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)

TYPES OF PARASITIC RELATIONS

The basic ecological division is into obligate and facultative (occasional) parasites. However, as was already written at the end of the chapter on symbioses, sharp ecological boundaries cannot be strictly defined (not even between parasitism and saprotrophy), and even the distinguishing criteria underwent changes over time.

Previously, cultivability on nutrient media was taken as a criterion for defining biotrophic parasites. It is a fact that it is difficult to cultivate biotrophs on nutrient media (cell functions, e.g. of stomata, must also be simulated on a non-cellular nutrient medium) and to a limited extent on tissue cultures (it is actually cultivation of living plant cells from which the parasite is fed biotrophically), however, for example a yeast-like stage or a haploid mycelium (but no longer a dikaryotic mycelium) can be grown in smut fungi – according to the original definition, smut fungi would be biotrophic, but facultative parasites.

Cultivation is usually not possible in biotrophic mycoparasites, which (with the exception of those forming macroscopic structures) have been so far largely out of attention and are recently known mainly from DNA extractions.

Obligate parasites are **biotrophic** – they live exclusively on living hosts or their tissues; typical examples are *Peronosporales*, *Taphrinales*, powdery mildews, rusts, smuts or *Exobasidiales*. They do not cause rapid dying out of the tissues (the death of the host would also lead to their death), but they often cause deformations of organs and plant parts (usually associated with their enlargement).

Melampsora salicina

Biotrophs influence physiological processes in the cells and tissues of the host (more than necrotrophs, which simply kill cells, see below) – usually increased supply of nutrients to the attacked cells (to „satisfy the demands“ of the pathogen), increased intensity of respiration (oxidative metabolism), releasing energy during the breakdown of sugars leads to increase the temperature in the cells. Transpiration is little affected, if the epidermis is not ruptured during sporulation of the parasite in the places where the sporomata (conidiomata) have been formed => then it results in a rapid loss of water and wilting of the plant.

Even if the host is damaged by penetration into the cells and possible disruption of the tissue, in general the biotrophic parasites try to harm the host as little as possible – they form mycelium only on the surface of the host body or in the intercellular spaces and do not create toxic metabolites, at most substances which inhibit (*Ustilago violacea*) or more commonly stimulate the growth.
In certain cases, biotrophs can even „maintain“ their host – a delayed aging of plant cells attacked by rust during its sporulation has been recorded.

Host specificity is common – usually at the genus level (a parasite species is able to attack individuals of one plant genus, for example smut species of the genus *Tilletia*), the parasite can also be targeted at a certain ontogenetic stage of the host (*Bremia lactucae* attacks lettuce seedlings). High specialisation is conditioned genetically (host gene – pathogen gene relationships); quite often a co-evolution and „arms races“ (development of „offensive capabilities“ of the parasite versus „defensive capabilities“ of the host) can be recorded.

Bremia lactucae, leaf symptoms, sporangiophores with sporangia.

Photo I. Petrželová, M. Sedlářová, http://botany.upol.cz/atlasy/system/nazvy/bremia-lactucae.html
Bottom right photo Magnus Gammelgaard, http://www.plante-doktor.dk/salatskimmel.htm

Host specificity is often accompanied by organ specificity (*Plasmopara viticola* – leaves, *Claviceps purpurea* – ovaries), but on the other hand, for example some *Peronosporales* or *Albuginales* cause systemic infections of entire shoots.

Photo Ladislav Hoskovec, http://botany.cz/cs/claviceps-purpurea/

Photo Harry Regin, http://www.pilzfotopage.de/Ascomyceten/slides/Claviceps_purpurea.html

Top: Stromata of *Claviceps purpurea* growing up from pseudosclerotia, formed by conversion of the ovaries.

Bottom: *Plasmopara viticola*, symptoms on upper side of the leaves, mycelial coating on the underside, sporangiophores with sporangia.

