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Lignin-degrading ability of litter-decomposing basidiomycetes from *Picea* forests of Hokkaido

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The frequency of occurrence of the litter-decomposing basidiomycetes of *Picea abies* and *P. glehnii* forest floors in Hokkaido was investigated. In both the *P. abies* and *P. glehnii* forest plots (each 10 m × 10 m), litter-decomposing basidiomycetes of the genera *Collybia* and *Mycena* were frequently observed. Species composition, frequency of occurrence, and basidioma numbers of each species were different between the two forest plots, but several species were common to both. Seven species isolated from the *P. glehnii* forest plot (*C. acervata, C. pinastris, Marasmius pallidocephalus, Ma. wettsteinii, My. aurantiidisca, My. clavicularis, Mycena* sp. 1) and four species from the *P. abies* forest plot (*C. pinastris, My. alphitophora* (=*My. osmundicola*), *Mycena* sp. 1, *My. vulgaris*) were tested for their ability to degrade lignin by a simple plate test for extracellular phenoloxidases and by measuring Klason lignin loss from needle litter of spruce. All the strains of the litter-decomposing fungi tested showed positive reactions on the plate test. Lignin contained in the needle litter was degraded by all strains tested (only *My. alphitophora* was not tested), and rates varied from 9% to 40% over a two-month period in vitro. Seven species with ligninolytic ability in the *P. glehnii* forest plot and four such species in the *P. abies* forest plot were found respectively in 77% and 60% of the 100 subplots in each plot. The results of this study suggest that lignin decomposition of needle litter by litter-decomposing basidiomycetes in the forest floor is a common event in the studied *Picea* forests of Hokkaido and that the diversity of the ligninolytic activity among the species or strains may cause spatial heterogeneity of litter decomposition in the *Picea* forest floor.

Key Words——basidiomycetes; lignin-degrading ability; litter decomposition; *Picea* forest.

Many studies have indicated that fungi proficient in lignin-decomposition belong to the Basidiomycetes, and that the ability to decompose lignin varies considerably among fungal species (Lindeberg, 1944, 1947; Mikola, 1955; Tanesaka et al., 1993). However, in most cases, the results of early studies may not supply sufficient data for understanding the activity of lignin-decomposing fungi in a specific ecosystem, because few works give detailed account of the habitats of the tested fungi. The measurable decomposition rate of litter in the laboratory varies with both the origin and history of the litter used as material, i.e., the tree species which supplied the litter and the degree of weathering and received microbial attack of the litter (Mikola, 1956; Saito, 1958; Dix and Simpson, 1984). From field observation, some litter-decomposing fungi are known to have substrate preference or specificity and to be restricted in their distribution to the O horizon under a certain tree species (e.g., Smith, 1947; Antonín and Noordeloos, 1993). Therefore, the litter material used for the investigation of the litter decomposition rate in the laboratory needs careful consideration in these points.

The use of sterilized material may also influence the decomposition rate. Material sterilized by autoclaving decomposed more rapidly than fumigated or irradiated materials, since its chemical and/or physical properties are changed by autoclaving (Saito, 1958; Hering, 1967). The litter material used in earlier work was generally autoclaved.

Recent studies on the lignin-decomposing fungi have concentrated on the screening of fungi for commercial applications such as lignin biodegradation of wood pulp or transformation of agricultural waste into food (Crawford, 1981; Eriksson and Kirk, 1985; Zadrazil, 1985; Valmaseda et al., 1990; Malek et al., 1994), and not on the relationship between the activity of fungi and the nature of their original habitat. Consequently, we do not have sufficient data to judge the ecological importance of fungi as litter-decomposers in forest ecosystems.

The objectives of the present study were to investigate the lignin-degrading ability of some basidiomycetes inhabiting in the O horizon of *Picea* forests in Hokkaido and to provide additional data for better understanding of the importance of the fungi in the spruce needle litter decomposition of spruce forests. Production of extracellular phenoloxidases was investigated using a simple plate test. To confirm the decomposition of

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lignin in needle litter by the fungal species used, Klason lignin loss was examined using natural substrates collected from *Picea* forest floors. They were used after sterilization by irradiation.

