

***Ganoderma* on Trees - Differentiation of species and studies of invasiveness**

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Summary

The relative abilities of *Ganoderma applanatum*, *G. resinaceum* and *G. adspersum* to overcome the reaction zone (R-zone) of *Platanus x acerifolia* were assessed under controlled conditions using wood blocks containing naturally induced R-zones. Also, the effect of physically damaging the R-zone on fungal spread was examined. During incubation, fungal entry into each block was controlled by coating it with paraffin wax, so as to leave only one side available for colonisation. The results were examined mainly in the context of the different colonisation strategies and wood-degrading mechanisms of these fungi. In order to allow for possible intra-specific differences, two isolates of each fungus were used.

There were clear differences between the fungi, on the basis of both histological criteria and drilling resistance measurements, as determined after four and eight weeks' incubation. Both *G. adspersum* and *G. resinaceum* breached the R-zone, but the *G. adspersum* was more aggressive in this respect (Fig. 11). On the other hand, *G. applanatum* did not breach the R-zone, due to an inability to modify the defensive compounds in this region.

When wood blocks were drilled before incubation, so as to breach the R-zones physically, *G. applanatum* was able to colonise and degrade the adjacent sapwood. This pre-treatment also enhanced the ability of *G. resinaceum* and *G. adspersum* to enter the sapwood. *Ganoderma resinaceum* preferentially exploited the sapwood before starting to degrade the polyphenolic barrier of the R-zone, whereas *G. adspersum* began to degrade this barrier at an early stage.

Within control blocks, containing no R-zones, *G. applanatum* caused the most rapid loss of cell wall structure, followed by *G. resinaceum* and *G. adspersum*. These results were confirmed by weight loss data.

Keywords: *Ganoderma* spp., London plane, reaction zone, invasiveness, “IML-Resi”

Introduction

Bracket fungi of the genus *Ganoderma* are known by mycologists for the crust-like upper surfaces of their fruit bodies, which in some species, such as *G. pfeifferi* and *G. resinaceum*, have a varnished appearance. Arborists and managers of plantation crops know them collectively as a cause of decay in a very wide range of tree species all over the world (FLOOD *et al.*, 2000). Among amenity and roadside trees, their presence is often taken to indicate that a hazard assessment may be necessary. Identification to species-level is frequently not attempted, despite the availability of information about the hazard-potential of particular species. We consider here some existing and new information about four species affecting broadleaved trees in various parts of Europe.

The genus *Ganoderma* belongs to the family of the Ganodermataceae within the Basidiomycetes (‘higher fungi’). Its members possess a trimitic hyphal system, which consists of binding, skeletal and generative hyphae. All *Ganoderma* spp. cause a white-rot, but they can degrade the woody cell walls in a number of ways, including selective delignification and simultaneous rot (BLANCHETTE; 1984, SCHWARZE, 1995). Recent studies have shown that *G. adspersum* is even able to cause a soft-rot (SCHWARZE and BAUM, 2000).

In the early stages of decay by *Ganoderma* spp., bleached zones usually appear in the wood, as a result of selective delignification. Elsewhere within the affected wood, there are less decolorised zones. These remain either relatively intact or show alterations typical of a simultaneous rot (CAMPBELL, 1932). The wood becomes progressively softer as the decay continues, it loses relatively little tensile strength until a late stage, but there is a marked loss of stiffness (SCHWARZE and FINK, 1994; SCHWARZE, 2000).

Selective delignification is now regarded as being of less concern for tree safety than other kinds, having been shown in recent studies to cause only a slow decrease in strength (SCHWARZE, 2000). Also, in trees with a relatively good ability to lay down new wood, there are usually clear biomechanical signs of such decay before any increased likelihood of failure occurs (MATTHECK and BRELOER, 1994; SCHWARZE *et al.*, 1999). In the later stages of decomposition, the wood disintegrates with a soft or spongy texture (SCHWARZE *et al.*, 1999)

In temperate zones, decay caused by *Ganoderma* spp. is often limited to the roots and the lower stem. The presence of the fungus can usually be detected quite easily due to the development of the perennial fruit bodies. However there are some species, for instance *G. resinaceum*, which form only annual fruit bodies and which can therefore be easily overlooked. Typical signs that accompany the decay include alteration in the shape of the stem (e.g. bulges, including ‘bottle-butt’), and perennial cankers, as well as a strongly decreased speed of sound within the wood (SCHWARZE and FINK, 1994; SCHWARZE *et al.*, 1999).

Diagnosis and differentiation

In the UK there are four main un-stalked species that occur on urban trees, these have well-marked differences, which are described in more detail as follows (see Figs. 1A-1C).

***Ganoderma applanatum* (Pers.) Pat.**

Ganoderma applanatum (fig. 1A) is widespread in the northern hemisphere. It has a broad host spectrum, mainly consisting of deciduous genera, e.g. *Acer*, *Fagus*, *Tilia*, *Populus*, *Platanus*, *Quercus*, *Aesculus*, *Betula*, *Alnus*, *Fraxinus* and *Salix*, but also occasionally including conifers such as *Abies* and *Picea*. It commonly causes a root- and butt-rot but, being confined mainly to trees with dysfunctional xylem associated with large wounds on the roots, it is regarded as predominantly saprotrophic (PETERSEN, 1983). ROSS (1976) showed that, on aspen, *Populus tremula*, it was unable to infect roots less than 7.5 cm in diameter.

