БИОРАЗНООБРАЗИЕ, СИСТЕМАТИКА, ЭКОЛОГИЯ

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SEASON DYNAMICS OF SPORULATION OF MYXOMYCETES IN MOSCOW CITY AND MOSCOW REGION

ГМОШИНСКИЙ В. И., МАТВЕЕВ А. В. СЕЗОННАЯ ДИНАМИКА СПОРОНОШЕНИЯ МИКСОМИЦЕТОВ В УСЛОВИЯХ МОСКВЫ И МОСКОВСКОЙ ОБЛАСТИ

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The paper covers phenological features of myxomycetes sporophore formation in Moscow city and Moscow Region. The research was based on long-term field survey of myxomycetes. The representatives of the order *Trichiales* were shown to be most abundant in spring and autumn months, while in summer their number was markedly reduced. The relative abundance of the order *Stemonitales* was maximal in late spring and in early summer. The peak of spore formation by the order *Ceratiomyxales* was observed in June, while in spring and autumn the species were not detected in Moscow and Moscow Region. The representatives of the order *Physarales* were most abundant in August—early September. Definite peaks of spore formation have not been detected for *Liceales*. Comparison of our data with the results of A. V. Vlasenko and Yu. K. Novozhilov obtained for pinewoods of the right bank of the Upper Ob river revealed similar dynamics. The work includes polygonal charts for phenology of species comprising the core of myxomycetes biota in Moscow city and Moscow Region.

Key words: myxomycetes, species diversity, phenology, Moscow and Moscow Region.

Работа посвящена изучению фенологических особенностей миксомицетов Москвы и Московской обл. В работе использовались многолетние данные полевых сборов миксомицетов. Было показано, что в весенние и осенние месяцы наибольшей численностью обладают представители порядка *Trichiales*, в то время как их численность в летние месяцы резко снижается. Порядок *Stemonitales* обладает наибольшей относительной численностью в конце весны—начале лета. Пик образований спороношений *Ceratiomyxales* приходится на июнь, в то время как весной и осенью образцы этого вида на территории Москвы и Московской обл. обнаружить не удалось. Представители порядка *Physarales* достигают максимальной относительной численности в августе—начале сентября. Для представителей порядка *Liceales* четкие пики образования спороношений нами выявлены не были. Сходная динамика была показана при сравнении наших данных с результатами, полученными А. В. Власенко и Ю. К. Новожиловым для сосновых лесов правобережной части Верхнего Приобья. В работе также приводятся полигональные графики фенологии видов, составляющих ядро биоты миксомицетов в Москве и Московской обл.

Ключевые слова: миксомицеты, видовое разнообразие, фенология, Москва и Московская обл.

Myxomycetes (class *Myxogasteromycetes*) make a unique group of spore-forming protists with a lifecycle that includes a motile vegetative stages without cell wall (myxamoebas, myxomonads, plasmodium) and a fertile stage represented by sporophores of various structure (Martin, Alexopoulos, 1969). Under unfavorable conditions, myxomycetes transform into resting forms (microcystae, spherules, sclerotia) and thus survive extensive dry periods, low and high temperature.

The group was originally divided into 5 orders: *Echinosteliales*, *Liceales*, *Trichiales*, *Stemonitales*, and *Physarales* (Martin, Alexopoulos, 1969). The status of order *Ceratiomyxales* that includes a single genus *Ceratiomyxa* and three species, two of which are tropical, has remained disputable for a long time. Recent studies of phylogenetic relations within the group consider order *Ceratiomyxales* as myxomycetes (Fiore-Donno et al., 2010).

In central Russia, myxomycetes form spores throughout the entire snow-free period. Both humidity and temperature determine the rate of sporocarp formation (Keller, Braun, 1999). Groups of highly specialized nivicolous species were shown to form spores only in early spring in areas adjacent to melting snow (Ronikier, Ronikier, 2009).

The studies of phenological features of sporophore development by myxomycetes in our country were carried out by A. V. Vlasenko and Yu. K. Novozhilov in pinewoods on the right bank of the Upper Ob river (Vlasenko, Novozhilov, 2011). The authors analyzed 920 samples that belonged to 115 species. Peaks of spore formation were detected in late spring, early summer and autumn, whereas in June spore formation was less obvious.

Materials and methods

The samples were collected from 1980 to 2012 in Moscow city and Moscow Region. Analysis was performed using 4076 samples obtained from field surveys. The study was based on the data obtained by the authors as well as on herbarium specimens kindly provided by the Department of Mycology and Algology of the Biological faculty of Lomonosov Moscow State University (Gmoshinskiy et al., 2011). Most of herbarium specimens were collected by T. P. Sizova and T. N. Barsukova during summer workshop for students of the Biological faculty.

The Department's herbarium material does not define the most favorable periods of myxomycetes sporulation because the sampling was not regular. Most samples were obtained during summer workshop on the biological research station at Zvenigorod biological station from early June to the end of July. At the same time, many samples were collected in Moscow recreation forests by M. F. Akimova and Ye. N. Vinogradskaya from early September to the middle of October. The number of species collected in different months is represented in Table.

Taking into account the irregularity of sample collection, relative values were calculated instead of absolute ones. Relative values reflected the relation of samples that belonged to a certain taxonomy group to the total number of samples collected in a certain month. Five and eleven samples were gathered in December and March, respectively, and these months were excluded from the analysis due to the lack of data.

To compare our data with the results obtained by A. V. Vlasenko and Yu. K. Novozhilov, we normalized the number of samples that belonged to certain species (or to higher taxa) to the total number of samples collected in each month.

