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)*

# LIFE STRATEGIES AND INTERACTIONS OF FUNGI

## LIFE STRATEGIES OF FUNGI

Life strategies are a way to deal with the influence of abiotic and biotic factors. Negative influence of the environment is determined by limiting factors, stress, disturbances and competition.

- **Competition** means „rivalry" for nutrients between different species (interspecific) or strains of the same species (intraspecific); fast germination of spores, fast growth and activity of depolymerases, allowing wide use of the substrate, are the advantageous traits. /*Competition mechanisms will be later described in detail.*/
- **Stress** is a state induced by long-term and usually stable influence of environmental factors, which limits the growth of most species or strains (lack of nutrients or water, temperature or other physical factors far from optimal values – different fungi have different adaptation limits). The adapted species/strains, which are not limited in growth under such conditions, have an advantage against the others.

• The effect of **disturbance** can play a specific role in the habitat – some habitats are regularly disturbed (e.g. coastal zones), but mostly the disturbances affect a stable habitat suddenly and unpredictably.
This term usually means destructive disturbance, where the fungal biomass is (partly or entirely) destroyed by a sudden but passing change of conditions (fire, flooding, animal biting, trampling, litter removal, human intervention); in nature, however, enriching disturbances are also common, due to which the hitherto uncolonised organic matter is supplied and the fungi are thus exposed to a new selection pressure at the site.

(Beware of confusion between disturbance and stress - while the term stress means long-term exposure to environmental factors, disturbance is a sudden intervention that changes the habitat and community of organisms living there.)

A sequence of disturbances is represented in the crop cultivation – tillage, changeover of bare soil and soil with vegetation cover, changes in chemistry (either as a result of fertilisation or use of herbicides, fungicides, insecticides) => the effect on fungal communities is usually decreasing the total amount of fungi as well as the species richness – saprotrophs (e.g. *Eurotiales*) subside, ectomycorrhizal fungi disappear completely, whereas phytopathogenic fungi can expansively spread.

The strategies can be characterised as a set of similar physiological traits in particular species, or within the community. The division into r and K strategists (Pianka 1970) is not suitable for fungi; strategies of particular species are between three primary types – **„R“, „S“ and „C“ strategists** (Grime 1977, see also diagram on the next page):

– little stress and rare disturbance, strong competitors prevail
=> application of „C“ strategy;

– considerable stress and rare disturbance, strestolerant species prevail
=> application of „S“ strategy;

– little stress and frequent disturbance, fast-growing fungi prevail
=> application of „R“ strategy;

– considerable stress and frequent disturbance => fungi growing in these conditions (e.g. in deserts) are classified by some authors as „D“ strategists; due to similarity of their characteristics (they form a lot of spores, they germinate easily, but they are not strong competitors) these fungi are here also assessed as „R“ strategists.

Combined influence of environmental factors commonly occur in nature
=> we then record transient, secondary strategies of various fungi:

– presence and enforcement of competitors is affected by disturbance, stress is minimal
=> „C-R“ combination;

– adaptation to colonisation of slightly disturbed substrates/habitats with lower nutrient availability
=> „S-R“ combination;

– competition strategy in low stress conditions
=> „C-S“ combination;

– competition low, limited by moderately intense stress and disturbances
=> „C-S-R“ combination.

