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FULL PAPER

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Decomposition of Japanese beech wood by diverse fungi isolated from a cool temperate deciduous forest

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Abstract We assessed 62 fungal strains in 31 species of wood decay fungi in the ability to decompose wood blocks of Japanese beech (*Fagus crenata*) under a pure culture condition. Fungi were collected in a cool temperate beech forest in Japan and isolated from the inside of beech logs and from sporocarps fruiting on logs and snags of beech that were different in diameter and decay class. Fungi in Holobasidiomycetidae showed marked decomposition of lignin and carbohydrate. These fungi were divided into three groups according to the pattern of lignin and carbohydrate utilization. *Phanerochaete filamentosa* decomposed lignin selectively. *Lampteromyces japonicus*, *Steccherinum rhois*, *Trichaptum biforme, Stereum ostrea*, *Mycena haematopoda*, *Antrodiella albocinnamomea*, *Daedalea dickinsii*, *Daedaleopsis tricolor*, *Ganoderma tsunodae*, and *Trametes versicolor* decomposed lignin and carbohydrates simultaneously. *Psathyrella candolleana*, *Lenzites betulinus*, and *Trametes hirsuta* decomposed carbohydrates selectively. Species in the Phragmobasidiomycetidae and in the Ascomycota caused low mass loss of wood.

Key words Carbohydrates · *Fagus crenata* · Lignin · Wood decay fungi

Introduction

Fungi play central roles in wood decomposition (Rayner and Boddy 1988). Wood decay by fungi is broadly grouped into three types: white-rot, brown-rot, and soft-rot (Rayner and Boddy 1988). These changes occur as a result of enzymatic differences of fungi that utilize chemical components of wood such as lignin and polymeric carbohydrates (cellulose and hemicellulose) in variable proportions (Eriksson et al. 1990). The wood-decay type of fungi have been studied with pure culture decay test under laboratory conditions, in which sapwood of beeches (*Fagus* spp.) has commonly been utilized (Savory and Pinion 1958; Fukuda et al. 1984; Enoki et al. 1985; Fukuda and Haraguchi 1985; Tanaka et al. 1988; Abe 1989; Tanesaka et al. 1993). The study of diverse wood-decay fungi and their decay types will support understanding the role of fungal wood decomposition in nature as well as its biotechnological applications.

In the present study, we assessed 62 fungal strains in 31 species of wood-decay fungi in the ability to decompose wood blocks of Japanese beech (*F. crenata* Bl.) under a pure culture condition. Fungi were collected in a cool temperate forest in Kyoto, Japan, and isolated from the inside of beech logs and from sporocarps fruiting on logs and snags of beech.

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Materials and methods

Fungi

The 62 strains in 31 species were used in the pure culture decay test (Table 1). During May to December 2001, 1–7 strains in each species were collected from a cool temperate deciduous forest dominated by *F. crenata* in the Ashiu experimental forest of Kyoto University (35°18′ N, 135°43′ E) about 40 km north from Kyoto City, Japan. The details of the study area were described in Fukasawa et al. (2002). Isolations were made from beech wood (Fukasawa et al. 2002, 2005) and from basidiocarps, mass basidiospores, or ascocarps on snags and fallen logs of beech that were different in diameter and decay class. *Trametes versicolor* IFO30340 and *Daedalea dickinsii* IFO 30766 were obtained from the culture collection of Institute for Fermentation, Osaka (IFO). All fungal strains were maintained on slants of 2% malt agar [MA: malt extract (Nacalai Tesque, Kyoto, Japan) 20 g, agar 20 g, and distilled water 1000 ml] at 20°C in darkness until the test.

