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FULL PAPER

Geographical distribution of myxomycetes on coniferous deadwood in relation to air temperature in Japan

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Abstract This study obtained information on the biogeographical distribution of lignicolous myxomycetes in temperate regions in Japan. It examined how climatic variables are related to patterns of occurrence in myxomycete communities. Sixty-four taxa were recorded on coniferous wood in 15 forest sites in summer. Common species that were abundant and widely distributed in Japan included *Stemonitis axifera*, *Lycogala epidendrum*, and *Cribraria cancellata*. In addition, *Lindbladia cribrarioides* was characteristic on dead *Pinus densiflora* wood in southwestern Japan. The species diversity index (H') of the myxomycete communities was positively correlated with the annual mean temperature. The distribution of myxomycete communities was analyzed using nonmultidimensional scaling (NMDS). The ecological nature of the gradients expressed by the first two NMDS axes was that the first axis was found to correspond strongly to changes in the average minimum temperature and the latitude, and the second axis was related to a complex of factors, including altitude. The relative abundance of certain species in a myxomycete community on Japanese red pine changed in relation to the annual mean temperature, e.g., *Lycogala epidendrum* correlated negatively while *Stemonitopsis hyperopta* did so positively. We conclude that air temperatures can be used to predict the geographical distribution of lignicolous myxomycetes in this temperate region of Japan.

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Introduction

Myxomycetes inhabit deadwood, leaf litter, and plant debris humus (Lister 1918) and are abundant worldwide (Gray and Alexopoulos 1968). Generally, myxomycetes have small fruiting bodies, ranging in size from a few centimeters to less than 1 mm. The fruiting bodies are frequently overlooked in the field because they occur sporadically and are ephemeral and fugacious, being preyed on by microbes (Madelin 1984) or disintegrated by rainfall (Alexopoulos 1963; Eliasson 1981). Therefore, studies of the flora and ecology of myxomycetes are difficult, resulting in a paucity of data and little ecological research. Most ecological reports have come from studies conducted in Europe (Ing 1983; 1994; Lado 1993) and North America (Stephenson 1983, 1988, 1989, 2004), with a few from subtropical communities (Novozhilov et al. 2001) and arctic and subarctic regions (Stephenson et al. 2000). These suggest that the distribution of myxomycetes is associated with altitude, vegetation, or humidity. Stephenson (1988) found that the species diversity and abundance in a temperate forest in Virginia (USA) were higher in habitats with increased humidity levels, while Schnittler and Stephenson (2000) reported that myxomycete diversity and abundance decreased in subtropical forests as altitude and humidity increased.

The factors limiting myxomycete distribution are unclear. Although climate (temperature and humidity), substrate type, and substrate pH are all important for determining myxomycete occurrence (Gray and Alexopoulos 1968; Venkataramani and Kalyanasundaram 1986; Ing 1994; Schnittler and Novozhilov 1996), it is unclear which of these factors are the main determinants of myxomycete distribution. Studies have not fully examined which factors limit the myxomycete distribution in every climate region. Relationships between seasonal sporulation and the occurrence of myxomycetes and air temperature have been recognized in Neotropical (Maimoni-Rodella and Gottsberger 1980), subtropical (Ogata 1996), warm temperate (Takahashi and Hada 2008a), and cool temperate (Eliasson 1981; Stephenson 1988) regions. Therefore, it is reasonable to postulate that temperature may also strongly influence the geographical distribution of myxomycetes. However, comparative studies have never been conducted.

The islands of Japan are distributed across a wide area, and range in climate from subtropic to subboreal, with heterogeneous climates and different vegetation. The vegetation distribution corresponds to the thermal sum index (Kira 1977). Myxomycete communities in Japan appear to be rich, with 500 or more species reported, representing about 60% of all described species (Yamamoto 1998). Therefore, the region is a suitable one in which to study the distribution of myxomycete communities and species. To study the effects of air temperature on the distribution of myxomycetes in forests, we devised the following new approach to this type of investigation. Fallen Japanese red pine or other coniferous woods, which dominate the study forests, were selected as a common substrate across study sites. This enabled us to compare the myxomycete communities inhabiting ecologically similar microhabitats among various climatic regions, since Japanese red pines, *Pinus densiflora*, are distributed throughout most of Japan, with the exception of Hokkaido Island. Pine wilt disease, which was prevalent in Nagasaki prefecture in western Japan about 100 years ago, has occurred in most pine forests in Japan (Yamamoto et al. 2000). Recently, the disease has provided abundant deadwood that myxomycetes can use as substrate over a wide range of climatic conditions in forests. This feature is considered important for the study of air temperature effects on myxomycete distribution.

