential is inversely proportional to the concentration of solutes (see right) – environment with low osmotic pressure has a high osmotic potential, and on the contrary, environment with high concentration of inorganic ions has a low potential (marine and salt-marsh habitats – here we find obligate halophiles such as *Scopulariopsis halophilica*).



Matric potential of sandy, sandy-loamy and clayey soils

http://www.colorado.edu/eeb/courses/4140bowman/lectures/4140-07.html



http://www.steve.gb.com/science/water_potential.html

• Matric potential determines how much the water bound in solid substrate (soil, wood) is available for fungi; its absolute value is inversely proportional to porosity of the substrate (various factors may play a role, e.g. surface tension, capillarity), dry substrates have a low matric potential – in such environment the filamentous fungi have an advantage that they can grow to places where water may be better accessible.

• The value of turgor in the cells, important for transport of solutes and growth of the hyphae, is called pressure potential.

Turgor in otherwise very fragile hyphal cells can exert very strong pressure – the photo shows how the fruitbody of *Phallus impudicus* can even penetrate asphalt (recalculated, one fruiting body, might lift up 133 kg).

Source: Niksic et al. 2004,
taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_2.ppt

(For completeness: in addition to the above-mentioned basic values, the values of gravity and humidity are added to the complete formula for calculating the water potential.)

To some extent, fungi are able to compensate differences in **osmotic pressure** of the cell and environment. Thanks to the solid cell wall, they relatively well tolerate a hypotonic environment (where they are at risk of plasmoptysis), definitely better than a hypertonic environment, in which the cells lose water and die (due to plasmolysis).

Adaptation to an environment with changing water potential is represented by ability to change the cell osmotic potential:
– *Thraustochytrium* absorbs ions in brackish water (it is possible up to a certain limit, high concentrations of inorganic ions such as Na^+ can negatively affect enzyme functions);
– osmotolerant yeasts */see "S" strategies in the chapter Life strategies/* form polyhydric alcohols (glycerol, mannitol, arabitol) from insoluble storage sugars (glucose <=> glycerol <=> glycogen) – in the deficit of available water, metabolic processes take place in glycerol instead of water; the disadvantage is slow reaction to sudden change of conditions, but on the other hand, there may be a surplus of these alcohols in the cell and this reserve may then be useful.

Apical ends of thin-walled hyphae are the most prone to plasmoptysis (cell wall rupture). This is the reason why the yeast-like form of dimorphic fungi is more favourable for life in environment with unstable humidity (e.g. leaf surface, where the osmotic potential is increased by plant exudates and decreased by rain).

Cells without solid cell wall (slime moulds, zoospores) use contractile vacuoles for osmoregulation.

Oxygen is essential for obligately aerobic fungi, which obtain energy exclusively through oxidative metabolism (respiration); on the contrary, it is not necessary for fungi that obtain energy by fermentation. In an anaerobic environment, fungi obtain oxygen bound in organic matter through various enzymatic reactions.

• Facultatively anaerobic fungi, which are capable of both types of metabolism, but prefer respiration in aerobic conditions for growth, are referred to as facultatively fermentative (various imperfect fungi or typically yeasts – the single-cell form is advantageous for more energy-intensive fermentative metabolism).

• Facultatively anaerobic but obligately fermentative fungi tolerate the presence of oxygen, but prefer high concentrations of CO_2 (5–20%, e.g. *Blastocladia*).

• Obligatory anaerobes (*Neocallimastigales*) cannot survive in the presence of oxygen (they must be able to survive in the form of spores – the spores are transferred to next generation of their hosts).

Increased amount of oxygen in the environment is not favourable even for aerobic fungi; it can be caused by a simple increase of atmospheric pressure – this is used in industry and laboratories to prevent contamination by undesirable fungi in fermentation processes. Also increased concentration of CO_2 is toxic to aerobic fungi; it is probably directly caused by changes of pH in the environment.

In addition to respiration, oxygen is also important for the production of sterols, unsaturated fatty acids and some vitamins.

Oxygen transfer can take place in cytoplasm (at the cellular level) or in tissues („air cavities“ inside the rhizomorphs allow growth even through oxygen-poor wood substrate).

While in the atmosphere there is almost 21% oxygen and less than 0.04% CO_2, in the soil the O_2 content can drop to 10% and in decaying wood even to 1%; heavy soils with dense clods or decaying trunks of large diameters have worse gas permeability. Oxygen gas is also poorly soluble in water, thus its diffusion is slowed down in wet substrates.

In contrast, as a result of intensive metabolism the proportion of carbon dioxide in the substrate increases (not only product of microorganisms, but also of plant roots) and volatile growth-limiting compounds may be released (by bacteria and fungi).