G. W. Martin's and K. A. Alexopoulos' system of myxomycetes (Martin, Alexopoulos, 1969; Ing, 1999; Stephenson, Stempen, 2000) was used in paper with minor modifications. The concepts and names of genera, species and intraspecies taxa are based on the works of C. Lado (Lado, 2001, 2011; Lado et al., 2005).

Moscow climate is determined by the location in middle latitudes with corresponding radiation and circulation regimes. Both land and ocean have impact on climate of Moscow located between the center of Eurasia and the Atlantic Ocean. The climate is considered as moderate continental. In winter persistent frost is accompanied by thaw, in summer fine and rather hot weather alternates with rainy and cool (Alisov, Poltaraus, 1974). Average annual air temperature is 3.8 °C, absolute minimum is –42 °C, absolute maximum is 37 °C. Average annual precipitation is 704 mm. Autumn frosts in Moscow usually start in late September—early October, spring frosts end up in April in the central urban part of the city, and in the middle of May in the suburbs. Usually, the frost-free period lasts for 214 days. Crossing 5 °C mark, considered as the beginning and the end of vegetation period, is usually observed on April 18 and on October 11. Vegetation period lasts for 175 days. However the fluctuations of vegetation period in Moscow are rather high (Shechtman et al., 1969).

Results

Relative abundance of myxomycetes orders in different months is represented in Fig. 1. For the most of the year order *Trichiales* dominates in Moscow city and Moscow Region by the number of samples. The representatives of order *Trichiales* can be detected from early spring to the late autumn, some species can form sporophores even after snow cover sets in. In spring and autumn the species of *Trichiales* are dominant, while other orders do not form sporophores. The observed phenomenon might be explained by ability of *Trichiales* to form sporophores numerously at low temperature. Similar results were obtained by A. V. Vlasenko and Yu. K. Novozhilov. In pinewoods on Upper Ob right bank the representatives of *Trichiales* were dominant in May and October, i. e. soon after snow melting and just prior to snow cover set-in (Fig. 2) (Vlasenko, Novozhilov, 2011).

In April, the representatives of *Liceales* start to form sporophores regularly. They constitute 15 % of total myxomycetes samples over the indicated period due to abundant aethalia formation by the species of genera *Lycogala* and *Reticularia* (Table). Other orders were represented by single samples. The species of *Tubifera* were detected only in summer and early autumn (Table).

In the middle of May the weather in Moscow city and Moscow Region is usually relatively warm and humid, spring frosts are rare, which result in mass development of myxomycetes of various orders. Sporophores formation of *Ceratiomyxales*, represented in Moscow city and Moscow Region by a single species *Ceratiomyxa fruticulosa*, starts in May, reaches maximum (9.46 %) in June, and ends up by September (Table). We suggest that the representatives of order *Ceratiomyxales* prefer warmer climate. The assumption is indirectly supported by the fact that two other species of *Ceratiomyxales* — *C. morchella* A. L. Welden and *C. sphaerosperma* Boedijn. have been detected only in the tropics (Cavalcanti et al., 2008; Rojas et al., 2008). In the pinewoods on Upper Ob right bank the peaks of sporophore formation by *Ceratiomyxales* have been detected in June and August (Fig. 2) (Vlasenko, Novozhilov, 2011). In July, sporophore formation by *C. fruticulosa* has not been observed. The phenomenon might result from torrid summer, while in the end of May and in early August high temperature is associated with significant substrate moistening.

Abundance of order *Physarales* reaches maximum in the end of summer, then it gradually decreases until snow cover set in. We suggest that warm weather is the major

