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Autor: Küffer, Nicolas / Senn-Irlet, Béatrice
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Wood decay and enzyme activities of green alder inhabiting fungi

Nicolas Küffer[1] & Béatrice Senn-Irlet[2]

Institut für Pflanzenwissenschaften, Universität Bern,
Altenbergrain 21, CH-3013 Bern, Schweiz

Summary – The wood decay ability of eight fungal species was tested with fresh and strongly decayed wood of green alder in an experimental study. The fungi tested were all isolated from fruit-bodies on dead wood of green alder. These species show considerable differences in their wood decay ability. *Polyporus arcularius* was the strongest decomposer on fresh green alder wood and *Megalocystidium leucoxanthum* on decayed green alder wood. The decay capabilities correspond fairly well with the main taxonomical groups of basidiomycetes, with the heterobasidiomycetes having a significantly lower decay ability than corticioid fungi and polypores.

In order to get quick information on functional qualities of additional wood and litter inhabiting fungi of green alder, five enzyme-tests, i.e. Guaiacol, Blue Cellulose, Tannin- and Anilin-Agar, and artificial PolyR-Lignin, were performed. All fungi were able to degrade cellulose, agarics displayed stronger laccase activities than aphyllophorales. However, the differences between the systematic groups nor the ecological groups were statistically significant. *Saccoblastia farinacea,* a very abundant heterobasidiomycete on green alder wood, is characterised by very weak enzyme activities.

Zusammenfassung – In einer Laboruntersuchung wurde die Holzabbautätigkeit von 8 Pilzarten getestet, die alle als Fruchtkörper auf Grünerlenholz gesammelt worden waren. Auf frischem Grünerlenholz ist *Polyporus arcularius* der stärkste Holzabbauer, auf bereits abgebauten Grünerlenholz, zeigt *Megalocystidium leucoxanthum* die grösste Abbautätigkeit. Die Abbaufähigkeit ist mit den wichtigsten taxonomischen Gruppen korreliert: Die Heterobasidiomyceten zeigen eine signifikant niedrigere Abbaufähigkeit als corticioide Basidiomyceten oder Porlinge.

[1] Present address: Université de Neuchâtel, Laboratoire de Microbiologie, Rue Emile-Argand, C.P. 2, CH-2007 Neuchâtel
[2] Present address: Swiss Federal Institute for Foresty, Snow and Landscape, Zürcherstrasse 111, CH-8903 Birmensdorf

Um schnell Informationen über funktionelle Eigenschaften von holz- und streubewohnenden Pilzarten zu bekommen, wurden zusätzlich 9 Pilzarten der Grünerle mit fünf verschiedenen Enzymtests untersucht: Guaiacol, Azur-Zellulose, Tannin- und Anilin-Agar und künstliches PolyR-Lignin. Alle 17 getesteten Arten konnten Zellulose abbauen, wobei Agaricales grössere Laccase-Aktivitäten zeigten als Aphyllophorales. Hingegen war kein Unterschied weder zwischen taxonomischen Gruppen noch zwischen ökologischen Gruppen signifikant. *Saccoblastia farinacea,* ein häufiger Grünerlenholzbewohner, kann durch sehr schwache Enzymtätigkeiten charakterisiert werden.

Keywords: green alder, *Alnus viridis,* basidiomycetes, succession.

An important issue in modern ecology is quantifying the impact of the various species involved in the decomposition process under natural conditions and estimating the ecosystem effect of biodiversity (McCann 2000). Processes in the nutrient cycling of forest ecosystems are only understood if a better knowledge of the role of various destruents are achieved. Among the decomposing organisms, fungi play a substantial role, especially in the decomposition of woody substrates. Wood with a low nutrient content, the presence of chemical inhibitors and a low surface/volume ratio, which hamper a fast colonisation (Aber & Melillo 1991), is a very unfavourable substrate for most organisms, even most fungi. Specialised ascomycetes and basidiomycetes are the principle wood-decayers in temperate forests (Boddy & Watkinson 1995). Over 600 heterobasidioid and aphyllophoroid basidiomycetes are described from Europe which are thought to decompose wood. Most species colonise a wide range of woody substrates and only a few are known to be restricted to selected host genera or even host species. The ecology of most species is poorly known. Which factors control the establishment of a species, what is the exact role of abiotic, i.e. microclimatic factors in comparison with biotic factors such as the age of the substrate, the volume of the substrate as expressed in the diameter of the twigs and trunks respectively? In general it is known that temperature, moisture, substrate quality and size of a woody substrate must be taken into consideration to describe a decay rate (Harmon et al. 1986).