Materials and Methods

Fungal flora The frequency of occurrence of litter-decomposing basidiomycete species was investigated in two *Picea* forests at Uryu Experimental Forest of Hokkaido University, Uryu-gun, Horokanai-cho, Hokkaido: a plantation of approximately 40-yr-old *Picea abies* Karst. and a natural forest of *Picea glehnii* (Fr. Schmidt) Mast. in which the most oldest tree was at least 280 yr old (Noda, 1996). These sites are situated at an elevation of 300 m. Mean annual precipitation and temperature during 1956–1989 were 1540 mm and 3.0°C, respectively (Experimental Forest of Hokkaido University, 1990). Snowfall persists from November to April. At each site, one plot was established with a size of 10 m × 10 m (subdivided into 1 m × 1 m subplots). The canopy is almost closed at both plots. At the plot of *P. glehnii*, 94.2% of the basal area of all trees over 1.3 m in height was occupied by *P. glehnii*. Several species of understory tree, mainly *Abies sachalinensis* (Fr. Schmidt) Mast. and *Quercus mongolica* var. *grosseserata* Rehd. et Wils. were also present. There were no other tree species in the plantation of *P. abies*. The plots were separated by a distance of about 400 m. From May to November, 1992, each plot was visited 15 times at 10-d intervals in principle, but sometimes with more intensive observation after rainfall. The number of basidiomata of each species growing on litter or humus was counted in each subplot. The frequency of occurrence of a species in a plot was expressed as the percentage of subplots in which its basidiomata were recognized. The results are shown in order of frequency of occurrence (over 9th) (Table 1). We defined litter-decomposing basidiomycetous fungi as those forming basidiomata on needle litter or humus. Taxonomic identifications except for previously reported species (Miyamoto et al., 1998a, 1998b, 1998c) were mainly made after Halling (1983), Maas Geesteranus (1983, 1984, 1988a, 1988b, 1989a, 1989b), and Antonín and Noordeloos (1993).

Collection and isolation The basidiomata from which the basidiospores harvested for isolation were collected from inside and around the plots during 1992–1994, and the multispore isolates were obtained from the fungi. The dikaryotic strains were maintained on 2% malt extract agar slants in test tubes. For the purpose of comparison, basidioma tissue isolates of two wood-rotting fungi, *Fomitopsis pinicola* (Swartz: Fr.) Karst. and *Fomes fomentarius* (L.: Fr.) Fr., were used. Voucher strains are

Table 1. Fequencies of occurrence and basidioma numbers of litter-decomposing basidiomycetes in the *Picea* forests of Hokkaido.

Tree species[a]	Species	Frequency (%)[b]	Number of basidiomata[c]
Picea abies	*Mycena sanguinolenta* (Alb. & Schw.: Fr.) Kummer	46	285
	Collybia pinastris (Kauffman) Mitchel & Smith	42	2567
	Mycena alphitophora (Berk.) Sacc. (=*My. osmundicola* J. Lange)	42	1214
	Mycena stylobates (Pers.: Fr.) Kummer	42	280
	Mycena pura (Pers.: Fr.) Kummer	33	131
	Mycena vulgaris (Pers.: Fr.) Kummer	23	1380
	Mycena sp. 1	15	349
	Mycena aurantiidisca (Murrill) Murrill	14	120
	Mycena amicta (Fr.) Quélet	12	19
	Collybia acervata (Fr.) Kummer	11	43
	Marasmius sp. 1	7	42
P. glehnii	*Collybia pinastris* (Kauffman) Mitchel & Smith	28	148
	Mycena aurantiidisca (Murrill) Murrill	24	545
	Mycena sp. 1	13	35
	Mycena clavicularis (Fr.) Gillet	11	184
	Mycena polygramma (Bull.: Fr.) S. F. Gray	9	18
	Mycena sanguinolenta (Alb. & Schw.: Fr.) Kummer	9	12
	Marasmius pallidocephalus Gilliam	9	357
	Marasmius sp. 1	5	20
	Collybia acervata (Fr.) Kummer	5	13
	Marasmius wettsteinii Sacc. & Sydow	3	70

a) Dominant tree species in the canopy of each plot (10 m × 10 m).
b) Frequency = number of subplots (1 m × 1 m) in which basidiomata were found/total subplots (100) × 100.
c) Total number of basidiomata found in each plot from May to November, 1992.

deposited in the first author's culture collection.