Species relative abundance according to month of sampling

Taxa	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
Ceratiomyxales	—	—	5.45	9.46	5.99	2.38	0.22	—	—	—
Ceratiomyxaceae	—	—	5.45	9.46	5.99	2.38	0.22	—	—	—
Ceratiomyxa fruticulosa (O. F. Müll.) T. Macbr.	—	—	5.45	9.46	5.99	2.38	0.22	—	—	—
Echinosteliales	—	—	—	—	—	0.26	0.44	—	—	—
Clastodermataceae	—	—	—	—	—	0.26	0.44	—	—	—
Clastoderma debaryanum A. Blytt	—	—	—	—	—	0.26	0.44	—	—	—
Liceales	—	14.29	11.82	20.7	18.35	12.7	13.27	14.41	18.18	—
Cribrariaceae	—	—	4.55	7.1	10.11	6.08	0.88	0.65	1.82	—
Cribraria argillacea (Pers. ex J. F. Gmel.) Pers.	—	—	—	1.97	1.08	1.06	0.22	—	—	—
C. atrofusca G. W. Martin et Lovejoy	—	—	—	0.07	—	—	—	—	—	—
C. aurantiaca Schrad.	—	—	—	0.39	0.49	0.26	—	—	1.82	—
C. cancellata (Batsch) Nann.-Bremek.	—	—	—	2.83	4.61	1.06	0.44	0.65	—	—
C. intricata Schrad.	—	—	—	0.46	0.69	—	0.22	—	—	—
C. languescens Rex	—	—	—	—	0.1	—	—	—	—	—
C. macrocarpa Schrad.	—	—	—	0.13	—	—	—	—	—	—
C. microcarpa (Schrad.) Pers.	—	—	—	0.13	0.39	0.53	—	—	—	—
C. minutissima Schwein.	—	—	—	0.07	0.1	—	—	—	—	—
C. piriformis Schrad.	—	—	—	—	0.2	0.53	—	—	—	—
C. rufa (Roth) Rostaf.	—	—	4.55	0.26	0.69	—	—	—	—	—
C. tenella Schrad.	—	—	—	0.07	0.69	2.12	—	—	—	—
C. vulgaris Schrad.	—	—	—	0.66	0.88	0.53	—	—	—	—
Lindbladia tubulina Fr.	—	—	—	0.07	0.2	—	—	—	—	—
Reticulariaceae	—	14.29	7.27	13.6	8.15	6.08	12.17	12.9	16.36	—
Dictydiaethalium plumbeum (Schumach.) Rostaf. ex Lister	—	—	—	—	0.1	0.26	0.44	0.22	—	—
Lycogala conicum Pers.	—	—	—	0.07	0.1	—	—	—	—	—
L. epidendrum (L.) Fr.	—	7.14	5.45	8.48	3.63	2.12	5.53	8.39	12.73	—
L. exiguum Morgan	—	5.36	0.91	2.56	2.55	0.79	1.99	1.94	1.82	—
L. flavofuscum (Ehrenb.) Rostaf.	—	—	0.91	0.2	0.39	0.26	0.22	—	—	—
Reticularia intermedia Nann.-Bremek.	—	—	—	—	—	—	—	0.43	1.82	—
R. lycoperdon Bull.	—	1.79	—	0.46	0.2	1.59	1.77	0.65	—	—
R. splendens Morgan	—	—	—	0.07	—	—	0.22	0.22	—	—
Tubifera ferruginosa (Batsch) J. F. Gmel.	—	—	—	1.77	1.18	1.06	1.99	1.08	—	—
Liceaceae	—	—	—	—	0.1	0.53	0.22	0.86	—	—
Licea minima Fr.	—	—	—	—	—	0.26	—	—	—	—
L. pusilla Schrad.	—	—	—	—	0.1	0.26	—	—	—	—
L. variabilis Schrad.	—	—	—	—	—	—	0.22	0.86	—	—
Trichiales	85.71	82.14	51.82	24.84	26.99	40.48	52.21	53.12	60	40
Arcyriaceae	7.14	1.79	7.27	12.02	16.29	22.75	17.26	14.62	12.73	—
Arcyodes incarnata (Alb. et Schwein.) O. F. Cook	—	—	—	—	—	—	0.44	0.65	—	—
Arcyria affinis Rostaf.	—	—	—	2.07	1.77	2.65	2.65	1.08	7.27	—
A. cinerea (Bull.) Pers.	7.14	1.79	0.91	1.71	3.73	3.44	1.33	1.72	—	—
A. denudata (L.) Wettst.	—	—	—	1.84	2.45	1.32	3.32	1.51	—	—
A. ferruginea Saut.	—	—	—	0.07	—	0.79	1.11	0.86	1.82	—
A. incarnata (Pers. ex J. F. Gmel.) Pers.	—	—	1.82	2.04	1.86	3.97	2.21	1.51	—	—
A. insignis Kalchbr. et Cooke	—	—	2.73	0.26	0.79	0.53	0.88	—	—	—
A. magna Rex	—	—	—	—	—	0.79	—	—	—	—
A. minuta	—	—	—	0.2	0.29	2.91	0.22	0.22	—	—
A. obvelata (Oeder) Onsberg	—	—	0.91	2.10	3.83	2.65	1.99	0.86	1.82	—
A. occidentalis (T. Macbr.) G. Lister	—	—	—	—	—	0.26	—	0.22	—	—
A. oerstedii Rostaf.	—	—	—	0.26	0.79	—	0.88	0.43	—	—
A. pomiformis (Leers) Rostaf.	—	—	0.91	1.51	0.79	2.91	0.88	2.58	—	—
A. stipata (Schwein.) Lister	—	—	—	—	—	0.26	1.33	2.8	1.82	—
A. versicolor W. Phillips	—	—	—	—	—	0.26	—	0.22	—	—
Trichiaceae	78.57	80.36	44.55	12.81	10.7	17.72	34.96	38.49	47.27	40
Hemitrichia abietina (Wigand) G. Lister	—	—	—	—	—	—	0.22	0.22	—	—
H. clavata (Pers.) Rostaf.	—	10.71	11.82	1.18	1.67	1.06	5.97	6.67	3.64	—
H. intorta (Lister) Lister	—	—	—	—	—	—	0.22	—	—	—