Even laboratory assays are scarce which could give first indications of the possible function in an ecosystem, despite strong arguments against such an approach (Blumenfeld 1984). Such assays have mainly focused on detecting enzymes involved in fungal wood decomposition (e.g. Boidin 1951, Marr 1978). In addition some few studies describe culture morphologies of wood-inhabiting fungi (e.g. Stalpers 1978, Nakasone 1990). Another approach is followed by studies which focus on the decay rates in situ (e.g. Harmon & Chen 1991).

Green alder (*Alnus viridis* (Chaix) DC.) is the most prominent bush-like tree in the upper subalpine zone of the Alps. Often it forms rather homogenous stands on moist, mostly Northern oriented slopes between 1400 and 2100 m asl with a constant favourable microclimate for fungal growth and fruiting. Among the wood decay fungi found in green alder stands, corticioid basidiomycetes play an important role in number and frequency. Küffer & Senn-Irlet (2000) found 40 species of corticioid basidiomycetes, all white-rotters, in green alder stands in the Swiss Alps. Species with a strong host-specificity, e.g. *Peniophora aurantiaca, Plicatura nivea,* were dominating both in abundance and frequency. By far the most abundant species was *Peniophora aurantiaca,* which covered large amounts of dead green alder branches and stems.

In the natural wood decomposition process, the ascomycetes are preceding aphyllophoroid basidiomycetes followed in a final decomposing stage by agarics. Is this common pattern also found in subalpine green alder bushes where the single stems only reach 60 to 80 years (Wettstein 2001) and where field observations suggest a very rapid decomposition and high turnover. Up to 3.45 t dead woody biomass per ha could be found in pure green alder stands representing 42% of all the litter collected (unpublished data). In relation to the standing biomass in green alder bushes of about 16 t/ha this is a very high amount of dead woody biomass on the ground. Is the turnover rate of green alder branches especially high and is green alder wood an especially soft, easily degradable substrate for fungi or is the high amount of dead wood better explained by especially slow decomposition processes based on wood properties, high moisture content and cool climate?

Material and methods

Cultures of seventeen fungal species of different taxonomical groups were isolated from fruit-bodies and their spore-prints found on green alder wood in the Swiss Alps (Table 1), and cultivated on 2% malt extract agar (MEA). Most species are represented by one single isolate.

Wood decay experiment

For the wood decay experiment eight species were chosen out of the 17 species in Table 1, including both agaricoid and aphyllophoroid basidiomycetes. To test the decay ability of these species, two branches of green alder wood of two different stages of decay, fresh undecayed wood and strongly decayed wood, were sawn into small cubes of about 0.5 cm side length (i.e. of approx. 0.125 cm^3). Undecayed wood was defined as corticated wood with a relative density (= 0.45–0.6 g/cm^3, with an average of 0.51 g/cm^3 following Sell

Table 1. The species used in the present study and their origin in the Swiss Alps.

