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FULL PAPER

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Distribution of Myxomycetes on coarse woody debris of *Pinus densiflora* at different decay stages in secondary forests of western Japan

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Abstract The relationship between myxomycete species and the decay stage of wood of *Pinus densiflora* coarse woody debris was investigated in warm temperate secondary forests of western Japan. The number of species and species diversity of the myxomycete community reached the maximum on moderately decayed wood. The 25 dominant species recorded from 8 or more samples of the total 1530 samples were arranged in order of the succession index corresponding to the stage of decay. Species on slightly decayed hard pine wood were characterized by *Stemonitis splendens*, *Enerthenema papillatum*, and *Physarum viride*, whereas species of Cribrariaceae were found on brittle decayed soft wood increasing abundance according to the decay stages. Most of the species occurred where there was sufficient moisture preserved in the environment of the decaying wood, although *S. splendens* specifically emerged in low-moisture environments. Because the myxomycete species had preference to different decay stages of wood, it appears that they change sequentially during myxomycete community succession on dead pine wood according to the progression of decay.

Key words Decay stage · Moisture · Myxomycetes · *Pinus densiflora* · Succession

Introduction

Myxomycetes are microbes that inhabit various humus environments. In the life cycle of myxomycetes, myxoamoebae and swarms prey on decomposer bacteria (Lister 1890; Indira 1969; Carlile 1974), and plasmodia feed on fungi in the heterotrophic phase (e.g., Lister 1888; Howard and Currie 1932; Madelin 1984; Ali and Kalyanasundram 1991). A few studies have investigated the relationships between myxomycetes and substrates in the decaying state. On decaying wood, Elliott and Elliot (1920) reported the occurrence of two species of myxomycetes associated with the dead and decaying part of a branch of a living tree. Hamashima (1965) reported the occurrence of myxomycetes associated with old, well-used wood on which shiitake mushrooms were cultivated. Ing (1994) reviewed many taxonomic studies and noted that the species found on slightly decomposed wood differ from those characteristic of well-decayed wood.

However, quantitative study on the relationship between myxomycetes and decaying wood has not yet been fully investigated. Takahashi (1999, 2004) found that moderately decaying deciduous broadleaf and coniferous wood harbored the maximum number of species and density of individuals. This result suggests that the myxomycete species community has some relationship with the decomposition state of woody debris and that the particular species of myxomycetes may appear at the limited decay stages of woody debris in forests. As the myxomycetes are one group of microbes that inhabit decaying wood, an ecological understanding of the myxomycetes may provide important information on a dystrophic food chain and the whole forest ecosystem.

This study was performed to clarify the myxomycete species diversity on decaying *Pinus densiflora* wood and the specific relationships between occurrence of myxomycetes and decaying stage of wood, including the moisture content of the wood.

Materials and methods

Study site

This study was carried out in warm temperate secondary forests dominated by *Pinus densiflora* Siebold & Zucc. in

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Okayama and Tottori prefectures in western Japan. Samples were collected at eight sites located along approximately 110 km from the northernmost site (35.40° N, 133.85° E) to the southernmost site (34.51° N, 133.52° E) through a range of altitudes from 20 to 680 m as follows: (1) Masumizukogen (altitude 650–680 m), Houki-cho, Saihaku-gun, Tottori Pref.; (2) Rashomon (440 m), Niimi-shi, Okayama Pref.; (3) Utukusiimori (430 m), Takahashi-shi, Okayama Pref.; (4) Nichiouji (360 m), Okayama-shi, Okayama Pref.; (5) Yokoi (170 m), Okayama-shi, Okayama Pref.; (6) Shyukuhonmati (50 m), Okayama-shi, Okayama Pref.; (7) Daianji (20 m), Okayama-shi Okayama Pref.; (8) Yukasan (250 m), Kurashiki-shi, Okayama Pref. In these locations, epiphytotic disease of pine was epidemic in the forests from the 1980s to the 1990s (Ishibashi 1992). *Pinus densiflora* trees continue to die sporadically, resulting in an abundance of fallen dead wood in various states of decay.

The climate of the study area is warm and dry in the south, coastal in the Setouchi Inland Sea region, and cool and moist in the northern highland areas. The normal annual mean air temperature was 15.8°C, and the monthly mean air temperature ranged from 4.8°C in January to 27.9°C in August near the Okayama Meteorological Station (altitude 2.8 m, 34.66° N, 133.55° E). The average annual precipitation was 1141 mm, and the monthly mean precipitation ranged from 26 mm in December to 185 mm in June.

Field survey

A rigorous field survey was carried out during July–August of 2006 and 2007 because the annual occurrence of myxomycetes peaks in July of the rainy season end (Takahashi 1995, 2001a). It is the warmest and wettest time of the year in this area. We searched for myxomycete fruiting bodies on fallen logs (more than 10 cm in diameter) of *P. densiflora*. Most of the fallen pine wood studied was partially or totally decorticated. A single sample was recorded as a single colony that may have arisen from one plasmodium, and whenever several colonies of the same species appeared within a 30-cm area on a part of rotten wood they were regarded as a single colony (Elliasson 1981). At one site, 100 or more samples of myxomycete colonies were observed.

