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# Effect of fungal competition on decay rates in bicultured soil bottle assays

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**Abstract:** For decades, wood scientists and preservative formulators have employed the monocultured soil bottle assay to test efficacy of wood treatment in the laboratory as a rapid predictor of field performance. This study examines the effects of bicultured soil bottle assays on the decay by common wood decay fungi. Mycelial interactions were noted in early stages of colonization. With only two exceptions, a single fungus was apparent in each soil bottle, indicating dominance. The dominant fungi were not always the most efficient wood rots, and the rot type, white or brown, did not affect the dominance outcome on the preferred wood type.

**Keywords:** accelerated decay test, fungal competition, soil microcosm, wood decay fungi

## Introduction

The AWPA E-10 soil-block bottle assay is one of the standardized laboratory methods for determining the efficacy of wood protectants or naturally durable wood species against monocultured wood decay fungi under optimal conditions conducive to fungal activity (AWPA 2014). The soil bottle assay was originally developed for laboratory testing of preservative treated wood and offers more rapid results and uniform decay than standard field tests (Leutritz 1946). The implication is that the results can be correlated to expected field performance; however, the diversity present in a real-world scenario is far more complex than that simulated in monoculture in laboratory. In the present study, the effects of replacement of the monocultured fungal soil bottle assay with a more complex bicultured fungal laboratory assay are investigated.

Simultaneous fungal interaction is the most realistic scenario in nature. Studies on standing, dead, even processed timber demonstrate how changing and diverse the micro-environments in wood can be (Shigo 1984; Boddy 2000, 2001; Boddy and Heilmann-Clausen 2008). The strategies of wood decay fungi are also highly variable and not yet fully understood (Schwarze 2011). Hulme and Shields (1972) evaluated the effects of primary colonizers on the rate of colonization and subsequent decay by secondary invaders on both hardwoods (HWs) and softwoods (SWs). The quoted authors indicated that pre-colonization by primary saprophytic fungi reduced decay by all but one fungus (*Hypocrea gelatinosa*). Other studies have shown that some saprophytic fungi (molds), such as *Trichoderma harzianum* and *Scytalidium lignicola* (Bruce and Highley 1991), can exclude wood decay fungi, presumably through the production of secondary metabolites that inhibit decay fungi. Exo-chitinases of similar mold fungi have also been shown to have antagonistic effects against sap stain and decay fungi (Lee et al. 2012). Moreover, yeasts and bacteria can also be biological antagonists against mold and stain fungi. Their volatiles were shown to significantly reduce radial growth and discoloration by most of the fungi tested (Payne et al. 2000). Phillips-Laing et al. (2003) isolated and tested isolates from soils with indigenous *Serpula lacrymans* and found that the secondary metabolite production of this fungus killed other decay fungi. The *Trichoderma harzianum* strain (T25) was much less effective with this regard. On the other hand, the presence of certain fungi can also promote subsequent colonization, and this can be interpreted that some form of chemical signaling in the substrate must have been effective (Heilmann-Clausen and Boddy 2005).

Holmer and Stenlid (1993, 1996) studied the effect of inoculum size on competitiveness of fungi via the percent coverage by mycelium and found that this could be a factor influencing fungal competition in nature. However, results obtained on artificial media did not agree with those experiments based on wood disks. Holmer and Stenlid (1997) found that species that normally fruit in the field during late succession were strong competitors in the

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laboratory, but combative mycelial replacement occurred in a random fashion both within and among successional stages. Laboratory studies based on selective replacement revealed that late successional species are much better competitors in the laboratory setting (Holmer et al. 1997) than early to mid-successional species. HW species colonized by multiple fungal species often exhibit lines of demarcation where the fungal masses encounter each other and attempt to restrict access of the opposing fungus through the production of metal rich exudates (Boddy and Heilmann-Clausen 2008).

Environmental conditions also impact diversity and activity of decomposer fungi. Toljander et al. (2006) demonstrated that niche partitioning may be important in maintaining species diversity and promoting decay activity under variable temperatures. Fukami et al. (2010) conducted timing experiments and found that early changes to the order of fungal colonizers resulted in a three-fold change in fungal species richness and composition and a similar increase in rate of decomposition and carbon release. Dickie et al. (2011) studied the effects at an ecosystem level concerning the assembly history, i.e. the order of fungal arrival, in an old growth forest in order to compare the results to laboratory studies of Fukami et al. (2010) and found that the assembly history was not as pronounced as the data suggested from laboratory studies, though some significant effects were detected with regards to timing of arrival of individual decomposer fungi and nutrient turnover. No doubt, early colonizers play an essential role in the decay process, thus these effects should also be considered in laboratory studies.