The perennial fruit bodies of *G. applanatum* have often been confused with those of *G. adspersum*, but the following characteristics can help to differentiate these species. If the lower surface of the fruit body bears the galls of the larvae of the mushroom fly *Agathomyia wankowici*, the fungus can be identified as *G. applanatum*, as it is the only European species of *Ganoderma* affected (BREITENBACH and KRÄNZLIN, 1986). However, the absence of these galls does not prove the converse, especially in regions where the fly does not occur. Another feature of the fruit bodies of *G. applanatum* is that they are usually thinner than those of *G. adspersum* (20 – 60 mm, compared with 40 – 100 mm) at the base. Also their undersides tend to emerge sharply at right angles from the host stem, whereas those of *G. adspersum* usually have a decurrent attachment. Moreover, *G. applanatum* has a thinner crust, which can be indented with a fingernail. With a hand lens, a difference in the pore structure can be seen in a radial section; in the older parts of the fruit body, the pores of *G. applanatum*, become filled with a white mycelium, whereas those of *G. adspersum* remain empty (BREITENBACH and KRÄNZLIN, 1986).

Microscopic features are also useful in distinguishing *G. applanatum* from *G. adspersum*. Its basidiospores are, on average, smaller (7 – 9 x 4.5 – 6.0 µm, compared with 8.5 – 12.0 x 6.5 – 8.0 µm) (BREITENBACH and KRÄNZLIN, 1986). Also, it has been reported by FERNER (2000) to produce broader hyphae at the growing margins of pure cultures on agar, having an average diameter of 3.50 µm, compared with 2.10 µm in *G. adspersum* (see Fig. 1A). As both spore size and hyphal diameter show overlap between individuals of the two species, another criterion, recently described by FERNER (2000), should be applied; i.e. the formation of thin hyphal strands at the margins of colonies of *G. adspersum* growing on cellophane overlying agar; this does not occur in the case of *G. applanatum*.

***Ganoderma adspersum* (Schulz.) Donk**

Ganoderma adspersum is found in built-up areas and parks and more rarely in closed-canopy forests BREITENBACH and KRÄNZLIN (1986), JAHN (1990) and SCHWARZE *et al.* (1999) (Fig. 1B). Its geographic range is mainly in subatlantic – submediterranean zones, and completely excludes Fennoscandia (JAHN, 1990). On its hosts, which include the genera *Tilia*, *Quercus*, *Fagus*, *Platanus* and *Aesculus*, it is thought to

begin its colonisation as a parasite, later developing saprotrophically (PETERSEN, 1983). Its perennial fruit bodies may form on various parts of the lower stem, but most commonly at the base. Its formation of hyphal strands (Fig. 1B) at the margins of pure cultures (FERNER, 2000; FERNER and SCHWARZE, 2002), described above, distinguishes it both from *G. applanatum* (Fig. 1A) and *G. resinaceum*, and perhaps from other species which have yet to be studied in detail.

***Ganoderma resinaceum* Boud. in Pat.**

In contrast to the two species described above, *G. resinaceum* is found predominantly in warmer areas (for example, it has a local stronghold in the Freiburg area of S.W Germany). It occurs in southern Britain, affecting *Quercus* spp. In central Europe, its main host species are *Q. rubra* and *Platanus* spp. (BREITENBACH and KRÄNZLIN (1986). Its fruit bodies (Fig. 1C) are annual and contain a light brown, cork-coloured trama which distinguishes it from other European *Ganoderma* species. Another feature is that its resinous crust, like that of *G. pfeifferi*, melts when heated with a match flame. At the microscopic level, a very useful distinguishing feature is the production of chlamydospores in pure culture (Fig. 1C), which are not found in cultures of *G. applanatum* or *G. adspersum*. The chlamydospores probably allow the fungus to survive unfavourable conditions.

Ganoderma resinaceum can certainly be classed as a butt-rot fungus, but this may represent an over-simplified view of its colonisation strategies on various host species. Thus, in *Quercus* spp., it sometimes remains below ground level, while in *Platanus* it extends some metres up the stem (SCHWARZE *et al.*, 1999).

***Ganoderma pfeifferi* Bres.**

The fruit bodies of *G. pfeifferi*, like those of *G. adspersum* and *G. applanatum*, are woody and perennial, but they have some resemblance to the annual ones of *G. resinaceum* in having a varnish-like resinous surface layer, which melts in a match flame, becoming smooth and glossy on cooling (RYVARDEN, 1976). The surface is, however, harder than that of *G. resinaceum*. Apart from the perennial growth and the harder surface, another means of distinguishing *G. pfeifferi* from *G. resinaceum*, and indeed from the other two species mentioned above, is that the actively growing

whitish margin and lower surface turns yellow and resinous while maturing and then brown with yellowish patches. Also, the wood decayed by *G. pfeifferi* contains strikingly dark, reddish-brown regions,

Prognosis of decay dynamics

Trees usually form chemically modified barriers, termed R-zones by SHAIN (1979), which help to arrest the extension of xylem dysfunction, in response to the early stages of fungal colonisation of living sapwood (BODDY & RAYNER, 1983; SCHWARZE and BAUM, 2000a, b). These R-zones are represented in the CODIT-model of SHIGO and MARX (1977), as “walls” 1 to 3 (Fig. 2). One feature of this modification is the occlusion of vessel lumina by tyloses, which may contain lignin and more rarely suberin (PEARCE and HOLLOWAY, 1984; PARMESWARAN *et al.*, 1985; PEARCE, 1990; SCHWARZE and BAUM, 2000a, b). The tyloses impede the development of decay fungi within the vessels, both by severely restricting aeration and also by the inhibitory effects of phenolic substances, including lignin and suberin, on fungal metabolism. Inhibition of fungal growth within R-zones is also effected by the infiltration of fungistatic substances into the lumina of the fibre tracheids and the parenchyma cells (Fig. 2). These substances are formed by the living parenchyma cells and are deposited on the internal wall surfaces, without, however, penetrating deeply into the walls (SCHWARZE *et al.*, 1999).