The state of decay of any given part of a log differs even along the same decaying log (Showalter 1992; Fukasawa et al. 2002). The hardness of a part of the wood on which fruiting bodies occurred was estimated using a soil hardness tester (Fujiwara Scientific Company, Tokyo). The resistance value (x mm) of a spring (8.0 kg/40 mm) for intrusion in the wood was measured by pressing a cone (40 mm in length) against the wood surface. Then, the hardness (P kg/cm^2) was calculated following the formula: $P = 100x/(0.7952(40 - x)^2)$.

The hardness was divided into eight logarithmically regular intervals, and the physical decay was classified into stages I–VIII (Table 1) as follows: (I) 280–176 kg/cm^2, (II) 176–38 kg/cm^2, (III) 38–14 kg/cm^2, (IV) 14–6.3 kg/cm^2, (V) 6.3–3.0 kg/cm^2, (VI) 3.0–1.4 kg/cm^2, (VII) 1.4–0.5 kg/cm^2, and VIII) ≤0.5 kg/cm^2.

The moisture content of the wood (% dry weight) was measured electronically using a wood-moisture tester (Turk H type; Kett Electric Laboratory, Tokyo, Japan). The moisture content of the wood samples, ranging from 4% to 120%, was estimated relative to the moisture content and electrical resistance of the wood. For all collected specimens, the microhabitat features of the myxomycetes such as the hardness and moisture content of the woody environment were noted in the field.

Identification of myxomycetes and data analysis

Specimens of common and easily recognized myxomycetes were usually identified by detailed observation of sporangial structures under a magnifying glass in the field. A portion of the colony fructifications was always sampled for the species that were difficult to identify in the field. The collected specimens were identified by microscopic examination, and the nomenclature used in the present study essentially follows that of Yamamoto (1998).

Species diversity indices for myxomycete communities were calculated using Shannon's formula as described in a previous study (Stephenson 1989). Species diversity (H′), defined as $H' = -\sum_{i=1}^{s} P_i \ln P_i$, where P_i is the proportion of the total number of samples represented by species i, was calculated for the different decay stages. The evenness component (J′) of species was calculated using the formula

Table 1. The decay stages of wood samples classified into eight logarithmically regular intervals by hardness, decay state in the field, and number of samples, moisture of the wood, number of species, species diversity (H′), and evenness component (J′) in each decay stage

Decay stage	Hardness (kg/cm^2)	Decay state of wood observed in the field	No. of samples	Moisture (%)[a]	No. of species	H′	J′
I	280–176	Undecayed hard wood with bark	3	14 ± 7	1	–	–
II	176–38	Hard wood, partially decorticated	48	55 ± 27	18	2.59	0.90
III	38–14	Hard wood, bark already loose	115	64 ± 22	25	2.74	0.85
IV	14–6.3	Soft wood, some decayed wood without bark	140	70 ± 23	29	2.99	0.90
V	6.3–3.0	Soft, decayed wood; shallow indentation made with finger	279	74 ± 23	36	3.02	0.84
VI	3.0–1.4	Softer, decayed wood; slight indentation made with finger	356	79 ± 21	32	2.82	0.81
VII	1.4–0.5	Brittle, strongly decayed wood; log shape retained	393	83 ± 22	29	2.75	0.82
VIII	0.5–0	Brittle wood, log partly destroyed and log shape lost	196	77 ± 23	18	2.55	0.88

[a]The values of moisture are expressed as % dry weight as means ± standard deviation of mean

$J' = H'/\ln S$, where S represents the number of species present in the community.

The distributions of 25 dominant species that were recorded from more than eight samples on the decay wood were quantified by the succession index. The succession index (SI) and the successional deviation (D) for a given species were calculated by the following formula (Hasegawa 1997):

$$SI = \left(\sum_{i=1}^{8} i \cdot n_i\right) \Big/ N \qquad D = \sqrt{\left(\sum_{i=1}^{8} n_i (i - SI)^2\right) \Big/ N}$$

where i is the decay stage, n_i is the number of samples of the species, and N is the total samples of the species throughout the survey. Therefore, SI indicates preference of a given species for decay stage.

Relative abundance of a given species was calculated by percentage of number of the samples for the total number of samples in the different decay stage. The Spearman rank correlation was used to assess the relationship between the relative abundance of a given species and progression of decay stage.

Results

Myxomycete community

The abundance and number of species (including varieties as species) and species diversity for each decay stage are shown in Table 1. Forty-one species and three varieties of 14 myxomycete genera from a total of 1530 samples were observed on the decaying wood of *P. densiflora*. Species of myxomycetes and numbers of samples on different decay stages of wood are shown in Table 2. Thirteen species (including varieties as species) were recorded over 48 samples (≥3% of all samples). Twenty-five species (including varieties as species) were recorded from 8 or more samples (≥0.5% of all samples). The most abundant species was *Stemonitis axifera*, which made up 16% of the total samples, followed by *Ceratiomyxa fruticulosa*, *C. fruticulosa* var. *porioides*, *Lindbladia cribrarioides*, *Arcyria cinerea*, *Lycogala epidendrum*, *Cribraria cancellata*, and *Stemonitopsis gracilis*. These species were commonly found on dead pine wood.