A certain concentration of carbon dioxide (around 7%) can stimulate the growth, but at a higher concentration (above 10% CO_2, still calculated at 20% O_2) it is already slowed down and in soils with a balanced concentration of O_2 and CO_2 (both at 20%) the species spectrum is changed (resistant species dominate); further changes in the species spectrum can be recorded when the CO_2 concentration is significantly higher than O_2 concentration (wet soils, wood).

Chemical composition and **pH** of the substrate can affect the fungi directly (effect of acidic / basic environment on the cell surface, affecting enzyme activity or membrane function) or indirectly, due to different nutrient availability at different pH (Al^{3+}, Cu^{2+}, Fe^{3+} ions are released and available in low pH, while in high pH the metals are insoluble, resulting in lack of e.g. Cu^{2+}, Mn^{2+}, Zn^{2+}).

Different fungal species prefer low or high pH values (growth at pH 0 /*Cephalosporium* sp., *Trichosporon cerebriae*/ and pH 9 /*Saccharomyces fragilis*/ was recorded in laboratory conditions, of course the range is narrower in nature).

• Acidophilous fungi grow on soil with an acidic bedrock (sandstone, svory, granite, gneiss), but process of peat formation or deposition of acid litter can also play a significant role => e.g. acidophilic fungi can grow on an acidic humus layer in spruce stand on limestone bedrock.

• Basiphilic fungi, on the other hand, can be found on soils with a basic bedrock (basalt, phonolite, serpentine), but also in forests with nutrient-rich mull-type humus (e.g. herb-rich beech or beech-fir forests).

• Specific case represent calciphilous species, requiring presence of calcareous substrate (limestone, dolomite, marl bedrock; they occur also in places where limestone was deposited during liming, road consolidation, building construction).

Slightly acidic pH, between 5 and 6.5, is optimal for most fungi; with sufficient nutrients, there is a wider tolerance in the range of approx. 4 to 7 (but inside the hyphae, the pH is almost constant around 7). However, fungi mostly dominate in more acidic soils (pH approx. 3 to 6), which are not so optimal for bacteria.

Physical properties of the substrate:
Soil structure is important, especially for soil fungi. It is mainly influenced by the solid phase (particles of rocks and minerals, organic material), forming its porosity => it affects the liquid (soil solution or just water film on the surface of the particles, its pH, leachate content) and gas phase (O_2 vs. CO_2 content) – water availability and gas permeability depend on pore size.

On the other hand, distances between the dispersed soil particles are increased by pores – the fungi must overcome empty spaces (here the mycelium is more advantageous over the yeast-like form). It has been observed that fungi grow more often along the pores than across (thigmotropism, reaction to contact with a solid, is assumed here) – forming of aerial mycelium represents a larger investment.
In addition, in sufficiently small pores, hyphae can be protected from nematodes, mites or springtails.