Table 1. Fungal isolates used in the decay test: their mass loss of wood, lignin, and carbohydrates, lignin/wood loss ratio (L/W), and lignin/carbohydrate loss ratio (L/C)

Fungus[a]	Isolation		Mass loss (% original mass)				
	Code	Source[b]	Wood	Lignin	Carbohydrates	L/W	L/C
Basidiomycota							
Holobasidiomycetidae							
Agaricales							
Armillaria sp.	AR5	W	3.3 ± 1.3				
Lampteromyces japonicus	1062235	B	13.3 ± 3.1	14.6	9.8	1.1	1.5
L. japonicus	1062802	B	26.8 ± 3.7	33.0	56.7	1.2	0.6
L. japonicus	LJ1	W	21.6 ± 8.2	27.0	9.7	1.3	2.8
L. japonicus	LJ2	W	20.6 ± 1.0	28.1	15.7	1.4	1.8
L. japonicus	LJ3	W	17.4 ± 2.2	29.6	16.4	1.7	1.8
L. japonicus	LJ4	W	22.7 ± 4.1	35.0	20.5	1.6	1.7
L. japonicus	LJ5	W	17.3 ± 1.9	19.7	36.3	1.1	0.5
Mycena haematopoda	1052508	B	1.6 ± 0.7				
M. haematopoda	1062206	B	7.0 ± 0.8	11.1	13.4	1.6	0.8
Psathyrella candolleana	1062237	B	6.9 ± 2.2	3.9	15.0	0.6	0.3
P. candolleana	F2-10-10	W	6.5 ± 0.8	6.3	25.4	1.0	0.2
P. candolleana	F2-3-12	W	8.1 ± 0.8	5.7	16.6	0.7	0.3
P. candolleana	PC5	W	1.0 ± 0.1				
Cortinariales							
Crepidotus mollis	1062240	B	1.4 ± 0.7				
C. mollis	1082827	B	1.0 ± 0.2				
Ganodermatales							
Ganoderma tsunodae	1062222	B	23.8 ± 6.7	22.2	15.4	0.9	1.4
G. tsunodae	1070501	B	1.4 ± 0.1				
Poriales							
Antrodiella albocinnamomea	AA5	W	14.9 ± 5.5	19.9	25.5	1.3	0.8
Daedalea dickinsii	IFO30766		18.0 ± 0.6	22.2	22.8	1.2	1.0
Daedaleopsis tricolor	1091905	B	30.9 ± 5.9	42.1	49.8	1.4	0.8
Lenzites betulinus	1070510	B	46.5 ± 6.1	45.4	65.3	1.0	0.7
L. betulinus	1082402	B	24.5 ± 1.9	25.1	37.7	1.0	0.7
Panus rudis	1060422	B	8.7 ± 0.7	13.4	22.8	1.5	0.6
Pleurotus ostreatus	1082401	B	2.6 ± 0.8				
P. ostreatus	1082826	B	0.7 ± 0.1				
P. ostreatus	F2-1-26	W	3.1 ± 0.5				
Trametes hirsuta	1072401	B	22.0 ± 1.0	21.6	46.7	1.0	0.5
Trametes versicolor	1070515	B	2.7 ± 1.0				
T. versicolor	107312	B	22.7 ± 1.4	30.4	35.0	1.3	0.9

Decay test

Wood blocks ($17 \times 17 \times 5\,mm^3$) were cut out from a living beech tree in the study site. The blocks were air-dried at 40°C for 1 week, weighed, and preserved in a paper box until the test was started.

Fungal inocula for each assessment were cut out with a sterile cork borer (5 mm diameter) from the margin of the colony previously cultured on a 2% MA plate. One fungal plug was inoculated on the surface of 30 ml 2% MA plate (9 cm diameter). The plates were incubated at 25°C in darkness for 1 week. One wood block sterilized by ethylene oxide gas at 60°C for 3 h was then inoculated on the mycelium in each plate. The plates were further incubated for 12 weeks at 25°C in darkness. After the incubation, the blocks were retrieved and the external mycelium was carefully removed using forceps. The blocks were then oven-dried at 40°C for 1 week and weighed. Mass loss of wood block was determined as a percentage of the original mass. Three replicates were prepared in each strain, and three uninoculated plates served as control. One wood block that showed intermediate mass loss of three replicates was used for chemical analyses.