The myxomycetes appeared in all the decay stages from I to VIII, but the abundance and number of species were very poor in stage I. As decay progressed, the number of species increased and reached a maximum, 36 species, at decay stage V (hardness range, 3.0–6.3 kg/cm^2), then decreased in the later decay stages. The abundance values also increased and reached a peak at decay stage VII, with 26% (393 occurrences) of all samples, and decreased in the final stage.

The myxomycete community structure was different at all decay stages. The species diversity index (H′) was the highest (H′ = 3.02) at the decay stage V (see Table 1), corresponding to the stage where species richness was maximum. The number of species decreased gradually toward the final stage of decay. Many species of myxomycetes occurred on moderately decayed wood, whereas a few species were restricted to slightly decayed wood and a few to heavily decayed wood. The evenness component (J′) changed slightly with decay stages and was 0.84 at stage V. When dominance was shared among a relatively large number of species, the evenness component was higher.

Species arrangement in decay stages

Changes in the dominant species (recorded as occurring in eight or more samples) along the decay progression were expressed by SI and D values (Fig. 1). The values, ranging from 1 to 8, correspond to the decay stages (I–VIII). Occurrence of myxomycete species changed as the decay of the pine wood progressed.

Stemonitis splendens (SI = 2.1) occurred on little decayed or hard wood not inhabited by other species. The following species were arranged on slightly decayed wood: *Enerthenema papillatum*, *Physarum nutans*, *P. viride*, and *Arcyria obvelata* were followed by *Fuligo septica*, *S. pallida*, and *P. flavicomum*. In decay stage V (moderately decayed wood), different seven species were continuously arranged in order of SI = 5.5–5.9. Subsequently, in decay stage VI (moderately decayed softer wood), nine species were continuously arranged in order of SI = 6.1–6.4: four were species of *Cribraria*, i.e., *C. cancellata*, *C. tenella*, *C. intricata* var. *dictydioides*, and *C. intricata*, along with two species of *Stemonitopsis*. No species except *Lindbladia cribrarioides* (SI = 6.7) was found on brittle decayed wood.

D ranged from 1.0 (*L. cribrarioides* and *C. tenella*) to 1.9 (*A. denudata*) and averaged 1.4 in all. Some species, including *C. cancellata*, *Stemonitopsis hyperopta*, *C. tenella*, *C. intricata* var. *dictydioides*, and *L. cribrarioides*, showed low deviations (≤1.2). These low-D species composed half of the high-SI species having an SI over 6.1. These species inhabited the softer and brittle wood and demonstrated a specific preference for that decay stage, being distinctly different from the species with high deviations, such as *A. denudata* (1.9 D) and *P. viride* (1.8 D).

Abundance relative to the decay stage

The abundance of species changed as wood decay proceeded. Eleven species that were recorded in more than 20 samples showed correlation with the progression of decay (Table 3). Five species significantly decreased with the progression of decay. Six species significantly increased. For example, *Physarum viride* and *P. nutans* dominated on slightly decayed wood, but their relative abundance significantly decreased with the decay progression (both of $r = -0.964$, respectively, $P < 0.01$), as shown in Fig. 2. In contrast, in relative abundance *Ceratiomyxa fruticulosa* var. *porioides* and *L. cribrarioides* were dominant on the well-decayed wood, and they increased with the progression of decay ($r = 0.976$, $r = 1.00$, respectively; $P < 0.01$). Furthermore, *Cribraria cancellata*, *C. intricata* var. *dictydioides*, and

Table 2. Number of myxomycete species recorded from different decay stages of *Pinus densiflora* wood