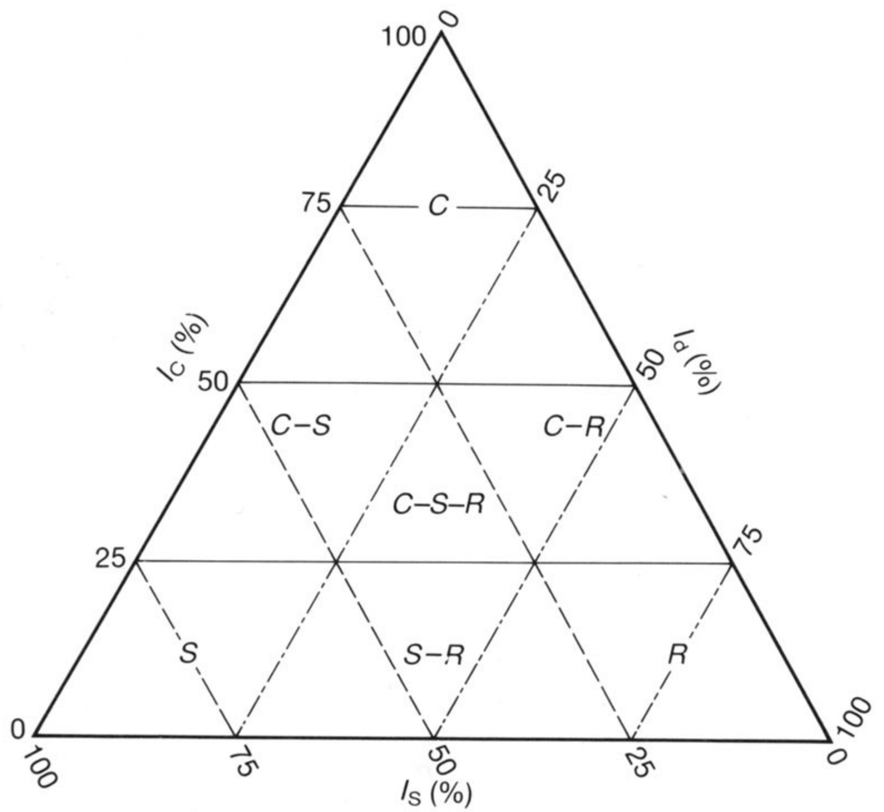



**Fig. 1.2** Model of location of primary and secondary strategies in relation to selection forces: $I_c$, relative importance of competition; $I_d$, relative importance of disturbance; $I_s$, relative importance of stress. For a full explanation of other symbols see text (from Grime, 1977, *American Naturalist*, **111**, by permission of University of Chicago Press, © 1977, University of Chicago Press).

Source: Cooke & Whipps 1993, taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_5.ppt

• **Ruderal („R“) strategists** are species with a simple life cycle, rapid development and growth, producing a number of (often mainly asexual) spores with long-term viability and rapid germination (they do not „prolong their life" by extensive mycelial growth and invest energy mainly in formation of reproductive particles) => these fungi prevail in habitats with good conditions, but either there is a rapid depletion of nutrient sources (e.g. fungi living on sugar substrates, so-called "sugar fungi") or there is frequent disturbance of the substrate;

– in the case of succession they represent pioneer stages, they easily germinate and perform rapid decomposition of substrates with simple carbohydrates, the presence of which can stimulate the germination;

– they inhabit habitats rich in readily available nutrients; they usually do not have very strong enzymatic equipment, therefore they cannot utilise e.g. polysacharides as nutrient sources;

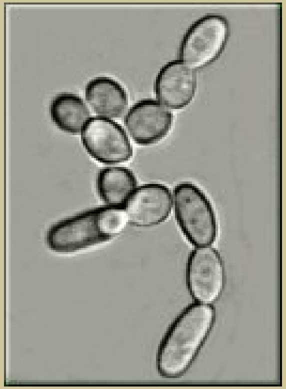
– this group includes various yeasts (common in anaerobic conditions), *Mucorales*, imperfect fungi such as *Penicillium* (opportunistic fungi forming large amount of conidia); among macromycetes, all coprophilic and anthracophilic (fire eliminates stronger competitors) fungi belong here.