Photo I. Petrželová, M. Sedlářová, http://botany.upol.cz/atlasy/system/nazvy/plasmopara-viticola.html

Some rusts create so-called „pseudoflowers“ formed by spermogonia, which attract insects with their shape and smell (they release aldehydes, aromatic alcohols and esters); smells are specific for the insect species, hence there is a high probability that the right pollinator of the plant species will come (to save gametes).

Puccinia monoica
Photo Doug Waylett, http://www.flickr.com/photos/dougcwaylett/3488852835/

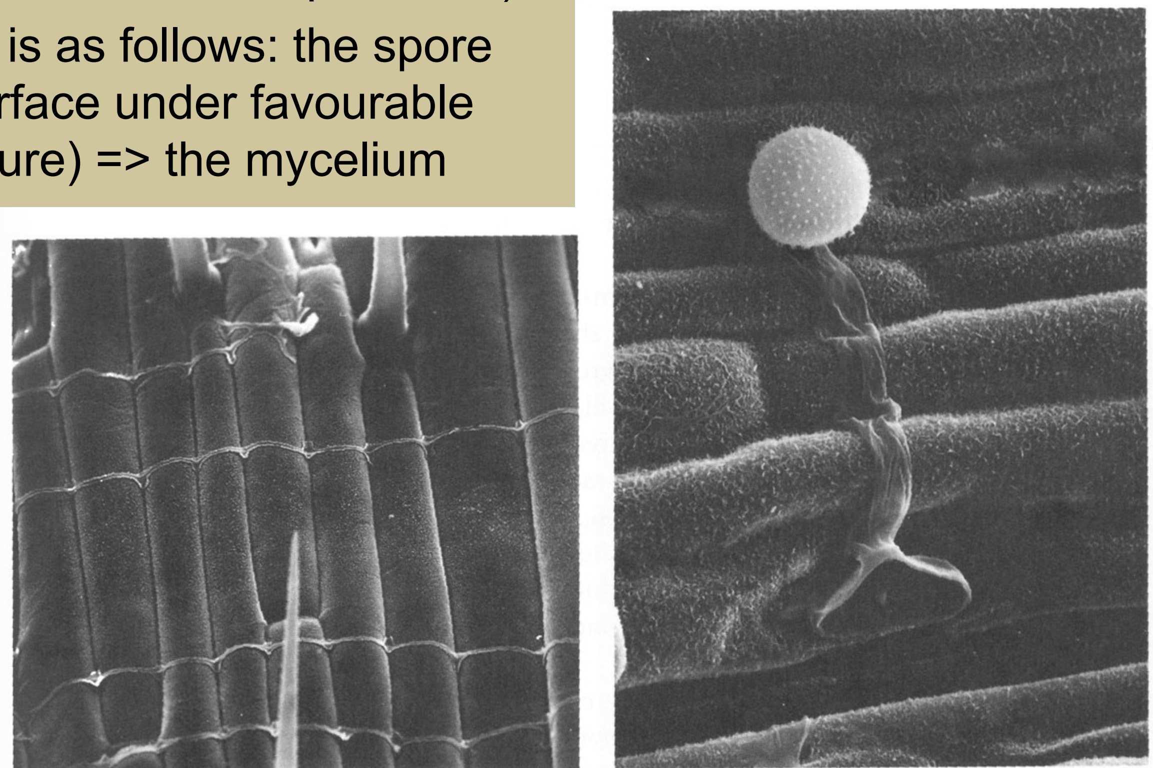
Exobasidium vaccinii or *Monilinia vaccinii-corymbosi* (also a biotrophic parasite on Vaccinium species) cause the enlargement of flowers to attract pollinators, who then also spread the spores of the fungus; in addition, the growing hypha of this fungus „looks like a pollen tube“ – it penetrates the flower through the stigma, where it uses a convenient path intended for the pollen tube.