In the previous studies on seasonal occurrence and sporulation of myxomycetes (Maimoni-Rodella and Gottsberger 1980; Takahashi and Hada 2008a), average minimum temperature strongly influenced seasonal distribution of myxomycetes. The present study thus sought to elucidate the characteristics of the myxomycete community that inhabits coniferous wood in summer and to discuss the relationships between myxomycete distribution and air temperature, such as the average minimum temperature, from warm temperate to subboreal regions in Japan.

Materials and methods

Study sites

The study was conducted at 15 sites in coniferous forests located between 31°54′N, 130°50′E on Kyushu Island and 43°38′N, 144°26′E on Hokkaido Island, Japan (Table 1). In the warm-temperate region of southwestern Japan, the natural vegetation consists of evergreen forests; in the cool-temperate regions, the natural vegetation consists of deciduous broadleaf trees; and in the subboreal regions of northern Japan, the natural vegetation consists of mixed forests that contain conifers and deciduous broadleaf trees (Kira 1977). However, most of these forests now contain substitute vegetation that has been generated by human activity. Many forests in western Japan today are composed of Japanese red pine (*Pinus densiflora* Sieb. et Zucc.) and deciduous oak (*Quercus serrata* Thunb. ex Murray), and Japanese red pine forest is distributed throughout the Japanese islands with the exception of Hokkaido. The pine forests have been damaged by pine wilt disease; consequently, fallen dead logs are abundant on the forest floor.

Geographic and climatic data from every site are listed in Table 1. Twelve sites were in Japanese red pine forests located in low-lying mountains, and the others were in a natural forest composed of *Abies firma* Sieb. et Zucc.; a subalpine natural forest composed of coniferous trees, such as *Abies veitchii* Lindley and *Tsuga diversifolia* (Maxim.) Masters; and in a subboreal natural forest composed of *Picea glehnii* (Fr. Schm.) Masters. In the present study, we focused on Japanese red pine forests located in the warmer areas of the Japanese islands, rather than other coniferous forests, which are distributed in highlands, subalpine, and subboreal regions.

Field surveys

In this study, we avoided surveying sites with steep inclines, and selected sites that were easy to access and had abundant fallen logs. Fallen logs occurred sporadically and were scattered at different densities within forests. We searched for fallen logs that had the same bark as that of dominant coniferous trees in the survey forest, diameters over 10 cm and lengths over 100 cm. Coniferous logs were distinguished from hardwood logs by observing the residual bark of the logs. Thus myxomycetes on hardwood were ruled out. Sufficient fallen coniferous logs in each survey site occurred to allow at least 100 colonies of myxomycete fruiting bodies to be sampled. Each individual colony that may have arisen from one plasmodium was recorded as a single sample. Whenever several colonies of the same species appeared within a 30 cm area on a log, they were regarded as a single colony (Eliasson 1981).

Table 1 Description of the geographical features, climatic variables, mean hardness of wood (kg/cm^2) on which myxomycete fruiting bodies occurred, number of samples, number of species, Shannon-Wiener species diversity (H'), and evenness component (J') of myxomycete communities at individual survey sites

Survey sites[a]	Od	Os	Ok	Oy	Tr	On	Ot	Or	Sk	Tm	Mk	Nt	Ko	Hk	Ny
Dominant forest tree species	*Pinus densiflora*												*Abies firma*	*Picea glehnii*	*Abies veitchii*
Environmental variables															
Latitude (°N)	34.67	34.70	34.51	34.71	36.64	34.77	34.80	34.94	35.53	35.37	31.96	36.02	31.92	43.64	36.05
Altitude (ca. m)	30	60	255	70	100	240	420	440	460	580	1170	1040	1130	140	2130
Annual mean temperature (°C)	15.6	15.5	14.2	13.7	13.0	12.6	11.8	11.6	11.4	10.3	9.5	8.0	9.4	4.8	1.4
Average minimum temperature (°C)	11.5	11.4	10.9	8.6	9.4	7.5	7.4	7.3	7.4	5.5	6.2	3.2	6.5	−0.6	−3.4
Average maximum temperature (°C)	20.5	20.5	18.1	19.8	17.3	18.8	18.2	17.3	16.7	16.1	15.4	14.9	15.7	10.4	8.3
Annual precipitation (mm)	1,254	1,254	1,146	1,254	2,410	1,399	1,470	1,446	1,556	2,835	5,500	1,408	5,500	1,162	1,408
Precipitation in summer (mm)[b]	528	528	413	538	605	538	507	491	458	638	2502	539	2502	111	539
Mean hardness of wood (kg/cm^2)	14.8	12.1	15.1	17.0	18.5	12.9	12.6	11.2	17.3	14.9	18.6	23.1	16.4	17.7	22.5
Myxomycete community															
Number of samples	110	111	107	110	436	138	114	156	128	104	130	147	113	109	105
Number of species	19	22	18	25	34	23	21	16	22	17	20	18	23	17	20
Species diversity (H')	2.48	2.52	2.53	2.84	3.06	2.68	2.72	2.11	2.30	2.45	2.40	2.37	2.55	2.21	2.16
Evenness (J')	0.63	0.56	0.69	0.68	0.63	0.63	0.72	0.52	0.45	0.68	0.55	0.59	0.56	0.54	0.43