Table continuation

Taxa	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
Hemitrichia minor G. Lister	—	—	—	—	0.1	—	—	—	—	—
H. serpula (Scop.) Rostaf. ex Lister	—	10.71	2.73	0.46	0.9	0.26	0.88	0.65	—	—
Metatrichia floriformis (Schwein.) Nann.-Bremek.	—	3.57	0.91	0.46	0.59	—	0.44	—	3.64	—
M. vesparia (Batsch) Nann.-Bremek. ex G. W. Martin et Alexop.	14.29	12.50	9.09	2.83	2.45	6.08	7.08	6.24	12.73	—
Perichaena chrysosperma (Curr.) Lister	—	—	—	0.13	—	—	—	0.22	—	—
P. corticalis (Batsch) Rostaf.	—	—	0.91	0.2	0.29	—	0.88	0.65	—	—
P. depressa Lib.	—	—	—	0.07	0.1	—	—	—	—	—
P. liceoides Rostaf.	—	—	—	—	—	—	—	0.22	—	—
Trichia botrytis (J. F. Gmel.) Pers.	—	—	0.91	0.07	0.1	0.53	0.22	0.65	3.64	—
T. brevicapillata Sizova. Titova et Darakov	—	—	—	—	—	0.26	—	—	—	—
T. contorta (Ditmar) Rostaf.	—	—	0.91	—	0.1	0.53	—	0.86	—	20
T. decipiens (Pers.) T. Macbr.	28.57	7.14	6.36	2.17	1.08	2.12	4.42	6.24	1.82	—
T. favoginea (Batsch) Pers.	7.14	8.93	5.45	2.1	2.26	1.32	0.66	0.22	1.82	20
T. lutescens (Lister) Lister	—	—	—	0.07	—	—	0.44	0.22	1.82	—
T. persimilis P. Karst.	14.29	5.36	1.82	0.33	0.1	1.32	2.88	4.52	3.64	—
T. scabra Rostaf.	7.14	5.36	1.82	1.97	1.28	1.59	2.65	3.66	1.82	—
T. subfusca Rex	—	—	—	—	—	—	—	0.22	0	—
T. varia (Pers. ex J. F. Gmel.) Pers.	7.14	16.07	1.82	0.79	0.2	2.65	7.96	7.1	12.73	—
Physarales	7.14	1.79	7.27	18.27	22.77	32.8	21.9	21.08	10.91	60
Didymiaceae	—	—	3.64	7.56	5.59	7.14	4.87	3.23	1.82	—
Diachea leucopodia (Bull.) Rostaf.	—	—	—	0.07	0.29	—	—	0.22	—	—
Diderma alpinum (Meyl.) Meyl.	—	—	—	—	—	—	0.22	—	—	—
D. chondrioderma (de Bary et Rostaf.) G. Lister	—	—	—	—	0.1	—	—	—	—	—
D. effusum (Schwein.) Morgan	—	—	—	—	—	0.26	—	—	—	—
D. floriforme (Bull.) Pers.	—	—	—	0.07	—	—	—	—	—	—
D. hemisphaericum (Bull.) Hornem.	—	—	—	—	—	—	0.22	—	—	—
D. radiatum (L.) Morgan	—	—	—	0.07	0.2	0.26	—	—	—	—
D. spumarioides (Fr.) Fr.	—	—	—	—	0.1	—	—	—	—	—
D. testaceum (Schrad.) Pers.	—	—	—	—	—	0.26	—	—	—	—
Didymium clavus (Alb. et Schwein.) Rabenh.	—	—	—	0.07	0.29	1.59	0.66	—	—	—
D. crustaceum Fr.	—	—	—	0.07	—	0.26	0.22	—	—	—
D. difforme (Pers.) Gray	—	—	—	0.07	—	0.26	0.22	0.22	—	—
D. dubium Rostaf.	—	—	0.91	0.07	0.29	—	—	—	—	—
D. iridis (Ditmar) Fr.	—	—	—	0.13	0.1	—	0.22	—	—	—
D. melanospermum (Pers.) T. Macbr.	—	—	—	1.84	0.69	1.32	1.11	1.08	1.82	—
D. minus (Lister) Morgan	—	—	0.91	1.38	1.37	1.59	—	—	—	—
D. nigripes (Link) Fr.	—	—	0.91	0.59	0.59	0.26	0.22	—	—	—
D. perforatum Yamash.	—	—	—	0.07	0.1	—	—	—	—	—
D. serpula Fr.	—	—	—	0.07	—	—	—	—	—	—
D. squamulosum (Alb. et Schwein.) Fr.	—	—	0.91	2.83	1.08	1.06	0.88	1.72	—	—
Mucilago crustacea F. H. Wigg.	—	—	—	0.2	0.39	—	0.88	—	—	—
Physaraceae	7.14	1.79	3.64	10.71	17.17	25.66	17.04	17.85	9.09	60
Badhamia affinis Rostaf.	—	—	—	0.07	—	—	—	0.43	—	—
B. capsulifera (Bull.) Berk.	—	—	—	—	0.1	—	—	—	—	—
B. foliicola Lister	—	—	—	0.07	0.29	0.26	0.88	0.65	—	—
B. lilacina (Fr.) Rostaf.	—	—	—	—	0.1	0.53	0.22	—	—	—
B. macrocarpa (Ces.) Rostaf.	—	—	—	0.26	0.1	1.06	1.33	1.51	—	20
B. melanospora Speg.	—	—	—	0.07	—	0.26	—	0.22	—	—
B. panicea (Fr.) Rostaf.	—	—	—	—	0.29	0.26	0.44	0.22	—	—
B. utricularis (Bull.) Berk.	—	—	—	0.07	—	—	—	—	—	—
B. versicolor Lister	—	—	—	—	—	—	—	—	—	20
Craterium aureum (Schumach.) Rostaf.	—	—	—	—	0.1	0.26	—	—	—	—
C. concinnum Rex	—	—	—	—	—	0.26	—	—	—	—
C. leucocephalum (Pers.) Ditmar	—	—	—	0.33	0.39	0.79	—	—	—	—
C. minutum (Leers) Fr.	—	—	—	0.07	0.1	1.06	0.22	0.43	—	—
Fuligo gyrosa (Rostaf.) E. Jahn	—	—	—	—	0.2	—	—	—	—	—