Exobasidium vaccinii
Photo Jeffrey Pippen, http://www.duke.edu/~jspippen/fungi/mushrooms.htm

Ectoparasitism is if the fungus grows on the plant surface (some parasites colonise the area above the epidermis, but under the cuticle – so-called subcuticular infection) and only sends haustoria to the epidermal cells (or into the mesophyll). For more efficient and rapid spread, sexual reproduction of the parasite is often suppressed (common for ecto- and endoparasites).

Typical course of infection is as follows: the spore germinates on the host surface under favourable conditions (primarily moisture) => the mycelium grows over the surface – typical is thigmotropism, perception of the surface by the growing hypha (the growth reaction is often targeted to increase probability of reaching the stoma) ...

Both thigmotropism and chemotropism determine the direction of hyphal growth along the leaf surface towards the stomata; this phenomenon occurs in both ectoparasites and penetrating endoparasites (see here).



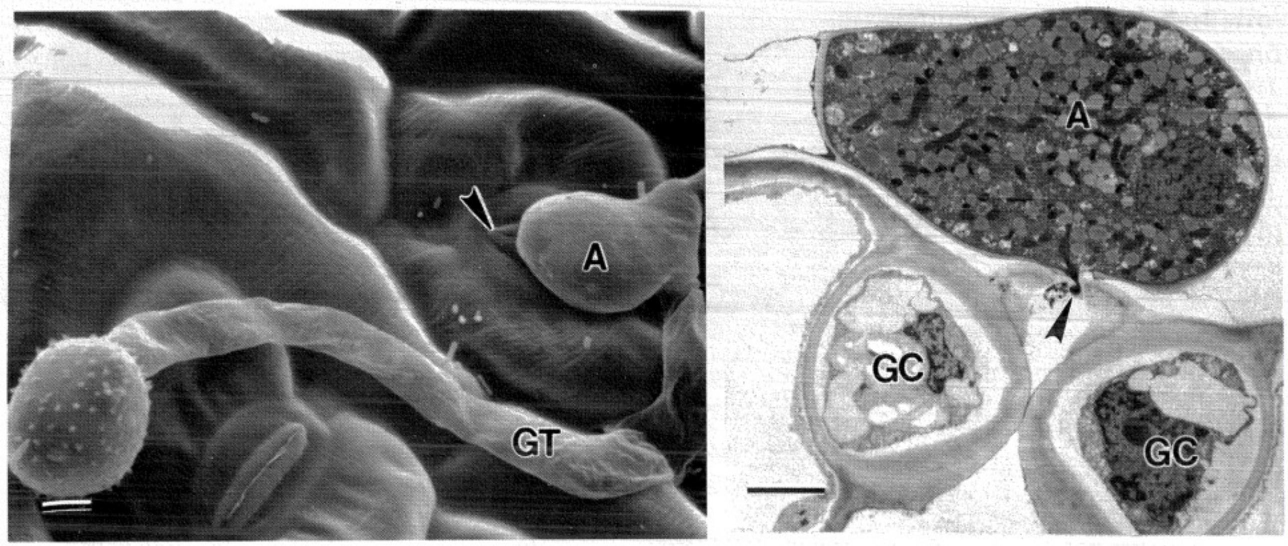
(a) (b)

taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_6.ppt

Fig. 9.2 Directional growth of urediniospore germ tubes. (a) *Puccinia graminis tritici*, four germ tubes growing across a wheat leaf at right angles to the long axis of the leaf (from Lewis & Day, 1972, © British Mycological Society); (b) *Puccinia sorghi*, urediniospore on a maize leaf with the germ tube extending at right angles to the long axis of the epidermal cells. A terminal appressorium has formed over a stoma (photograph by W.K. Wynn, by courtesy of V.A. Wilmot).

Source: Alexopoulos 1994

=> appressoria are formed on hyphae
=> penetration hyphae grow from them, penetrate the cell wall (or the stomatal aperture)
=> a haustorium is formed, which does not penetrate into the cytoplasm, but „pushes“ the plasmalemma inside => in the gap between it and the cell wall, nutrients are accumulated and absorbed by the fungus.