[a] *Od* Dianji, Okayama-shi, Okayama Pref. (133.89°E, July 7, 2006), *Os* Syukuhonmachi, Okayama-shi, Okayama Pref. (133.94°E, July 10, 2006), *Ok* Yukasan, Kurashiki-shi, Okayama Pref. (133.85°E, July 12, 2006), *Oy* Yokoikami, Okayama-shi, Okayama Pref. (133.92°E, July 10, 2006), *Tr* Ranjonomori, Tonami-shi, Toyama Pref. (137.04°E, July 23, 2007), *On* Nichiouji, Okayama-shi, Okayama Pref. (133.87°E, July 20, 2006), *Ot* Matuyama, Takahashi-shi, Okayama Pref. (133.65°E, July 25, 2006), *Or* Rashyomon, Niimi-shi, Okayama Pref. (133.56°E, July 24, 2006), *Sk* Kinomoto-cho, Ika-gun, Siga Pref. (133.22°E, July 20, 2006), *Tm* Masumizu-kogen, Houki-cho, Tottori Pref. (133.50°E, July 10, 2006), *Mk* Kosikidake, Ebino-kougen, Miyazaki Pref. (130.85°E, July 30, 2006), *Nt* Toyohira, Chino-shi, Nagano Pref. (138.24°E, August 10, 2006), *Ko* Ohnami, Makizono-cho, Kagoshima Pref. (130.84°E, July 31, 2006), *Ny* Yatugatake Koumimachi, Minamisaku-gun, Nagano Pref. (138.36°E, August 11, 2006), *Hk* Kawayuonsen. Teshikaga-cho, Hokkaido (144.43°E, August 6, 2006). Longitudes and survey dates are shown *in parentheses*

[b] Total precipitation values for June and July

Myxomycetes occur most abundantly on decaying wood in the summer in Japan (Takahashi 2001; Takahashi and Hada 2008a). In all, 14 surveys were conducted in the summer of 2006 and 1 survey in the summer of 2007. Myxomycetes are only identifiable by observing their fruiting bodies. The fruiting bodies of common, recognizable myxomycetes were identified in the field using a magnifying glass. Other, unidentifiable myxomycetes were collected, and these specimens were identified in the laboratory under a microscope. The nomenclature used in this study follows Yamamoto (1998). The occurrence of myxomycetes on deadwood is reported to be related to the decay state of the wood (Heilmann 2001; Takahashi and Hada 2008b, 2009). Therefore the hardness of the wood on which fruiting bodies occurred was estimated using a soil hardness tester (No. 351, Fujiwara Scientific), following the method of previous studies (Takahashi 2004). For all samples, the hardness of the wood, measured in kg/cm^2, was treated as the microhabitat feature of the myxomycetes.

Meteorological data

Meteorological records from the measuring station nearest to each survey site were used (Japanese Meteorological Agency, 2007). The temperature at each survey site was calculated using a standard temperature lapse rate of −0.0065°C/m (Meteorological Society of Japan 2004), adjusted according to the difference in altitude (m) between the station and survey site. For meteorological data on the survey sites, annual mean temperature, average minimum temperature, average maximum temperature, and annual precipitation were collected. The precipitation levels recorded in summer were total values for June and July (Table 1).

Data analysis

The species diversity of the myxomycete community at each site was calculated using the Shannon-Wiener index (Magurran 2004). The species diversity (H') was calculated as $H' = -\Sigma P_i \ln P_i$, where P_i (the relative abundance of species i) is the proportion of the total number of samples represented by species i. In addition, the evenness component (J') of the species diversity was estimated using Pielou's index (Pielou 1966): $J' = H'/\ln S$, where S represents the number of species present in the community. J' has a value of 1 when component species are distributed evenly. In this study myxomycete communities from different sites were subjected to nonmultidimensional scaling (NMDS) using the program PAST (Hammer et al. 2001). This computer application program (http://folk.uni.no/ohammer/past/) was chosen because of its efficacy in other studies. NMDS proved to be the best strategy for recovering simulated two-dimensional gradient data (Kenkel and Orlóci 1986). The ordination was based on Morisita's similarity index (Morisita 1959) using the number of samples of every species from every study site. Each site was arranged in order on the first and second axis, and relationships between their NMDS values and several environmental variables, such as geography, climate, and hardness of the portion of wood on which myxomycete fruiting bodies occurred, were analyzed using correlation coefficients.

