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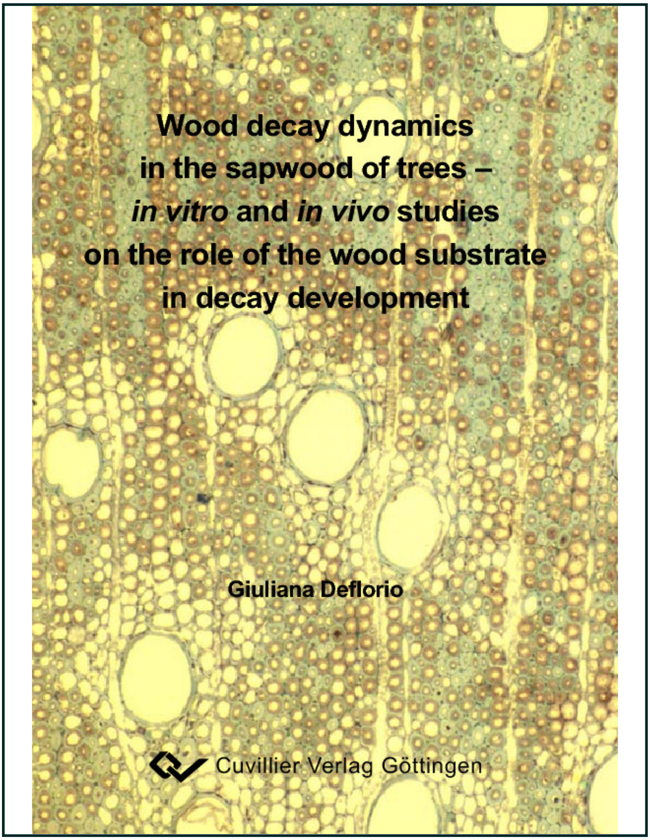
Wood decay dynamics in the sapwood of trees - in vitro and in vivo studies on the role of the wood substrate in decay development



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1. General introduction

1.1 The problem of decay for urban and plantation trees

Trees grown in urban and plantation forestry are usually subjected to a great number of both abiotic and biotic stress factors. Among the abiotic sources of stress, deficit in water and mineral nutrients, as well as air and soil pollution, are known to affect tree vigor (Gregg *et al.*, 2003; Mohammed *et al.*, 2004). Trees which become less vigorous are predisposed to damage by biotic stress factors, such as insects and fungi.

Among the fungi occurring on trees, wood decay fungi are considered an important source of damage to both living trees and solid wood products. In standing trees, most wood decay fungi require wounds on tree trunks and roots which they use as entry courts to invade living hosts and cause decay. By contrast, wood products (such as sawn logs, pulpwood, etc.) are degraded by decay fungi only if environmental and wood physical conditions are suitable for decay.

Unlike the beneficial ecological function they serve in natural forests (Franklin *et al.*, 1987), wood decay fungi are potentially destructive organisms in timber production and urban forestry. In forests managed for timber production, wood decay decreases the amount and/or quality of timber which can be sold on the market (Dickinson, 1982; Butin, 1996; Kile and Johnson, 2000). For example, Australian eucalypt plantations suffer from internal defects caused by decay fungi. This is due to silvicultural operations such as thinning and pruning which provide entry courts for infection of living hosts (Mohammed *et al.*, 2000; Wardlaw, 2003).

In urban systems, the colonization of standing trees by decay fungi poses a substantial hazard to public safety. In standing trees, the dead central part of the tree (heartwood or ripewood) is usually the first tree portion to be colonized by wood decay fungi. For this reason, decayed wood is usually restricted to the centre of the tree. However, decay fungi which are capable of spreading into the living sapwood can render trees hazardous. Therefore, infected trees can easily fail, killing people and/or damaging public infrastructures.

To counteract these potential hazards, information on the decay dynamics in host-fungus interactions is needed, so that the public demand for green city areas can be safely met, and the timber volumes produced in commercial forestry are not dramatically reduced by fungal decay.

1.2 Host-fungal interactions

To explain host-fungus interactions in plants, Agrios (1997) introduced the concept of “disease triangle”. In this concept, the amount of disease, or disease severity, is the result of the interaction among the host, the fungus, and the environment. Similarly, the application of this concept in forest pathology exemplifies decay severity as the result of three interacting factors: the standing tree, the decaying fungus, and the environment. Fig. 1 illustrates all of these factors.