(A) (B) Source: Alexopoulos 1994

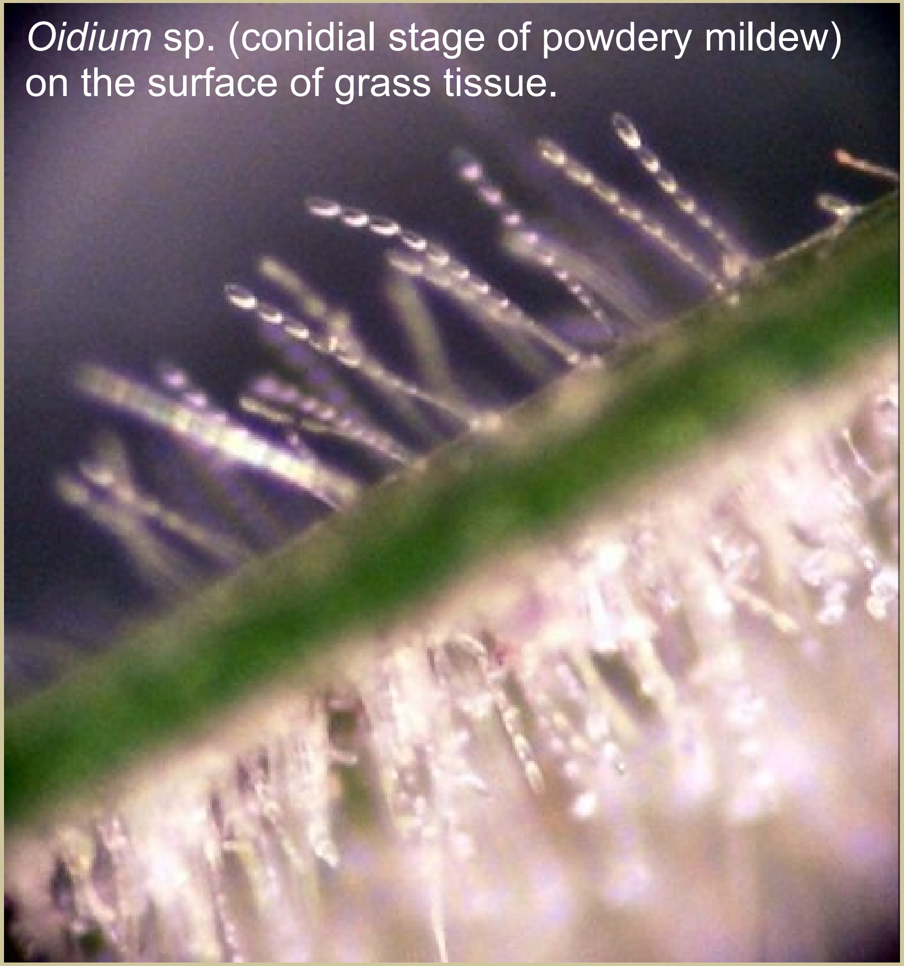
Figure 2-14 (A) SEM of an appressorium (indicated by A) of a plant pathogenic fungus on a leaf surface. The appressorium developed from the tip of a germ tube (GT) that grew over a stoma. The guard cell lips are barely visible at the arrowhead. (B) TEM of an appressorium over a stoma. A tiny peg (arrow) had emerged from the appressorium and grown between the lips of the guard cells (GC). Bars = 2.5 μm. [From Mims et al. (1989).]

taken from http://botany.natur.cuni.cz/koukol/ekologiehub/EkoHub_6.ppt

The space between the cytoplasmic membranes of the haustorium and the host cell is called the apoplast. A „neck“ is formed at the place where the haustorium entered the cell – the two membranes merge here, which isolates the „apoplast compartment“ from the surrounding space (formation of such „neck“ is found in parasites, but not in symbionts, e.g. in the case of arbuscular mycorrhiza).