Myxomycetes	Abbreviation of species name	Decay stage								Total number
		I	II	III	IV	V	VI	VII	VIII	
Species recorded in eight or more samples										
Stemonitis axifera (Bull.) T. Macbr.	sa		5	17	19	40	60	73	30	244
Ceratiomyxa fruticulosa (Mueller) T. Macbr.	cf		2	20	15	34	39	42	16	168
Ceratiomyxa fruticulosa var. *porioides* (Alb. & Schw.) Lister	cfp		2	4	8	18	32	39	25	128
Lindbladia cribrarioides (Emoto) Farr & Alexop.	lc				2	12	33	46	30	123
Arcyria cinerea (Bull.) Pers.	ac		2	11	12	21	17	19	12	94
Lycogala epidendrum (L.) Fr.	ly			4	12	21	21	18	12	88
Cribraria cancellata (Batsch) Nann.-Bremek.	cc		1		5	16	28	20	10	80
Stemonitopsis gracilis (G. Lister) Nann.-Bremek.	sg			4	3	14	17	21	10	69
Tubifera ferruginosa (Batsch) J. F. Gmel.	tf		2	2	6	12	16	16	7	61
Cribraria intricata Schrad.	ci			1	5	6	13	18	13	56
Stemonitopsis hyperopta (Meylan) Nann.-Bremek.	sh				7	6	19	15	6	53
Cribraria intricata var. *dictydioides* (Cooke & Balf.) Lister	cid			1	1	13	12	13	12	52
Physarum viride (Bull.) Lister	pv		11	11	7	7	4	8		48
Stemonitis axifera var. *smithii* (T. Macbr.) Hagelst.	sas			2	5	9	9	11	2	38
Physarum nutans Pers.	pn		5	9	2	5	4	1		26
Arcyria obvelata (Oeder) Onsberg	ao		2	6	7	6	1	2		24
Physarum flavicomum Berk.	pf		1	3	3	5	4	2	2	20
Stemonitis pallida Wingate	sp			5	3	5	3	4		20
Stemonitis fusca Roth	sf		1		1	2	4	6	2	16
Arcyria denudata (L.) Wettst.	ad			2	1	1	1	3	5	13
Fuligo septica (L.) Wiggers	fs		1	1	4	2	3	1		12
Enerthenema papillatum (Pers.) Rostaf.	ep		3	4	1		1	1		10
Stemonitis splendens Rostaf.	ss	3	4	1		1				9
Cribraria minutissima Schw.	cm		1			3	1	3		8
Cribraria tenella Schrad.	ct					2	3	2	1	8
Species recorded in fewer than eight samples										
Cribraria languescens Rex			1	2	3	1				7
Stemonitopsis subcaespitosa (Peck) Nann.-Bremek.						1	2	4		7
Cribraria vulgaris Schrad.						3	1	1		5
Stemonitis virginiensis Rex						1	1	2	1	5
Fuligo candida Pers.				1		2		1		4
Lamproderma arcyrionema Rostaf.						1	3			4
Lindbladia tubulina Fr.			1			2	1			4
Physarum rigidum (G. Lister) G. Lister			3	1						4
Stemonitis flavogenita Jahn					2	1		1		4
Arcyria ferruginea Sauter				1	1	1				3
Clastoderma debaryanum Blytt					2		1			3
Physarum stellatum (Massee) G.W. Martin						3				3
Cribraria microcarpa (Schrad.) Pers.				1			1			2
Physarum roseum Berk. & Br.				1	1					2
Arcyria affinis Rostaf.						1				1
Arcyria pomiformis (Leers) Rostaf.					1					1
Comatricha elegans (Racib.) G. Lister					1					1
Physarum nucleatum Rex							1			1
Stemonaria nannengae (Lakhanpal & Mukerji) Nann.-Bremek.						1				1
Total samples		3	48	115	140	279	356	393	196	1530
Total species		1	18	25	29	36	32	29	18	44

C. intricata also increased significantly with the progression of decay ($r = 0.766$, $r = 0.821$, $r = 0.964$, respectively). The remaining species, e.g., *Ceratiomyxa fruticulosa* and *A. cinerea*, exhibited a different pattern, which had a peak in stages of moderate decay.

Decay stage and moisture level of the wood inhabited by myxomycetes

The level of wood moisture where fructifications occurred was estimated at every stage of decay (see Table 1). The moisture (% dry weight) of the wood increased in decay stage II, but there was no clear difference in the moisture content among the decay stages II–VIII, as they all fell within 55%–83%. The average moisture content when fructifications occurred was 76%.

The dominant species (recorded as occurring in eight or more samples) distributed in different decay stages provided sufficient moisture (Fig. 3). Most of the species occurred on wood with > 60% moisture content, although *S. splendens* appeared on slightly decayed wood under low moisture conditions (19%). On the well-decayed wood (range of 5–7 in SI), several species were distributed over a wide range of moisture. *Lindbladia cribrariodes* apparently grew on brittle decayed wood with a high humidity.