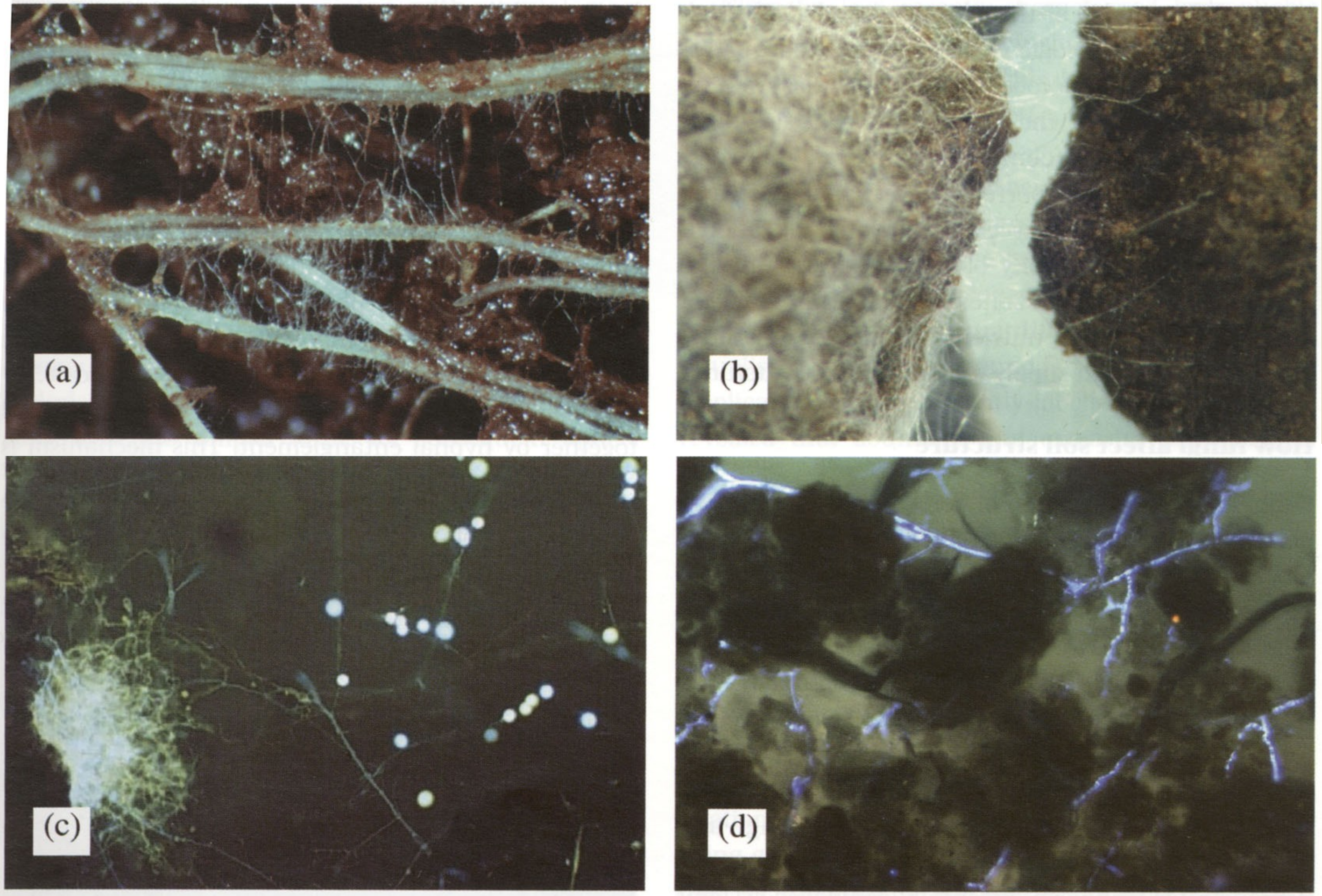


Fig 1 Fungal mycelia in the soil environment. (a) Unidentified hyphae bridging roots of *Plantago lanceolata* growing in non-sterile field soil. Note abundance of mucilage films. Image width = 2 cm. (b) Hyphae of *Fusarium oxysporum* f. sp. *raphani* colonising a pair of adjacent soil aggregates. Aggregate on left is sterile, hence extensive mycelial development. Aggregate on right is non-sterile; reduced mycelial growth is due to competitive effects of indigenous microflora and reduced nutrient levels therein. Image width = 1 cm. (c) Unidentified mycelium growing in soil pore, visualised in thin-section of undisturbed pasture soil, stained with Fluorescent Brightener 28. Note proliferation of hyphae on pore wall in left of image. Bright spherical objects are sporangia. UV epifluorescent illumination. Image width = 150 µm. (d) Mycelium of *Rhizoctonia solani* growing in sterilised arable soil, visualised in thin-section stained with SCRI Renaissance 2200. UV epifluorescent illumination. Image width = 150 µm. (Image sources: the authors)

Fungal mycelia in different soils. The methods used for their visualisation allow to detect and quantify the mycelium of soil fungi (including the distinction between living and dead mycelium).

Source:
Ritz & Young 2004, taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

Saprotrophic fungi prefer soils with high nutrient content
(soils with accumulated humus, also heavy clay soils are suitable for some species, although aeration also plays a role here).

Lighter and granular soils are more favourable for mycorrhizal fungi; they generally less occur at sites with higher nitrogen content.