Although in some cases, R-zones can be highly effective barriers against fungal development into sapwood, recent studies have shown this not to be the case when *Ganoderma adspersum* colonises species of *Tilia*, *Fagus*, *Acer* and *Platanus* (SCHWARZE, *et al.*, 1999; FERNER, 2000; BAUM, 2001). Microscopical examination of wood samples incubated under laboratory conditions showed that *G. adspersum*, unlike various other wood decay fungi, could not only breach R-zones, but could even utilise them as a nutritional substrate (SCHWARZE and BAUM, 2000a; SCHWARZE, 2002). This means that its invasiveness in the standing tree can be classified as high. It thus seems to contrast with *G. applanatum*, which appears from field observations not to breach R-zones.

From this level of understanding, the following questions emerged:

- Do species of *Ganoderma* differ in their invasiveness as sapwood colonisers?
- Can the above *Ganoderma* species be regarded as having a similar potential for extension within functional wood?
- If an R-zone is penetrated by the use of a diagnosis device, what is the effect on the decay dynamics of the fungus?
- To what extent can drilling resistance measurements with a micro-drill such as the “IML-Resi” allow the effectiveness of compartmentalisation to be appraised?

These questions were addressed in the course of a diploma project at the Department of Forest Botany at Albert-Ludwigs-University, Freiburg in Germany. This study involved two isolates each of *G. applanatum*, *G. resinaceum* and *G. adspersum*. Host material was obtained by the removal of sapwood containing naturally occurring R-zones from a single tree of *Platanus x acerifolia*, which was selected as a commonly planted street tree. Wood blocks extracted from this tree were sterilized and were each sealed on five sides with paraffin wax (KERSTEN, 2000), so as to set up challenge tests in which each of the test fungi was able to enter wood blocks from the unsealed side only (Fig. 3). In this way, its ability to breach the pre-existing R-zones was tested (FERNER 2000). The experiment also included blocks containing no R-zones or with holes drilled through the R-zones with the “IML-Resi”. For each treatment combination, two incubation times were used (4 and/or 8 weeks). Also, a series of non-incubated blocks were retained for 64 weeks in a long duration test.

Investigations of the aggressiveness of different *Ganoderma* species

Influence of injured and intact R-zones on the breakdown of fungistatic substances by *Ganoderma* species

It is apparent from Fig. 4 that the colour intensity and the width of the R-zone were altered due to colonisation by *G. adspersum* within four weeks. This macroscopically recognisable effect was confirmed by histological analysis of the test wood blocks (Fig. 5). In contrast, no such effect was induced by *G. applanatum*, even after eight weeks' incubation

Although, as shown in Fig. 5, *G. adspersum* became well established in the xylem ray parenchyma within the R-zone, the cell walls were evidently not attacked.

Ganoderma resinaceum occupied an intermediate position amongst the three fungal species studied. Like *G. adspersum*, it modified the polyphenolic deposits in the R-zone, but without degrading them to the same extent within the same incubation period.

The presence of a drill hole through the R-zone allowed *G. applanatum* and *G. resinaceum* to colonise the sapwood more easily (Fig. 12). Interestingly, *G. resinaceum* colonised the sapwood region, from which it then grew back so as to start degrading the R-zone. *Ganoderma applanatum* grew via the drill hole into the sapwood, but did not degrade the R-zone (Fig. 12).

In the test blocks containing no R-zones, a different picture of wood degradation emerged. *Ganoderma applanatum* caused the most intense decay and *G. adspersum* the least, with *G. resinaceum* occupying an intermediate position (cf. Fig. 9).

Influence of the R-zone on the intensity of decay caused by *Ganoderma* species

The second technique for assessing the activity of *Ganoderma* species in *Platanus* wood involved the measurement of dry weight loss. For each combination of fungal species and incubation time, eighteen wood blocks were inoculated. Fifteen of the blocks each contained an R-zone, while the three remaining blocks contained no R-zones. None of the blocks was drilled before inoculation. The resulting differences in weight loss confirmed the observations outlined in 4.1 above; principally that, of the three species studied, *G. adspersum* appeared to be the most able and *G. applanatum* the least able to grow in wood containing an R-zone (Figs. 6-7). In the absence of an R-zone, *G. adspersum* degraded the sapwood considerably more slowly than *G. applanatum* (Figs 8-9).