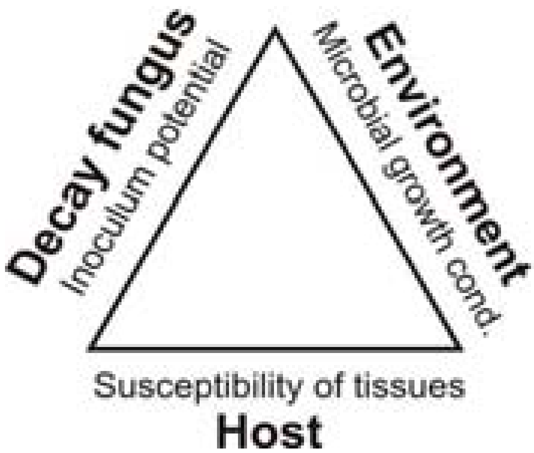

Fig. 1. Decay triangle. The severity of decay results from the interaction of host susceptibility, inoculum potential, and all of the conditions (environmental, physical, chemical) favorable to wood decay. Illustration modified from Rayner and Boddy (1988), Agrios (1997), and Schwarze (pers. comm.).

With regard to the environment, wood decay cannot become established without favorable environmental conditions. These are both exogenous and endogenous conditions. Exogenous factors relate to the external environment, i.e. the season of the year, air temperature, and rainfall. By contrast, endogenous factors relate to the physical and chemical wood conditions. Among the physical conditions, oxygen and wood moisture content are essential for the establishment of fungal decay. In particular, oxygen is critical to fungal growth, since fungi are obligate aerobes (Rayner and Boddy, 1988; Zabel and Morrell, 1992). In addition, wood moisture content is an indispensable prerequisite for the initiation of a decay process (Ammer, 1964; Thompson *et al.*, 1968; Boddy and Rayner, 1983; Redfern, 1993; Viitanen, 1997). At least 28-30% of wood moisture (based on dry wt.), equal to the fiber saturation point, is required by wood decay fungi. With regard to the chemical wood conditions, the amount and type of lignin, as well as the presence of accessory compounds, are also known to influence fungal activity. All of these aspects will be presented together with the host-related factors.

If the environmental conditions are favorable for fungal growth, the decay fungus may be capable of getting established into the host. On the one hand, factors linked with the standing tree, i.e. tree vitality, wood chemistry, and wood anatomy, are of major importance in host-fungus interactions (Rayner and Boddy, 1988; Fink, 2000; Roloff, 2001; Schwarze *et al.*, 2004). On the other, the decaying fungus influences decay severity by means of its inoculum potential. All of the aspects related to the host and the wood decay fungus will be briefly introduced in the following sections.

1.3 Wood decay fungi

Wood decay fungi are heterotrophic organisms which require organic matter for growth and reproduction (Isaac, 1992). Wood components are therefore depleted by means of their enzymatic systems, so that carbohydrates are gained and metabolized. In this regard, wood decay fungi are considered as necessary organisms inhabiting natural ecosystems such as forests, since they are capable of mineralizing and thereby recycling dead wood components, so that the life cycle can continue (Swift, 1982; Manion, 1991).

Depending upon the enzymes they possess, wood decay fungi are capable of depleting different wood cell wall components, i.e. hemicelluloses, cellulose, and lignin. In general, the classification of decay types follows the morphology of wood observed after fungal attack (Boyce, 1961; Rayner and Boddy, 1988). Consequently, wood decay fungi are classified as being “brown” or “white” rots.

Brown rot has a brownish appearance, since brown-rot fungi deplete hemicelluloses and cellulose but are generally unable to digest lignin. Brown-rot fungi are predominantly found on coniferous trees. They represent only about 6% of the total wood decay causing fungi (Gilbertson, 1980). Moreover, brown-rot fungi occur more frequently in the Northern than in the Southern hemisphere (Watling, 1982).

In contrast, white rot has a bleached appearance, because white-rot fungi metabolize all of the wood components. Furthermore, white-rot fungi are usually divided into simultaneous rots and fungi causing selective delignification. In the category of simultaneous rot, white-rots are capable of decomposing hemicelluloses, cellulose, and lignin simultaneously. In the category of selective delignification, the white-rot fungi first decompose lignin, and then gradually hemicelluloses and cellulose.

