Life cycle and pathological importance of the genus *Phytophthora*

Fungi of the genus *Phytophthora* (Greek: plant destroyer) are worldwide known as primary **parasites of fine roots and causal agents of root and collar rots and bark cankers** on young and mature specimens of hundreds of tree and shrub species. Many *Phytophthora* species belong to the most aggressive and most important plant pathogens of the world.

As a consequence of the root and bark damages the **crowns of affected trees develop typical symptoms**, eg. increased transparency, sparse ramification and stunted growth of lateral twigs leading to whip-like branch structures and clustering of leaves at the end of branches, and finally small-sized and often chlorotic foliage, dieback of branches and crown-dieback. Despite of lack of any scientific proof these symptoms are still erroneously assigned to air pollutants in the annual reports on forest condition of most European and German countries.

From a global perspective, **more than 66 % of all fine root diseases and more than 90 % of all collar rots of woody plants are caused by *Phytophthora* species**. However, *Phytophthora* is very often not detected leading to wrong diagnoses. The reasons are mainly based on the specific life cycle of *Phytophthora* which requires specific detection methods. Furthermore, when first symptoms become visible in the crown the destruction of the fine root system is already in an advanced stage. At this point the inoculum of the primary parasite *Phytophthora* has decreased to a low, nearly undetectable level, and the real cause of the disease is masked by a secondary disease process caused by high populations of secondary parasitic and saprophytic fungi.

The devasting dieback and mortality of the Jarrah-Eucalypt forests in **Western Australia** caused by the invasive soilborne pathogen *Phytophthora cinnamomi* shows which dramatic implications a *Phytophthora* disease can have for a whole ecosystem.

In **Europe**, *Phytophthora citricola, Phytophthora cactorum, Phytophthora cambivora, Phytophthora quercina, Phytophthora alni* and *Phytophthora pseudosyringae* are causing root and collar rots, and aerial, bleeding bark cankers on stems and branches of many tree species such as European beech (*Fagus sylvatica*), maples (*Acer platanoides* and *A. pseudoplatanus*), horse chestnut (*Aesculus hippocastanum*), sweet chestnut (*Castanea sativa*), limes (*Tilia* spp.), White fir (*Abies alba*), spruce (*Picea abies*), scots pine (*Pinus silvestris*) and several oak (*Quercus robur, Q. petraea, Q. cerris, Q. ilex, Q. frainetto, Q. pubescens*) and alder

species (*Alnus glutinosa*, *A. incana*, *A. cordata*, *A. viridis*). Since those *Phytophthora* species were introduced to Europe from other continents our native tree species are not adapted and therefore often highly susceptible.

Results from recent scientific studies indicate that the synergistic **interactions between root losses by introduced soilborne *Phytophthora* species and climatic extremes** are a major cause for the **general decline of forests** across Europe.
Between 1993 and 2004, my own investigations in more than 150 oak stands in 12 European countries have shown that on a broad range of site conditions *Phytophthora quercina* and nine other soilborne *Phytophthora* species are strongly involved in the etiology of **European oak decline** by causing a progressive destruction of the fine root system. These results were confirmed by several other studies.

Soilborne *Phytophthora* species are also known as causal agents of root rots and damping-off diseases of seedlings of many deciduous and conifer species, in particular in nursery environment. Since a few years, **nursery infestations** and **spread of harmful *Phytophthora* species via infested nursery stock** are increasingly recognised as a major threat to global forestry. In several studies by me and several research groups, more than 10 *Phytophthora* species were recovered from nursery fields in Germany and other European countries; some of them were almost ubiquitious.
In many amenity and forest plantations trees are dying during the first years due to *Phytophthora* infections making expensive replacement plantings necessary. Then, during the first 50-70 years of their lifes trees have a high reactivity enabling them to replace fine root losses by *Phytophthora* sufficiently. Younger trees are usually only suffering from *Phytophthora* infections on wet sites or after heavy or unseasonal rain. However, with increasing age the balance between fine root losses due to *Phytophthora* attacks and fine root replacements by the trees becomes more and more imbalanced leading to crown decline and increasing mortality, often caused by secondary invaders of the weakened trees.