Comparison of histological results with drilling resistance measurements

In a further study, the “IML-Resi” was used for the measurement of drilling resistance in wood blocks, containing R-zones, following incubation with each of the three test

fungi. The same device had been used prior to incubation in order to bore holes in R-zones in one series of the wood blocks. As in the assessment of decay across the radius of a standing tree, the pattern of drilling resistance along the length of each block provided a means of mapping the intensity of wood decomposition (Fig. 10). However, the values for high drilling resistance (in unaltered wood and R-zones) and low resistance (decayed wood) were relative and not absolute, since the readings were dependent partly on the sharpness of the probe and the condition of the rechargeable battery. As shown in Fig. 11A-F, the measurements of resistance amplitude allowed the following observations:

- A. In all cases, the tracings showed a transition between the R-zone and the sapwood. The R-zone showed a peak value, probably due to the presence of deposited compounds (mainly polyphenolics), which was clearly highest in the case of *G. applanatum* which, unlike *G. resinaceum* and *G. adspersum*, was unable to modify these compounds.
- B. In the blocks incubated with *G. resinaceum*, the R-zone peak, although distinct, was somewhat lower than in the case of *G. applanatum*; this reflects the moderate ability of *G. resinaceum* to degrade the polyphenolic compounds.
- C. The measurements indicate clearly which zones of the wood blocks were strongly decomposed. In the case of *G. adspersum*, the peak within the R-zone was very low and broad, indicating that this fungus was able to degrade the polyphenolic compounds successfully and then to colonise the sapwood. Interestingly, the sapwood contained amplitude peaks as great as the peak within the R-zone.
- D. Although the R-zone was more easily penetrated by the fungi when pre-drilled, it still showed a recognisable peak on the tracing. This was most marked in the case of *G. applanatum*, due to its inability to degrade the polyphenolic compounds in the R-zone. Penetration of the R-zone did, however, enhance fungal colonisation of the sapwood, which showed a low amplitude on the tracing.
- E. In the blocks incubated with *G. resinaceum*, the R-zone peak, although distinct, was somewhat lower than in the case of *G. applanatum*; this reflects the ability of *G. resinaceum* to degrade the polyphenolic compounds.

- F. After incubation with *G. adspersum*, a recognisable R-zone peak remained even in the pre-drilled blocks, even though the overall amplitude of the tracing was very low.

Overall, the drilling resistance data reflected those of the histological study.

Overview

The above results seem to illustrate the importance of evaluating decay-related hazards in the light of the propensities of the fungal species concerned. The ability of *G. adspersum* to penetrate intact R-zones (Fig. 12) could clearly be a hazard factor, by allowing the development of potentially extensive decay, even within trees of high vitality. Trees colonised by this species may often have adequate residual walls of sound wood at the time of initial assessment. However, they would seem to have a poor long-term prognosis, compared to trees colonised by *G. applanatum*, which probably remains confined within previously dysfunctional columns of wood.

Ganoderma resinaceum occupies an intermediate position in this respect, which could mean that, despite having some ability to penetrate R-zones in the wood of *Platanus*, it can be kept in check within trees of high vitality.

As the present study did not include *G. pfeifferi*, the only information about the ability of this species to colonise functional wood comes from field observations, which have sometimes revealed extensive decay in *Fagus sylvatica* (D. LONSDALE, unpublished data.) and the death of extensive areas of bark, or even of entire trees (BURDEKIN, 1979).

Although both *G. applanatum* and *G. resinaceum* are less likely than *G. adspersum* to cause very extensive decay, they can both cause an intense degradation of the wood that they occupy. In the present study, this was more rapid in the case of *G. applanatum*, but it appears from field observations (BURDEKIN, 1979) that *G. resinaceum* causes a more complete loss of tensile strength.

The major differences between the above *Ganoderma* species make it highly advisable to identify them correctly, so as to aid prognosis of decay. This can be done by a mycologist, using morphological features seen in pure culture (Fig. 1A-1C.). If

G. applanatum, or perhaps *G. resinaceum* is identified, and if visual observation indicates that any weakening from decay is currently not a significant hazard, internal investigations may be unnecessary. The use of invasive devices can markedly increase the ability of these two species to extend into previously sound wood (KERSTEN, 2000).

Further work is in progress, so as to assess more fully the relevance of the above laboratory data to the development of *Ganoderma* spp. within living trees.

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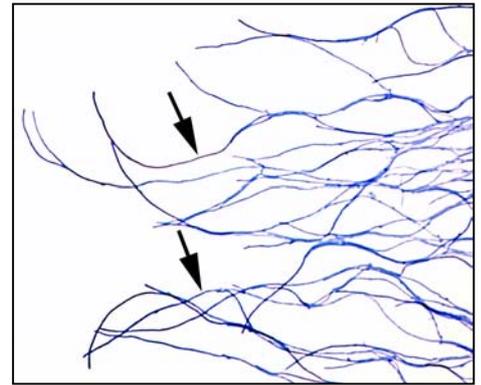
We appreciate the assistance of Mrs. Nardos Streit and Mrs. Karin Waldmann in preparing sections for light microscopy. The authors also wish to thank Dr. David Lonsdale for comments on the manuscript.