There is a geographical difference in distribution between Japanese red pine wood and the other coniferous wood in this study (Satake et al. 1989). We performed Fisher's exact probability test of independence (e.g., Sokal and Rohlf 1973) to compare data between Japanese red pine wood and the other coniferous wood in total, using the SSRI computer application (Social Survey Research Information 2004, Tokyo). When the occurrence of species on any type of wood was significantly higher ($P < 0.01$) than 0 by Fisher's exact probability test, the species was regarded as frequent and as having a preference for a specific wood, except species with ten or fewer total records.

Results

Frequent species on coniferous wood

In total, 64 species or varieties were recorded from 2,118 samples at 15 survey sites during the summer (Table 2). The myxomycetes communities were distributed on dead coniferous wood across the wide climatic range from warm temperate to subboreal in Japan. Three species appeared at all study sites: *Stemonitis axifera* (Fig. 1a), *Lycogala epidendrum* (Fig. 1b), and *Cribraria cancellata* (Fig. 1c). Two species, *Stemonitis axifera* and *Ceratiomyxa fruticulosa* (Fig. 1d), were the most abundant with the highest relative abundance (P_i) ≥ 0.1 of all samples. Five additional species, *Lycogala epidendrum*, *Physarum viride* (Fig. 1e), *Ceratiomyxa fruticulosa* var. *porioides* (Fig. 1f), *Arcyria cinerea*, and *Cribraria cancellata* were abundant with $P_i \geq 0.05$ across all samples. These seven species were commonly found on coniferous wood in summer.

Characteristic distribution of myxomycetes

In Japanese red pine forests, which are mainly distributed in low-lying mountains and the southwestern region of Japan, several myxomycetes have been recorded abundantly (Table 2). The following nine species were found significantly frequently on wood of *P. densiflora*: *Cribraria*

Table 2 Myxomycetes that occurred on dead *Pinus densiflora* wood and other coniferous deadwood at the 15 survey sites in Japan. The number of samples is given

Species	Survey sites[a]	Od	Os	Ok	Oy	Tr	On	Ot	Or	Sk	Tm	Mk	Nt	Ko	Hk	Ny	Log types	
	Fallen logs	*Pinus densiflora*												*Abies firma*	*Picea glehnii*	*Abies veitchii*	*P. densiflora*	Other logs
Stemonitis axifera (Bull.) T. Macbr.		15	4	11	3	37	32	13	36	7	19	11	35	2	22	20	223	44
Ceratiomyxa fruticulosa (Mueller) T. Macbr.		29	36	9	23	17	2	12	3	45	11	11	3	5		3	201**	8
Lycogala epidendrum (L.) Fr.		2	7	1	6	37	2	7	11	10	13	33	19	4	13	5	148	22
Ceratiomyxa fruticulosa var. *porioides* (Alb. & Schw.) Lister		1	7		4	35	5	6	21	21	16	9		10	1	1	125*	12
Cribraria cancellata (Batsch) Nann.-Bremek.		9	5	11	6	40	8	5	15	6	1	7	10	5	2	6	123*	13
Physarum viride (Bull.) Pers.		2		7	6	49	16	3	1	1	1	13	24	12	6	26	123	44**
Arcyria cinerea (Bull.) Pers.		2	12		11	10	5	17	4	9	7	22	2	34		2	101	36**
Lindbladia cribrarioides (Emoto) Farr & Alexop.			3		8	3	19	3	44	3	6			1			89**	1
Tubifera ferruginosa (Batsch) J. F. Gmel.		4	4	23		12	2		4	5	4			7			58	7
Stemonitopsis hyperopta (Meylan) Nann.-Bremek.		6		5	5	24		3	2	1	4	3		1	1		53*	2
Physarum flavicomum Berk.		2	2		6	23		5	1	4	2		1	2			46*	2
Stemonitopsis gracilis (G. Lister) Nann.-Bremek.			2	2	5	1	6	14	4	1	10		1			1	46*	1
Physarum nutans Pers.		7	4		2	9	2	7		1			13	6	2	1	45	9
Cribraria intricata var. *dictydioides* (Cooke & Balf.) Lister		8	6	8	1	11	5			2		4		7			45	7
Stemonitis axifera var. *smithii* (T. Macbr.) Hagelst.		7	1	1	2	6	3	1	5	1	2	1	5	1	2		35	3
Cribraria intricata Schrad.		4	3	10	4	6		4			1						32*	
Arcyria denudata (L.) Wettst.						24	6							1			30	1
Arcyria obvelata (Oeder) Onsberg			3	4	4	1	4	4		2		1			1		23	1
Fuligo septica (L.) Wiggers		1		4		14	2							1	6		21	7
Cribraria tenella Schrad.			5	1		13		1		1							21*	
Stemonitis pallida Wingate				3		9	1	4	2			1		2			20	2
Stemonitis splendens Rostaf.						1	4			1	4		9		6	1	19	7
Stemonitis fusca Roth			2		1	5	4	2	2			3		3	3		19	6
Lamproderma arcyrionema Rostaf.			1			7				2	1	1	3				15	
Enerthenema papillatum (Pers.) Rostaf.		7			1		2			3		2					15	
Arcyria virescens G. Lister						13						1					14	
Cribraria minutissima Schw.				5		1	3					2					11	
Cribraria langescens Rex						10			1								11	
Cribraria macrocarpa Schrad.													11				11	