The soil bottle test offers the opportunity of additional control over fungal interactions on a small scale. The present study is aimed at changes in wood decay capacity of commonly studied fungi when paired in a soil bottle test. Our hypothesis is that either synergetic or competitive effects may occur and can be quantified by measuring percent weight loss (PWL). To our knowledge, these types of tests have not been attempted in this particular scenario.

## Materials and methods

Soil bottles were prepared according to AWPA E10-12 (AWPA 2014). The softwood (SW) species studied was Southern pine (*Pinus taeda* L.). Feeder strips were placed on the soil surface in each bottle and inoculated with either two plugs from a single fungal culture (one plug at each end of the feeder strip) or one plug each from two different fungal species of common wood decay fungi. Selection of fungi was based on the list in the AWPA E10 standard. Four experiments were conducted with two groups of four fungi each, in combinations such that all four fungi "competed" against each other. All fungi were obtained from the Center for Forest Mycology Research (CFMR) culture collection, Madison, WI, USA.

One group of test fungi included three brown rot basidiomycetes, *Gloeophyllum trabeum* Pers. (Murrill) (Mad-617-R), *Postia placenta* (Fr.) MJ Larsen & Lombard (Mad-698-R), and *Fomitopsis palustris* (Berk. & M.A. Curtis) Gilb. & Ryvarden (TYP-6137) and a white rot fungus *Trametes versicolor* L. (Loyd) (Mad-697). After 3 weeks incubation at 27°C, 70% relative humidity (RH), feeder strips were fully covered with mycelium. Square cubes (20 mm) of southern pine were added to bottles. The cubes were preconditioned at 27°C and 30% RH and weighed. Five replicate bottles were incubated at 27°C, 70% RH for 12 weeks before scraping off mycelium and re-conditioning blocks for PWL determination.

A second group of test fungi included two white rot basidiomycetes, *Phanerochaete chrysosporium* (Fr.) P. Karst (ME-461), and *Irpex lacteus* (Fr.) Fr. (HHB-7328-Sp), and two brown-rot basidiomycetes, *Coniophora puteana* (Schum.: Fr.) P. Karst (Mad-515), and *Neolentinus lepideus* (Fr.) Redhead & Ginns (Mad-534-R).

These two groups of test fungi were also applied in identical experiments with the hardwood (HW) red maple (*Acer rubrum* L.) including feeder strips and cubes of to compare the fungal performance on HW vs. SW. The experimental design was identical for both SW and HW soil bottle tests.

**Statistical methods and results:** Bar plots in the figures give the raw average PWL and STD for each group. Dominance in these figures is based on four out of five bottles exhibiting a dominant relationship. The PWL was analyzed assuming a mixed effect model with 10 treatment groups (each Fungus 1-Fungus 2 pairing) with five bottles per treatment group and subsampling with two blocks per treatment bottle. All PWLs fell between zero and 100%, and were modeled assuming a beta distribution with SAS® (SAS Institute Inc. Cary, NC, USA) 9.4 proc GLIMMIX (Stroup 2013). Within each experiment, all pairwise least squares means on the beta scale were compared by the Tukey multiple comparison adjustment procedure held at the 0.05 significance level. The raw average PWLs were quite comparable to the modeled means of PWL based on the inverse-logit of the beta-derived means.

Within each experiment, the statistical differences were highly significant (Expt. I-F9, 40=116.85, $P<0.0001$; Expt. II-F9, 40=38.63, $P<0.0001$; Expt. III-F9, 40=13.36, $P<0.0001$; Expt. IV-F9, 40=7.61, $P<0.0001$). The raw means presented in the figures are comparable to the inverse-logit of the beta means from on which the statistical comparisons are based. Means within an experiment (within a figure) that have the same Tukey letter are not significantly different at an adjusted 0.05 level. For each bottle in a fungal pairing, a dominant fungus could typically be determined. A two-sided sign test (a test for paired observations based on the binomial distribution (Gibbons 1985) was used to determine statistical dominance, i.e. a fungus in a fungal pairing was declared statistically dominant if all five bottles had the same dominant fungus (corresponds to a two-sided P-value=0.0624 with the sign test). A direction was implied if four out of five bottles had the same dominant fungus and the fifth bottle was indeterminate (two-sided P-value=0.1250). An overall schematic diagram summarizing the statistical relevant relationships between the fungi in the four experiments is presented in Figure 1. The dominant fungus is indicated by arrows with solid lines representing significant differences and dashed lines indicating non-significance.