Chemical analyses

Wood blocks were ground in a laboratory mill to pass a 0.5-mm screen. The amount of lignin in the samples was estimated by gravimetry according to a standardized method using hot sulfuric acid digestion (King and Heath 1967). Total carbohydrate content was estimated by the phenol-sulfuric acid method (Dubois et al. 1956) according to Fukui (1969). The details of the procedures were described in Fukasawa et al. (2005).

Lignin/wood loss ratio (L/W) and lignin/carbohydrate loss ratio (L/C) are useful indices of substrate utilization pattern of fungi (Worrall et al. 1997; Osono and Takeda 2002). L/W and L/C in each fungal isolate were calculated according to the following equations:

L/W = mass loss of lignin (% of original lignin mass)/ mass loss of wood (% of original wood mass)

L/C = mass loss of lignin (% of original lignin mass)/mass loss of carbohydrate (% of original carbohydrate mass)

Table 1. Continued

T. versicolor	F1-7-8	W	39.7 ± 4.2	49.1	55.5	1.2	0.9
T. versicolor	F2-1-20	W	29.8 ± 1.2	27.7	64.6	0.9	0.4
T. versicolor	IFO30340		8.8 ± 4.8	7.5	14.4	0.8	0.5
Trichaptum biforme	1091906	S	13.0 ± 5.4	14.0	9.0	1.1	1.6
Stereales							
Phanerochaete filamentosa	1070506	B	9.9 ± 1.1	26.0	0.0	2.6	—[c]
Schizopora cf. *paradoxa*	1120503	B	10.5 ± 3.4	15.9	23.3	1.5	0.7
Steccherinum rhois	1070513	B	5.5 ± 1.6				
S. rhois	1073111	B	5.8 ± 1.0				
S. rhois	F4-9-15	W	9.5 ± 1.8	16.7	7.2	1.8	2.3
S. rhois	F6-7-6	W	8.0 ± 1.2	13.3	10.6	1.7	1.3
Stereum gausapatum	1120506	B	4.8 ± 1.3				
Stereum ostrea	1070508	B	14.6 ± 1.9	30.1	19.5	2.1	1.5
Phragmobasidiomycetidae							
Auricularia auricula	1062207	S	0.9 ± 0.7				
A. auricula	10622341	S	4.4 ± 0.4				
Dacrymyces sp.	1062209	S	0.7 ± 0.1				
Dacrymyces sp.	1062232	S	0.0 ± 0.1				
Exidia glandulosa	1052501	S	6.0 ± 3.3	7.2	6.7	1.2	1.1
E. glandulosa	1052502	S	4.6 ± 1.1				
E. glandulosa	F1-1-25	W	−0.3 ± 0.4				
Unidentified Basidiomycota							
Basidiomycete 1	B12	W	19.0 ± 2.8	21.4	16.4	1.1	1.3
Basidiomycete 2	B24	W	16.1 ± 1.5	19.2	32.8	1.2	0.6
Basidiomycete 3	B35	W	6.0 ± 0.4	19.9	0.0	3.4	—[c]
Ascomycota							
Ceratostomella cirrhosa	F1-1-6	W	1.3 ± 0.1				
Trichoderma sp.	TR3	W	0.4 ± 0.0				
Trichoderma sp.	TR4	W	0.6 ± 0.2				
Trichoderma sp.	TR5	W	0.2 ± 0.2				
Xylaria polymorpha	1072409	A	2.7 ± 0.6				
Xylaria sp.	F1-2-1	W	4.4 ± 1.0				
Xylaria sp.	F2-2-2	W	5.4 ± 0.9				
Sterile mycelia							
White sterile mycelium	F1-4-11	W	0.4 ± 0.0				
White sterile mycelium	F2-7-1	W	0.6 ± 0.2				
White sterile mycelium	SM2	W	0.3 ± 0.1				

Values indicate means ± SE ($n = 3$)
[a]The classification follows Hawksworth et al. (1995); the Ascomycota includes their anamorphs
[b]W wood; B, basidiocarp; S, spores; A, ascocarp
[c] L/C was not calculated because there was no mass loss of carbohydrates

Contents of lignin, carbohydrates, and nitrogen in initial wood block were 29.8%, 61.4%, and 0.10%, respectively.