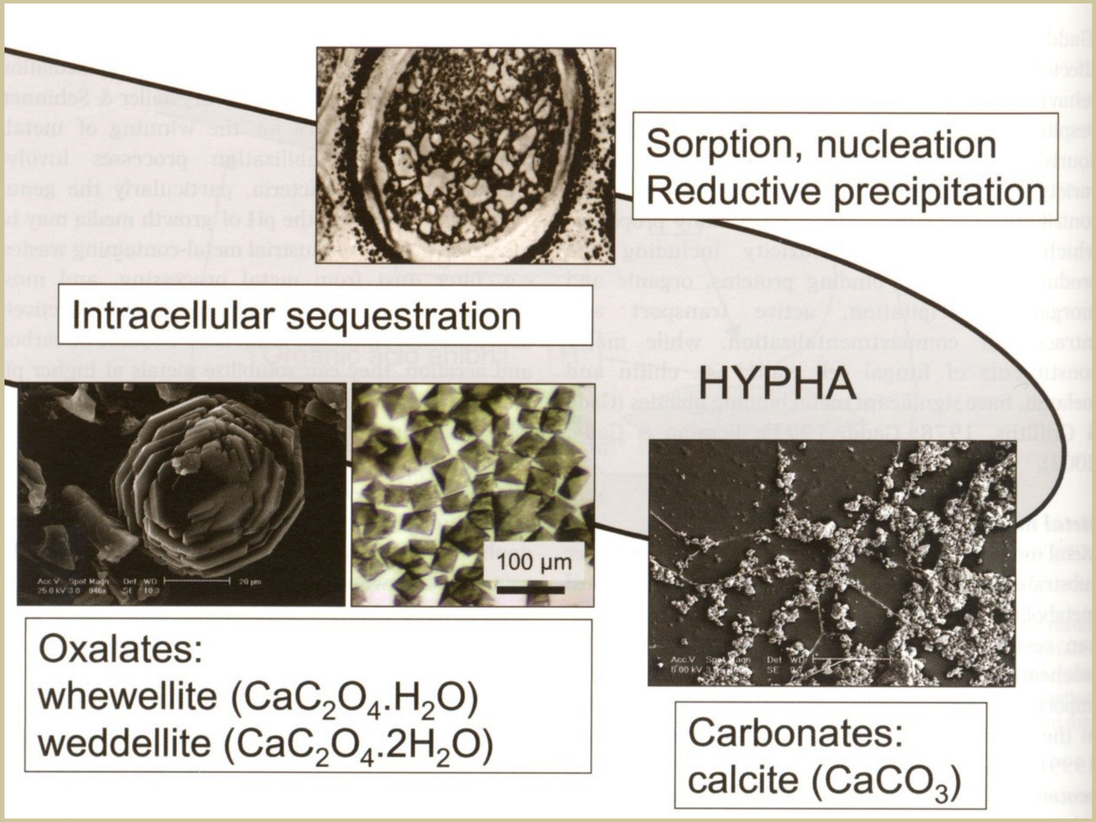
Mycologically the poorest are ravine habitats (especially mycorrhizal species are absent here); the reasons can be seen in the imperfectly developed soil horizon and large fluctuations of the microclimate.

Psammophilic fungi (some species of gasteromycetes and gilled fungi) thrive on sandy soils (Polabí region, southern Bohemia, southern Moravia).

For some fungi, **relief of the terrain** is an important factor – for example, *Suillus grevillei* more frequently grows "below" the larch than "above" it on the slope
(in this case, the availability of the partner tree roots is decisive).

The fungi themselves **affect the physicochemical properties** of the soil (when desiccated, colonised soil has a different structure than sterile). The hyphae connect soil particles with hyphae and at the same time the excrete compounds which cause aggregation of particles, bind elements, are hydrophobic or difficult to degrade (e.g. melanin or glomalin /*more about this topic see in the chapter dealing with mycorrhizal symbiosis*/).

The hyphae can also form aggregation nuclei for mineral formation; in addition, they also form micropores in the soil, which remain after their death, and also participate in weathering of the bedrock or subsoil (*more in the chapter dealing with soil fungi*).



Source: Gadd 2004, taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_4.ppt

Temperature – different fungi have different minimum, optimum and maximum temperatures (when the limit values are exceeded, the activity of cells stops due to denaturation of key enzymes or collapse of regulatory mechanisms of their metabolism => the cells die). Mycelium is the most sensitive to temperature fluctuations; on the contrary, survival structures (sclerotia, chlamydospores, to varying degrees conidia, sexual spores) can withstand considerable fluctuations.

The rate of growth and metabolic processes is the highest at optimal temperature and decreases towards the minimum and maximum – this is absolutely true in laboratory conditions, while growth in the nature can be affected by competition of other organisms. The temperature optimum may not be the same for vegetative growth and for fructification (e.g. *Flammulina velutipes* has an optimum of 25 C for growth, but 5–10 C for fruitbody formation); in general, the temperature optimum range for fructification tends to be narrower.

Flammulina velutipes

Photo Josef Hlásek, http://www.hlasek.com/flammulina_velutipes_a8875.html

Similarly to water requirements, according to relation to the temperature we distinguish psychrophilic (unable to grow above 20 C), psychrotolerant (grow even at low temperatures, but optimum around 15–20 C), mesophilic, thermotolerant and thermophilic (unable to grow below 20 C, optimum approx. 35–40 C) fungi.
Sometimes the first impression can be deceiving – e.g. *Fusarium nivale*, considered to be psychrophilic, overwinters under snow, where, however, the temperature can rise to 20 C during the melting.
Similarly, species that can be found under piles of plant remnants, where the matter heats up, are mesophilic rather than psychrophilic.