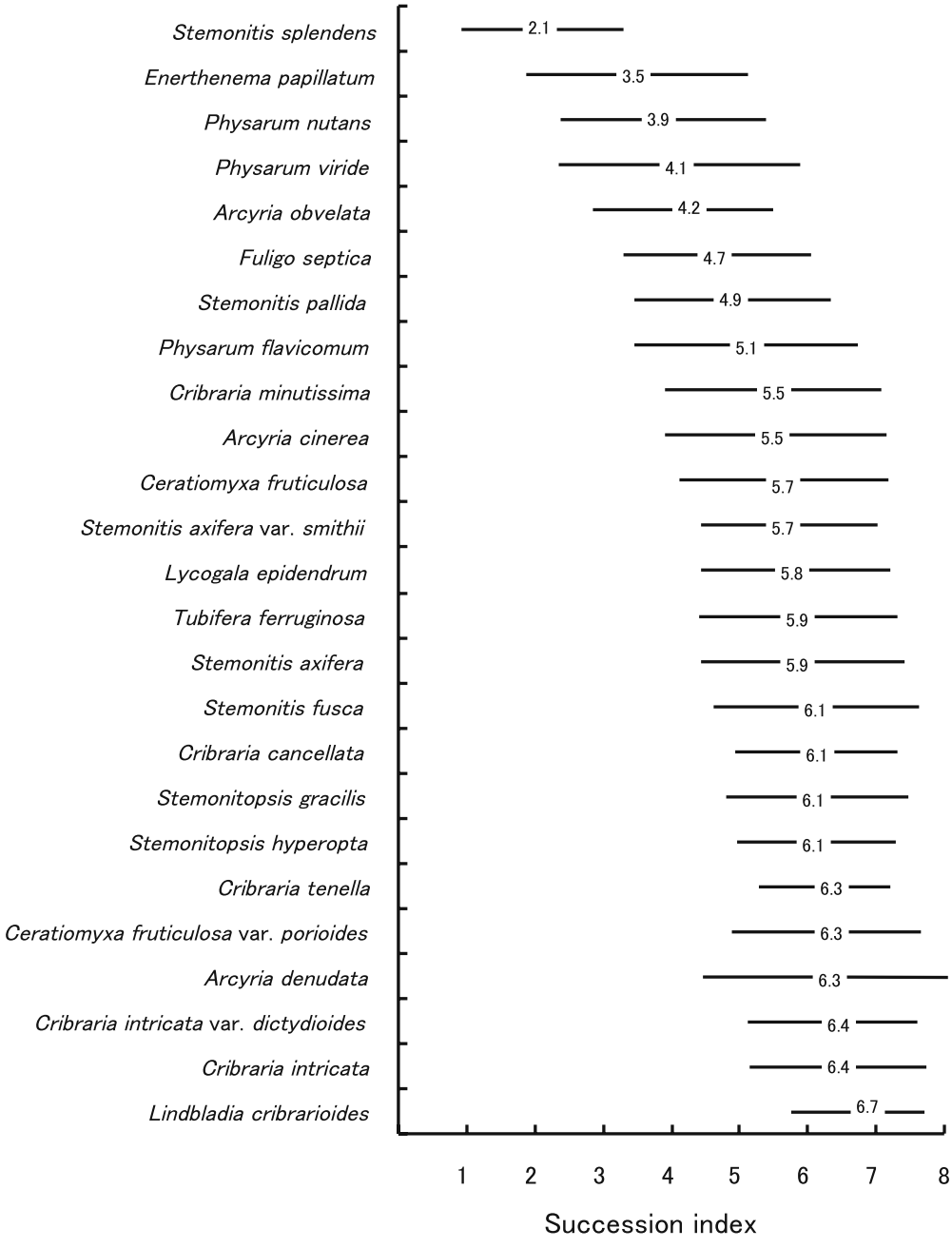

Fig. 1. Arrangement of the dominant 25 species recorded in more than eight samples relative to the succession index according to decay stage. The *transverse axis*, ranging from 1 to 8, corresponds to the decay stages (I–VIII). *Bars* indicate succession index and deviation

Discussion

Evaluation of the decay state

In fungal studies, logs have generally been classified into decay classes I–V using a visual decay class system (Crawford et al. 1990; Renvall 1995; Pyle and Brown 1999). A determination of decay class was also made in a survey of myxomycetes based on observed decay characteristics (Schnittler and Novozhilov 1998). This investigation found that a log could be classified into four stages, and the maximum number of myxomycete species was reached in stages 3–4, which was the last stage of decaying.

However, the myxomycetes occurred on a partially dead and decomposed section of a fallen tree trunk. Rayner and Boddy (1988) identified the fruiting bodies of specific myxomycetes on the partially decaying wood of a log. Ostrofsky and Shingo (1982) reported that myxomycetes occurred on a partially dead and decomposed section of a living tree trunk. Thus, myxomycetes do not always use the whole log as a substrate, but inhabit sections of decaying wood.

In our study, an evaluation of the decay state was performed physically on the parts of logs on which fructifications occurred. Then, the decay stage of wood was classified, particularly into the eight stages (I–VIII). We found that the richest and greatest diversity of myxomycete species occurred on wood in decay stage V (6.3–3.0 kg/cm^2). Many myxomycete species primarily inhabit moderately decayed

Table 3. Spearman's correlation coefficients between progression of decay stage and relative abundance in species in which were recorded more than 20 samples

Species	Spearman's correlation coefficient	Significant difference[a]
Physarum nutans	–0.964	**
Physarum viride	–0.964	**
Stemonitis pallida	–0.943	**
Arcyria obvelata	–0.857	*
Physarum flavicomum	–0.857	*
Stemonitis axifera var. *smithii*	0.143	
Ceratiomyxa fruticulosa	0.238	
Arcyria cinerea	0.262	
Stemonitopsis hyperopta	0.314	
Tubifera ferruginosa	0.333	
Lycogala epidendrum	0.393	
Cribraria cancellata	0.766	*
Cribraria intricata var. *dictydioides*	0.821	*
Stemonitis axifera	0.857	**
Stemonitopsis gracilis	0.893	**
Cribraria intricata	0.964	**
Ceratiomyxa fruticulosa var. *porioides*	0.976	**
Lindbladia cribrarioides	1.000	