Table continuation

Taxa	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
F. leviderma H. Neubert. Nowotny et K. Baumann	—	1.79	0.91	0.13	0.2	0.79	1.77	1.08	—	—
F. septica (L.) F. H. Wigg.	—	—	1.82	1.71	3.93	1.59	1.11	0.86	—	—
Leocarpus fragilis (Dicks.) Rostaf.	—	—	—	0.33	1.08	1.06	0.22	0.22	—	—
Physarum album (Bull.) Chevall.	—	—	—	2.23	2.75	7.94	5.97	7.53	7.27	—
P. auriscalpium Cooke	—	—	—	—	0.29	—	—	—	—	—
P. bitectum G. Lister	—	—	—	—	—	—	0.44	—	—	—
P. bivalve Pers.	—	—	—	0.13	0.2	0.26	—	—	—	—
P. cinereum (Batsch) Pers.	—	—	—	0.53	0.69	0.53	0.44	0.22	—	—
P. citrinum Schumach.	—	—	—	0.07	0.1	—	0.22	0	—	—
P. compressum Alb. et Schwein.	—	—	—	0.07	—	0.79	0.66	0.43	—	20
P. confertum T. Macbr.	—	—	—	0.26	0.29	0.26	—	—	—	—
P. contextum (Pers.) Pers.	—	—	—	—	—	0.53	—	1.08	—	—
P. didermoides (Pers.) Rostaf.	—	—	—	—	—	0.26	0.22	0.65	—	—
P. flavicomum Berk.	—	—	—	0.07	0.2	—	—	—	—	—
P. globuliferum (Bull.) Pers.	—	—	—	0.26	0.69	0.79	0.22	—	—	—
P. leucophaeum Fr.	7.14	—	—	0.13	0.49	1.59	0.22	1.51	1.82	—
P. leucopus Link	—	—	—	1.25	0.69	1.32	1.55	0.43	—	—
P. limonium Nann.-Bremek.	—	—	—	0.07	—	0.26	—	—	—	—
P. mutabile (Rostaf.) G. Lister	—	—	—	—	0.1	—	—	—	—	—
P. notabile T. Macbr.	—	—	—	—	0.1	0.26	0.22	—	—	—
P. nudum T. Macbr.	—	—	—	—	0.2	—	—	—	—	—
P. pezizoideum (Jungh.) Pavill. et Lagarde	—	—	0.91	—	—	—	—	—	—	—
P. polycephalum Schwein.	—	—	—	—	0.1	—	—	—	—	—
P. psittacinum Ditmar	—	—	—	1.51	1.18	0.53	0.22	—	—	—
P. pusillum (Berk. et M. A. Curtis) G. Lister	—	—	—	—	0.2	—	—	—	—	—
P. serpula Morgan	—	—	—	—	0.1	0.26	—	—	—	—
P. tenerum Rex	—	—	—	—	0.2	—	—	—	—	—
P. vernum Sommerf.	—	—	—	0.07	0.39	—	—	0.43	—	—
P. virescens Ditmar	—	—	—	0.13	0.1	—	—	—	—	—
P. viride (Bull.) Pers.	—	—	—	0.85	1.18	1.59	0.44	—	—	—
Willkommlangea reticulata (Alb. et Schwein.) Kuntze	—	—	—	—	0.1	0.26	—	—	—	—
Stemonitales	7.14	1.79	23.64	26.74	25.91	11.38	11.95	11.4	10.91	—
Stemonitidaceae	7.14	1.79	23.64	26.74	25.91	11.38	11.95	11.4	10.91	—
Collaria arcyrionema (Rostaf.) Nann.-Bremek. ex Lado	—	—	—	0.99	0.69	0.26	0.22	—	—	—
Comatricha alta Preuss	—	—	—	—	—	—	—	0.22	—	—
C. dictyospora L. F. Celak.	—	—	0.91	0.26	0.1	0.26	0.22	—	—	—
C. elegans (Racib.) G. Lister	—	—	0.91	0.59	0.2	0.79	0.22	0.43	—	—
C. ellae Härk.	—	—	—	0.13	—	—	0.44	0.43	—	—
C. laxa Rostaf.	—	—	—	—	—	—	0.22	0.43	—	—
C. longipila Nann.-Bremek.	—	—	—	—	0.1	—	—	—	—	—
C. nigra (Pers. ex J. F. Gmel.) J. Schröt.	—	1.79	4.55	1.38	1.57	1.59	3.54	5.38	9.09	—
C. pulchella (C. Bab.) Rostaf.	—	—	—	0.53	0.49	0.53	0.44	—	—	—
C. tenerrima (M. A. Curtis) G. Lister	—	—	—	0.33	0.1	0.26	—	—	—	—
Enerthenema papillatum (Pers.) Rostaf.	—	—	3.64	1.58	0.98	0.79	0.88	1.29	—	—
Lamproderma arcyrioides (Sommerf.) Rostaf.	—	—	—	0.26	0.39	0.26	0.22	—	—	—
L. atrosporum Meyl.	—	—	—	0.13	—	—	—	—	—	—
L. columbinum (Pers.) Rostaf.	—	—	—	0.26	0.39	—	0.22	—	—	—
L. scintillans (Berk. et Broome) Morgan	—	—	0.91	0.72	—	—	—	—	—	—
Paradiacheopsis solitaria (Nann.-Bremek.) Nann.-Bremek.	—	—	—	0.07	—	—	—	—	—	—
Stemonaria gracilis Nann.-Bremek. et Y. Yamam.	—	—	—	—	0.1	—	—	—	—	—
S. irregularis (Rex) Nann.-Bremek. R. Sharma et Y. Yamam.	—	—	1.82	—	0.29	—	0.22	0.22	—	—
Stemonitis axifera (Bull.) T. Macbr.	7.14	—	4.55	12.09	10.01	2.91	0.88	0.86	1.82	—
S. flavogenita E. Jahn	—	—	—	—	0.1	—	—	—	—	—