*Penicillium chrysogenum* (scale bar 10 μm)
Photo Alena Kubátová, http://www.sci.muni.cz/ueb/mik/Miniatlas/pen-chr.htm

• **Stress-tolerant („S“) strategists** include fungi able to grow in conditions which do not allow survival of other species (extreme temperatures, osmotic potential, lack of nutrients); they occur even under normal conditions, but thrive better in the environment where extreme factors limit stronger competitors;

– this group includes thermo-/psychrophilic, xerophilic, halophilic species or those that live in a symbiotic relationship (including lichens), as well as some ligninolytic, chitinolytic, keratinophilic fungi;

– osmophilic fungi tolerate low water availability (*Zygosaccharo-myces rouxii* withstands a water activity of 0.61, *Xeromyces* /*Monascus*/ *bisporus* 0.62), they cope it by formation of glycerol or other alcohols in the cell (which protect membranes and enzymes from denaturation due to lack of water or accumulation of ions);



*Zygosaccharomyces rouxii*
http://www.biomed.cas.cz/~sychrova/staff.php

– extremely psychrophilic fungi can withstand temperatures below –3  C, extremely thermophilic ones can withstand above 65  C – for example they occur inside compost, where rising temperature kills other species /*see Saprotrophs*/;

– some strestolerant fungi are so adapted that they even do not grow (or have reduced metabolism) in „less stressful“ conditions;

– in unfavourable conditions, they are usually able to survive in the stage of dormant spores.

• **Competitive („C“) strategists** are able to be successful against other species in the community due to their high ability to occupy and utilise the substrate – mainly macro-mycetes with long endurance of mycelia at the site (fungi forming „fairy rings“), long fructification time (perennial polypores of the genera *Ganoderma*, *Fomes*, *Phellinus*), formation of many fruitbodies which cover the substrate (*Stereum hirsutum*, *Trametes versicolor*, *Armillaria* spp.)

Top: *Ganoderma applanatum* (= *G. lipsiense*)
Photo Dalibor Matýsek, http://www.nahuby.sk/obrazok_detail.php?obrazok_id=5758

Bottom: *Stereum hirsutum*
Photo Standa Jirásek, http://www.nahuby.sk/obrazok_detail.php?obrazok_id=66867

– they need habitats with stabilised conditions (optimally climax), without disturbance of the mycelium (dead wood, meadows);

– communities of climax stands, with well-developed network of mutual relationships, usually do not tolerate greater disturbance or stress;

– they perform slower but stronger decomposition; this group usually includes cellulolytic or ligninolytic species (only they are able to use these substrates), species able to degrade substances of the character of waxes or polyphenols;

– also mycorrhizal species are included to „C“ strategists.

Competition may not be manifested if there are enough nutrients in the environment or if different fungi have different nutritional requirements – they need some space, water, oxygen, organic nutrients as a source of energy for their growth and reproduction.
If there are not enough resources in the environment, the fungi try to suppress potential competitors using various **competition mechanisms**:

– **primary resource capture**: gaining access to a substrate that has not yet been colonised, rapid growth and coverage of the substrate, influencing of the contents of nutrients and their potential utilisation, frequent sporulation („R" strategy combined with efforts to „maintain the conquered land"; contrary to plants or algae, where access to light is of great importance to take the habitat, gaining a substrate and contained nutrients is primary in the case of fungi);

– **special niche** (used by „S" strategists);

– **combat**: an effort to maintain (defend) the substrate or „fight" the substrate already occupied by other species, production of growth inhibitors of other fungi and, conversely, elimination of inhibitors produced by other competitors
(in principle this is the „C" strategy).

**INTERACTIONS OF MYCELIA**

Contact of different mycelia on the same habitat (substrate) can be of different nature – we are considering following **interactions**:

- **neutral** – nothing happens (rather a hypothetical case, it is impossible to prove that nothing happens);
- **commensal** – one mycelium benefits from the activities of the other without causing harm to it; a typical case is decomposition of structural polysaccharides by fungi with cellulolytic or ligninolytic capabilities, on the products of which the other species feed on (secondary „sugar fungi“, typically *Mucoromycota*);
- **mutualistic** – both mycelia benefit from their activity, for example when one of them primarily decomposes the substrate, while the other one removes intermediates that the former one cannot use or contributes with its enzymes; the decomposition of structural polysaccharides by fungi with different sets of cellulolytic or ligninolytic enzymes can be mentioned as an example too;
- **parasitic** – close cohabitation, from which one mycelium benefits at the expense of another one (if only mycelia are involved in this interaction, we do not call it predation);
- **competitive** – competition for a substrate will elicit an antagonistic response in both mycelia that will adversely affect one or both of them.