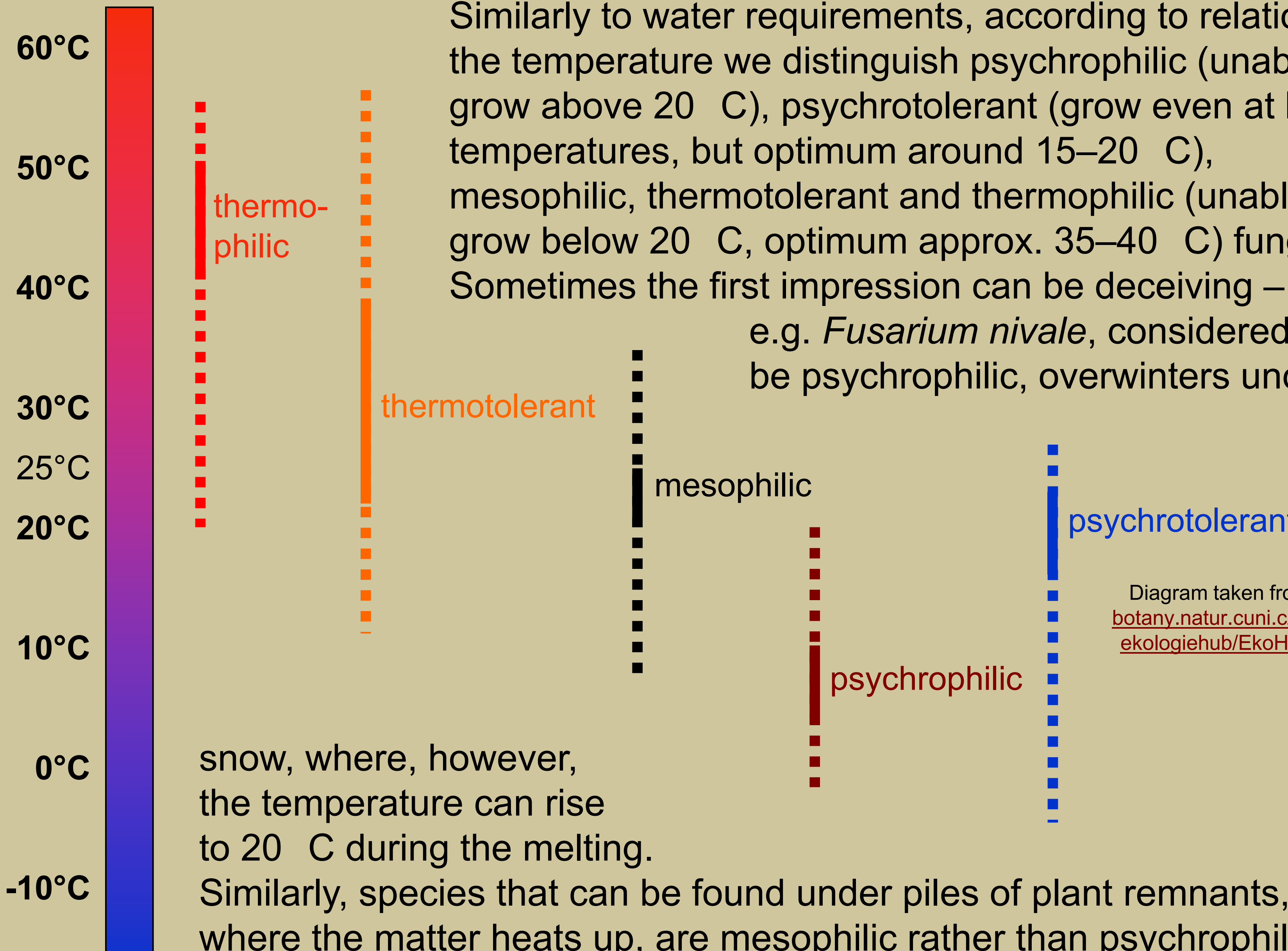
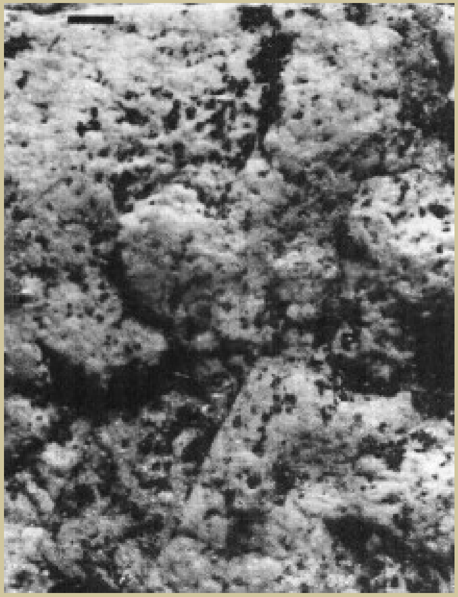


Diagram taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_2.ppt

Extreme psychrotolerance can be observed in polar regions – only soil yeasts grow at temperatures below 0 C. However, in sites with temperatures above zero and occurrence of bryophytes and vascular plants e.g. *Geomyces pannorum* or *Mortierella* species can be found, and in subantarctic regions with woody plants also hymenomycetes of the genera *Galerina* or *Omphalina* occur – mostly psychrotolerant strains of mesophilic species.