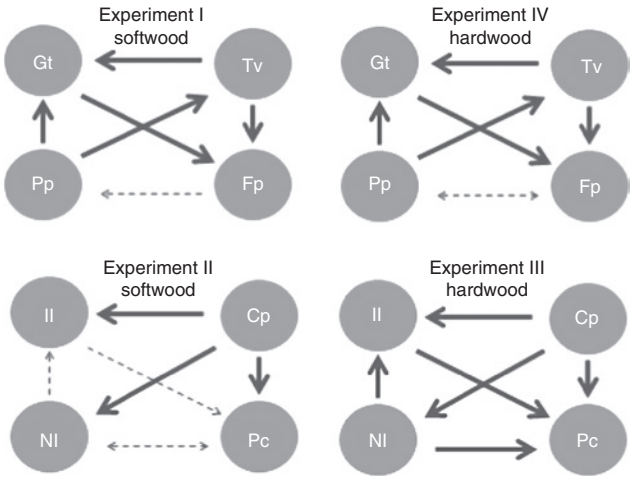


**Figure 1:** Schematic diagrams of the relationships between decay fungi in the different experiments, with solid arrows indicating dominance (by the sign test) and dashed lines indicating non-significance. In each comparison, the more dominant fungus is indicated by arrows pointing towards it.

## Results and discussion

Early in the experiments, before blocks were added, zones of hyphal incompatibility could be seen between the two growing fungi on a feeder strip (Figure 2). However, upon completion, one of the two fungi added in each bottle could be identified by phenotypical observation as the dominant fungus (Figure 3), which are documented in Figures 4–7. There are two sets of fungi combinations, where a clear winner could not be determined: *P. chrysosporium* and *N. lepideus* on SW (Figure 5) and *F. palustris* and *P. placenta* on HW (Figure 7), and this fact is indicated by gray shaded bars in the corresponding figures. For all other pairings, there was a clear dominant fungus in at least four out of five bottles. Owens et al. (1994) tested interspecific interactions among both white and brown rot fungi and found that most of the brown rot either deadlocked or replaced white rot fungi and that brown rot fungi may be capable of invading and occupying domains within white rotted wood.

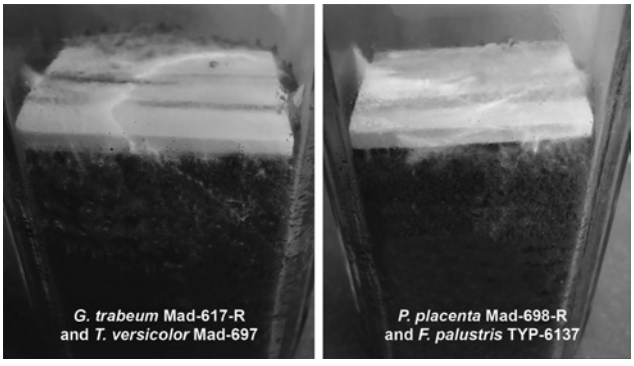


**Figure 2:** Zone of interaction on pine feeder strips due to competition between *G. trabeum* Mad-617-R and *T. versicolor* Mad-697 (left) and between *P. placenta* Mad-698-R and *F. palustris* TYP-6137 (right) in 3 week old soil bottle cultures before adding test blocks.

In the first SW experiment, *G. trabeum* caused the most decay with the highest PWL (57%) and outcompeted other test fungi, with the exception of *F. palustris*. The PWL was significantly less when *F. palustris* dominated the bottle, but the difference is not statistically significant as judged from the mean PWL observed in the monocultured *F. palustris* bottles. *Gloeophyllum trabeum* also showed a slight increase in PWL (63%), when paired with *P. placenta*, but the PWL increment is statistically not significant, either. *Fomitopsis palustris* outcompeted all fungal pairings except against *P. placenta*, which resulted in a significantly higher PWL (56%). When paired with *T. versicolor* (38%), the apparently better performance of *F. palustris* is statistically not significant compared to the PWL of *F. palustris* alone (32%). *Postia placenta* and *T. versicolor* both outcompeted only one of three test fungi, i.e. in case of *F. palustris* and *P. placenta*. *Postia placenta* showed a significant PWL increment when paired with *F. palustris*, from 43% to 56%. *Trametes versicolor* had very low PWL (13%) on Southern pine and showed no change when paired with *P. placenta*.