Species	Origin	Herbarium number
Basidiomycetes		
Heterobasidiomycetes		
**Saccoblastia farinacea* (Höhn.) Donk	Mürren, Bern	NK 97/09[a]
Agaricales		
**Armillaria cepistipes* Velen.	Steinboden, Uri	BSI 97/34[b]
**Kuehneromyces mutabilis* (Schaeff.: Fr.) Singer & Smith	Steinboden, Uri	BSI 97/77
Marasmius androsaceus (L.: Fr.) Fr.	Rivera, Ticino	BSI 99/251
Mycena alnetorum Favre	Andermatt, Uri	BSI 99/33
Mycena amicta (Fr.) Quél.	Gletsch, Valais	BSI 99/18
Mycena haematopoda (Pers.: Fr.) Kummer	Andermatt, Uri	BSI 99/100
Sarcomyxa serotina (Schrad.: Fr.) P. Karst.	Rivera, Ticino	BSI 99/260
Aphyllophorales		
Athelia sp.	Château d'Oex, Bern	BSI 98/10
Hapalopilus rutilans (Pers.: Fr.) P. Karst.	Andermatt, Uri	BSI 99/28
**Megalocystidium leucoxanthum* (Bres.) Jülich	Riggisberg, Bern	BSI 97/213
**Merismodes fasciculatus* (Schw.) Donk	Château d'Oex, Bern	BSI 98/9
**Peniophora aurantiaca* (Bres.) Höhn. & Litsch.	Riggisberg, Bern	BSI 97/212
**Plicatura nivea* (Sommerf.: Fr.) P.Karst.	Andermatt, Uri	BSI 98/1061
**Polyporus arcularius* (Batsch) Fr.	Gletsch, Valais	BSI 98/177
Stereum hirsutum (Willd.: Fr.) S.F.Gray	Andermatt, Uri	BSI 99/120
Ascomycetes		
Rutstroemia bolaris (Batsch: Fr.) Rehm	Gletsch, Valais	BSI 99/20

* species were chosen for the wood decay experiment (see text for explanations)

[a] NK: Herbarium N. Küffer

[b] BSI: Herbarium Helveticum Fungi, B. Senn-Irlet

(1989). Decayed wood was defined as wood with a relative density (= 0.24–0.44 g / cm^3 and an average of 0.34 g / cm^3). Each wooden cube was weighted and in addition length, width and height were measured to determine the relative density for an estimation of its stage of decay (Maser & Trappe 1984; Boddy et al. 1987).

The wooden cubes were sterilised by autoclaving for 20 minutes with 120 ° C, then one wooden cube was put into Petri dishes together with one small plug of cultivated mycelium. Each setting had been performed with five replicates.

The Petri dishes with mycelia and wooden cubes were kept for six months at about 16 °C in a incubator, densely closed to minimise humidity loss. According to Blumenfeld (1984) six months is as a sufficient long period to obtain reasonable results in wood decay experiments. After this period the wooden cubes were cleaned from the attached mycelia, dried and weighted again. The weight loss for each wood cube was calculated in absolute number and percentage.

Differences between the two decay stages within one species and differences between species were analysed with Students t-tests.

Enzyme tests

Enzyme activities were checked using five different tests:

With the PolyR-Lignin test (Hutchinson 1990) the lignase activity becomes visible when a modified Melin-Norkrans-medium (Marx 1969) turns from purple to yellow. This reaction is based on a discoloration of the polyanthraquinon colour PolyR-478 by phenoloxydases, enzymes able to degrade polyphenols such as PolyR-lignin, a polymeric dye.

The Guaiacol test (Boidin 1951) visualises laccase activities. Guaiacol is also composed of phenolic structures, therefore it is generally assumed that laccase degrading Guaiacol are also able to degrade lignin. Though mainly laccases are reacting in the Guaiacol test, tyrosinase may also play a certain role (Marr 1978).

With Blue Cellulose (Smith 1977) as a substrate the presence of cellulase can be tested, cellulase turns the blue colour of the medium into a lilac to purplish colour.

The Tannin test developed by Bavendamm (1928) and the recently proposed Anilin test (Alberto & Wright 1997) to detect extracellular enzymes in acid milieu are used to separate different groups within the white-rot fungi.