Statistical analysis

A one-way analysis of variance (ANOVA) (SYSTAT version 5.2; Systat, Evanston, IL, USA) was performed to evaluate the difference in mass loss rate of wood, lignin, and carbohydrates and in L/W and L/C among fungal taxa. Scheffe's test was used for multiple comparisons.

Results

Mass loss

Mass loss of beech wood block ranged from −0.3% to 46.5% (see Table 1). *Lenzites betulinus* 1070510 caused the highest mass loss, followed by *Trametes versicolor* F1-7-8, *Daedaleopsis tricolor* 1091905, *T. versicolor* F2-1-20, and *Lampteromyces japonicus* 1062802. At the species level, *L. betulinus* caused the highest mean mass loss (35.5%) followed by *D. tricolor* (30.9%), *T. hirsuta* (22.0%), *T. versicolor* (20.7%), and *L. japonicus* (19.9%). Mean mass loss of wood block caused by Holobasidiomycetidae was significantly ($P < 0.05$) higher than those of Phragmobasidiomycetidae and Ascomycota (Fig. 1).

Lignin and carbohydrates were measured for the wood blocks that indicated mass loss of more than 6% (see Table 1). Mass loss of lignin ranged from 3.9% to 49.1%. *Trametes versicolor* F1-7-8 caused the highest mass loss of lignin, followed by *L. betulinus* 1070510 and *D. tricolor* 1091905. At the species level, *D. tricolor* caused the highest mass loss of lignin (42.1%), followed by *L. betulinus* (35.3%), *Stereum ostrea* (30.1%), *T. versicolor* (28.7%), *L. japonicus* (26.7%), and *Phanerochaete filamentosa* (26.0%). Mass loss of carbohydrates ranged from 0.0% to 65.3%. *Lenzites betulinus* 1070510 caused the highest mass loss of carbohydrates, followed by *T. versicolor* F2-1-20, *L. japonicus* 1062802, and *T. versicolor* F1-7-8. At species level, *L. betulinus* caused the highest mean mass loss of carbohydrates (51.5%), followed by *D. tricolor* (49.8%), *T. hirsuta* (46.7%), *T. versicolor* (42.4%), and unidentified Basidi-

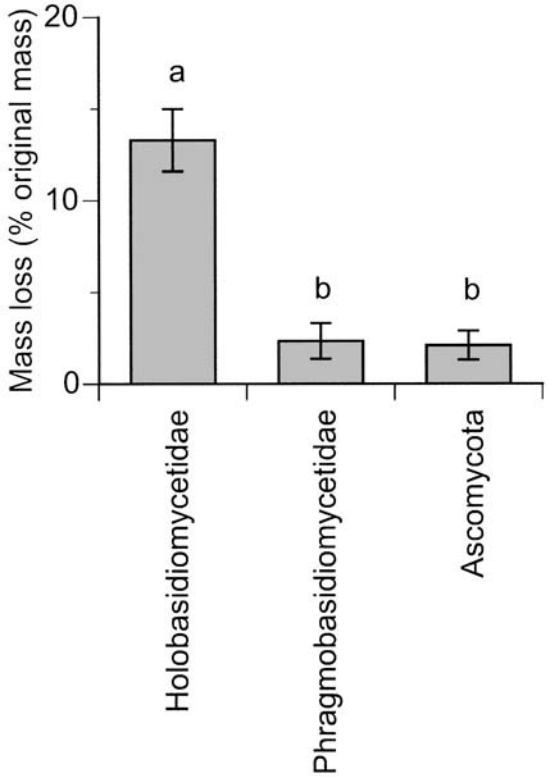

Fig. 1. Comparison of mass loss of wood among higher fungal taxa. Values indicate means ± SE (Holobasidiomycetidae, $n = 42$; Phragmobasidiomycetidae, $n = 7$; Ascomycota, $n = 7$). The same letters indicate not significantly different at 5% level by Scheffe's test