Figure Captions

1A. *Ganoderma applanatum*

Perennial fruit body

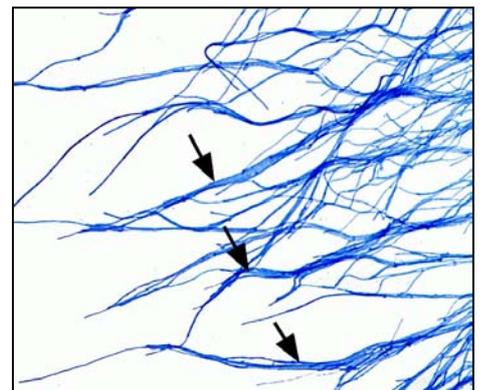
Mycelium without strands (arrow); diameter of peripheral hyphae: 3.5 µm



1B. *Ganoderma adspersum*

Perennial fruit body

Mycelium with strands (arrow); diameter of peripheral hyphae: 2,1 µm



1C. *Ganoderma resinaceum*

Annual fruit bodies

Chlamydospores (arrows)

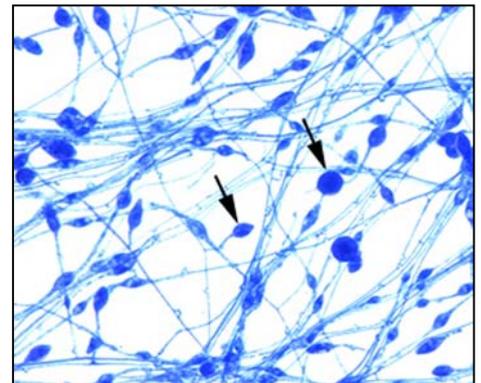


Figure 1A - 1C. Fruit bodies of *Ganoderma* spp. frequently causing decay, together with important morphological features in pure culture.

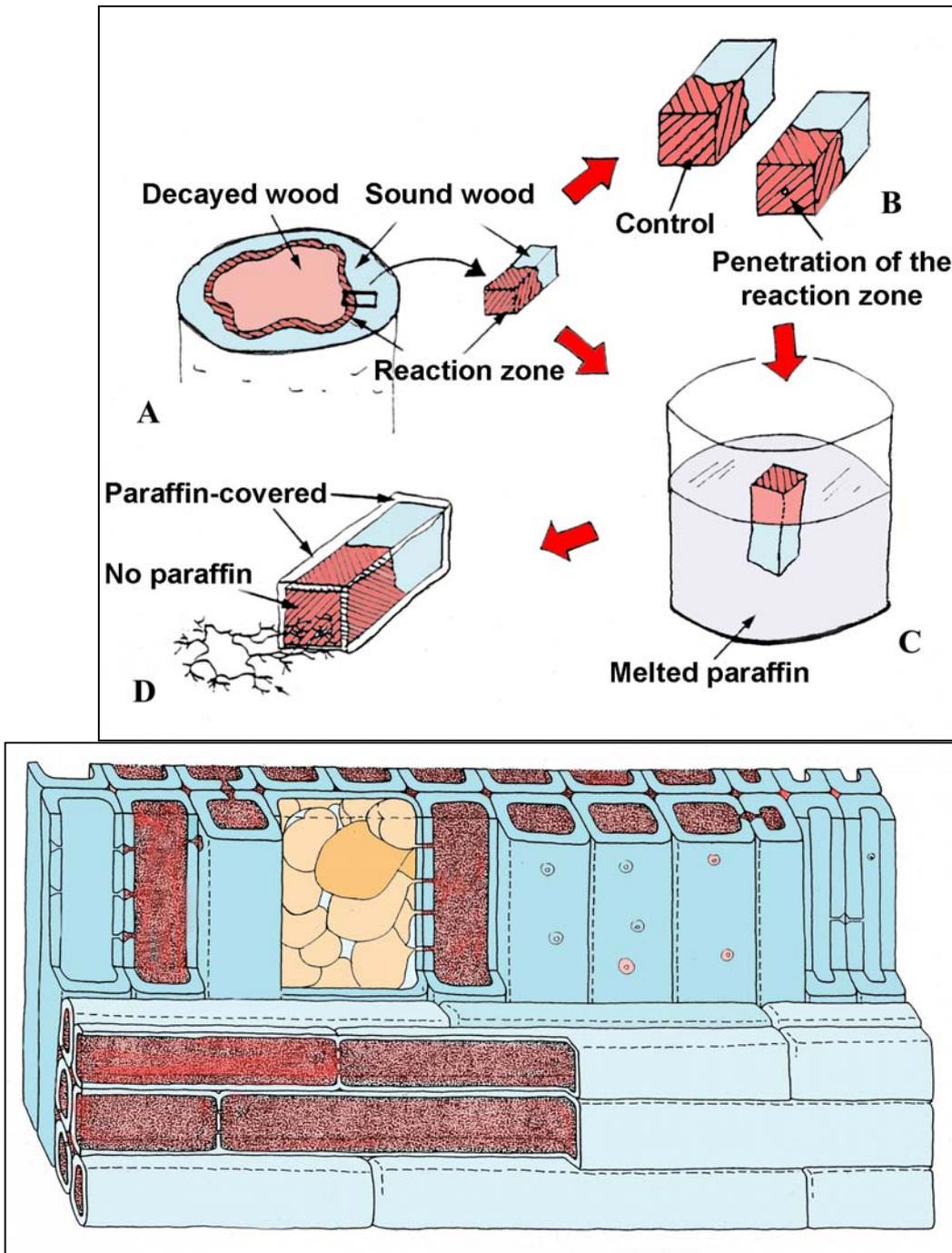


Figure 3. Artificial and healthy wood sterilization wood (intact RZ) were remaining unsealed pure cultures of