As seen in Figure 5, the white rot fungi *P. chrysosporium* and *I. lacteus* individually produced very low PWL on Southern pine, two and 11.7%, respectively, as white rot fungi preferentially decay HW species. In biculture, *P. chrysosporium* and *I. lacteus* caused only 4.7% PWL. Similarly, when *P. chrysosporium* and *N. lepideus* were combined, they produced 16.7% PWL, while these fungi alone produced 2 and 35.7% PWL, respectively. All other instances, where two fungi were grown in biculture, resulted in similar PWL compared to the exposure of monocultures. Monocultures of the brown-rot fungi *C. puteana* and *N. lepideus* produced higher PWL than *P. chrysosporium* and *I. lacteus*, 28% and 36%, respectively. However, *C. puteana* was not better in any of these pairing experiments, and *N. lepideus* only outcompeted *C. puteana*.

The PWL of the white rot fungi, *P. chrysosporium* and *I. lacteus* (Figure 6) was higher on HW (34%) than on SW (26%). Highley and Scheffer (1970) found lower decay rates by white rot fungi in laboratory decay tests and concluded that this observation may be due to the inadequate moisture in the blocks. Conversely, the brown rot fungi *C. puteana* and *N. lepideus* produced lower PWL on HW (17.6%) than on SW (26.4%). *Phanerochalte chrysosporium*

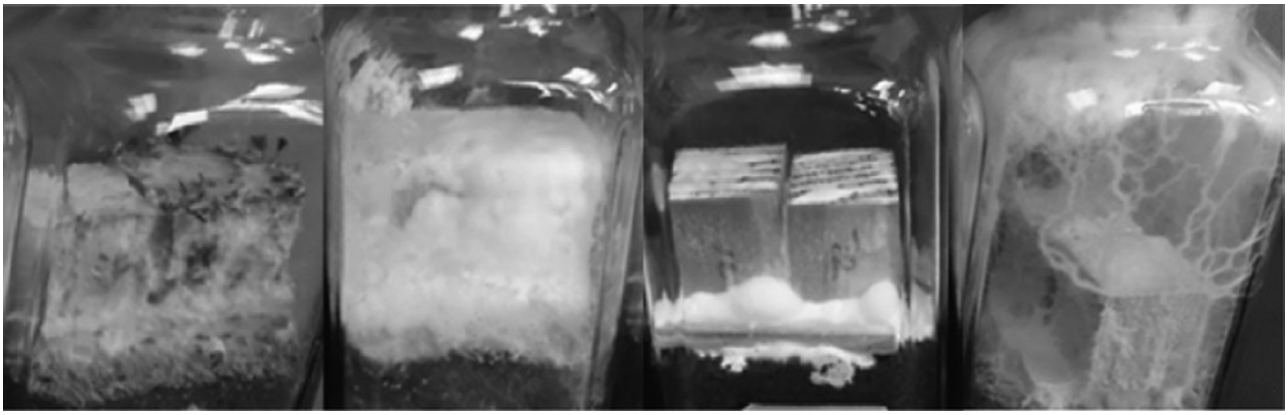

**Figure 3:** Examples of phenotypical dominance seen in the first set of bottles. Fungal species from left to right are: *G. trabeum*, *F. palustris*, *T. versicolor*, and *P. placenta*. Dominant fungus in each pairing was recorded prior to obtaining final weights.