Examples of ectoparasites are powdery mildews (*Erysiphales*) or scabs (*Venturia*), which additionally help themselves with extracellular enzymes to break the cuticle on the leaf or fruit surface (here they successfully attack ripening fruits, while the hypha usually cannot overcome the „finished“ lipid layer of mature fruits).

Photo Jose Rodriguez, http://www.mycolog.com/CHAP4b.htm



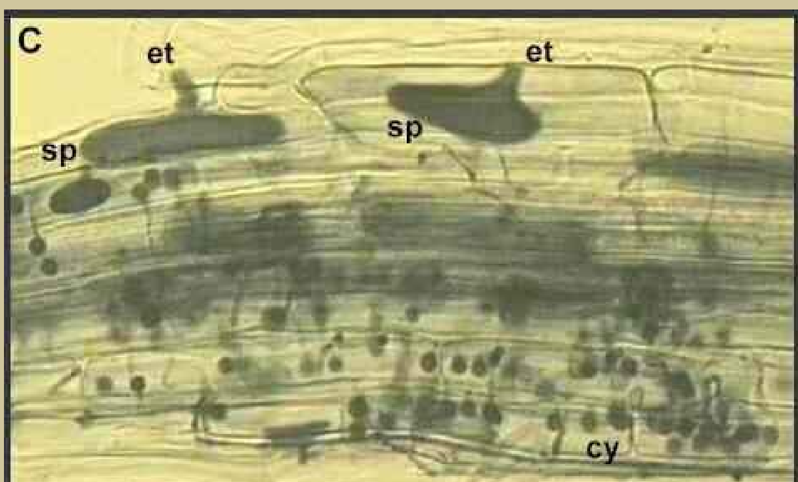
Oidium sp. (conidial stage of powdery mildew) on the surface of grass tissue.

In the case of **endoparasitism**, the process is similar, but the mycelium does not only grow on the surface, but also grows through the intercellular spaces of tissues. Common endoparasites are *Peronosporales, Taphrinales* or *Pucciniales*.

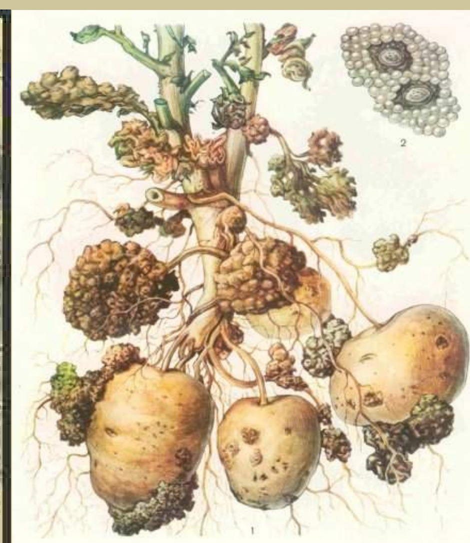
Haustoria mostly serve to absorb nutrients (but they may not be the only means of absorbing – e.g. the forming sclerotium of *Claviceps purpurea* is nourished by intercellular mycelium, which has replaced the plant tissue at the base of ovary).

Endobiotic parasites such as *Olpidium* (formerly *Chytridiomycota*, now incertae sedis), *Synchytrium* or *Plasmodiophora* grow directly in the host cells (the entire thallus, not only haustoria) – they do not kill the attacked cells, on the contrary, they induce their enlargement (hypertrophy) and proliferation (hyperplasia).

Olpidium brassicae (cysts and sporangia; **et** – exit tube), *Synchytrium endobioticum* (tumours and permanent sporangia in potato tuber tissue), *Plasmodiophora brassicae* (hypertrophy of roots).