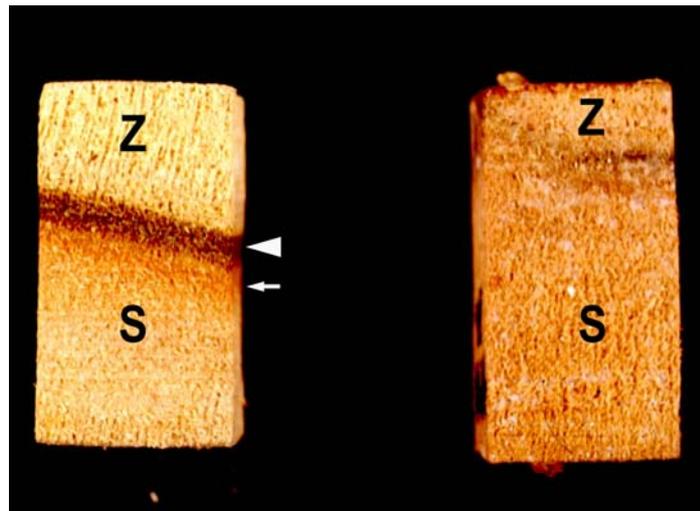


Figure 4. Comparison of reaction zone: Left: Clear transition between naturally decayed wood, reaction zone and intact sapwood. Right: After 8 weeks' *Ganoderma adspersum* has completely breached the reaction zone **Z** → naturally decayed wood; **S** → sapwood; Arrowhead → reaction zone; Arrow → transition zone

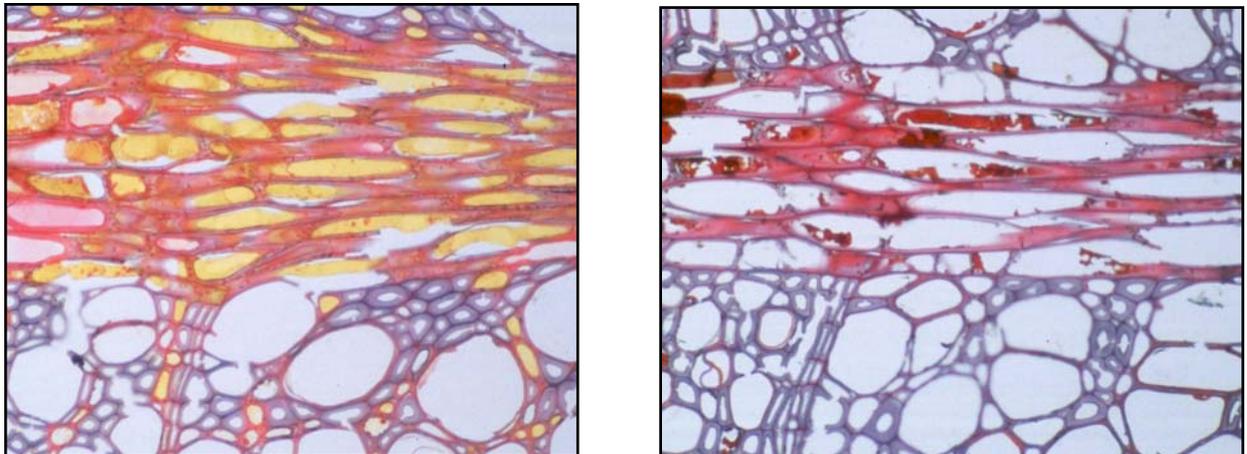


Figure 5. Left: Xylem ray in R-Zone before incubation with *Ganoderma adspersum*. Right: Xylem ray in R-Zone after four-week incubation *Ganoderma adspersum*. Note preferential degradation of the polyphenols within cells of the xylem ray parenchyma.