Results

Wood decay experiment

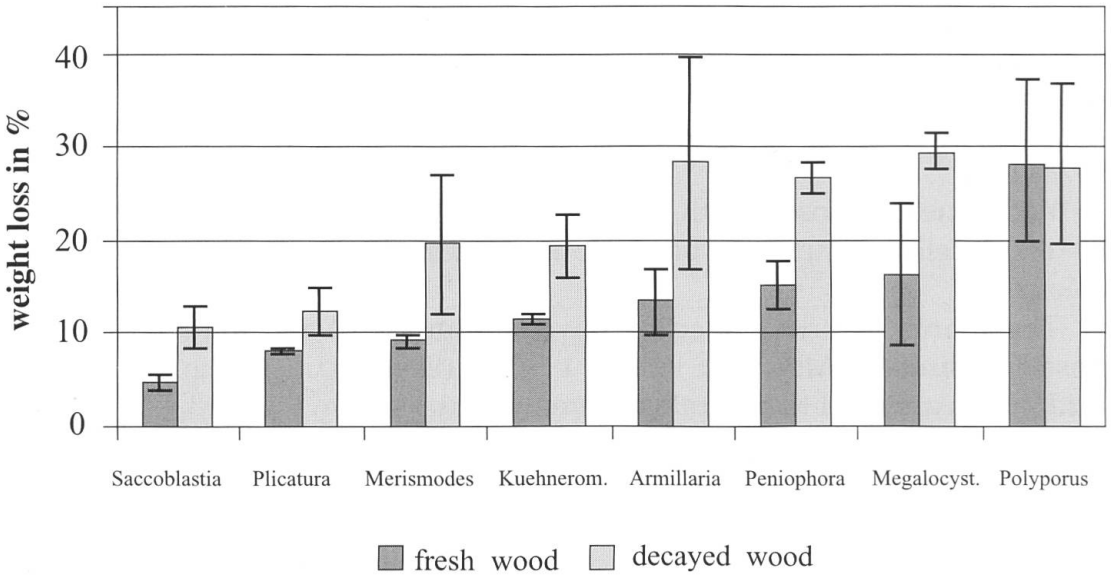
The relative decay capabilities of the nine species tested are summarised in Fig. 1. The weight loss of the wood blocks in these six months ranged from 30 mg in *Saccoblastia farinacea* up to 80 mg in *Polyporus arcularius*. The two substrate types, fresh wood and strongly decayed wood respectively, influenced the activities of the fungi considerably: all but one species (*Polyporus arcularius*) showed higher activities on decayed wood when the relative weight loss of the wood cubes were analysed.

Remarkable differences were found among the species (Table 2). Almost every species showed its own characteristic decay ability. However, *Saccoblastia farinacea* and *Plicatura nivea* form a cluster of two species with distinctly different wood decay abilities: compared with the rest they are very weak decomposers. *Peniophora aurantiaca, Megalocystidium leucoxanthum, Merismodes fasciculatus, Polyporus arcularius, Kuehneromyces mutabilis* and *Armillaria cepistipes* form the group of strong decomposers of green alder wood.

The differences in the decay rates were more pronounced with decayed wood than with fresh wood. Therefore, the results of the t-tests show more significant correlations on fresh wood (see Table 2). Taken all species into account, the two decay stages exhibit each a characteristic decay rate ($p < 0.001$).

Enzyme tests

Most species out of the various taxonomic groups displayed enzyme activities which are associated with the wood decay process (Table 3). All fungi



tested were able to grow on Blue Cellulose, but four species (*Saccoblastia farinacea, Mycena amicta, Megalocystidium leucoxanthum* and *Plicatura nivea*) did not provoke a colour reaction indicating no cellulase activities. The presence of at least one enzyme out of the group of phenoloxydases, indicating a possible role in the lignin decomposition, was found in all species tested, with the exception of *Saccoblastia farinacea.*

Guaiacol performed the strongest and quickest reactions of all enzymes tested. On PolyR-lignin (the polymeric dye) and Anilin-agar only few species displayed enzyme activities. Based on the activity of laccases three groups of

Table 2. Comparison of the decay abilities for fresh and decayed wood, results from t-statistics. Only species pairs with significant differences are shown.