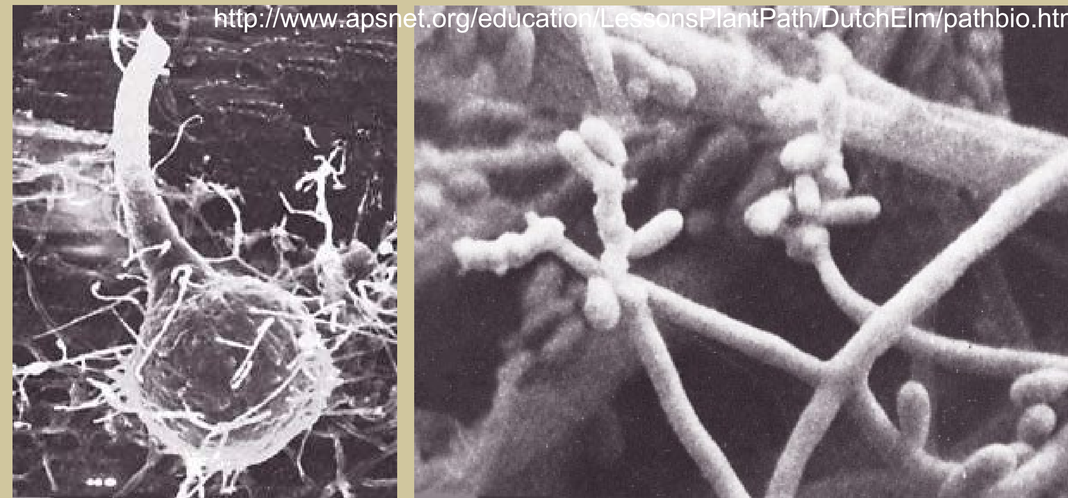


http://www.biology.ed.ac.uk/research/groups/jdeacon/microbes/chytrid.htm#The%20obligately%20parasitic%20species



http://botany.upol.cz/atlasy/system/nazvy/synchytrium-endobioticum.html, http://botany.upol.cz/atlasy/system/nazvy/plasmodiophora-brassicae.html

A special case of endoparasitism is the growth of fungus in the conductive tissues of the host – examples are the causative agents of tracheomycosis of elms *Ophiostoma novo-ulmi* or oaks *Ceratocystis fagacearum*, which, in addition to mechanically clogging the conductive pathways, also affect the plant with products of their metabolism, produce viscous substances and some fungi also toxins. Mycelium grows in the intercellular spaces of xylem (it never spreads through phloem) and thousands of conidia (blastospores) are formed on it, which travel through the flow in the conductive tissue and attach a little further, where they again germinate into hyphae => result is a limited function of the conductive tissues.

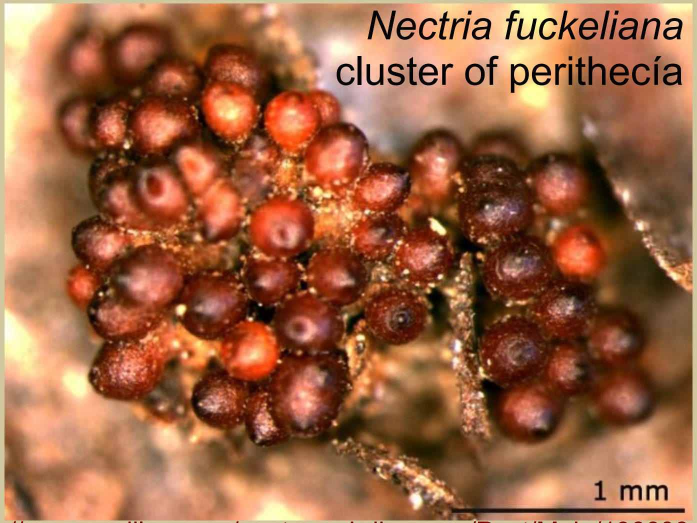


Ophiostoma novo-ulmi, perithecium and conidiophores with conidia (forming free in the wood of living trees, while in dead trees synnemata are formed in the bark and beetle galleries).

Note: Fungi that parasitise exclusively in conductive tissues are referred to as fungi causing tracheomycoses (see above), although other parasites (causing, for example, systemic infections) can also penetrate conductive tissues.