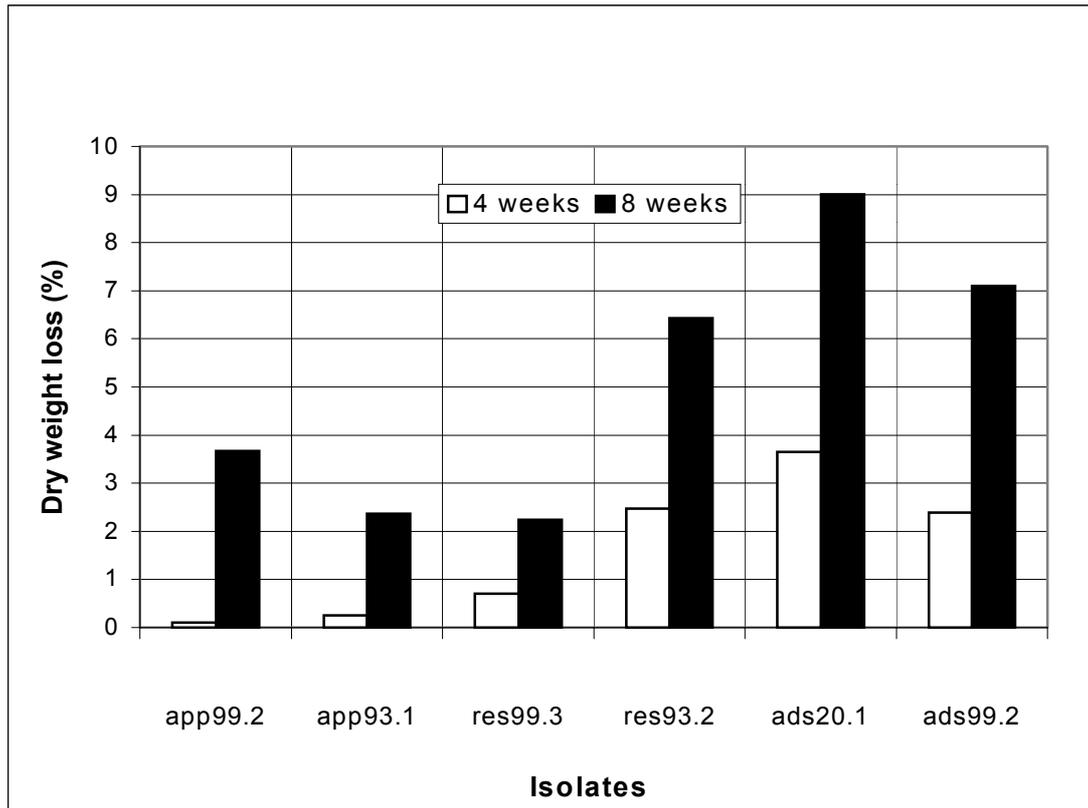


Figure 6. Weight-loss of wood blocks containing reaction zones



Figure 7. Wood blocks with reaction zones after 64 weeks' incubation. Left: *Ganoderma applanatum* = weakly colonised, Middle: *Ganoderma resinaceum* = moderately colonised. Right: *Ganoderma adspersum* = strongly colonised and degraded.

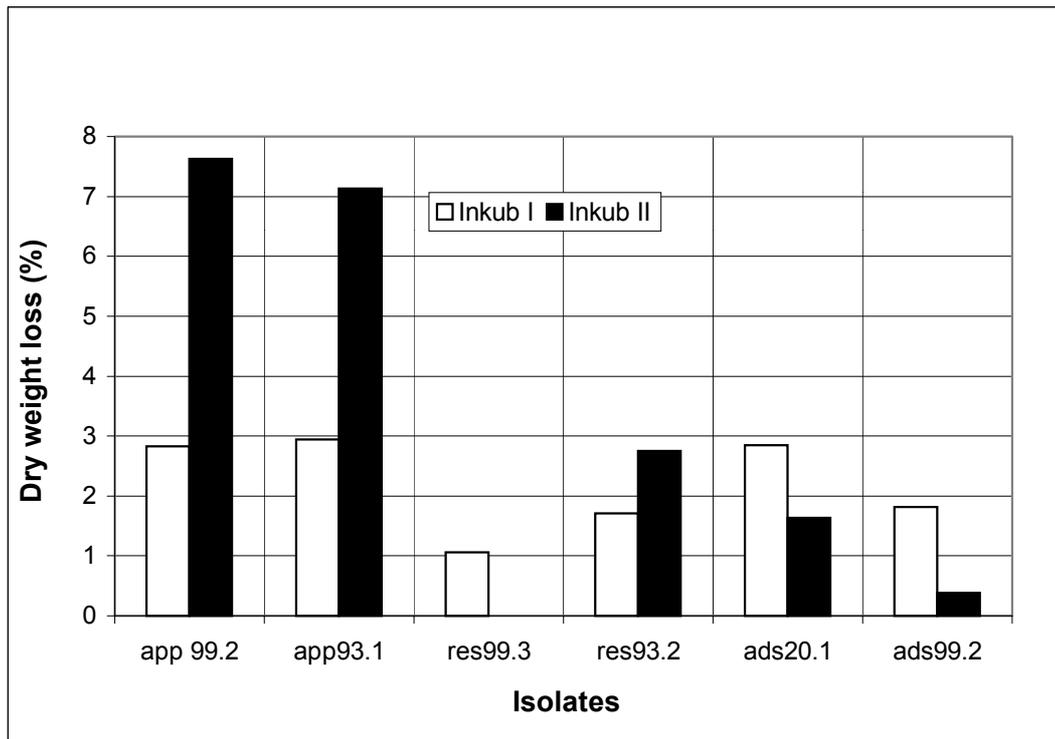


Figure 8. Weight-loss of wood blocks without reaction zones



Figure 9. Wood blocks without reaction zones after 64 weeks' incubation. Left: *Ganoderma applanatum* = strongly colonised, Middle: *Ganoderma resinaceum* = moderately colonised. Right: *Ganoderma adspersum* = weakly colonised and degraded.