In order for the traits of competitively strong species to manifest, the interaction must take place in a relatively stable habitat with as constant conditions as possible. Typical habitats are, for example, tree trunks/logs, deeper soil horizons, coniferous litter (or another type of plant litter which is difficult to decompose).

The competitive relationships between lignicolous species of fungi have long been studied and are best explored, as tree trunks provide space and opportunities for interactions of different mycelia for several years to decades.

**Hyphal interactions** can be direct or indirect. An example of indirect interaction can be depletion of certain nutrients by hyphae of one species, which in turn suppresses the growth of another species, depending on the specific source (direct contact of hyphae is not needed for suppression – on the contrary, the mentioned species can intertwine without limits if they have sufficient nutrients).

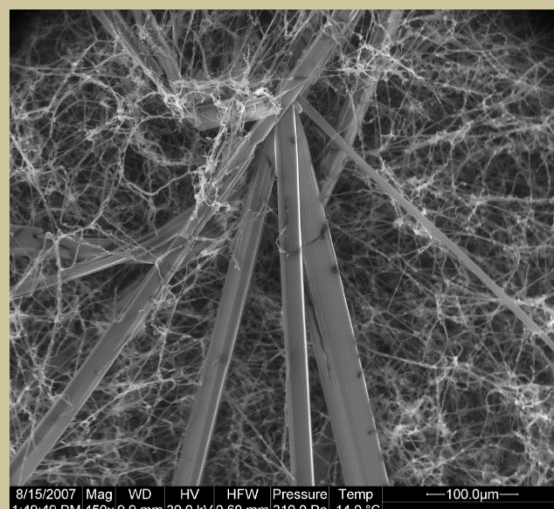
Under the term direct interaction we understand the interaction of different species by the action of inhibitors (allelopathy) or direct contact of hyphae.

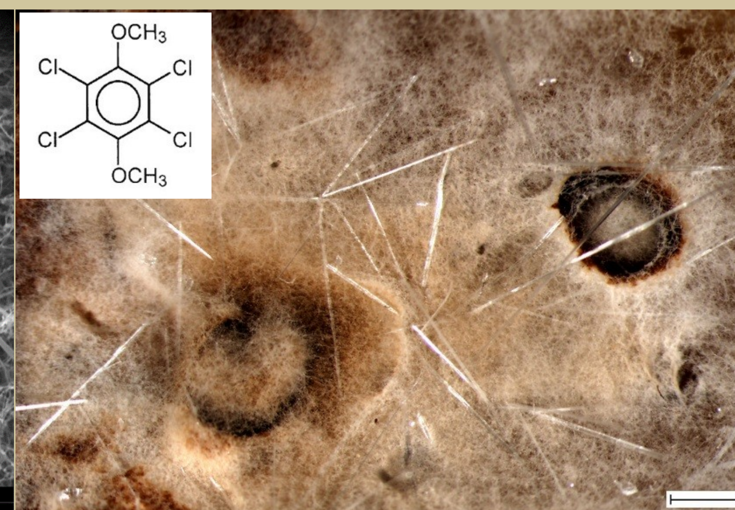
An interaction between two populations in which one destroys the other through the excretion of secondary metabolites, acting antibiotically on other species (often only in worse conditions), is called **allelopathy**.

Many substances are excreted only during competition; these are often toxic compounds which, on the other hand, can stimulate the excretion of detoxifying substances.