Table continuation

Taxa	Mar	Apr	May	June	July	Aug	Sep	Oct	Nov	Dec
Stemonitis fusca Roth	—	—	0.91	1.84	2.55	0.53	2.43	1.08	—	—
S. herbatica Peck	—	—	—	0.07	—	—	—	—	—	—
S. pallida Wingate	—	—	—	0.39	0.2	—	0.22	0.22	—	—
S. smithii T. Macbr.	—	—	1.82	1.38	2.26	—	0.22	—	—	—
S. splendens Rostaf.	—	—	—	0.07	0.2	0.26	—	—	—	—
S. virginiensis Rex	—	—	—	0.13	0.2	—	—	—	—	—
Stemonitopsis aequalis (Peck) Y. Yamam.	—	—	—	0.07	—	—	—	—	—	—
S. gracilis (G. Lister) Nann.-Bremek.	—	—	—	0.07	0.2	—	—	—	—	—
S. hyperopta (Meyl.) Nann.-Bremek.	—	—	0.91	0.13	0.2	—	—	0.43	—	—
S. typhina (F. H. Wigg.) Nann.-Bremek.	—	—	2.73	3.15	4.32	2.65	1.11	0.22	—	—
Symphytocarpus amaurochaetoides Nann.-Bremek.	—	—	—	—	0.1	—	0.22	0.22	—	—
S. confluens (Cooke et Ellis) Ing et Nann.-Bremek.	—	—	—	0.13	0.2	0.26	—	—	—	—
Total number of samples	14	56	110	1522	1019	378	452	465	55	5

factor of sporophore formation for the order. As a result, the rate of sporophore formation is sufficiently increased and then it is gradually decreased by early November. Similar dynamics is observed in pinewoods of Upper Ob right bank (Fig. 2) with the exception that abundance of the order reaches maximum in July rather than in August, during minimal moistening (Vlasenko, Novozhilov, 2011). The phenomenon can be explained by the presence of phaneroplasmodium, which is resistant to dry conditions due to its mucous sheath. The order might have another sporulation peak observed as a result of sporophore formation by genus *Badhamia*. Some species of the genus form sporophores in the end of snow-free season (Lister, 1925), just prior to snow cover set in. In Moscow and Moscow Region species of *Badhamia* can sporulate in summer, although at reduced rate, while in pinewoods of Upper Ob right bank the representatives of the genus are detected only from September to November (Vlasenko, Novozhilov, 2011).

At family level myxomycetes exhibit similar dynamics (Fig. 3). *Trichiaceae* dominate in spring and autumn, while in summer its abundance is markedly decreased. We were unable to determine sporulation peaks for *Reticulariaceae* since aethalia of genus *Lycogala* were found during the entire snow-free period in Moscow and Moscow Region — from April to November (Fig. 4). The abundance of *Reticulariaceae* reaches maximum in August (6.2 %) and in November (16.4 %) due to intense development of aethalia by *Reticularia* when sporophore formation of other species is decreased (Table).

Families *Ceratiomyxaceae* and *Stemonitidaceae* have sporophore formation peaks in early summer and end up sporulation by August. Possible reasons underlying the phenomena are discussed above. In June and July the representatives of *Cribrariaceae* richly form sporophores (up to 10.1 % in July), in August the number of detected sporophores was reduced to 4.3 %, but sporocarps can be detected even in the end of November. In autumn the most abundant species of *Cribrariaceae* are *Cribraria cancellata* and *C. argillacea* (Table). These species sporulate in summer and exhibit high ecological plasticity, which enables them to form sporophores during an extensive period. These species are known to have similar type of sporula-

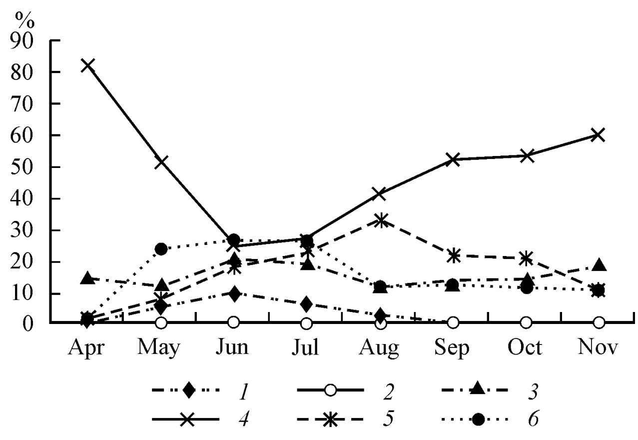

Fig. 1. Seasonal dynamics of abundance at order level (Moscow city and Moscow Region).

1 — Ceratiomyxales, 2 — Echnosteliales, 3 — Liceales, 4 — Trichiales, 5 — Physarales, 6 — Stemonitales. The same — for fig. 2.

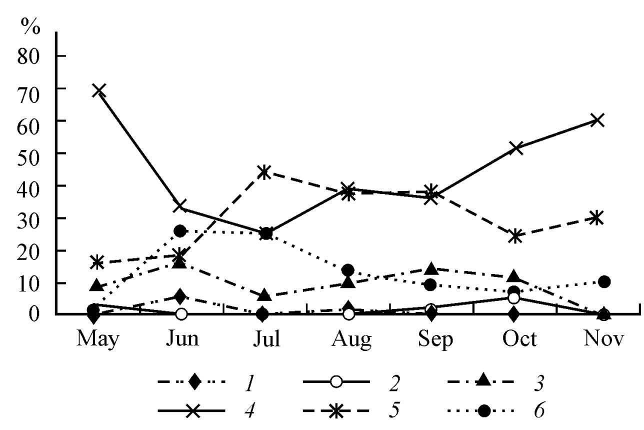

Fig. 2. Seasonal dynamics of abundance at order level (pinewoods, the right bank of the Upper Ob). The data from Vlasenko and Novozhilov (2011).