[a] Significant differences: $*P < 0.05$; $**P < 0.01$

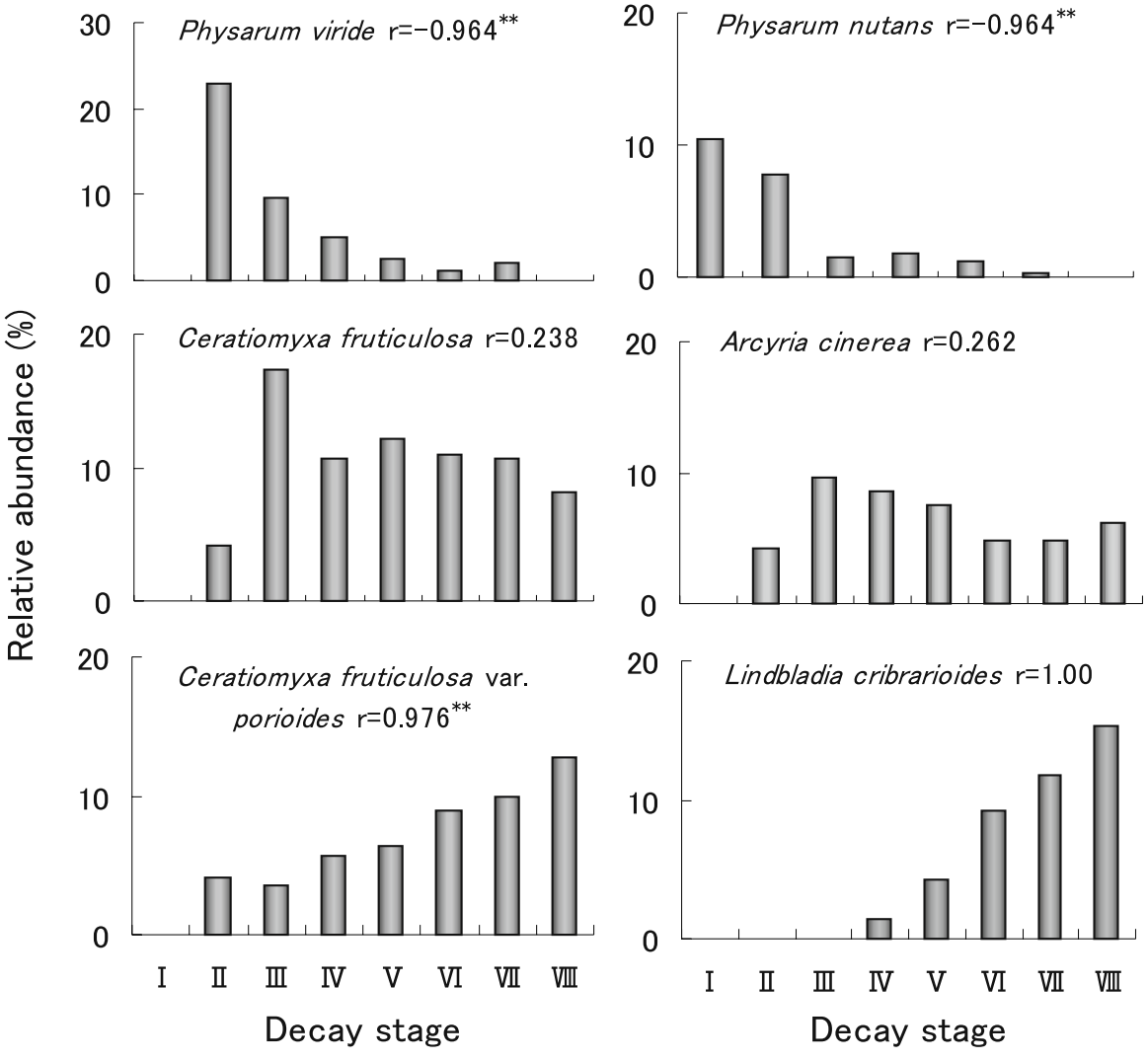

Fig. 2. Typical patterns of relative abundance of myxomycete species recorded in more than 20 samples relative to the decay stage. Spearman correlation coefficients between relative abundance in every decay stage and progression of decay stage are indicated (significant differences: $*P < 0.05$*, $**P < 0.01$)