Most antibiotics are produced by hyphomycetes (generally by imperfect fungi), for example soil species of the genera *Trichoderma*, *Penicillium*, *Aspergillus* – they produce specific antibiotics (e.g. plectasin acts on bacteria, trichodermin against other fungi, aflatoxins are toxic to mammals) and substances with a wide range (disruption of synthesis of DNA and proteins in various organisms). Fungi often produce esquiterpene-type compounds (they also have a wide range, they also act on bacteria or invertebrates; in addition, they can remain in the substrate and positively/negatively affect its further colonisation) or halogen derivatives, such as drosophilin A (methyl ether).

http://atlashub.wz.cz/atlashub_soubory/houbywebs/spicka.htm




Drosophilin crystals on *Gymnopus (Setulipes) androsaceus* culture

Taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_5.ppt

Among macromycetes, *Armillaria* spp. or *Hypholoma fasciculare* act allelopathically; mycelium of *Marasmius oreades* (see left) secretes hydrogen cyanide (!) into the soil.

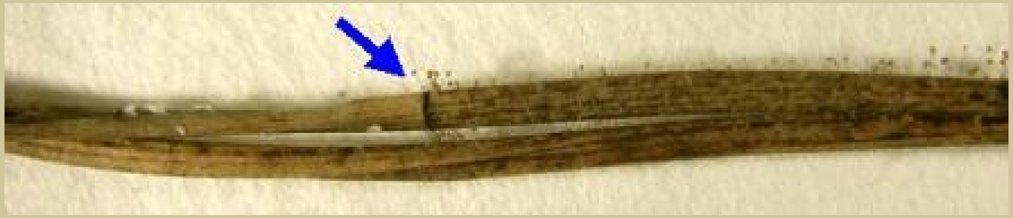

Cases of **direct contact of hyphae** are known in lignicolous fungi, whose mycelium forms „border zones“ (often dark-coloured) in the wood – in many cases these fungi do not allow the other species to grow into the confined space.
Another example of micromycetes can be seen on fallen needles, where dams formed by *Lophodermium pinastri* restrict the growth of *Verticicladium trifidum*.

Clear results of the mycelial interactions can be often seen on cross sections of logs.

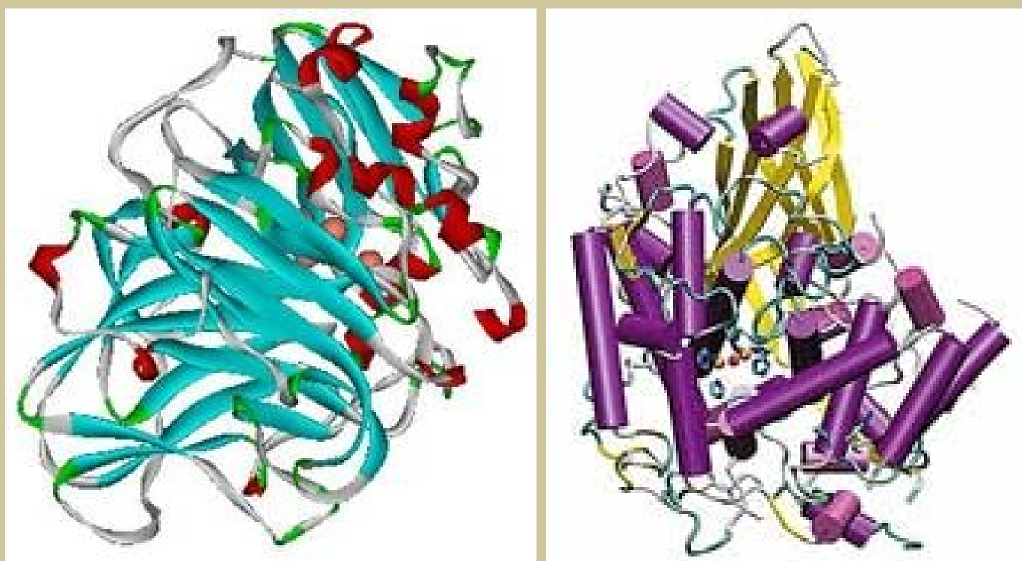
Lynne Boddy (2000): Interspecific combative interactions between wood-decaying basidiomycetes. – FEMS Microbiology Ecology 31(3): 185–194. http://onlinelibrary.wiley.com/doi/10.1111/j.1574-6941.2000.tb00683.x/full

Needles with conidiophores of *Verticicladium trifidum* (anamorph of *Desmazierella acicola* /*Pezizales*/); the arrow indicates a dam behind which the growth of this fungus is not visible.

Taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_5.ppt



Compared to freely growing ones, the competing mycelia often secrete different enzymes; the main changes are in the production of laccase and tyrosinase. Both enzymes are intracellular and are involved in the oxidation of polyphenols and tyrosine, as well as in the formation of pigments (melanin) and at the same time in „switching“ the mycelial growth between air and substrate; this has been proven at the molecular level (mRNA reverse transcription).



Laccase on the left,
tyrosinase on the right.

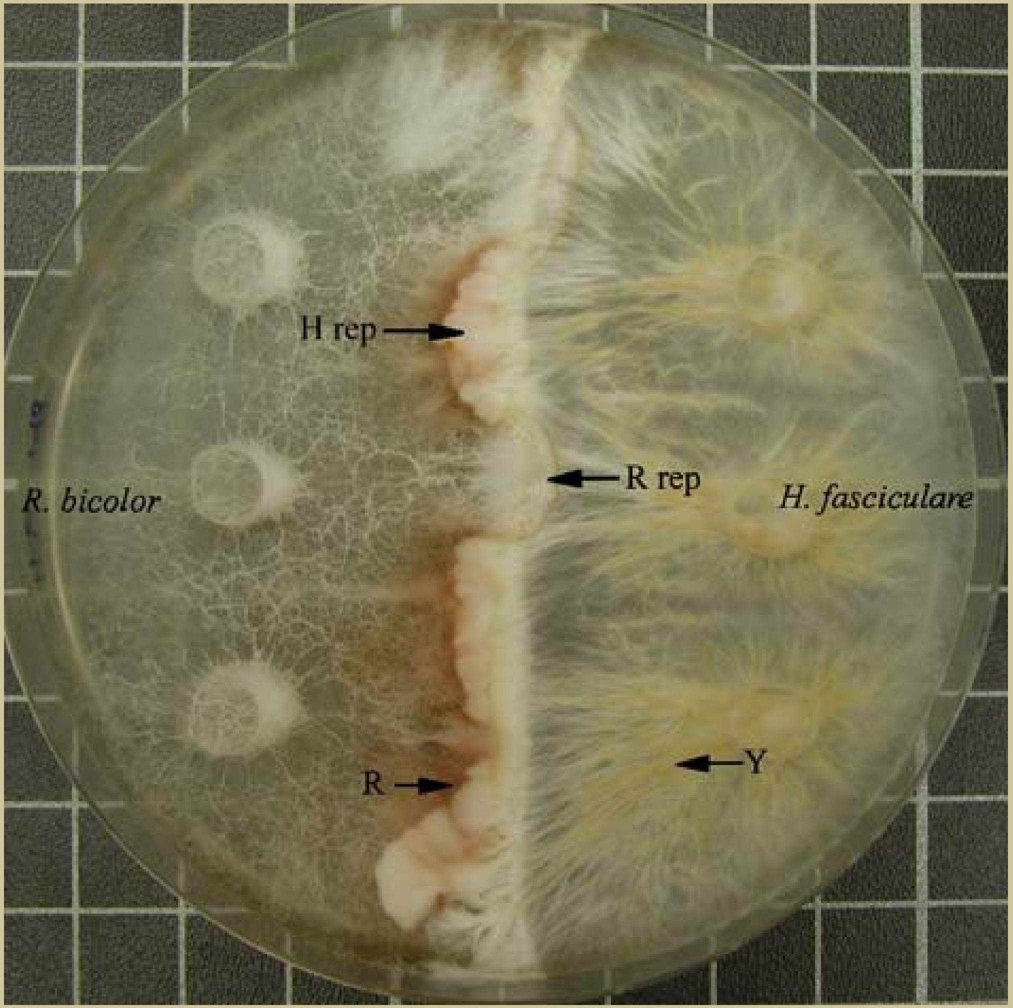
http://www.udel.edu/chem/bahnson/chem645/websites/laccase/index_files/image5951.jpg

http://www.geoscience-online.de/redaktion/focus/bild3/albino25m.jpg

Taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_5.ppt

Direct contact was monitored in detail in growth experiments on agar and sterile wood. Competition in laboratory conditions may result in:

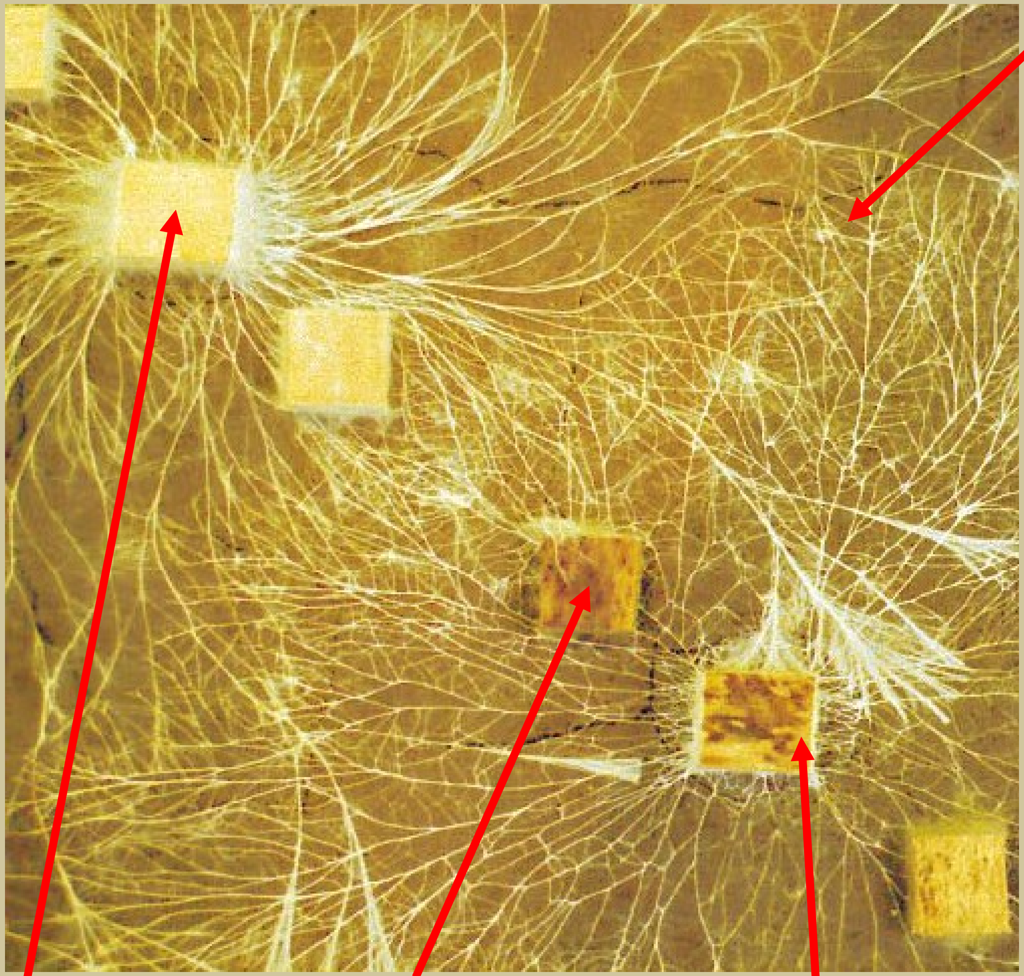
- replacement – only one fungus remains, the other is removed (at least partly);
- overgrowth – only ostensible replacement, but the overgrown fungus is still viable;
- deadlock – indecisive result, both fungi have no access to each other.