Species pair	fresh wood			decayed wood		
	df	t-value		df	t-value	
Polyporus – Saccoblastia	5	6.23	**	5	4.53	**
Polyporus – Plicatura	5	5.32	**	4	4.09	**
Polyporus – Merismodes	4	5.04	**	8	1.71	n.s.
Polyporus – Kuehneromyces	4	4.43	*	5	2.19	n.s.
Polyporus – Armillaria	5	3.66	*	7	0.06	n.s.
Polyporus – Peniophora	5	3.33	*	4	0.33	n.s.
Megalocystidium – Saccoblastia	3	2.83	n.s.	2	10.30	**
Megalocystidium – Plicatura	3	2.00	n.s.	7	9.07	**
Megalocystidium – Merismodes	3	1.75	n.s.	5	2.73	*
Megalocystidium – Kuehneromyces	3	1.22	n.s.	3	5.00	*
Peniophora – Saccoblastia	4	7.79	**	6	12.53	***
Peniophora – Plicatura	3	5.37	*	7	10.90	***
Peniophora – Merismodes	3	4.46	*	4	2.14	n.s.
Peniophora – Kuehneromyces	3	2.70	n.s.	6	4.95	**
Armillaria – Saccoblastia	5	5.44	**	4	3.40	*
Armillaria – Plicatura	4	3.33	*	4	3.08	*
Kuehneromyces – Saccoblastia	6	12.75	***	7	5.38	**
Kuehneromyces – Plicatura	4	9.02	***	8	4.20	**
Kuehneromyces – Merismodes	7	4.92	**	5	0.03	n.s.
Merismodes – Saccoblastia	6	8.88	***	5	2.57	n.s.
Merismodes – Plicatura	5	3.05	*	5	2.09	n.s.
Plicatura – Saccoblastia	4	8.19	**	8	1.05	n.s.

* = $p<0.05$; ** = $p<0.01$; *** = $p<0.001$; n.s. = not significant

Table 3. Results of the five enzyme activity experiments (foot notes are on next side).

Target woody substance Enzyme	Cellulose Blue Cellulose[1] (cellulase)	Lignin Guaiacol[2] (laccase)	Tannin[3]	R-Lignin[4] (lignase)	Anilin[5]
Basidiomycetes					
Heterobasidiomycetes					
Saccoblastia farinacea	+	–		–	–
Agaricales					
Armillaria cepistipes	++++	+++++	++	–	++
Kuehneromyces mutabilis	++	++++	++++	(+)	(+)
Marasmius androsaceus	+++	++++	+++	–	
Mycena alnetorum	++	++++	++++	–	
Mycena amicta	+	+++	+++	–	
Mycena haematopoda	++++	+++	+++	–	
Sarcomyxa serotina	++++	+++	+++++	++	
Aphyllophorales					
Athelia sp.	+++	–	–	(+)	–
Hapalopilus rutilans	++++	–	–	–	
Megalocystidium leucoxanthum	+	++	+	–	–
Merismodes fasciculatus	++++		–	–	–
Peniophora aurantiaca	+++	+++	++	–	+
Plicatura nivea	+	–	++	–	–
Polyporus arcularius	++++	++	++++	+	–
Stereum hirsutum	+++	++++	++++		
Ascomycetes					
Rutstroemia bolaris	+++	+++	+++	++	

fungi can be formed. A first group characterised with strong enzyme activities (*Armillaria cepistipes, Kühneromyces mutabilis, Mycena alnetorum, Sarcomyxa serotina* and *Stereum hirsutum*), a second group with medium laccase activities (*Marasmius androsaceus, Mycena amicta, M. haematopoda, Peniophora aurantiaca, Polyporus arcularius, Rutstroemia bolaris*) and a third with very weak signs of laccase activities (*Athelia spec. Hapalopilus rutilans, Megalocystidium leucoxanthum, Plicatura nivea*).

[1] Blue cellulose test (Smith 1977) after 14 days
– = no reaction, no mycelium growth
+ = mycelium growth, but no colour reaction
++ = mycelium growth and lilac coloration without diffusion zone
+++ = mycelium growth and lilac coloration with distinct diffusion zone
++++ = mycelium growth and purple colouration with distinct diffusion zone

[2] Guaiacol test (Boidin 1951) after 7 days
– = no reaction
+ = inoculation is coloured vine–red
++ = vine–red colour only under the inoculation
+++ = diffusion zone till 10 mm
++++ = diffusion zone between 10 and 25 mm
+++++ = diffusion zone between 30 and 40 mm

[3] Tannin test (Bavendamm 1928) after 20 days
– = no reaction
+ = diffusion zone till 5 mm (yellowish colour)
++ = yellowish colour between 5 – 10 mm
+++ = diffusion zone till 20 mm
++++ = diffusion zone between 20 and 25 mm
+++++ = diffusion zone over 25 mm, very strong coloration

[4] R-Lignin (Hutchison 1990)
– = no reaction
+ = weak yellowish colour around the inoculation
++ = clear coloration 10 to 25 mm around the inoculation

[5] Anilin test (Alberto & Wright 1997) brown coloration after 20 days
– = no reaction
+ = till 5 mm, very weak
++ = 5–10 mm, weak
+++ = strong reaction, 10–20 mm
++++ = very strong, >20 mm

Discussion

Wood decay experiment

The various wood-inhabiting fungi showed remarkable differences in their abilities to decay fresh and decayed wood. The experiment divides the species into weak decomposers and fairly active decomposers.