Parasites penetrate the tissues most often through natural openings – stomata (in herbs), lenticels (in the cork layer of woody plants), and in the root system through root hairs (here is the thinnest cell wall).

Facultative parasites are most often **saproparasites**, having the ability to use both living and dead host tissues (and also live as saprotrophs on a completely dead substrate). These fungi have little ability to attack healthy adult individuals, they usually successfully attack only very young/old or weakened plants (due to injury, frost, lack of nutrition, etc.).

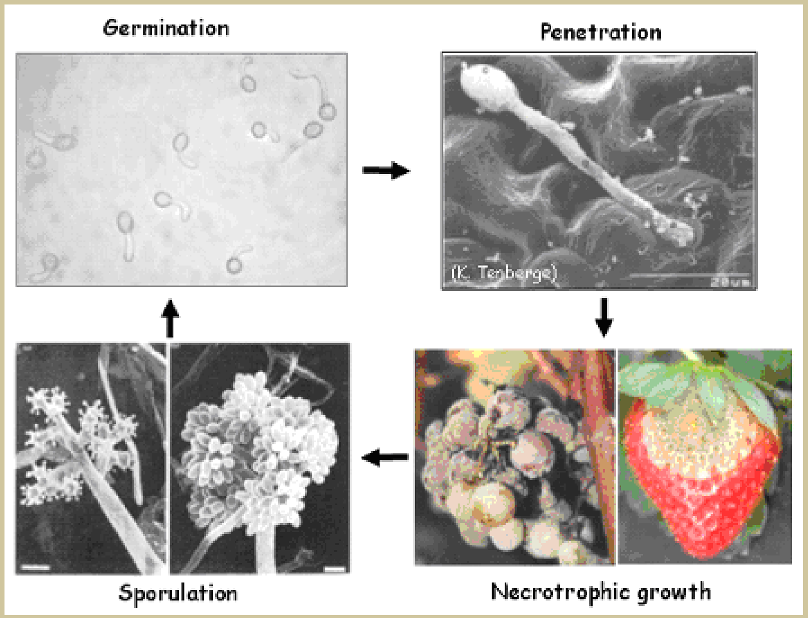


http://www.padil.gov.au/pests-and-diseases/Pest/Main/136608

The basic difference from biotrophic parasites is the fact that the host cells are killed by secreted enzymes or toxins (so, in principle, it is necrotrophy). Most facultative parasites are **perthotrophs** (perthophytes) – organisms which feed on the dead tissue of a still living host. (Even here, the concept of terms is not entirely uniform, e.g. Urban used the term perthotrophs also for necrotrophic parasites, while by the term necrotrophs he denoted saprotrophs.)

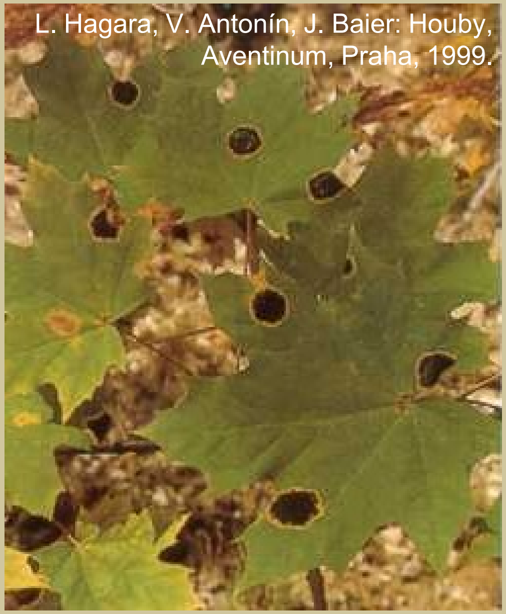
Soil fungi colonising the root surface and living from dying or dead tissue can also be included in this group; they multiply and invade the living tissue when the plant defence is weakened (usually due to a stress factor). Their reproduction can be eliminated by the presence of a mycorrhizal partner or by the competition of other species (e.g. saprotrophic and parasitic species of the genera *Rhizoctonia* or *Fusarium* compete in the rhizosphere).