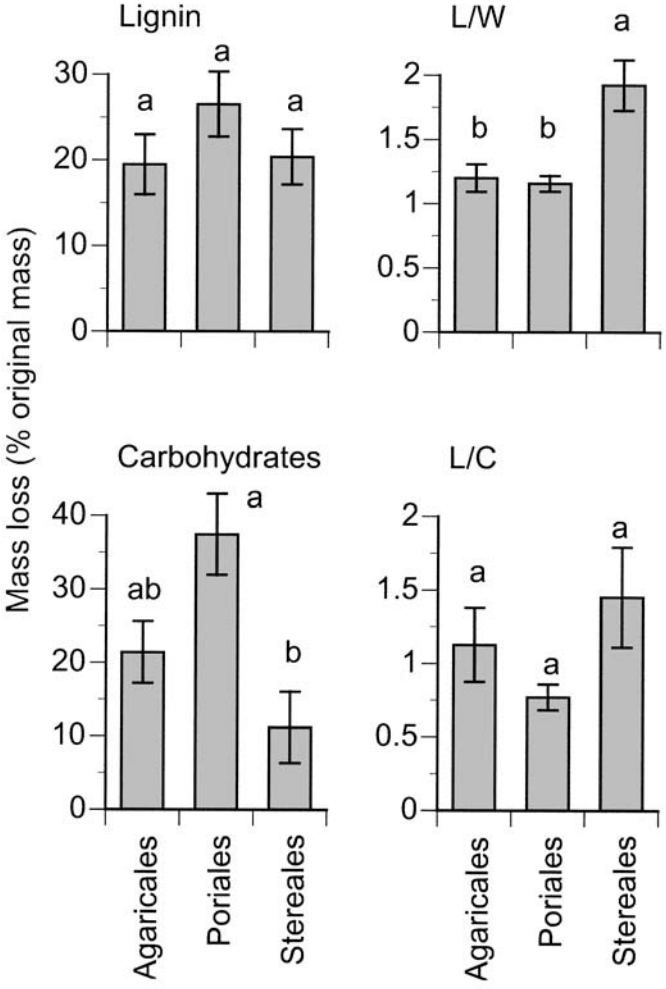

Fig. 2. Comparison of mass loss of lignin and carbohydrates, lignin/wood loss ratio (*L*/*W*), and lignin/carbohydrate loss ratio (*L*/*C*) within Holobasidiomycetidae. The same letters indicate not significantly different at 5% level by Scheffe's test

omycete 2 (32.8%). In Holobasidiomycetidae, mean mass loss of lignin was not significantly ($P > 0.05$) different among three orders, but that of carbohydrates was significantly ($P < 0.05$) higher in Poriales than in Stereales (Fig. 2).

Substrate utilization

Lignin to wood mass loss ratio (L/W) ranged from 0.6 to 3.4 (see Table 1). Unidentified Basidiomycete 3 B35 showed the highest L/W, followed by *P. filamentosa* 1070506 and *S. ostrea* 1070508. On the other hand, *Psathyrella candolleana* 1062237 and *P. candolleana* F2-3-12 showed the lowest L/W. At species level, L/W ranged from more than 2 in unidentified Basidiomycota 3 (3.4), *P. filamentosa* (2.6), and *S. ostrea* (2.1) to less than 1 in *P. candolleana* (0.7) and *Ganoderma tsunodae* (0.9), with intermediate values in the other species tested. Lignin to carbohydrate mass loss ratio (L/C) ranged from 0.2 to 2.8.