In late stages of wood decay nutrient content is lower compared with early stages (Boddy & Rayner 1988). Yet, in our experiment the fungi displayed a significant higher activity in decomposing already decayed, fragile wood than in the undecayed wood. Do additional fungi, not covered by our experiments, play a crucial role or is it due to several specific chemical compounds in fresh green alder wood (Sell 1989) which hamper an early colonisation by basidiomycetes? The fact that much greater species-specific differences are found on fresh wood than on decayed wood can be interpreted in this sense. The colonisation of such an unfavourable substrate such as fresh wood of green alder requires a high specialisation, although it contains more nutrients than partly decayed wood. Therefore we assume that the species tested here do not belong to the so-called sugar-fungi, which are the first colonisers with low decay abilities and low competition potential, decomposing mainly the easy soluble sugar compound of the wood (Levy 1982).

A further possibility might be considered: Fresh wood may primarily be attacked by other than fungal destruents such as arthropods or woodlice. However, no such field observations were made.

According to our initially formulated hypothesis, there is also a, however weak, systematical gradient from weak decomposers to stronger ones. *Saccoblastia farinacea,* at the lower end, is a heterobasidiomycete and regarded as weak decomposer, as all the other heterobasidiomycetes, which are able to decompose wood (Worrall et al. 1997). Homobasidiomycetes are found at the other end of the scale, mostly fast growing and strong decomposers, e.g. *Peniophora aurantiaca.* Agarics seem to take an intermediate position.

The species found at both ends of the scale in Fig.1, i.e. *Saccoblastia farinacea* and *Polyporus arcularius,* are among the most abundant aphyllophoroid fungi in green alder stands and must therefore be considered as very good competitors, too. The other species are all rather rarely fruiting and were found only in a few samples together with many additional aphyllophoroid fungi and agarics (Küffer & Senn-Irlet 2000, unpublished data) with the exception of *Peniophora aurantiaca* being by far the most frequent species.

A strong competitive ability for secondary decay species compared with their preceding species was found by Holmer et al. (1997). This observation fits

only partly with the results of our study. We found a broad range of competitive abilities in species classified as secondary decay species. An intermediate position both in growth rate and decay ability, paired with a medium competitive ability, leads to the highest species richness whereas species with weak or very strong decay abilities are few. Highest species diversity on intermediate positions would be in agreement with a general pattern in ecology described by Huston (1994).

The highest decay ability and the only species, which has a higher decay ability in fresh wood is *Polyporus arcularius.* The genus *Polyporus* is known as good decomposer of deciduous wood (Worrall et al. 1997). The observation that a fungus decomposes fresh wood better than decayed wood is thought to occur rather in facultative parasites such as *Armillaria* (Boddy & Rayner 1988). A study in Northern Finland showed that in the Polyporales, in the present study only represented by *Polyporus arcularius,* most species are found on a medium stage of decay, in contrast to the Corticiaceae s.l., which rather prefer the later stages (Renvall 1995).

The preference of many species for decayed wood can be interpreted as one for later stages of the decay process. An additional indication that most of the species of this study belong to this group of so-called late stage species.

In absolute terms, the decay rates found in our laboratory experiments are low. With such decay rates the fallen twigs and branches of green alder would need many years to be completely decomposed. However, field observations suggest that decay rates in green alder stands are much higher, within three years fresh cut stem turned brittle and fairly rotten. Therefore we must conclude that additional species or different moisture regimes play a crucial role in a fast natural decomposition process. Yet, *Stereum* species, well-known for high decay abilities are rarely found fruiting. More observations are needed to understand in a quantitative way the succession of wood decomposing fungi in green alder.

Niemelä et al. (1995) found that the late stage species in Finnish boreal forests can be characterised as species with thin and often ephemeral fruit-bodies. In our study only *Plicatura nivea* match this observation. For the early stages of wood decay Niemelä et al. (1995) propose rather thick and perennial fruit-bodies, which applies for *Polyporus arcularius,* indeed showing a preference for undecayed wood.