Necrotrophic parasites are those that directly attack living tissue, kill cells and subsequently feed on the dead cells (we do not find specific structures to penetrate the cells – they do not even need them when they directly kill the cells).



Note: Some parasites cannot be strictly classified as biotrophic or necrotrophic because they can begin to parasitise living cells (via haustoria) and gradually or occasionally kill them (they thus change from biotrophs to necrotrophs and eventually to saprotrophs) – such are referred to as hemibiotrophic.

Necrotrophs (typically, for example, *Botrytis cinerea*) are not as host-specific as biotrophic parasites and can act either locally (manifestated as lesions, areas of dead tissue, e.g. light edges around the stromata of *Rhytisma acerinum*) or extensively => a general attack can also lead to death of the host.



Top: *Botrytis cinerea* (anamorph, sporulation = production of conidia); bottom: stromata of *Rhytisma acerinum* on leaves of *Acer platanoides*.

Normally saprotrophic fungi (for example, *Alternaria alternata*, but *Botrytis cinerea* can also be the case) which attack a host with damaged dermal tissues or weakened by another pathogen, become secondary parasites *(primary and secondary parasitism see below)*, typically necrotrophic.

In the case of necrotrophic mycoparasitism, questions arise as to what extent the relationship with the host is parasitism (sensu stricto) and to what extent the fungus tries to get rid of the competitor in an environment of limited resources, to obtain a substrate for itself by eliminating it, or to obtain nutrients obtained from the host. From this point of view, "targeted killers" (i.e. necrotrophic parasites in the typical interpretation of this term) may actually be just "very strong competitors".

Parasites of parasites are referred to as **hyperparasites**, sometimes at several levels – a parasite of another parasite can itself be parasitised (*Viscum album* – *Sphaeropsis visci* – *Xanthomonas* sp. – bacteriophage).
A commonly used concept is mentioned above, however, in a different meaning, the term hyperparasite may be used for secondary, tertiary etc. parasites.

http://www.forst.tu-muenchen.de/EXT/LST/BOTAN/LEHRE/PATHO/PILZE/DARLUCA/darluca.html

Sphaerellopsis filum (*Dothideomycetes*) in uredium of *Melampsora* sp. (left one is parasitised)

If we look among the **macromycetes**, we find no obligate biotrophic parasites; the vast majority of them are facultative parasites (the term saproparasites can be used), especially necrotrophic.
Among them, there are mostly wood-decaying fungi, especially polypores.

They can also be specialised for a certain tissue of the host, for example, *Porodaedalea pini* decomposes only the heartwood (it forms in the middle of older trees, after ca 50 years) – this Fungus does not take nutrients from the sapwood or cambium, but reduces strength of the trunk.

Porodaedalea pini (syn. *Phellinus pini*)

Photo Tomáš Přibyl,
http://www.zbelitovsko.cz/gh_kozovkovite.php

Bark is a reliable protection against fungi – most fungi penetrate the wood in the places where the bark is damaged (mechanical injury, lightning, frost cracks, insects); such fungi are called **secondary parasites**.

Only species of the genera *Heterobasidion* and *Armillaria* are able to penetrate through the roots – these are referred to as **primary parasites** (contrary to secondary parasites, which penetrate only through damaged bark, see above); their infection is usually successful when trees are weakened by external factors (insects, immissions,
low level of groundwater).

Armillaria ostoyae

Heterobasidion annosum

Parasitic fungi on herbs are more rare – for example *Pleurotus eryngii* occurring on the roots of *Apiaceae* and *Asteraceae*, *Gymnopus androsaceus* (synonym *Setulipes androsaceus*) on living heather or *Schizophyllum commune* on strawberry stolons.

Top *Gymnopus androsaceus*,
bottom left *Pleurotus eryngii*, right *Schizophyllum commune*.

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