Table 2 continued

Species	Survey sites[a]	Od	Os	Ok	Oy	Tr	On	Ot	Or	Sk	Tm	Mk	Nt	Ko	Hk	Ny	Log types	
	Fallen logs	*Pinus densiflora*												*Abies firma*	*Picea glehnii*	*Abies veitchii*	*P. densiflora*	Other logs
Cribraria vulgaris Schrad.				1	2						2				33		5	33**
Trichia botrytis (J. F. Gmel.) Pers.						3										27	3	27**

The following additional species were found [the two-letter study site abbreviation (see Table 1) followed by the number of samples is given]: *Stemonitis flavogenita* Jahn (Mk 2, Ok l, Oy 1, Ot 1, Ny 1, Hk 3); *Cribraria microcarpa* (Schrad.) Pers. (Oy 1, Ot 1, Tr 7); *Lindbladia tubulina* Fr. (Oy 2, On 1, Nt 4, Hk 1); *Stemonitis virginiensis* Rex (Ko 2, Os 1, Oy 1, M 1, Tr 1); *Tubifera casparyi* (Rostaf.) T. Macbr. (Hk 6); *Stemonitopsis reticulata* (H. C. Gilbert) Nann.-Bremek. & Y. Y. (Sk 1, Nt 3, Ny 1); *Arcyria ferruginea* Sauter (Od 2, Os 1, Sk 1); *Fuligo candida* Pers. (On 4); *Physarum rigidum* (G. Lister) G. Lister (Oy 4); *Cribraria piriformis* Schrad. (Ny 1, Tr 2); *Cribraria cancellata* var. *fusca* (Lister) Nann.-Bremek. (Ko 2, M 1); *Stemonitis uvifera* T. Macbr. (Ny 3); *Clastoderma debaryanum* Blytt (Tr 3); *Physarum globliferum* (Bull.) Pers. (Ko 3); *Stemonitopsis subcaespitosa* (Peck) Nann.-Bremek. (Ny 2); *Comatricha nigra* (Pers.) Schroet. (Mk 2); *Stemonitis splendens* var. *webberi* (Rex) Lister (M 2); *Elaeomyxa cerifera* (G. Lister) Hagelst. (Ny 1); *Lycogala exiguum* Morgan (Hk 1); *Cribraria filiformis* Nowotny & Neubert (Ny 1); *Physarum newtonii* T. Macbr. (Ny 1); *Stemonitopsis amoena* (Nann.-Bremek.) Nann.-Bremek. (Ny 1); *Arcyria affinis* Rostaf. (Os 1); *Arcyria pomiformis* (Leers) Rostaf. (Od 1); *Comatricha elegans* (Racib.) G. Lister (Oy 1); *Cribraria persoonii* Nann.-Bremek. (Ko 1); *Hemitrichia clavata* var. *calyculata* (Speg.) Y. Yamam. (Tr 1); *Physarum nucleatum* Rex (Os 1); *Physarum psittacinum* Ditmar (Ko 1); *Physarum roseum* Berk. & Br. (Tr 1); *Stemonaria nannengae* (Lakhanpal & Mukerji) Nann.-Bremek. (Od 1); *Stemonitis pallid Wingate var. rubescens* Y. Yamam. (Ot 1); *Stemonitopsis typhina* (Wiggers) Nann.-Bremek. (Mk 1)

Independent test significance level: ** $P < 0.01$, * $P < 0.05$

[a] The survey sites followed Table 1

cancellata, *Ceratiomyxa fruticulosa*, *Ceratiomyxa fruticulosa* var. *porioides*, *Stemonitopsis hyperopta* (Fig. 1g), *Lindbladia cribrarioides* (Fig. 1h), *Physarum flavicomum*, *Stemonitopsis gracilis*, *Cribraria intricata*, and *Cribraria tenella*.

On the other hand, several species had particular distributions in cool regions (Table 2), i.e., *Cribraria macrocarpa* appeared abundantly on highlands in central Japan, *Trichia botrytis* occurred in a subalpine forest in central Japan, and *Cribraria vulgaris* and *Tubifera casparyi* were found in a subboreal forest. *Physarum viride* and *Arcyria cinerea* were common in forests, but also frequently found in cool regions. These six species were associated with the cool regions and were distributed geographically in Japan. Thus the different distributions of the myxomycete species suggested a relationship with different air temperatures.