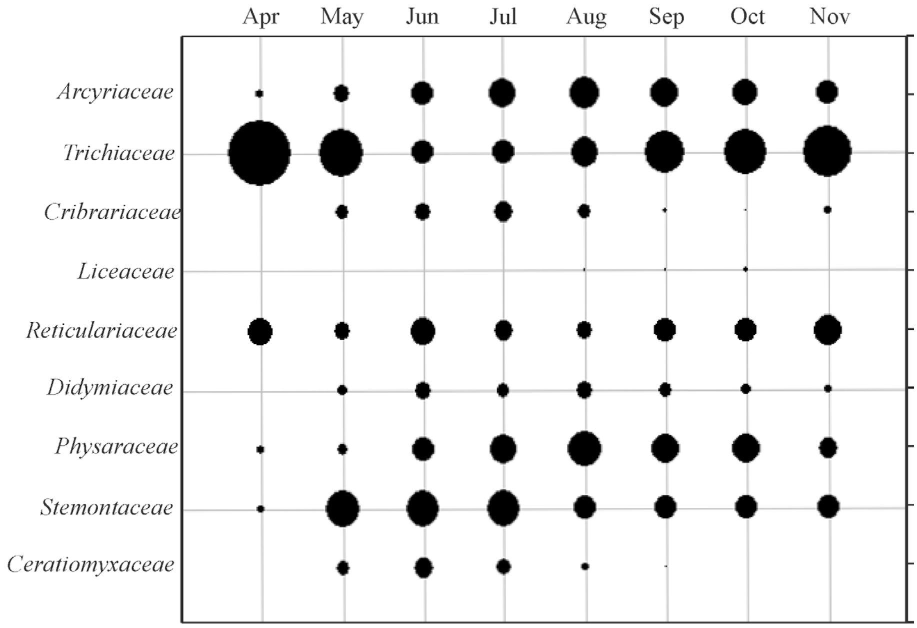

Fig. 3. Seasonal dynamics of abundance at family level (Moscow city and Moscow Region). Diameter of circles corresponds to the values of abundance.

tion represented by rather large clusters of sporangia that reach several centimeters in diameter. Sporangia of other species are usually dispersed throughout the substrate, and sporulation occupies a smaller area. However it should be noted that we revealed several cases of *C. aurantiaca* sporulation in the middle of November (Table).

In August the weather conditions are most favorable for the development of species from families *Physaraceae* and *Arcyriaceae* (Fig. 3). The sporophores were detected during the entire snow-free period. Starting from April, the percentage of these families is increased and reaches 26 and 23.2 %, respectively (Table), and then their relative abundance is gradually decreased. Species of *Didymiaceae* are found in Moscow and Moscow Region from May to November (Fig. 3), when the percentage of this family ranged from 5.6 to 7.6 %.

The phenology of five major genera obtained from field surveys is represented in Fig. 4. Overall, it is similar to the phenology of higher taxa. Dynamics of sporophore formation in these genera resembles the one observed in case of families and orders. Thus, two genera, *Arcyria* and *Physarum*, have definite peaks of sporophore formation in August (Fig. 4). *Stemonitis* species intensely sporulate in early summer, and slow down by August. Genus *Lycogala* does not have a pronounced peak of sporophore formation in Moscow and Moscow Region, and it is abundant during the entire snow-free season. *Trichia* species are detected all the year round, and in spring and autumn they become dominant (Fig. 4).

The phenology of sporophore formation by species that comprise the core of biota (with abundance exceeding 1.5 %) is represented in Fig. 5. It should be noted that the most widespread species form sporocarps during several months, yet peaks of its formation can be defined for almost all species. Most species that form sporophores in summer have a single peak, while species that sporulate in spring and autumn usually have two peaks, which might result from similar weather conditions in spring and autumn seasons. Such species include, for example, *Comatricha nigra*, *Hemitrichia clavata*, *Metatrichia vesparia*, *Trichia favoginea*, *T. scabra*, and *T. varia* (Fig. 5, *a—e*). Yet it should be noted that some species have two peaks of sporophore formation in the period from early to midsummer: *Arcyria denudata* and *Stemonitis fusca* (Fig. 5, *m*, *n*). Other species form sporophores from midsummer to cold season. The sporocarps of *Physarum album* (Fig. 5, *u*) are rarely found in spring, while the abundance from August to November is 6 % (Table). *Arcyria affinis* (Fig. 5, *g*) actively sporulates from early summer to the end of September, in October sporophores are detected rarely, while in November the abundance of the species is increased to 7.2 % in Moscow and Moscow Region.

It should be noted that sporophore formation by order *Stemonitales* is maximal from the end of May to the end of

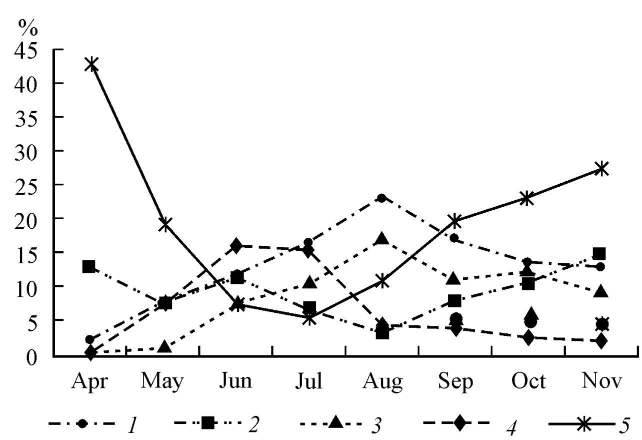

Fig. 4. Seasonal dynamics of abundance: dominant genera (Moscow city and Moscow Region).