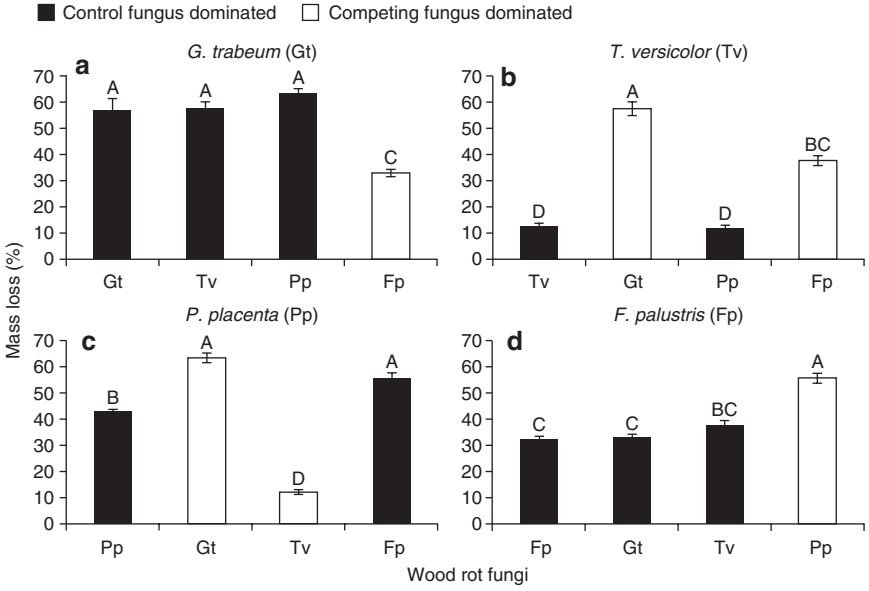


**Figure 4:** Percent weight losses of pairings of select wood rot fungi on softwood (*P. taeda*) blocks. Black or white shading indicates which fungus dominated each particular pairing. Blocks were exposed to each decay fungus alone or paired in a modified biculture soil bottle test and exposed for 12 weeks.

outcompeted test fungi in all three biculture soil bottle tests and had a slight increase in PWL when paired with *N. lepideus* on HW. *I. lacteus* was better in bicultured pairings in two of three fungi combinations, but not in combination with *P. chrysosporium*. *N. lepideus* outcompeted only one pairing against *C. puteana*, while *C. puteana* was not better in none of the three biculture soil bottle tests.

Brown-rot fungi preferentially decay SWs, so the results presented in Figure 7 are not surprising (Figure 7). *G. trabeum* produced a lower PWL (39%), while *P. placenta* a slightly higher one (44%), while the performance of *F. palustris* was with PWL 32% similar on HW and on SW (Figure 4). *Fomitopsis palustris* outcompeted two of three bicultured pairings and it could not be determined phenotypically that it outcompeted *P. placenta* when paired. *Postia placenta* also produced a higher PWL when paired with *G. trabeum* on HW. *G. trabeum* outcompeted two of three test fungi in biculture and additionally produced a higher PWL when combined with *T. versicolor*. *Trametes versicolor* was only able to outcompete *P. placenta* and *P. placenta* failed to dominate in any of the biculture pairings.

Regarding fungal synergy, *G. trabeum* paired with *P. placenta* resulted in a slight (not significant) increase in PWL on both SW (*P. taeda*) and HW (*A. rubrum*). Bicultured pairings of *F. palustris* and *T. versicolor* had slightly higher mean PWL on *P. taeda* than the monocultured soil bottles

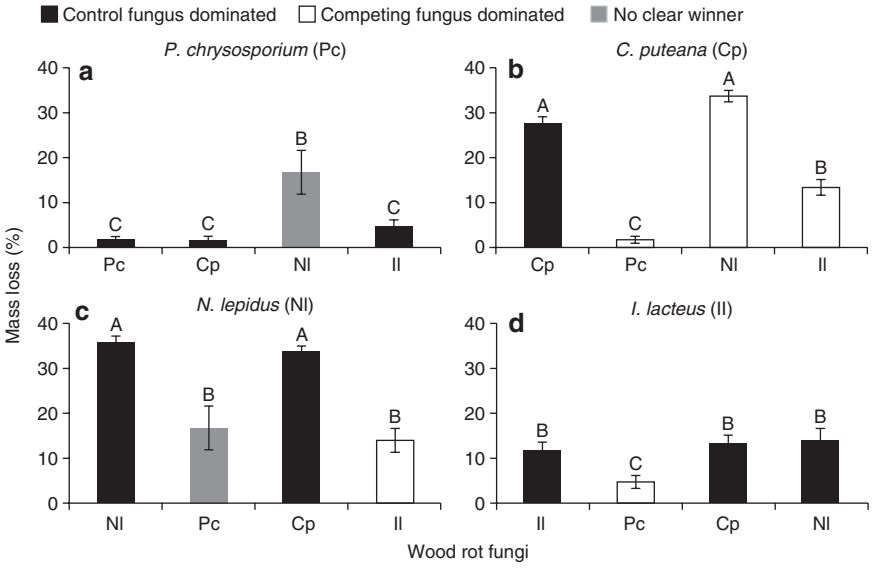


**Figure 5:** Percent weight losses of pairings of select wood rot fungi on softwood (*P. taeda*) blocks. Black or white shading indicates which fungus dominated each particular pairing and gray shading indicates where neither fungus dominated. Blocks were exposed to each decay fungus alone or paired in a modified biculture soil bottle test and exposed for 12 weeks.