The life cycle of soilborne *Phytophthora* species is illustrated in Figure 1. *Phytophthora* species are able to survive unsuitable environmental conditions over several years as dormant resting spores (oospores or chlamydospores) in the soil or in infected root tissue. When environmental conditions become suitable (high soil moisture, soil temperature > c. 10 °C) the resting spores germinate by forming sporangia which release motile, biflagellate

zoospores into the soil water. These zoospores are chemotactically attracted by young fine root tips. After penetrating the the exoderm (or the periderm in suberized fine roots) *Phytophthora* is growing inter- and intracellular inside the fine root with typical coralloid to irregular, non-septate hyphae. In the case of nutrient depletion, competition by secondary antagonistic fungi or strong defense reactions by the root the *Phytophthora* hyphae are forming resting spores. After decomposition of the root by saprophytic fungi the resting spores are set free into the soil environment, and the cycle starts again. Phytophthoras can increase and disseminate their inoculum from low, nearly undetectable levels during a relatively short time of favourable environmental conditions. On the other hand, the life cycle has to run million times, and it can take decades of inoculum build-up and progressive fine root destruction before a mature tree begins to show visible crown symptoms (Tsao, 1990). Therefore, the epidemiology of Phytophthora-induced fine root diseases is considered to be multicyclic (Erwin & Ribeiro, 1996). Predisposing factors such as waterlogging or planting of tree species which are not adapted to the site conditions as well as contributing factors, which either reduce the vitality of the tree (e.g. extreme droughts or defoliations) or favour the pathogen (e.g. excess soil moisture following heavy rain, flooding or irrigation) can accelerate the disease process or actually make it possible.

In contrast to soilborne Phytophthoras **airborne *Phytophthora* species** are spread by wind and rain splish splash via sporangia; they are causing aerial bark cankers, twig dieback and leaf necroses. Except from southern England where the invasive pathogens *Phytophthora ramorum* and *Phytophthora kernoviae* are currently causing damages on a series of tree species, airborne Phytophthoras are yet of minor importance to European forestry. However, in California and Oregon *Phytophthora ramorum* is responsible for a devasting dieback of oak trees commonly known as **‘Sudden Oak Death (SOD)’**.

Interactions between *Phytophthora* damages and weather conditions

Extent and progress of *Phytophthora* diseases are strongly depending on the weather conditions as exemplarily shown by the current epidemic of beech stands.