Conversely, desert microcolonial fungi (*Lichenothelia*) or species occurring in thermal springs (*Dactylaria gallopava*, recorded growth at 61.5 C) are extremely thermotolerant; under dry conditions, ascospores of *Talaromyces flavus* can survive even 80 C, and conidia of fungi of the family *Trichocomaceae* were isolated even from the bark after a fire (experimentally they survived 105 C). Some endomycorrhizal or endophytic fungi also show tolerance to high temperature (a positive effect of a fungus of the genus *Curvularia* on the growth of the herb *Dichanthelium lanuginosum* has been described).



Left: *Galerina autumnalis*

http://www.mykoweb.com/CAF/species/Galerina_autumnalis.html

Right: *Lichenothelia*, forming small colonies on the rocks (max. 100 μm), uses moisture from the dew. It has one more advantage over lichens – not needing light, it can grow in the dark.

Source: Palmer et al. 1997, taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_2.ppt

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

In general, fungi are more commonly adapted to lower temperatures, for example many parasitic species are able to grow at temperatures below 15 C; their growth in cold areas is usually not limited directly by temperature, but by short duration of the vegetation season – for example downy or powdery mildews (except for those that overwinter in host resting buds), are not able to complete the life cycle in short season.

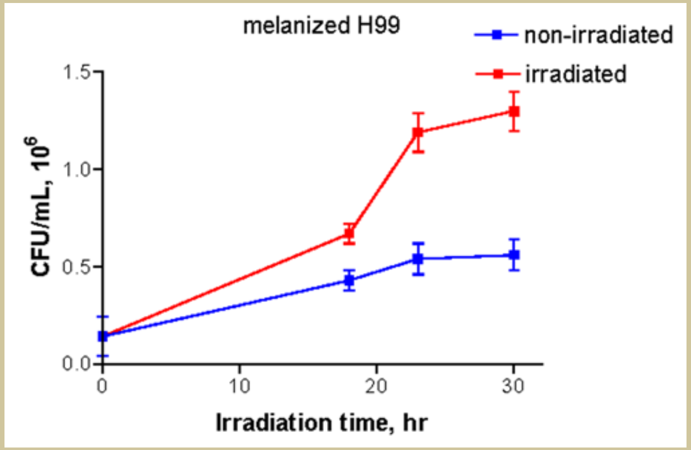
Stable conditions without large temperature fluctuations are necessary for life of „domesticated“ fungi – this fact is often more important than the absolute value of temperature, e.g. *Serpula lacrymans* grows commonly even at 15 C.
(The „domestication“ of some species is a clear example of how the long-term influence of environmental conditions may result in a shift of the ecological optimum – the evolutionary promotion of a chain of small mutations leads to gradual adaptation of the species to new conditions.)

Light is not a purely limiting factor for heterotrophic organisms, it does not affect the growth of vegetative mycelium, but has an effect on the formation of spores and fruitbodies. It was recorded that visible light stimulates, for example, formation of *Schizophyllum commune* fruitbodies or slime mould sporocarps, it is also needed for other species of fungi (*Pilobolus kleinii*, *Nectria haematococca*). In the dark, *Gloeophyllum*, *Neolentinus* or *Pleurotus* species form „mine forms" in which pileus and hymenophore is not formed (see photo). Fungi growing in deficit of light often lack pigments (it is not only the case of mine forms, the same has been observed in laboratory cultures).

Reactions to UV radiation and near blue light have been observed in some fungi. Absorption of radiation by some substances in the cell can lead to the formation of free radicals, and subsequent oxidation damages the cell components – to prevent such damage, formation of carotenoids, which play a protective role against these oxidants, is induced under the influence of radiation.

Radiation also induces the formation of melanin, providing „universal protection“ against UV radiation, radioactivity, drying (it binds large amount of water), extreme temperatures, reactive compounds (H_2O_2, free radicals), lytic enzymes (chitinase, glucanase), which also strengthens cell walls, binds and accumulates metals (Zn, Fe, Cu up to 50 times more than in the environment) and in pathogenic species it can also be a virulence factor.

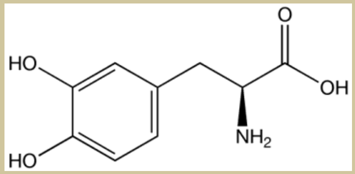
In some species with melanised mycelium, a positive effect of γ-radiation on their growth was also observed (isolation from soils in the vicinity of Chernobyl, see results in the graph).