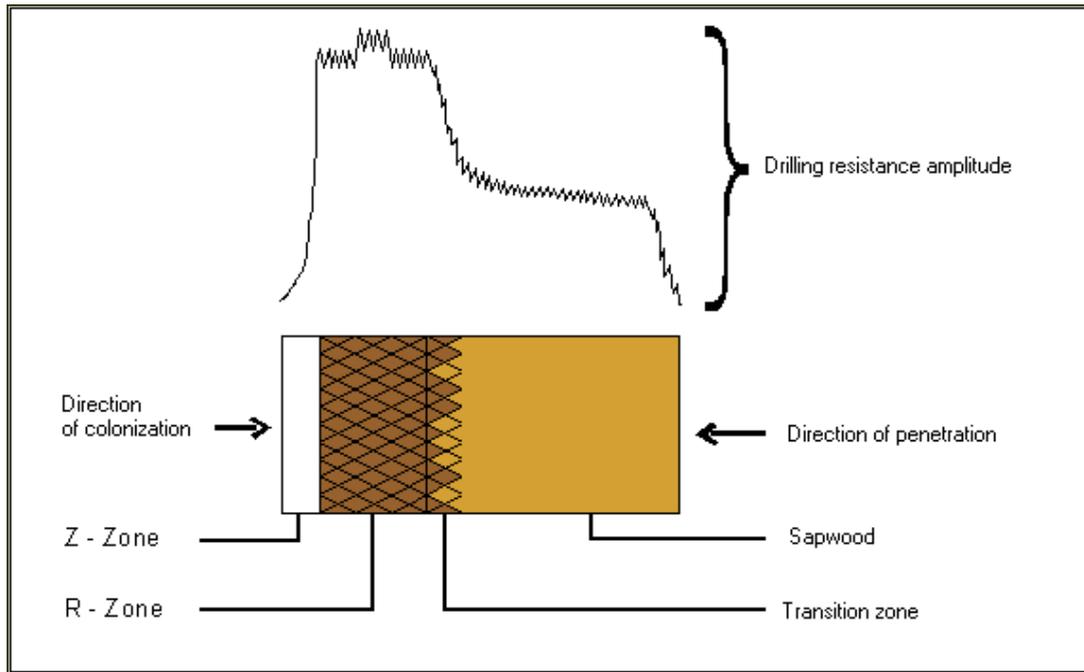


Figure 10. Schematic illustrations of drilling resistance amplitude of control wood blocks. Z - Zone = previously decayed ripewood; R- Zone = reaction zone.

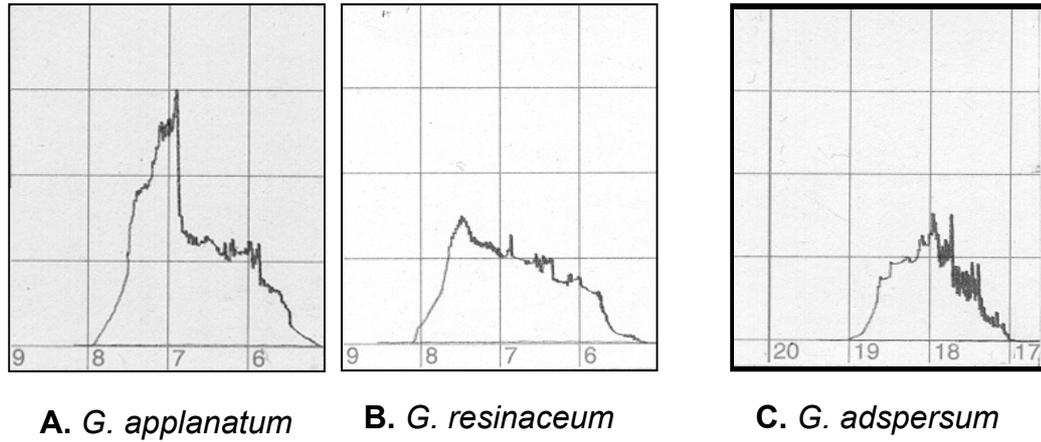


Figure 11A-C. Drilling resistance amplitude of wood blocks with non-drilled reaction zones (see text for explanation of the individual drill traces).

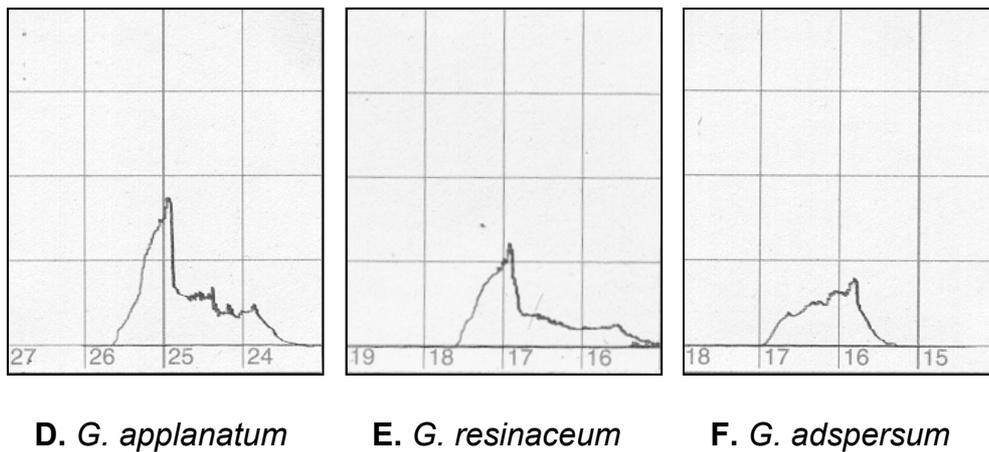


Figure 11D-F. Drilling resistance amplitude of wood blocks with reaction zones drilled before incubation (see text for explanation of the individual drill traces).

Figure 12. Left: Penetration (arrow) of the R-zone with the “IML-Resi” enhanced fungal colonisation of the sapwood by *Ganoderma applanatum*. (Tangential longitudinal section). Right: Note the ability of the fungus to overcome the reaction zone (RZ) and subsequent degradation of the adjacent sapwood (arrows) (Transverse section). See text for comparison of the individual drill trace as described in Figure 11D.