Species diversity on coniferous wood

The average number of species across the study sites was 20, the range being 16–34 species. The median species diversity index (H') for all study sites was $H' = 2.48$ with a range across sites of $H' = 2.11$–3.06 (Table 1). Forest type was not related to species diversity, but numerous samples had high values, as seen in Table 1, with Tr ($H' = 3.06$) being the highest. The median evenness (J') was 0.59 and ranged from 0.43–0.72. Where J' was lower, particular species were abundantly found.

Species diversity (H') was significantly correlated with air temperature (Table 3); the correlation coefficient with annual mean temperature was $r = 0.554$ ($P < 0.05$) for H' and $r = 0.565$ ($P < 0.05$) for evenness (J'). However precipitation and hardness of the wood where the myxomycete fruiting bodies occurred were not significantly correlated with species diversity. Thus, the warmer region of southwestern Japan tended to have higher species diversity in the myxomycete community.

Ordination of myxomycete communities

The locations of all study sites on a two-dimensional NMDS ordination are shown in Fig. 2. Myxomycete communities showed a distinct hierarchical ranking along the ordination axes. The first axis correlated most closely with latitude and temperature, with communities in Hokkaido and subalpine regions located on the right side and communities in the southwestern region located on the left. The correlation of NMDS sample scores on the first axis with the temperature was highly significant for average minimum temperature ($r = -0.774$, $P < 0.01$), average maximum temperature ($r = -0.739$, $P < 0.01$), and annual mean temperature ($r = -0.731$, $P < 0.01$) (Table 3). The average minimum