1 — Arcyria, *2 — Lycogala*, *3 — Physarum*, *4 — Stemonitis*, *5 — Trichia.*

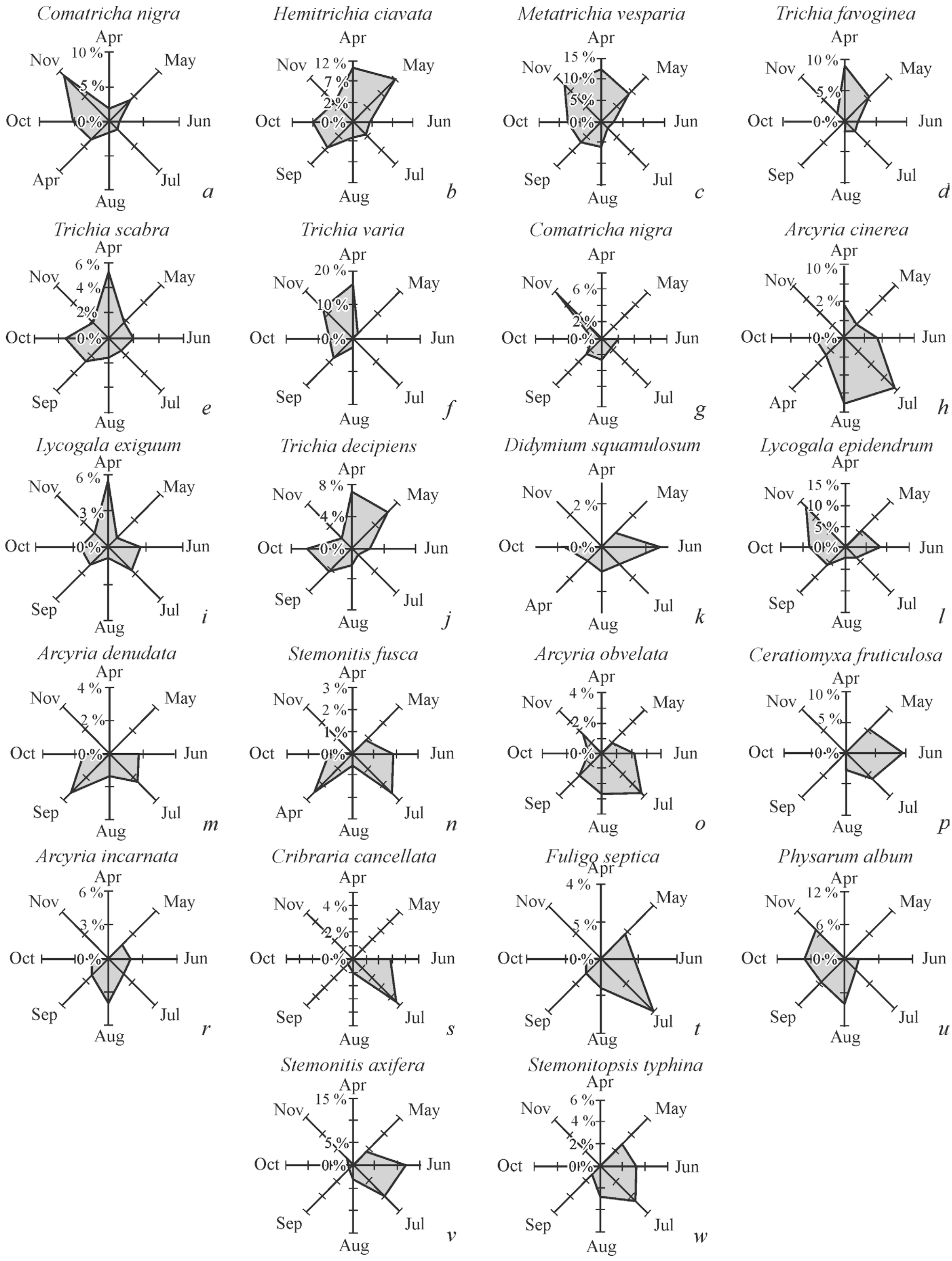

Fig. 5. Phenology of dominant species (Moscow city and Moscow Region).

The references to details of the figure — sec in the text.

July. Then the rate of sporulation is reduced, predominantly due to the decreased sporophore formation by species of genus *Stemonitis* s. l., because their number is decreased from 15.5 in July to 3.8 % in August. Such dynamics might be explained by the phenology of the most widely spread species — *Stemonitis axifera* (Fig. 5, *v*) and *Stemonitopsis typhina* (Fig. 5, *w*), which form sporophores in the beginning of summer, and rarely sporulate later. However some species of the order have peaks of spore formation in autumn (e. g., *Comatricha nigra*) (Fig. 5, *a*). The sporophore relative abundance in May is 4.55, in summer it is 1.38—1.59 %, and in autumn intense sporophore formation is observed again with a peak in November (9.09 %) (Table).

Discussion

The results of the study demonstrate that most of myxomycete species have pronounced phenological features of sporophore formation. Major peaks of sporulation can be defined for individual species. All abundant species in Moscow city and Moscow Region can be divided into several groups regarding the period of active sporophore formation: 1) a group of species that form sporophores in spring and autumn; 2) summer species with maximal sporulation during hot and humid periods; 3) autumn species. During the study we have not detected the representatives of nivicolous species, which include many species of *Lamproderma*, *Diderma* and some other genera.

The obtained data indicate that phenological features of sporophore formation by myxomycetes in Moscow city and Moscow Region similar to the ones observed by A. V. Vlasenko and Yu. K. Novozhilov in pinewoods of Upper Ob right bank (Vlasenko, Novozhilov, 2011).

Further studies of phenological features of myxomycetes in Moscow city and Moscow Region should focus on revealing sporophores in early spring, late autumn and under snow in winter, since the obtained data indicate the possibility of sporophore formation in these periods.

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