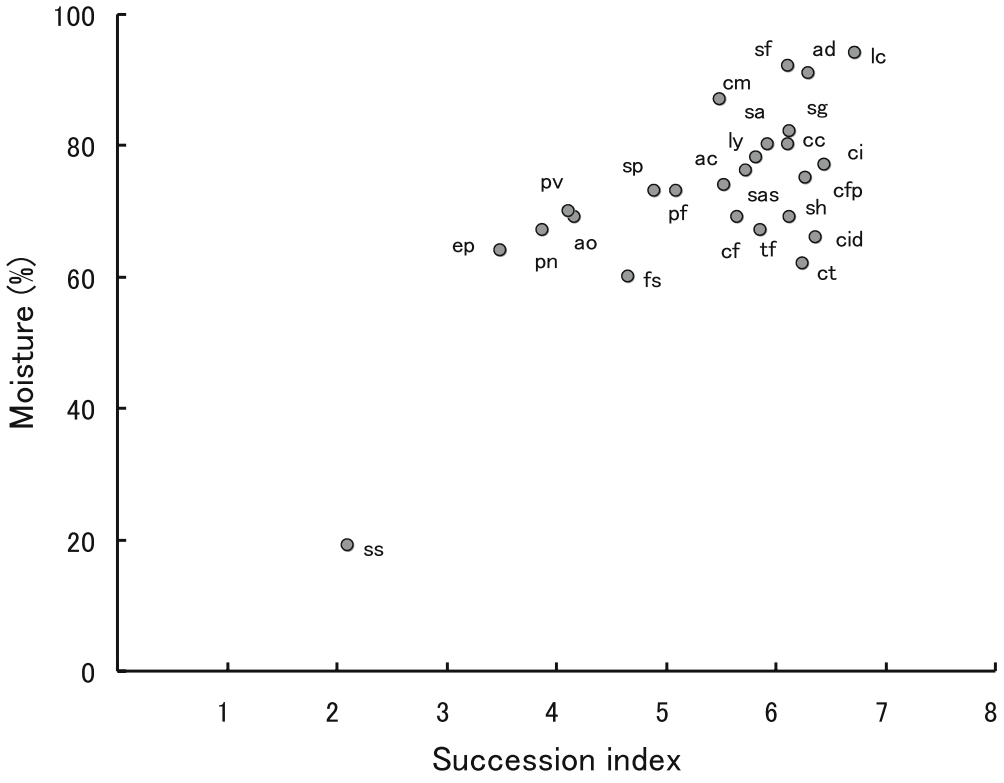

Fig. 3. Moisture of wood (% dry weight) relative to succession index in the dominant 25 species recorded in more than eight samples. Abbreviations of species names are shown in Table 2. The *horizontal axis*, ranging from 1 to 8, corresponded to the decay stages (I–VIII)

soft wood. Moreover, the method of evaluating the hardness of the part of a log where myxomycete fruiting bodies occurred allowed a more detailed analysis, namely, that certain species preferred a specific decay state.

Wood decay is accompanied by increasing water content of the wood (Renvall 1995), the moisture content of the wood being dependent on its state of decay (Lumley et al. 2001; Fukasawa 2008). The trophic stages in the life cycle of myxomycetes require water. Consequently, distribution of myxomycetes is strongly influenced by the decay stage and moisture of wood.

In this study, we estimated the amount of moisture preserved in decaying wood simultaneously with measuring wood hardness. Every decay stage from II to VIII retained more than 55% moisture content on average. We found that the region of the wood where fruiting sporangia were found contained sufficient moisture for fructification to occur. The distribution of almost all species was attributed to a narrow range of moisture content, which was restricted to 60%–100% moisture content on average, except for *Stemonitis splendens*, which occurred on low-moisture wood (mean ± SE; 19% ± 4%). In the present study, under conditions of sufficient moisture the species of myxomycetes were distributed extensively corresponding to the decay stage. Thus, the decay stage of wood strongly influences the distribution of myxomycetes found on it.

Occurrence patterns of species relative to the decay stages

It is experientially assumed that the species composition of myxomycetes clearly differs on slightly decayed wood compared to well-decayed wood (Ing 1994). In recent studies on dead wood of *P. densiflora* (Takahashi 1999, 2000, 2001b, 2002), several species, such as *Arcyria ferruginosa*, *A. obvelata*, and *Physarum viride*, occurred on hard wood whereas species such as *Cribraria cancellata* and *Stemonitopsis hyperopta* occurred on very soft wood. In this quantitative study many different species appeared with the progression of wood decay. No species demonstrated a constant distribution pattern throughout the decay process. A few species decreased in abundance and others increased as decay progressed, with significant correlation. Thus, the distribution and abundance of myxomycete species are highly dependent upon the decay state of the wood, and certain species have preference for a specific decay state.

Successional changes in myxomycetes

Hamashima (1965) and Heilmann-Clausen (2001) suggested successional changes in myxomycete populations on the decaying wood of deciduous broadleaf trees. Previously, the characteristics of the successional species were unclear for lack of investigation associating time after wood had fallen with substrate decay. We have provided more quantitative information on the relationships between the occurrence of myxomycete species and decay state by using the succession index and succeeded in demonstrating that the successional changes in species composition correspond to the stage of decay.

Stemonitis splendens significantly preferred slightly decayed wood with less retained moisture. Species of *Physarum* emerged predominantly on slightly decomposed,

fairly hard wood but rapidly decreased in occurrence with the progression of decay. Conversely, five species of Cribrariaceae and *Ceratiomyxa fruticulosa* var. *porioides* increased significantly with the progression of decay. *Lindbladia cribrarioides* especially preferred soft and damp wood. Because several species of myxomycetes had a preference for a particular state of wood decay, the community composition changed in response to the progression of wood decay in *P. densiflora*.

Decomposing coarse woody debris in a forest provides habitats for decomposing fungi, microbes, and microscopic animals and can serve as a source of nourishment for trees (Swift 1977; Blanchette and Shaw 1978). As the myxomycetes are one group of microbes that inhabit decaying wood, this group may show the interactions of organisms living in a dystrophic food chain and play an important role in the whole forest ecosystem. The apparent natural succession of myxomycete species on decaying wood is likely the result of the changing availability of nutrients for the myxoamoebae and plasmodia. Different myxomycete communities and particular species may serve as indicators of different environments of the decaying wood in forests.