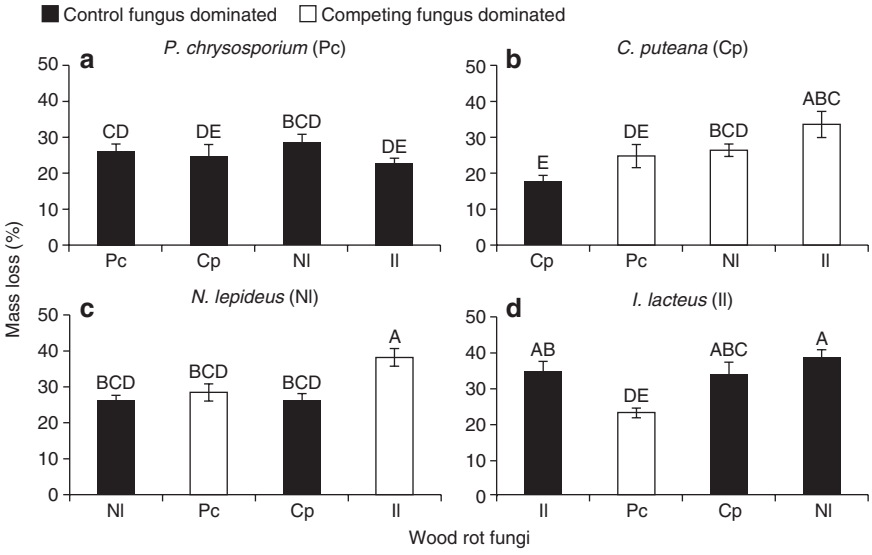


**Figure 6:** Percent weight losses of pairings of select wood rot fungi on hardwood (*A. rubrum*) blocks. Black or white shading indicates which fungus dominated each particular pairing. Blocks were exposed to each decay fungus alone or paired in a modified biculture soil bottle test and exposed for 12 weeks.

of each isolate. Bicultured pairings of *P. chrysosporium* and *N. lepidus* also resulted in slightly higher PWL on *A. rubrum,* as well as pairings of *I. lacteus* and *N. lepidus,* than their respective monocultures. Bicultured pairings of *P. placenta* and *F. palustris* had significantly higher mean PWLs on *P. taeda* than monocultures of each isolate in a soil bottle test. In addition, the combination of *G. trabeum* and *T. versicolor* resulted in a significantly higher PWL (55%) on *A. rubrum* than PWLs for either fungus in monoculture. The presence of one fungus may also stimulate metabolic activity of the other as described by Heilmann-Clausen and Boddy (2005), but this statement can only be substantiated by further studies. These results suggest that bicultured soil bottles, if utilized correctly, can be a useful tool for increasing the basic understanding of the complexity of colonization during development of incipient decay and the resulting effects on wood. The role of decay enzymes was not explored in the present study, but in the literature enzyme systems are described during combative interactions, both for brown rot (Boddy 2000) and

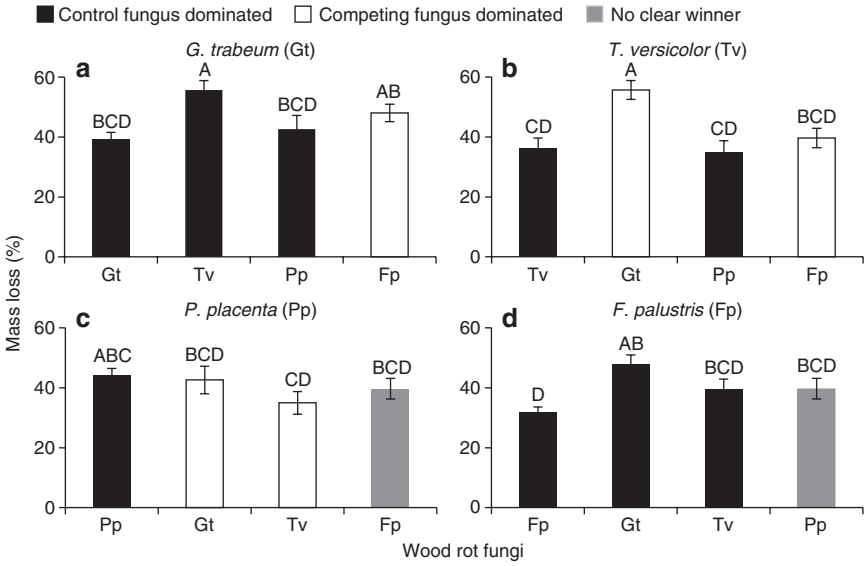


**Figure 7:** Percent weight losses of pairings of select wood rot fungi on hardwood (*A. rubrum*) blocks. Black or white shading indicates which fungus dominated each particular pairing and gray shading indicates where neither fungus dominated. Blocks were exposed to each decay fungus alone or paired in a modified biculture soil bottle test and exposed for 12 weeks.