Unfortunately it is hardly possible to compare the results of this study with similar experiments: the incubation period, the selection of species as well as the woody substrate and the temperature chosen give an very high number of

possible combinations not covered by the anyway scanty literature. A comprehensive overview on decay rates by lignicolous basidiomycetes is given by Worrall et al. (1997). A high number of fungal species was tested on two different woody substrates (i.e. *Betula alleghaniensis* Britton and *Pinus taeda* L) for a rather short incubation period of only 12 weeks. The decay abilities of Heterobasidiomycetes and Homobasidiomycetes differed not so obviously as in our study and amounts among closely related species (or sometimes even within one single species) varied considerably. A time extrapolation from this 12 weeks test (Worrall et al. 1997) to our study seems difficult as decomposition rates may vary with time (Boddy & Watkinson 1995).

Blumenfeld (1984) tested fungi on wood of two *Pinus* species, a substrate which is decomposed much more slowly than that of *Alnus viridis.* Nevertheless, the weight loss of the wood blocks in six months is similar to that found in the present study.

Enzyme tests

The results of the enzyme experiments show only small differences: Whereas the R-lignin test and the Anilin medium had only few positive reactions, the Guaiacol- and the Blue Cellulose test displayed almost only strong positive results. The R-lignin test seems to be very specific, and there are some doubts if this test can unambiguously be used as a lignin test allowing for an ecological statement. *Armillaria cepistipes,* a well-known white-rotting wood decomposer and even facultative parasite, shows no signs of reaction in agreement with other strains of this genus tested from various woody substrates (results not shown).

The decomposition of lignin is very costly and offers little nutrient value (Aber & Melillo 1991), so it is possible that some of these species are only weak lignin decomposers, although they belong all to the white-rot species, which are able to degrade both cellulose and lignin.

In general, the results from the wood decay experiment are in agreement with the results from the enzyme tests: weak decomposition ability in the wood decay experiment is paired with weak reactions in the enzyme assay. Except *Megalocystidium leucoxanthum,* which shows a rather high wood decay ability, but shows only weak reactions in the enzyme experiments. A possible explanation is that the conditions in the enzyme experiments simulate an early stage in the wood decomposition process, in which *Megalocystidium leucoxanthum* proofed to be a rather weak decomposer (see Fig. 1).

The ecological function of the only representative of the ascomycetes is not clear: it appears that at least this species is fairly able to degrade wood, but in which amount and in which stage of the decay process it is most effective remains unknown. Ascomycetes are classified as soft rotting decomposers (e.g.

Dix & Webster 1995), or as members of a very early stage of in the decay process (Worrall et al. 1997).

Stalpers (1978) tested a great number of species with different enzyme tests. Only two species overlap with our study: *Peniophora aurantiaca* and *Hapalopilus rutilans. Peniophora aurantiaca* reacted positively in tyrosinase, peroxidase and laccase tests in agreement with our observations. For *Hapalopilus rutilans* a positive reaction for tyrosinase and peroxidase is reported combined with a very weak reaction for laccase, whereas we could found a strong reaction for laccase, but no other reactions.

Peniophora aurantiaca and *Megalocystidium leucoxanthum* have also been studied by Nakasone (1990). They showed a positive reaction both on gallic acid media and in the tannin acid test, but negative reactions on a tyrosine agar. *Plicatura nivea* shows only slight positive reactions in the gallic acid media, but no reaction in the other tests. These results underline the strong decay ability found in the wood decay experiment of *Peniophora aurantiaca* and *Megalocystidium leucoxanthum* in comparison with *Plicatura nivea.*

Further studies, both laboratory and ecological studies in situ, are needed to highlight the role of fungal activity on the decay process in wood ecosystems.

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References

Aber J. D. & Melillo J. M. 1991. Terrestrial Ecosystems. Saunders College Publishing, Philadelphia. 429 pp.

Alberto E. & Wright J. E. 1997. Anilin Agar: a simple medium useful in characterising white-rot fungi in culture. Mycotaxon 62: 375–388.