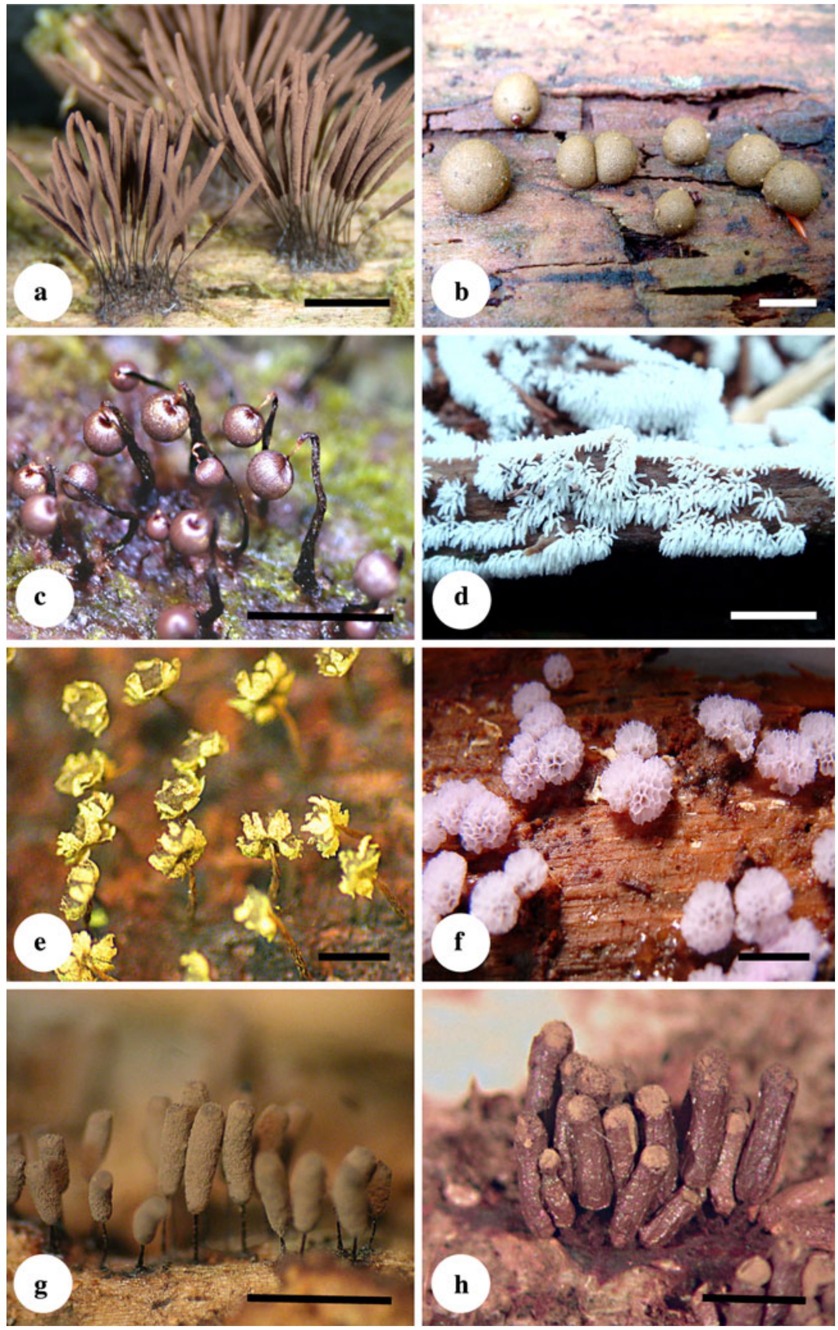

Fig. 1 Myxomycete fruiting bodies that were abundant on *Pinus densiflora* deadwood. **a** *Stemonitis axifer*. **b** *Lycogala epidendrum*. **c** *Cribraria cancellata*. **d** *Ceratiomyxa fruticulosa*. **e** *Physarum viride*. **f** *Ceratiomyxa fruticulosa* var. *porioides*. **g** *Stemonitopsis hyperopta*. **h** *Lindbladia cribrarioides*. *Bar* 5 mm

temperature had the highest coefficient correlation with the NMDS axis 1 among the environmental variables. In addition, the ordination of myxomycete communities along the first axis provided evidence for a relationship with latitude ($r = 0.645$, $P < 0.01$). The ordination along the second axis was apparently related to a complex of factors, including altitude ($r = -0.655$, $P < 0.01$) and precipitation in summer ($r = -0.641$, $P < 0.01$). Wood hardness had no effect on the ordination, probably because surveys at every study site were carried out on wood in various states of decay. Differences in the distributions of myxomycete communities across different sites were primarily characterized by air temperature related to the latitude and altitude. The distribution of myxomycete communities was strongly influenced by relative low temperature.

Distribution of species on Japanese red pine wood

The change in relative abundance (P_i) of every species in each community on Japanese red pine was compared with annual mean and minimum temperatures and wood hardness. The results showed that, for 3 of the 18 species that

Table 3 Correlation coefficients between the environmental variables and species diversity or NMDS axes for myxomycete communities

	Number of species	Species diversity (H')	Evenness (J')	NMDS axes	
				Axis 1	Axis 2
Latitude	−0.128	−0.229	−0.153	0.645**	0.270
Altitude	−0.206	−0.453	−0.530*	0.324	−0.655**
Annual mean temperature	0.280	0.554*	0.565*	−0.731**	0.477
Average minimum temperature	0.305	0.547*	0.520*	−0.774**	0.409
Average maximum temperature	0.254	0.556*	0.582*	−0.739**	0.395
Annual precipitation	0.139	0.070	−0.095	−0.178	−0.643**
Precipitation in summer	0.105	0.046	−0.124	−0.254	−0.641**
Wood hardness	0.114	−0.140	−0.367	0.379	−0.491

Significance level: ** $P < 0.01$, * $P < 0.05$

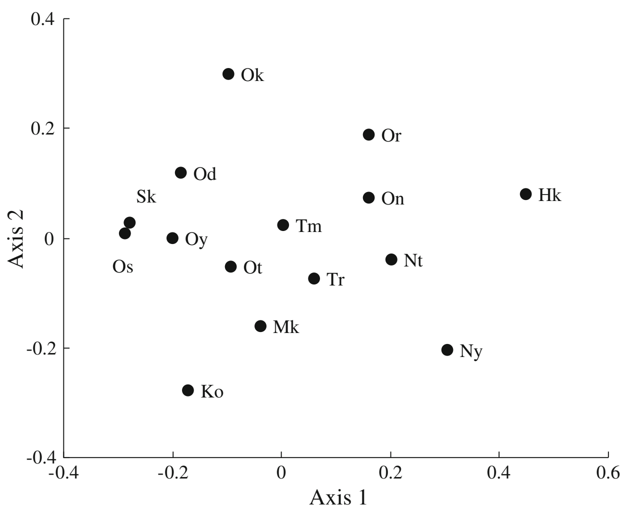

Fig. 2 Ordination of the myxomycete communities on coniferous wood in Japan on the two axes of nonmultidimensional scaling (NMDS). See Table 1 for survey site codes

appeared in seven survey sites or more, changes in P_i correlated significantly with one of the above three factors (Table 4). *Lycogala epidendrum* showed significantly negative correlations with annual mean temperature ($r = -0.713$, $P < 0.01$) and average minimum temperature ($r = -0.708$, $P < 0.01$), while *Stemonitopsis hyperopta* showed significantly positive correlations with annual mean temperature ($r = 0.679$, $P < 0.01$). On the other hand *Physarum viride* was strongly affected by wood hardness ($r = 0.655$, $P < 0.05$).

These results on deadwood of Japanese red pine show that the air temperature apparently influenced the occurrence of a few species, and the decay state of wood also influenced the distribution of particular species on deadwood in the forests.