white rot fungi (Baldrian 2003). Obviously, the detection of oxalate production may serve as a method of dealing with fungal competition by brown rot fungi (Dutton and Evans 1996, Micales 1997). Our results partially support this interpretation in case of the dominance of brown rot as indicated by PWL. Green and Clausen (2003) confirmed that the effectivity ranking of fungi is related to the relative oxalate accumulation. Similar results were found in tests with HW test blocks. It should also be kept in mind that enzyme production is highly variable within and between isolates and it is also influenced by culture conditions.

These experiments yielded several notable results. The brown rot fungi, *G. trabeum* and *P. placenta*, caused nearly equal PWL when exposed to SW or HWs. *Gloeophyllum trabeum* outcompeted all but one of the challenge fungi *F. palustris*, which is manifested in higher mean PWL than *F. palustris* in monoculture, and the data are nearly equal to that of *G. trabeum* in monoculture. However, on HW, *P. placenta* did not compete well in combination with other fungi demonstrating that decay and fungal survival are not the same: *P. placenta* can decay HW species but is not aggressively competitive against other fungi specialized to HWs. Our general observations are consistent with past studies that in laboratory decay tests brown rot fungi have equal capacity to degrade both HWs and SWs while white rots generally degrade HWs to a greater extent (Eslyn and Highley 1976).

In evaluation of the observations of this study, one should consider the following. First, these experiments compare a single isolate of each fungal species and decay fungi typically exhibit variation between isolates within a species (Hakala et al. 2004). Second, only two decay fungi were compared here. However, the reality of the natural decay environment is much more complex and typically involves several different fungi in a single biotope. Moreover, the timing of the colonization of the competing decay fungi was not taken into consideration, which is relevant in nature. Wood decay is typically a succession of multiple species that colonize, exploit and retreat (Rayner and Boddy 1998) opening new routes for secondary successional species and additional microorganisms that eventually convert the woody biomass into soil organic matter.

## Conclusions

In most cases, where two different wood rot fungi were grown together in a bicultured soil bottle test, there was a clear phenotypical "winner". In several cases the PWL was higher in case of a simultaneous attack than that in case of individual attack and in two cases the PWL was even significantly higher. In a few cases the PWL was lower in combined degradation compared to that of individual one. The underlying mechanisms of these observations are not clear.

The analysis of residual blocks of this study may contribute to additional interpretations. The oxalic acid hypothesis, as reported in the literature, may play a role in the paired interactions, but it does not explain why certain fungi are dominant in this study. Fungi with the highest overall individual PWL did not always dominate the other

fungus in bi-cultured tests. The competitive mechanisms underlying these interactions need further study.

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## References

American Wood Protection Association. Standard Method of Testing Wood Preservatives by Laboratory Soil-Block Cultures. AWPA E10-12, 2014, pp. 445–455.

Baldrian, P. (2003). Interactions of heavy metals with white-rot fungi. Enzyme Microb. Tech. 32:78–91.

Boddy, L. (2000). Interspecific combative interactions between wood-decaying basidiomycetes. FEMS Microb. Ecol. 31:185–194.

Boddy, L. (2001). Fungal community ecology and wood decomposition processes in angiosperms: from standing tree to complete decay of coarse woody debris. Ecol. Bull. 49:43–56.

Boddy, L., Heilmann-Clausen, J. (2008). Basidiomycete community development in temperate angiosperm wood. In: British Mycological Society, Manchester, UK, Symposia Series. Academic Press. Vol. 28, pp. 211–237.

Bruce, A., Highley, T.L. (1991). Control of growth of wood decay Basidiomycetes by *Trichoderma* spp. and other potentially antagonistic fungi. Forest Prod. J. 41:63–67.

Dickie, I.A., Fukami, T., Wilkie, J., Allen, R.B., Buchanan, P.K. (2011). Do assembly history effects attenuate from species to ecosystem properties? A field test with wood-inhabiting fungi. Ecol. Lett. 15:133–141.