Bavendamm W. 1928. Ueber das Vorkommen und den Nachweis von Oxydasen bei holzzerstörenden Pilzen. Zeitschrift für Pflanzenkrankheiten und Pflanzenschutz 38: 257–276.

Blumenfeld S. N. 1984. Studies on the degradation of pine wood blocks by Aphyllophorales. Material und Organismen 19: 253–262.

Boddy L., Bardsley D. W. & Gibbson O. M. 1987. Fungal communities in attached ash branches. The New Phytologist 109: 143–154.

Boddy L. & Rayner A. D. M. 1988. Fungal decomposition of wood. Its biology and ecology. John Wiley and sons, Chichester. 587 pp.

Boddy L. & Watkinson S. C. 1995. Wood decomposition, higher fungi, and their role in nutrient redistribution. Canadian Journal of Botany 73 [Supplement 1]: 1377–1383.

Boidin J. 1951. Recherche de la tyrosinase et de la laccase chez les Basidiomycètes en culture pure. Revue de Mycologie 16: 172–197.

Dix N. J. & Webster J. 1995. Fungal Ecology. Chapman and Hall, London. 549 pp.

Harmon M. E. & Chen H. 1991. Coarse woody debris dynamics in two old-growth ecosystems. BioScience 41: 604–610.

Harmon M. E., Franklin J. F., Swanson F.J., Sollins P., Gregory S. V., Lattin J. D., Anderson N. H., Cline S. P., Aumen N. G., Sedell J. R., Lienkaemper G. W., Cromack K. & Cummins K. W. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133–302.

Holmer L., Renvall P. & Stenlid J. 1997. Selective replacement between species of wood-rotting basidiomycetes, a laboratory study. Mycological Research 101: 714–720.

Huston M. A. 1994. Biological Diversity. Cambridge University Press, Cambridge. 681 pp.

Hutchinson L. J. 1990. Studies on the systematics of ectomycorrhizal fungi in axenic culture II. The enzymatic degradation of selected carbon and nitrogen compounds. Canadian Journal of Botany 68: 1522–1530.

Küffer N. & Senn-Irlet B. 2000. Diversity and ecology of corticioid basidiomycetes in green alder stands in Switzerland. Nova Hedwigia 71: 131–143.

Levy, J. F. 1982. The place of basidiomycetes in the decay of wood in contact with the ground. In: Frankland, J. C., J. N. Hedger & M. J. Swift (Eds.): Decomposer basidiomycetes, their biology and ecology. Cambridge University Press, Cambridge. pp. 161–178.

Marr C. D. 1978. Laccase and tyrosinase oxidation of spot test reagents. Mycotaxon 9: 244–276.

Marx D. H. 1969. The influence of ectotrophic mycorrhizal fungi on the resistance of pine root pathogenic fungi and soil bacteria. Phytopathology 59: 153–163.

Maser C. & Trappe J. M. 1984. The seen and unseen world of the fallen tree. General technical report, US Dept. of Agriculture and Forest Service PNW 164: 1–56

McCann K. S. 2000. The diversity-stability debate. Nature 405: 228–233.

Nakasone K. K. 1990. Cultural studies and identification of wood-inhabiting Corticiaceae and selected Hymenomycetes from North America. Mycologia Memoir 15: 1–412.

Niemelä T., Renvall P. & Penttilä R. 1995. Interactions of fungi at late stages of wood decomposition. Annales Botanici Fennici 32: 141–152.
Renvall P. 1995. Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in Northern Finland. Karstenia 35: 1–51.
Sell J. 1989. Eigenschaften und Kenngrössen von Holzarten. Baufachverlag, Zürich. 80 pp.
Smith R. E. 1977. Rapid tube test for detecting fungal cellulase production. Applied and Environmental Microbiology 33: 980–981.
Stalpers J. A. 1978. Identification of wood-inhabiting fungi in pure culture. Studies in Mycology 16: 1–248.
Wettstein, S. 2001. Der Einfluss abiotischer Faktoren auf die Morphologie der Grünerle in den Schweizer Alpen. Botanica Helvetica 111: 31–44.
Worrall J. J., Anagnost S. E. & Zabel R. A. 1997. Comparison of wood decay among diverse lignicolous fungi. Mycologia 89: 199–219.

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