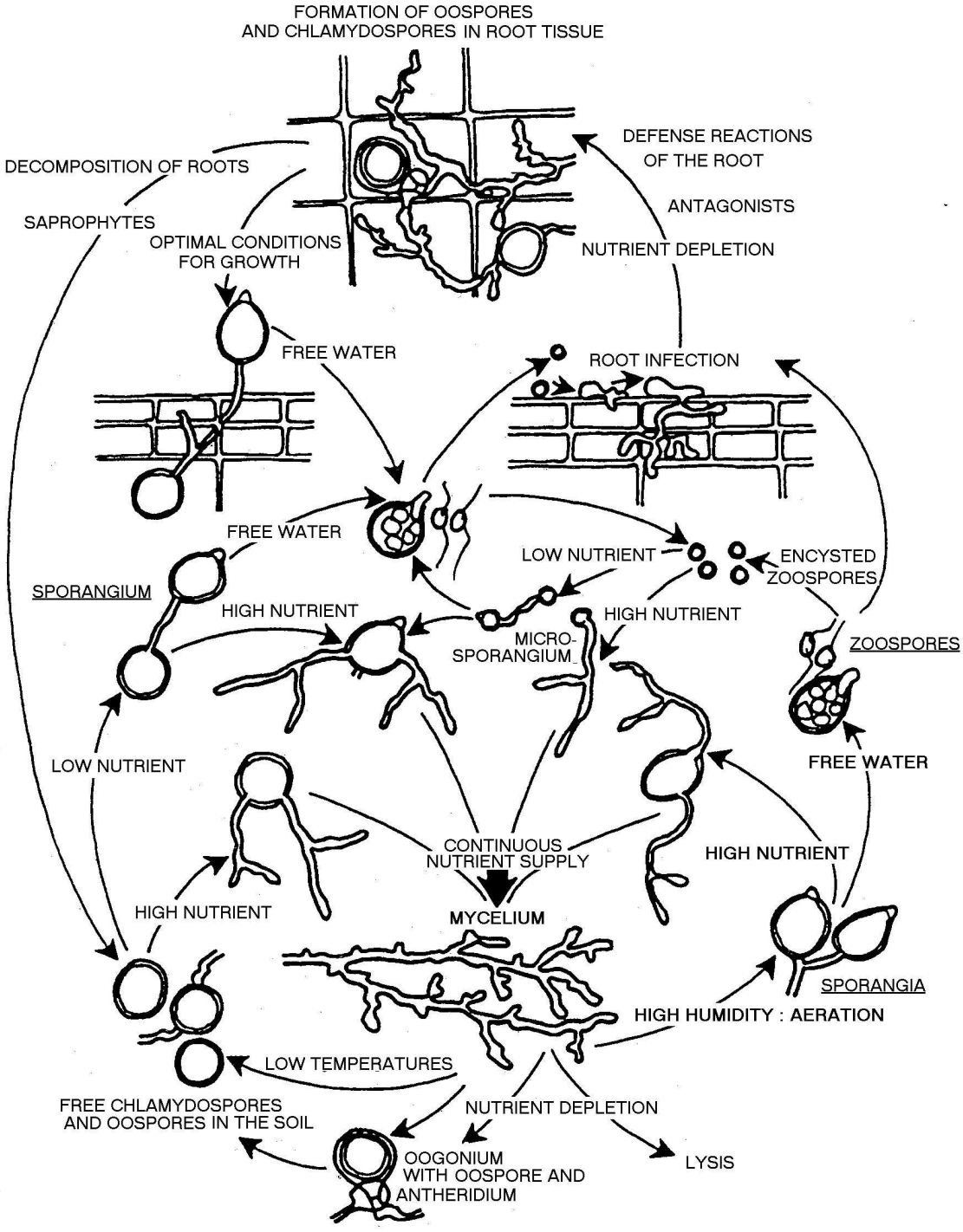
In Bavaria, the continuously high precipitations of summer 2002 led to excess soil moisture providing favourable conditions for multicyclic spread of soilborne *Phytophthora* species via zoospores. As a consequence, fine root systems of beech trees and other susceptible tree species became extensively destroyed. Moreover, due to the permanent soil saturation resistance mechanisms of many beech trees were reduced so that Phytophthoras could invade

the susceptible bark at the stem base causing collar rot and aerial bark cankers. Then, in spring and summer 2003 the weakened beech trees were faced with an exceptional and continuous drought which prevented the replacement of the extensive fine root losses from the previous year. As a consequence affected beech trees were extremely suffering and predisposed to attacks by secondary parasites, in particular *Armillaria*, *Nectria coccinea* and various species of bark beetles which often led to death.

The severe damages of beech trees are resulting from a fatal interaction between introduced root pathogenic *Phytophthora* species, the succession of an extremely wet and an extremely dry vegetation period and exploding populations of secondary parasites.

If the frequency of climatic extremes increases as predicted by most climatic models (note that the summer of 2005 was also extremely wet in Bavaria and parts of Austria and Switzerland) the frequency and severity of such complex tree damages will also increase.

Figure 1: Life cycle of soilborne *Phytophthora* species (adapted from Ribeiro 1978)



THE LIFE CYCLE OF PHYTOPHTHORA SPECIES IN SOIL AND AFFECTED ROOT TISSUE