Dutton, M.V., Evans, C.S. (1996). Oxalate production by fungi: its role in pathogenicity and ecology in the soil environment. Canadian J. Microb. 42:881–895.

Eslyn, W.E., Highley, T.L. (1976). Decay resistance and susceptibility of sapwood of fifteen tree species. Phytopathology 66:1010–1017.

Fukami, T., Dickie, I.A., Paula Wilkie, J., Paulus, B.C., Park, D., Roberts, A., Allen, R.B. (2010). Assembly history dictates ecosystem functioning: evidence from wood decomposer communities. Ecol. Lett. 13:675–684.

Gibbons, J.D. Nonparametric Methods for Quantitative Analysis, 2nd edn. American Sciences Press, Fullerton, CA, USA, 1985. p. 481.

Green, F. III, Clausen, C.A. (2003). Copper tolerance of brown-rot fungi: time course of oxalic acid production. Int. Biodet. Biodegr. 51:145–149.

Hakala, T.K., Maijala, P., Konn, J., Hatakka, A. (2004). Evaluation of novel wood-rotting polypores and corticioid fungi for the decay and biopulping of Norway spruce (*Picea abies*) wood. Enzyme Microb. Tech. 34:255–263.

Heilmann-Clausen, J., Boddy, L. (2005). Inhibition and stimulation effects in communities of wood decay fungi: exudates from colonized wood influence growth by other species. Microb. Ecol. 49:399–406.

Highley, T.L., Scheffer, T.C. (1970). A need for modifying the soil-block method for testing natural resistance to white rot. Mater. Organis. 5:281–292.

Holmer, L., Stenlid, J. (1993). The importance of inoculum size for the competitive ability of wood decomposing fungi. FEMS Microb. Ecol. 12:169–176.

Holmer, L., Stenlid, J. (1997). Competitive hierarchies of wood decomposing basidiomycetes in artificial systems based on variable inoculum sizes. Oikos 79:77–84.

Holmer, L., Stenlid, J. (1996). Diffuse competition for heterogeneous substrate in soil among six species of wood-decomposing basidiomycetes. Oecologia 106:531–538.

Holmer, L., Renvall, P., Stenlid, J. (1997). Selective replacement between species of wood-rotting basidiomycetes, a laboratory study. Mycol. Res. 101:714–720.

Hulme, M.A., Shields, J.K. (1972). Interaction between fungi in wood blocks. Canadian J. Bot. 50:1421–1427.

Lee, J., Huh, N., Hong, J.H., Kim, B.S., Kim, G.H., Kim, J.J. (2012). The antagonistic properties of *Trichoderma* spp. inhabiting woods for potential biological control of wood-damaging fungi. Holzforschung 66:883–887.

Leutritz, J. (1946). A wood soil contact culture technique for laboratory study of wood-destroying fungi, wood decay and wood preservation. AT&T Tech. J. 25:102–135.

Micales, J.A. (1997). Localization and induction of oxalate decarboxylase in the brown-rot wood decay fungus *Postia placenta*. Int. Biodeter. Biodegrad. 39:125–132.

Owens, E.M., Reddy, C.A., Grethlein, H.E. (1994). Outcome of interspecific interactions among brown-rot and white-rot wood decay fungi. FEMS Microb. Ecol. 14:19–24.

Payne, C., Bruce, A., Staines, H. (2000). Yeast and bacteria as biological control agents against fungal discolouration of Pinus sylvestris blocks in laboratory-based tests and the role of antifungal volatiles. Holzforschung 54:563–569.

Phillips-Laing, E.M., Staines, H.J., Palfreyman, J.W. (2003). The isolation of specific bio-control agents for the dry rot fungus Serpula lacrymans. Holzforschung 57:574–578.

Rayner, A.D., Boddy, L. Fungal Decomposition of Wood: Its Biology and Ecology. Wiley & Sons Ltd., Hoboken, NJ, USA, 1998.

Schwarze, F.W. (2011). Wood decay under the microscope. Fungal Biology Reviews 21:133–170.

Shigo, A.L. (1984). Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. Annu. Rev. Phytopath. 22:189–214.

Stroup, W.W. (2013). Generalized Linear Mixed Models – Modern Concepts, Methods and Applications. CRC Press, Boca Raton, FL, 2013. pp. 529.

Toljander, Y.K., Lindahl, B.D., Holmer, L., Högberg, N.O. (2006). Environmental fluctuations facilitate species co-existence and increase decomposition in communities of wood decay fungi. Oecologia 148:625–631.