Lignin-degrading ability Ligninolytic activity was estimated by the formation of a colored zone around a mycelium growing on wood powder and agar medium containing guaiacol as described by Nishida et al. (1988). The presence of the colored zone indicates extracellular phenoloxidases production. Nishida et al. (1988) noted that their method was suitable for measuring ligninolytic activity, because the results showed good agreement with the results of assays relying on the measurement of Klason lignin loss, and that there is a smaller risk of mistaking non-ligninolytic fungi for ligninolytic fungi in this test than in the Bavendamm test (Bavendamm, 1928). Discs of fungi were cut with a 4-mm diam cork-borer from the actively growing colony margins of isolates maintained on plates of 2% malt extract (Difco) agar. These discs were inoculated onto an agar plate containing 0.01% (v/v) guaiacol, 0.2% (w/v) beech (*Fagus crenata* Blume) wood-powder (100-mesh-pass), and 1.8% (w/v) agar. Plates were incubated at 23°C. The pH of the medium was adjusted to 5.0 before autoclaving at 121°C for 20 min, and guaiacol was added after the medium had cooled to 50–60°C. Nishida et al. (1988) used medium containing 1.6% agar. However, 1.8% agar was used in this study to obtain a more appropriate degree of solidity. All tests were performed in 9-cm diam non-vented Petri dishes contained 15 ml of medium per dish, and four replicates were performed. After 2 wk, the diameters of the colony and surrounding colored zone were measured in two directions at right angles to one another.

The needle litter of *P. abies* and *P. glehnii* was collected at several points from the O horizon of soil under each tree species by using metal cylinders with an opening of 10 cm in diam. Needles of the L and F layers were then carefully selected by using a sieve and a forceps. The litter was air-dried at room temperature, and an amount equivalent to a dry weight of 1 g was placed in a 100-ml Erlenmeyer flask. This was irradiated by ^{60}Co gamma-rays at 30 kG for 144 h. Five ml of sterilized distilled water was added, and the mixture was allowed to soak for a few hours before inoculation. Test fungi isolated from *Picea* forests were pre-cultured in liquid culture containing 2% malt extract (Difco). About 20 ml of the hyphal mass of each species was rinsed five times with sterilized distilled water, then homogenized with 20 ml of sterilized distilled water. The sterilized litter was inoculated with 1 ml of sterilized distilled water containing the homogenized hyphal suspension or with only 1 ml of sterilized distilled water as a control, then incubated at 23°C for 2 mo. After 1 mo, 5 ml of sterilized distilled water was added. Four or five replicates were made for each species and the control. The diameter of the colony was measured at intervals of 1 wk. After incubation, each sample was filtered and dried at 80°C. Three samples were then selected at random, and the Klason lignin content of the needle litter was determined by the modified method of King and Heath (1967). The lignin decomposition (%) was estimated by comparing the weight loss of Klason lignin in the test sample to that of the control. Although Klason lignin contains true lignin and lignin-like material (humic compounds produced during decomposition), we have used the term lignin here as employed by Berg et al. (1993).

Results and Discussion

Species composition and frequency In both the *P. abies* and *P. glehnii* forest plots, litter-decomposing basidiomycetes of the genera *Collybia* and *Mycena* were frequently observed (Table 1). These fungi were found in 97% of the 100 subplots in the former plot and 68% in the latter. Species composition, frequency of occurrence, and basidioma numbers of each species were different between the two plots, though several species were common to both (Table 1), and most of the observed species were known to occur commonly in coniferous forests. *Collybia pinastris* (Kauffman) Mitchel

Table 2. Strains used in this study.

Species	Strain	Substrate[a)]	Date of isolation
Collybia acervata	L94016	Needles, small twigs of Pg, small twigs of Qm	1994.9.27
Collybia pinastris	L92016	Needles of Pa	1992.7.9
Collybia pinastris	L93001	Needles of Pg	1993.7.24
Fomes fomentarius	W95002	Coniferous wood	1995.10
Fomitopsis pinicola	W95001	Wood of Be	1995.10
Marasmius pallidocephalus	L94008	Needles of Pg	1994.7.12
Marasmius wettsteinii	L94010	Needles of Pg	1994.7.12
Mycena alphitophora	L94015	Needles of Pa	1994.9.10
Mycena aurantiidisca	L94017	Needles of Pg	1994.10.27
Mycena clavicularis	L94009	Needles of Pg or As	1994.7.12
Mycena sp. 1	L94004	Needles of Pa	1994.7.1
Mycena sp. 1	L94006	Needles of Pg	1994.7.3
Mycena vulgaris	L92022	Needles of Pa	1992.10.5

a) As: *Abies sachalinensis*; Be: *Betula ermanii*; Pa: *Picea abies*; Pg: *Picea glehnii*; Qm: *Quercus mongolica* var. *grosseserata*.