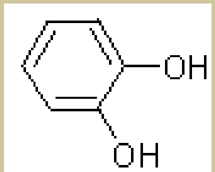


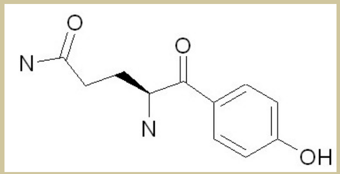
Growth comparison of growth of irradiated and non-irradiated cultures of melanized forms of *Cryptococcus neoformans*

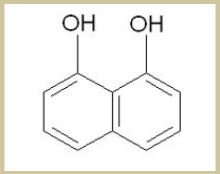
Source: Palmer et al. 1997, taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_2.ppt

Melanin is a dark macromolecular compound composed of several types of monomers (left to right): dihydroxyphenylalanine (DOPA; occurrence in mammals, in fungi perhaps only *Tuber* sp.), catechol (only *Ustilago* sp.), glutaminyl-4-hydroxybenzene (GHB; mostly *Basidiomycota*), 1,8-dihydroxynaphthalene (DHN; predominantly *Ascomycota*); it does not contain nitrogen, but is bound to proteins and polysaccharides in cell wall. It is a chemically and biologically very resistant substance (resistant to lytic enzymes, insoluble in boiling water or hot acid, degradable only in hot base).









Flavoprotein enzymes (flavonoids) bound to membranes in fungal cells are considered potential visible light receptors; mycochromes and mycosporins are considered to be UV receptors.
Photosensitivity may have appeared and disappeared several times in evolution of different groups, and a number of compounds are potential photoreceptors.

Not only hyphal growth, but also release of spores or sporangia (e.g. *Pilobolus*) can be oriented towards the light.
/*More about fungal growth and movements see in the end of the chapter Hyphae and vegetative thallus of fungi in the study material of General mycology*./

Sporulation of phytopathogenic fungi depends on the direction of the incoming light – the lighting signals the direction out of the tissue and the fungus thus ensures sporulation on the surface of the host tissue, where spores have a chance to release into the environment.
Because plant tissues are quite permeable to visible light, fungi are influenced more by UV radiation, which does not go through the tissue so much (induction of conidiogenesis or fructification of *Botrytis cinerea* or *Pleospora herbarum*).

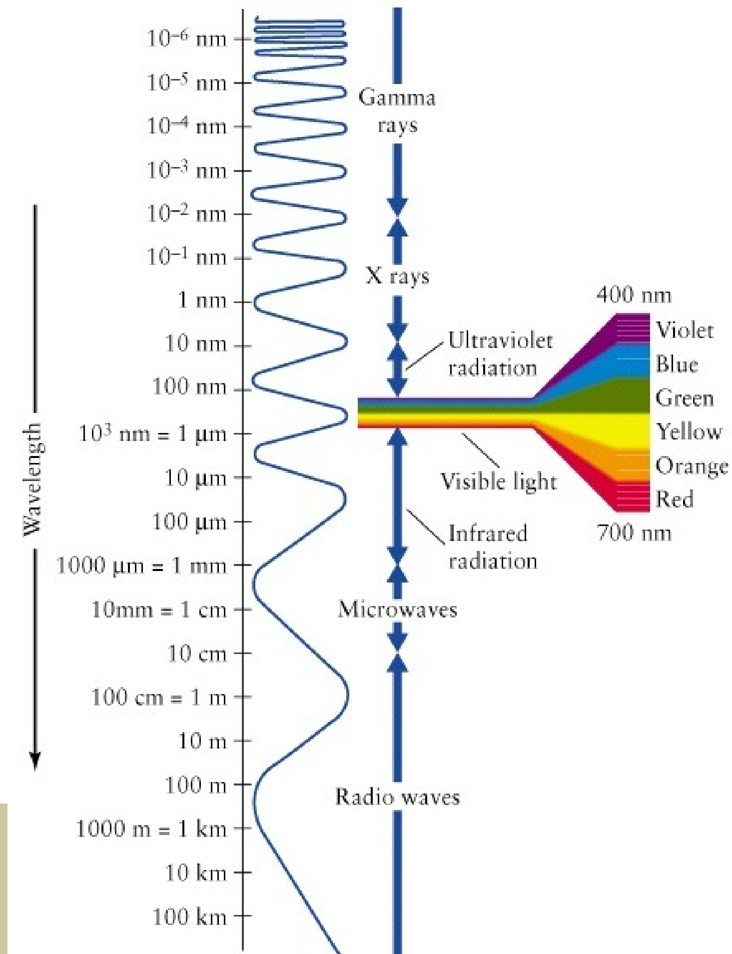
Some fungi germinate better in the light, others in the dark; in certain species, fructification (*Coprinus congregatus*) or sporulation (*Pilobolus kleinii*) occurs only when light and dark alternate. In laboratory conditions, sporulation was also induced by alternating darkness with „black light“ (300–380 nm, at the transition of UV and visible light; a 12h/12h cycle was applied for 3-4 days).

Source: Cooke & Whipps 1993, taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_2.ppt

Table 5.3 Examples of irradiance wavelengths stimulatory to reproduction (from Tan, 1978, © Edward Arnold).