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References

Ali NM, Kalyanasundram I (1991) Amylase as an extracellular enzyme from plasmodia of myxomycetes. Mycol Res 95:885–896

Blanchette RA, Shaw CG (1978) Associations among bacteria, yeasts, and basidiomycetes during wood decay. Phytopathology 68:631–637

Carlile MJ (1974) The myxomycete *Physarum nudum*: life cycle and pure culture of plasmodia. Trans Br Mycol Soc 62:213–215

Crawford RH, Carpenter SE, Harmon ME (1990) Communities of filamentous fungi and yeast in decomposing logs of *Pseudotsuga menziesii*. Mycologia 82:759–765

Eliasson U (1981) Patterns of occurrence of myxomycetes in a spruce forest in south Sweden. Holarct Ecol 4:20–31

Elliot WT, Elliot JS (1920) The sequence of fungi and mycetozoa. J Bot (Lond) 58:273–274

Fukasawa Y (2008) Fungal decomposition of coarse woody debris of beech (*Fagus crenata* Blume) in a cool temperate natural forest (in Japanese with English summary). Doctoral thesis, Kyoto University, Kyoto, pp 8–18

Fukasawa Y, Osono T, Takeda H (2002) Fungal community structure and physical and chemical properties of decaying beech logs in a cool temperate natural forest (in Japanese with English summary). Appl For Sci 11:7–14

Hamashima S (1965) The growth of slime molds on "Shiitake"-cultivating bed logs (in Japanese with English summary). Trans Mycol Soc Jpn 6:55–57

Hasegawa M (1997) Changes in collembolan and *Cryptostigmata* communities during the decomposition of pine needles. Pedobiologia 41:225–241

Heilmann-Clausen J (2001) A gradient analysis of communities of macrofungi and slime moulds on decaying beech logs. Mycol Res 105:575–596

Howard FL, Currie ME (1932) Parasitism of myxomycete plasmodia on fungus mycelia. J Arnold Arboret Harv Univ 13:438–446

Ing B (1994) The phytosociology of myxomycetes. New Phytol 126:175–201

Indira PV (1969) The life cycle of *Stemonitis herbatica*. Trans Br Mycol Soc 53:25–38

Ishibashi N (1992) The damage and alteration of pine forest by the pine wood disease in the Chugoku district (in Japanese with English summary). Bull Fac Sch Educ Hiroshima Univ Part II 14:127–135

Lister A (1888) Notes on the plasmodium of *Badhamia utricularis* and *Brefeldia maxima*. Ann Bot 2:1–24

Lister A (1890) Notes on the ingestion of food-material by the swarm-cells of Mycetozoa. J Linn Soc (Bot) 25:435–441

Lumley TC, Gignac LD, Currah RS (2001) Microfungus communities of white spruce and trembling aspen logs at different stages of decay in disturbed and undisturbed sites in the boreal mixed wood region of Alberta. Can J Bot 79:76–92

Madelin MF (1984) Myxomycetes, microorganisms and animals: a model of diversity in animal-microbial interactions. In: Anderson JM, Rayner ADM, Walton DW (eds) Invertebrate–microbial interaction. Cambridge University, Cambridge, pp 1–33

Ostrofsky A, Shingo AL (1982) A myxomycete isolated from discolored wood of living red maple. Mycologia 73:997–1000

Pyle C, Brown MM (1999) Heterogeneity of wood decay classes within hardwood logs. For Ecol Manag 114:253–259

Rayner ADM, Boddy L (1988) Fungal decomposition of wood: its biology and ecology. John Wiley & Sons, Chichester, pp 132–134

Renvall P (1995) Community structure and dynamics of wood-rotting Basidiomycetes on decomposing conifer trunks in northern Finland. Karstenia 35:1–51

Schnittler M, Novozhilov YK (1998) Late-autumn myxomycetes of the northern Ammergauer Alps. Nova Hedwigia 66:205–222

Showalter TD (1992) Heterogeneity of decomposition and nutrient dynamics of oak (*Quercus*) logs during the first 2 years of decomposition. Can J For Res 22:161–166

Stephenson SL (1989) Distribution and ecology of myxomycetes in temperate forests. II. Patterns of occurrence on bark surface of living trees, leaf litter, and dung. Mycologia 81:608–621

Swift MJ (1977) The ecology of wood decomposition. Sci Prog Oxf 64:175–199

Takahashi K (1995) An ecology of myxomycetes in secondary forests of coastal areas in Okayama Prefecture (in Japanese with English summary). Bull Okayama Pref Nat Conserv Center 3:23–31

Takahashi K (1999) Occurrence of myxomycetes in relation to the decaying state of *Pinus densiflora* and *Quercus acutissima*. Bull Okayama Pref Nat Conserv Center 7:53–60

Takahashi K (2000) Ecology of myxomycetes in relation to the decaying state of *Pinus densiflora* in Rashomon, Okayama Prefecture (in Japanese with English summary). Bull Okayama Pref Nat Conserv Center 8:33–41

Takahashi K (2001a) Ecological distribution of myxomycetes on beech forest on Mt. Daisen in the south-west of Japan (in Japanese with English summary). Bull Kurashiki Mus Nat Hist 16:55–64

Takahashi K (2001b) Occurrence of myxomycetes in relation to the decaying state of dead trees of *Pinus densiflora* at Mt. Sanbe (in Japanese with English summary). Bull Okayama Pref Nat Conserv Center 9:11–18

Takahashi K (2002) Occurrence of lignicolous myxomycetes associated with the progression of wood decaying of *Pinus densiflora* in a secondary forest in Rashomon (I) (in Japanese with English summary). Bull Okayama Pref Nat Conserv Center 10:25—34

Takahashi K (2004) Distribution of myxomycetes on different decay states of deciduous broadleaf and coniferous wood in a natural temperate forest in the Southwest of Japan. Syst Geogr Pl 74:133–142

Yamamoto Y (1998) The myxomycete biota of Japan (in Japanese). Toyo Shorin, Tokyo