& Smith, the most frequently observed species in the two plots, has been observed only on coniferous litter (Halling, 1983; Miyamoto et al., 1998a), as was also the case for some of the other species: *My. aurantiidisca* (Murrill) Murrill, *My. clavicularis* (Fr.) Gillet, and *My. vulgaris* (Pers.: Fr.) Kummer (Maas Geesteranus, 1989a, 1990; Miyamoto et al., 1998c), *Marasmius pallidocephalus* Gilliam (Gilliam, 1976; Miyamoto et al., 1998b), *Ma. wettsteinii* Saccardo & Sydow (Antonín and Noordeloos, 1993; Miyamoto et al., 1998b). The basidiomata formed on decaying *Picea* needles retained their original shape, and did not fruit from the humus (H layer). Of the species shown in Table 1, *My. polygramma* (Bull.: Fr.) S. F. Gray is known to grow only on deciduous tree litter (Maas Geesteranus, 1988a), and we also observed this species among the litter of *Q. mongolica* var. *grosseserata* mixed with spruce needles. *Collybia acervata* (Fr.) Kummer is able to live on decaying wood and coniferous or deciduous humus in nature (Halling, 1983) but seemed to inhabit both the needle litter of *Picea* and small twigs of *Q. mongolica* var. *grosseserata* at the study site. No correlation was found between species frequency and basidioma numbers of species. Finally, we obtained cultures of nine species (eleven strains) from among the species found in the two forests and tested their ability to degrade lignin (Table 2).

Lignin degrading ability All the strains of the litter-decomposing fungi tested produced dark red zones in the guaiacol-containing medium (Table 3). This suggests that they have ligninolytic activity. For comparison, we tested two woodrotting fungi, *Fomi. pinicola* and *Fome. fomentarius*, by the same method. *Fomitopsis pinicola* is a well known brown-rot fungus of coniferous wood and unable to degrade lignin. It grew well in the guaiacol-containing medium, but did not produce colored zones. On the other hand, *Fome. fomentarius*, which is known to cause white-rot of deciduous wood, produced colored zones.

The lignin-degrading ability of the fungi that produced dark red zones in the guaiacol medium was confirmed by measuring the decrease of the lignin in the needle litter (Table 3). The rate of loss for each strain was significantly different from that of the control (Mann-Whitney U test, $P<0.05$) and varied among the species. The growth rate of the mycelium on needle litter also varied among the species (Table 4). But no clear correlation was observed between the rate of loss of lignin and the growth rate of mycelium. This result may reflected partly the difference in total biomass and partly the difference in enzymatic activity among the strains.

It has been reported that measuring phenoloxidase activity in agar media introduces the risk of mistaking non-ligninolytic fungi for ligninolytic fungi (Sundman and Näse, 1971; Nishida et al., 1988). In this study, however, we found no inconsistency between the results of the phenoloxidase activity test on agar plates and the Klason lignin-degrading ability of the tested fungi. The reliability of the simple plate test has already been indicated by Nishida et al. (1988) for rot-type diagnosis. And we have not found any brown-rot species among the litter-decomposing basidiomycetes of *Picea* forests during this study.

The greatest lignin loss was produced by strains of *Ma. pallidocephalus* (40%). The lowest loss of 9% was

Table 3. The ligninolytic ability of selected litter-decomposing basidiomycetes collected from *Picea* forests.

Tree species[a]	Species/Strain	Colony diam[b]	Coloration zone diam[c]	Klason lignin loss (%)[d]
P. abies	*Collybia pinastris*/L92016	29±1	38±1	23±5*[g]
	Mycena alphitophora/L94015	16±0	30±1	—[e]
	Mycena sp. 1/L94004	30±2	41±2	29±3*
	Mycena vulgaris/L92022	21±1	40±1	9±2*
P. glehnii	*Collybia acervata*/L94016	17±1	36±0	33±0*
	Collybia pinastris/L93001	24±3	28±2	12±2*
	Marasmius pallidocephalus/L94008	25±1	41±3	40±2*
	Marasmius wettsteinii/L94010	13±1	28±1	12±1*
	Mycena aurantiidisca/L94017	10±1	20±1	9±0*
	Mycena clavicularis/L94009	30±0	40±0	33±0*
	Mycena sp. 1/L94006	32±0	41±1	18±4*
	Fomes fomentarius/W95002†[f]	41±4	44±6	—
	Fomitopsis pinicola/W95001†	73±2	0±0	—

a) Dominant tree species in the canopy where fungi were collected and of the needle litter used for Klason lignin loss.
b) The mean of four replications in colony diam (mm) on wood powder and agar medium containing guaiacol after 2 wk (±SD).
c) The mean of four replications in coloration zone diam (mm) on wood powder and agar medium containing guaiacol after 2 wk (±SD).
d) The mean of three replications in Klason lignin weight loss of the needle litter after 2 mo (±SD).
e) —, Not tested.
f) †, Wood-rotting fungi for comparison.
g) *, Significant difference from control ($P<0.05$) by Mann-Whitney U-test.