Soft-rot fungi are yet another category of wood decay fungi which was given a distinct classification (Savory, 1954; Courtois, 1963, 1965). Soft-rot fungi either erode the cell wall (soft-rot type I) or cause cavities in the secondary cell wall (soft-rot type II). From an evolutionary point of view, these fungi are considered to be an intermediate category between brown- and white-rot fungi (Takahashi, 1978; Schwarze *et al.*, 2004).

Recent investigations of several host-fungus combinations showed that several fungal isolates are capable of switching from one decay type to another within the same host (Blanchette, 1984; Schwarze and Fink, 1998; Schwarze and Baum, 2000b). This discovery suggests that the aforementioned classification may be too rigid, since the classifications of brown, soft, and white rot do not reflect the true complexity which can be found in nature (Eaton, 2000).

The development of wood decay largely depends on the colonization strategy adopted by the decay fungus. Nevertheless, the preference for a strategy by an individual fungus does not exclude its use in combination with other strategies. Rayner (1986) and Rayner and Boddy (1988) listed the five fungal strategies which are adopted by decay fungi for wood colonization. These are: heart rot, unspecialized opportunism, specialized opportunism, active pathogenesis, and desiccation tolerance. This theoretical distinction may be of help to "*classify fungal behavior but not fungi* per se" (Rayner and Boddy, 1988: page 332).

Heart rot fungi grow within the inner core of the tree (i.e. heartwood or ripewood) where living cells are absent or rare. These fungi get established through wounded roots or branches with exposed heartwood. Heart rots are capable of growing in a wood environment characterized by high oxygen content and great concentration in phenolic substances. Therefore, heart rot fungi are regarded as slow-growing fungi, lacking combative ability, and as host-specialized.

Unspecialized opportunists colonize the sapwood after accidental or deliberate wounding. These decay fungi are adapted to a wood environment with high oxygen content. Furthermore, they possess a wide range of colonization strategies, varying from ruderal to combative. Although these fungi are somewhat adapted to environmental conditions, this adaptation is less marked as in other strategies. Decay fungi such as *Trametes versicolor*, *Stereum sanguinolentum*, and *Chondrostereum purpureum* use this strategy to colonize standing trees.

Specialized opportunists also colonize the sapwood by taking advantage of the tree physiological stress due, for example, to root damage or drought conditions. In this colonization strategy, non-decay-causing microorganisms are almost absent. Moreover, extensive individual genotypes within the tree are often observed. These are often capable of developing wide decay columns. Mechanisms of 'latent invasion' which involve the movement of spores within the xylem sap have been proposed to explain the rapid development of decay (Boddy, 1994; Baum *et al.*, 2003).

Active pathogenesis is a strategy which involves direct penetration of the host by the fungal pathogen. The establishment of sufficient inoculum base is critical for successful active pathogenesis. This may occur through heart rot (ectotrophic root infection), unspecialized or specialized opportunism. The well-known pathogens *Heterobasidion annosum* and *Armillaria mellea* are classified as active pathogens (Woeste, 1956).

Lastly, fungi which adopt a **desiccation tolerance** strategy are those which create and maintain dry conditions in wood. This environment allows them to persist in the presence of potential competitors. Consequently, their ability to tolerate low or fluctuating water potentials is of advantage for the colonization of wood. Examples of fungi belonging to this category are *Hypoxylon mammatum* and *Daldinia concentrica*.

Although this theoretical classification is useful to understand the plasticity of fungal behavior, this distinction does not explain why some wood decay fungi are more often found on coniferous trees and some others by contrast on deciduous trees. This important aspect is introduced in the following section.

1.3.1 Adaptation of decay fungi to the wood substrate

Previous investigations have demonstrated that the risk of fungal infection is possibly linked with the adaptation to wood by decay fungi (Nobles, 1958; Gilbertson, 1980; Watling, 1982). In these studies, brown-rot fungi were mainly found in softwoods, whereby white- and soft-rots usually occurred in hardwoods.

Several factors are possibly involved with the adaptation of decay fungi to coniferous and deciduous trees. These are: wood anatomy, wood chemistry, proportion of cell types in the tree, and structure of the woody cell wall. Except for the latter (structure of woody cell wall), all of these elements have been summarized in the classification of the water conducting system published by Braun (1970) and subsequently modified by Baum (2000) and Schwarze (2000). Fig. 2