Discussion

It has been presumed that climatic factors affect the myxomycete distribution (Gray and Alexopoulos 1968). Ing (1994) claimed that temperature plays a significant role as a limiting factor in tropical, subtropical, Mediterranean, and alpine species, but did not mention temperate species. The ways in which temperature is related to patterns of occurrence in myxomycete communities and species has been poorly addressed and has never been studied quantitatively. Since myxomycetes cannot regulate their internal temperature, diurnal and seasonal fluctuations in environmental temperature have direct and immediate impacts on all aspects of their metabolism and life histories. Temperature imposes physiological limits on myxoamoeba and plasmodia and hence controls the rates of spore germination, growth, and sporulation (Gray and Alexopoulos 1968). Our research, from field studies in a temperate region, revealed a temperature-driven geographical distribution of myxomycetes. The primary emphasis was placed on determining the myxomycete species present on dead coniferous wood and on assessing their distributional relationships with air temperature. The average minimum temperature was significantly correlated with the distribution of myxomycete communities.

Studies of the distribution of myxomycete communities are complicated by the various substrates on which the fruiting bodies occur and/or climatic variables. Lado (1993) investigated myxomycete distribution in Mediterranean woodlands in terms of the vegetation zone corresponding to altitude. Furthermore, myxomycete distribution in the subtropical mountains was associated with different forest vegetation corresponding to altitude (Novozhilov et al. 2001). However which environmental factors influenced myxomycete distribution was not specified. Empirical

Table 4 Correlation coefficients between the relative abundance of 18 species of myxomycetes that appeared in seven or more survey sites on dead *Pinus densiflora* wood and air temperatures and/or hardness of wood

Species	Number of sites	Air temperature		Hardness of wood
		Annual mean temperature	Average minimum temperature	
Cribraria cancellata	12	0.291	0.381	0.045
Lycogala epidendrum	12	−0.713**	−0.708**	0.500
Stemonitis axifera	12	−0.467	−0.478	−0.033
Ceratiomyxa fruticulosa	12	0.494	0.477	−0.135
Stemonitis axifera var. *smithii*	12	0.159	0.119	0.019
Physarum viride	11	−0.364	−0.366	0.655*
Arcyria cinerea	11	−0.068	−0.110	−0.135
Ceratiomyxa fruticulosa var. *porioides*	10	−0.600	−0.493	0.057
Stemonitopsis gracilis	10	−0.096	−0.158	−0.360
Stemonitopsis hyperopia	9	0.679*	0.637	0.251
Physarum flavicomum	9	0.284	0.277	0.094
Physarum nutans	8	−0.347	−0.336	0.298
Cribraria intricata var. *dictydioides*	8	0.595	0.655	−0.553
Tubifera ferruginosa	8	0.251	0.381	0.120
Lindbladia cribrarioides	8	−0.224	−0.297	−0.570
Arcyria obvelata	8	0.696	0.651	−0.563
Stemonitis fusca	7	−0.545	−0.598	−0.150
Cribraria intricata	7	0.376	0.465	−0.109

Significance level: ** $P < 0.01$, * $P < 0.05$

taxonomic studies have shown that particular myxomycetes prefer certain types of substrate, such as coniferous or angiosperm wood (Ing 1994). In this study, the dataset was limited to a single type of substrate, i.e., coniferous deadwood, especially *P. densiflora* deadwood, which is distributed throughout Japanese pine forests. Coniferous tree species are distributed geographically in Japan according to latitude and altitude. Consequently the present study pointed out that myxomycete distribution strongly relates to air temperature.

The occurrence of myxomycetes has also been related to the decayed state of the wood (Takahashi and Hada 2008b, 2009). The heterogeneity of the decay state may influence the distribution of myxomycetes. The average decayed state of wood recorded in this study, however, ranged from 11.2 to 23.1 kg/cm^2 across the 15 sites and was not correlated with the species diversity and distribution of myxomycete communities.

The availability of water is of prime importance for myxomycete occurrence, and water-retaining substrates are essential. Humidity in forests influences the distribution of myxomycetes (Stephenson 1988; Heilmann 2001; Rubino and McCarthy 2003). However, precipitation had no correlation with species richness and species diversity. Thus the influence of precipitation on myxomycete distribution was negligible in this study. The humid climate of Japan, which is maintained through high precipitation during the rainy season, should reduce the importance of precipitation as a limiting factor in summer. Temperature factors are more effective indicators of a regional climate gradient than are the other factors that may be responsible for the distribution of myxomycetes.

This study exclusively examined abundant samples of myxomycetes that had fruited in the summer under natural conditions, and accidentally overlooking a tiny myxomycete fruiting body may lead to an underestimation of species richness. Moreover, there may be species of fruiting bodies that were not present at the survey time. Thus, the study of the distribution of myxomycetes over a wide geographical range needs further research.

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