Table 4. Hyphal growth of selected litter-decomposing basidiomycetes in *Picea* needle litter during 2 mo of incubation.

Tree species	Species/Strain	Time after inoculation (wk)				
		1	2	4	6	8
P. abies	*Collybia pinastris*/L92016	++/+++	++++	++++	++++	++++
	Mycena sp. 1/L94004	—	+/++	++++	++++	++++
	Mycena vulgaris/L92022	—	+	+/++	+/++	+/++
P. glehnii	*Collybia acervata*/L94016	+++	++++	++++	++++	++++
	Collybia pinastris/L93001	+++	++++	++++	++++	++++
	Marasmius pallidocephalus/L94008	—/++	++/+++	++++	++++	++++
	Marasmius wettsteinii/L94010	++/+++	++++	++++	++++	++++
	Mycena clavicularis/L94009	+	++	++++	++++	++++
	Mycena sp. 1/L94006	+	+++	++++	++++	++++
	Mycena aurantiidisca/L94017	—	+	++/+++	++++	++++

Diameter of colony: —, no growth; +, 0–15 mm; ++, 15–30 mm; +++, 30–45 mm; ++++, 45–60 mm.

observed for *My. aurantiidisca* and *My. vulgaris*. It is difficult to compare the results of lignin loss with those obtained by other investigations, because of the different conditions of incubation, especially the incubation period and the temperature. Lindeberg (1944, 1947) reported that *Marasmius* spp. (eight species) could decompose lignin in pine needles at a rate of 1.2% to 58.6% over 6 to 7 mo at 25°C, and that beech leaves could be decomposed at a rate of 19.4% to 76.5% over a period of about 5 to 7 mo at 25°C by *Collybia* spp. (four species), *Marasmius* spp. (five species) and *Mycena* spp. (seven species). The rate of lignin loss from *Picea* needles over 2 mo period at 23°C in the present study is not so low if one takes into account the shorter incubation period and the fact that decomposition of *Picea* needle litter is relatively slow (Takeda et al., 1987). Also, the needles used in the present study were sterilized by irradiation, whereas autoclaved substrates were used by Lindeberg (1944, 1947).

Because of the recalcitrant nature of lignin in degradation by microorganisms, lignin concentration regulates the rate of litter decomposition (Swift et al., 1979; McClaugherty and Berg, 1987; Takeda et al., 1987; Berg et al., 1993). Therefore, it is important to investigate lignin decomposition by litter-decomposing microorganisms in order to elucidate the mechanism of litter decomposition in forests. The composition and distribution of litter-decomposing basidiomycetes in the forest floor has received relatively little attention compared to microfungal species (e.g., Widden and Parkinson, 1973; Kjøller and Struwe, 1982), even though Basidiomycetes are known to be proficient in lignin decomposition and thought to be the most important functional group in litter decomposition. One reason for this seems to be the difficulty of obtaining precise data about the distribution of a species in soil or litter. The distribution of basidiomycetous fungi is usually investigated using the occurrence of basidiomata at a certain period as a marker. However, the absence of basidiomata of a certain species at a location does not mean the absence of the mycelium in soil or litter. This suggests that the abundance of each species observed in this experiment may be underestimated.

In this report, seven species with ligninolytic ability in the *P. glehnii* forest plot and four such species in the *P. abies* forest plot were found respectively 77% and 60% of the 100 subplots in each plot. The ligninolytic fungi are probably distributed more densely in the *Picea* forests, because their distributions may be underestimated. Therefore the results of this study suggest that lignin decomposition of needle litter by litter-decomposing basidiomycetes in the forest floor is a common event in the *Picea* forests of Hokkaido studied. Furthermore, there was considerable diversity in ligninolytic activity among the species or strains, and this may cause spatial heterogeneity of litter decomposition in the *Picea* forest floor.

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