Ultraviolet (200–320 nm)	Near ultraviolet and blue (330–500 nm)	Yellow/red/far-red (550–675 nm)
Conidiation *Alternaria chrysanthemi* *Helminthosporium oryzae* *Stemphylium botryosum* *Pyricularia oryzae* *Botrytis cinerea*	Sporangium initiation *Phycomyces blakesleeanus*	Ascospore formation *Saccharomyces carlsbergensis* *Leptosphaeria avenaria*
Pycnidium formation *Ascochyta pisi* *Septoria nodorum*	Conidiation *Aspergillus ornatus* *Penicillium isariiforme* *Trichoderma viride*	
Perithecium formation *Pleospora herbarum* *Leptosphaerulina trifolii*	Circadian rhythm of conidiation *Neurospora crassa*	
Ascospore formation *Leptosphaerulina* spp.	Coremium formation *Penicillium claviforme*	
	Perithecium formation *Gaeumannomyces graminis* *Nectria haematococca*	
	Ascospore formation *Saccharomyces carlsbergensis* *Saccharomyces cerevisiae*	
	Fruitbody initiation *Favolus arcularius* *Schizophyllum commune* *Sphaerobolus stellatus*	
	Sclerotium initiation *Sclerotinia sclerotiorum* *Sclerotium rolfsii*	

http://eosweb.larc.nasa.gov/EDDOCS/Wavelengths_for_Colors.html



Examples of the influence of visible and UV radiation and the alternation of light and dark phases on the fructification and sporulation of selected species

The influence of light on the circadian cycle can also be demonstrated by the example of downy mildews, which create spores in the dark – then, in the morning minimum with water present on the plant surface, they spread the spores. The first signal for sporulation is light in this case, but there is an obvious correlation of factors – temperature and precipitation go hand in hand with dawn.

Correlation of various **abiotic factors** can be demonstrated by interaction of temperature and humidity. Similar conditions are defined by the Lang factor – a fraction of the temperature and humidity values: lower temperature and lower precipitation have a similar effect as a combination of higher temperature and precipitation (temperature also affects the water regime of the fungus and precipitation must compensate for evaporation). In general, the highest tolerance to low water potential is in optimum temperature of the environment and the highest tolerance to extreme temperatures is related to optimum water potential (i.e. enough water). Water requirements are also related to pH – if the pH is not optimal, a higher water potential is needed for growth and spore germination.

Another example is the effect of environmental conditions on the amount of spores in the air; it is the highest in cloudy, foggy weather, smoke haze – if a layer that absorbs rays of certain wavelengths (mainly UV radiation in this case) is present. In some groups we can find peculiarities, such as the two-peak curve of *Phytophthora infestans*: in the water drop zoospores are released from sporangia, while at higher temperature the sporangium „germinates“ directly with hypha – overproduction of "conidia" (inaccurate term for germinating sporangia) may reflect unfavourable conditions in the environment.

Abiotic factors may **affect the fructification** more than vegetative growth:

• CO_2 – high concentration inhibits fructification of basidiomycetes, on the other hand it can induce fructification and sporulation in ascomycetes;

• humidity – too high humidity causes deformation of the fruitbodies (above-mentioned example of *Polyporus brumalis*), drought can be a signal to start fructification (desiccation => stress => secondary metabolism => fructification);

• water and moisture – many species cannot sporulate in submerged culture (some species of the genus *Penicillium*), whereas *Chytridiomycota* or *Peronosporomycota* need water for zoospore movement;

• temperature – optimum for sporulation is usually lower than the growth optimum; different temperature may affect the type of conidiogenesis (production of macro- vs. microconidia) as well as the ratio between conidiogenesis and sexual reproduction;

• fire => fructification of ectomykorrhizal ascomycetes – the reasons for this are still quite unknown...

/From physical factors, also time, gravitational and electromagnetic forces affect the development, growth and movements of fungal structures (vegetative and reproductive). Their influence will also be described at the end of the chapter Hyphae and vegetative thallus of fungi in the study material of General mycology./

It is always desirable to take into account the sum of all factors, the **ecologically optimal values** of which may differ from the physiologically determined ones (measured in the laboratory). The optimum, extreme values and tolerances for environmental conditions tend to be different for different strains of one species.

Shift of the values of environmental factors to the extreme values can affect the competition between fungi – the species, which better thrives in unfavourable conditions, wins in the competition (e.g. *Mycena galopus* vs. *Gymnopus androsaceus*, *Trichoderma koningii* vs. *Trichoderma hamatum*).

Biotic factors are especially important for parasites and species living in a symbiotic relationship with other organisms.

Depending on the environmental conditions, fungi can occur **in different forms**:
- fructification only at favourable temperature and sufficient humidity, otherwise they survive for many years only in the form of mycelium;
- occurrence in mycelial or yeast-like form in some groups;
- survival of unfavourable conditions in spores, while the vegetative thallus dies.