Phanerochaete filamentosa 1070506 and Basidiomycete 3 B35 caused undetectable mass loss of carbohydrates so that L/C was not calculated. Except for those two species, *L. japonicus* LJ1 showed the highest L/C, followed by *S. rhois* F4-9-15. On the other hand, *P. candolleana* F2-10-10, 1062237, and F2-3-12 showed the lowest L/C. At the species level, L/C ranged from less than 0.8 in *P. candolleana* (0.3), *T. hirsuta* (0.5), unidentified Basidiomycete 2 (0.6), *Panus rudis* (0.6), *L. betulinus* (0.7), and *Schizopora* cf. *paradoxa* (0.7) to *S. ostrea (1.5)*, *Trichaptum biforme* (1.6), and *Steccherinum rhois* (1.8), with intermediate values in the other species tested. In Holobasidiomycetidae, L/W was significantly ($P < 0.05$) higher in Stereales than in Agaricales and Poriales, but L/C was not significantly ($P > 0.05$) different among Agaricales, Poriales, and Stereales (see Fig. 2).

Discussion

Fungi in Holobasidiomycetidae showed marked decomposition of lignin and carbohydrates in beech wood, although fungi in the Phragmobasidiomycetidae and in the Ascomycota showed low mass loss of mean. However, some species in *Auricularia* and *Dacrymyces* in the Phragmobasidiomycetidae and xylariaceous Ascomycota are reported to cause higher mass loss rate of beech wood than observed in the present study (Seifert 1983; Abe 1989;

Nilsson and Daniel 1989; Tanesaka et al. 1993; Worrall et al. 1997).

At the species level, *L. betulinus*, *T. versicolor*, *D. tricolor*, and *L. japonicus* caused the highest mass loss of beech wood block with lignin and carbohydrate. These species are known as vigorous decomposers of lignocellulose and are regarded as white-rot fungi (Ander and Eriksson 1977; Setliff and Eudy 1980; Blanchette et al. 1985; Enoki et al. 1985; Imazeki and Hongo 1987, 1989; Tanesaka et al. 1993; Worrall et al. 1997). In addition, *Panus rudis*, *P. filamentosa*, *S. rhois*, *Stereum gausapatum*, *S. ostrea*, and *T. biforme* also caused mass loss of both lignin and carbohydrates. *Panus rudis* and *S. gausapatum* are known as white-rot fungi (Setliff and Eudy 1980; Tanesaka et al. 1993). To our knowledge, this is the first report of lignocellulose decomposition by *P. filamentosa*, *S. rhois*, *S. ostrea*, and *T. biforme*. *Armillaria* sp. and *Pleurotus ostreatus,* which have been reported as ligninolytic fungi (Tanesaka et al. 1993; Worrall et al. 1997), showed limited ability in the present study. *Daedalea dickinsii*, which is generally known as brown-rot fungus (Imazeki and Hongo 1989), showed ligninolytic activity in the present study, as reported previously (Enoki et al. 1985; Osono and Takeda 2003).

In the present study, tested fungi were divided into three groups according to their mean L/C values. The first group included *P. filamentosa* and unidentified Basidiomycete 3, which showed highly selective delignification associated with negligible mass loss of carbohydrates. *Phanerochaete chrysosporium* has been studied intensively as a model fungus that causes selective delignification of wood (Eriksson et al. 1990). The second group included *L. japonicus*, *Steccherinum rhois*, *T. biforme, S. ostrea*, *Mycena haematopoda*, *Antrodiella albocinnamomea*, *D. dickinsii*, *D. tricolor*, *G. tsunodae*, *T. versicolor*, and unidentified Basidiomycete 1, which caused simultaneous loss of lignin and carbohydrates with L/C in the range of 0.8–2. The third group included *P. candolleana*, *T. hirsuta*, unidentified Basidiomycete 2, *P. rudis*, *Schizopora* cf. *paradoxa*, and *L. betulinus*, which degraded carbohydrate in preference to lignin with L/C of less than 0.8.

Our results indicated that fungi in Holobasidiomycetidae were major decomposers of lignin and carbohydrates of Japanese beech logs. Fungi in Agaricales and Poriales showed similar decay ability. Fungi in Stereales caused more selective delignification. Fukasawa et al. (2005) showed that several species in these fungal taxa were dominant colonizers of beech logs in the study site and that the small-scale variation in contents of lignin and carbohydrates reflects within-log distribution and decay ability of these fungi. The present study will contribute to the understanding of the role of fungi in chemical changes of beech logs during decomposition.

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