Interaction of basidiomycetes *Resinicium bicolor* and *Hypholoma fasciculare*. „R rep“ refers to places where *R. bicolor* replaces *H. fasciculare*, whereas in „H rep“ the latter species „wins“. Also the pigment production is noteworthy: the red-brown pigment is produced by *R. bicolor* (R), and in contrast, the yellow pigment is produced by mycelial cords of *H. fasciculare* (Y).

Source: Hynes et al. 2007; taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_5.ppt

Competitive interactions on wood blocks inoculated with mycelia of *Phallus* a *Phanerochaete*.



interaction of mycelial cords

*Phallus impudicus*

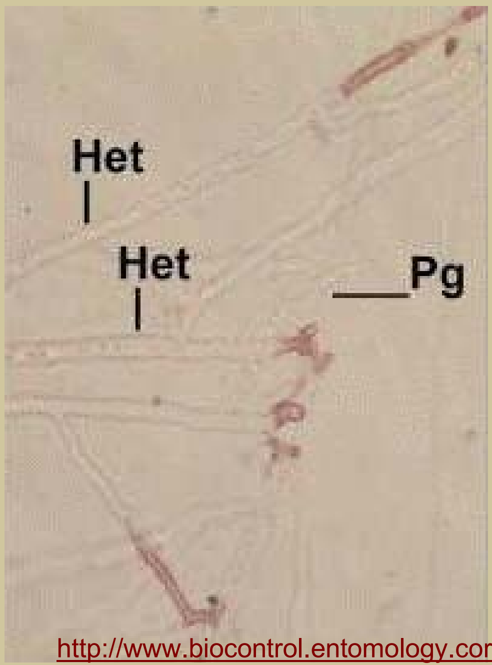
*Phanerochaete velutina*

mycelial cords of *Phanerochaete velutina* are colonising wood occupied by *Phallus impudicus*

Boddy (2000): Interspecific combative interactions between wood-decaying basidiomycetes. http://onlinelibrary.wiley.com/doi/10.1111/j.1574-6941.2000.tb00683.x/full

However, results of laboratory experiments also depend on conditions such as medium composition, size of the wood block, temperature, water potential, $CO_2$ concentration, fungal strain, age of colonies – in a paired experiment (test of two fungal species), opposite results may be obtained under different conditions. Unfortunately, biotic (presence of bacteria, invertebrates, etc.) and abiotic factors (substrate desiccation, changing amount of oxygen) are eliminated in these experiments – therefore it is a question to what extent the detected interactions are realised in nature.

The so-called **hyphal interferences** (also „contact phenomena“) were observed in basidiomacetes – at the point of contact of different hyphae, one of them „dies“ (stopped growth, vacuolation, protein coagulation, decrease of turgor, organelle breakdown).
From a human point of view, it is possible to use interferences to „fight“ against certain species (e.g. elimination of *Heterobasidion*, see example).




When *Heterobasidion annosum* hyphae come into contact with hyphae of *Phlebiopsis* (*Phanerochaete*) *gigantea* (left photo), their wall ruptures, membrane integrity is broken and protoplast spills out.

Orig. J. W. Deacon 1998;

http://www.biocontrol.entomology.cornell.edu/pathogens/phlebiopsis.html

Rarely, one hypha grows directly into another (in necrotrophs), but if the „infected“ hypha survives, a parasitic relationship can evolve (temporary or even long-term – in the case of asexual reproduction of the host).

Question in conclusion :
What is the nature of the competition in terms of profit for one or both mycelia?
A simple case is if one fungus „wins“– it obtains substrate and nutrients from the defeated opponent. However, some competition mechanisms may damage both mycelia (pigment production), changes in mycelial growth during competition may exhaust both competitors, or (used in experiments with ascomycetes) sporulation may be stimulated when mycelia meet – if the fungus sporulates rapidly, but at the cost of restricted vegetative growth, is it actually a profit or not?

The influence of competitive interactions of fungi on the substrate or other organisms have not been studied much so far (competition of saprotrophs causes changes in the substrate decomposition due to changes in the spectrum of secreted enzymes; decreased vitality of mycorrhizal fungus also affects its symbiotic partner).